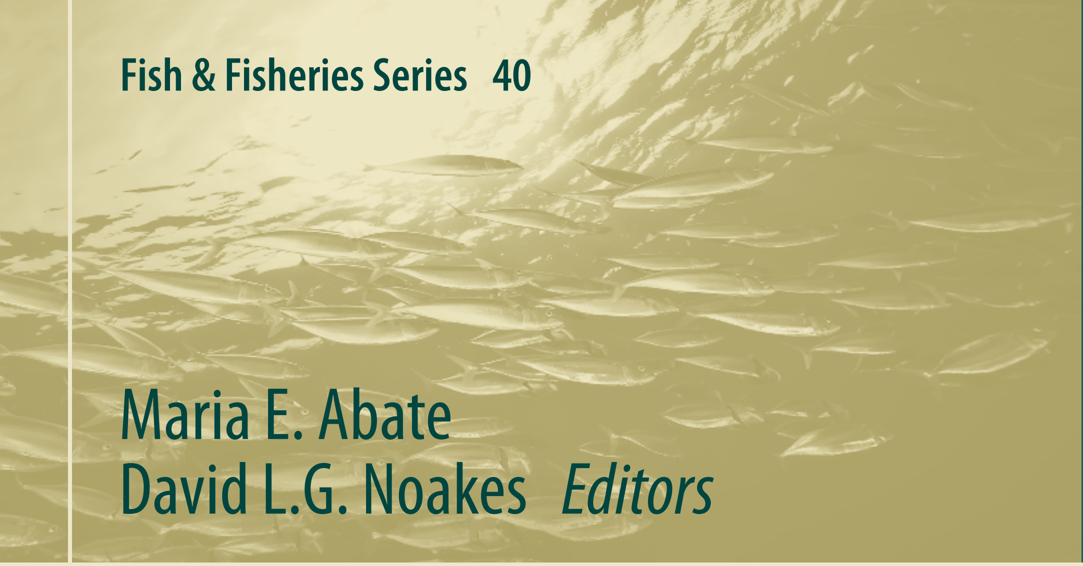

Fish & Fisheries Series 40

Maria E. Abate
David L.G. Noakes *Editors*

The Behavior, Ecology and Evolution of Cichlid Fishes

Springer

Fish & Fisheries Series

Volume 40

Series Editor

David L. G. Noakes, Fisheries & Wildlife Department, Oregon State University, Corvallis, USA

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With deep regrets we are informing our Readers that Prof. David Noakes, Editor in Chief of the journal *Environmental Biology of Fishes* and Series Editor of the *Fish and Fisheries* book series has suddenly passed away.

David's professional expertise and prompt advice has always been highly regarded and will be very much missed by all at Springer, who have known and worked with him.

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Maria E. Abate • David L. G. Noakes
Editors

The Behavior, Ecology and Evolution of Cichlid Fishes

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Editors
Maria E. Abate
Department of Biology
Simmons University
Boston, USA

David L. G. Noakes
Fisheries & Wildlife Department
Oregon State University
Corvallis, USA

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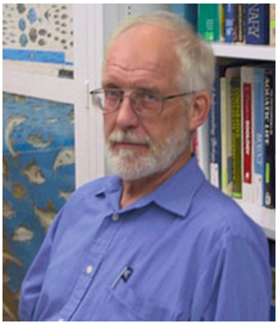
Dedication

Rosemary Helen Lowe-McConnell
24 June 1921–22 December 2014

From our initial conversations about the idea for this volume, we both agreed that it would be dedicated to Rosemary Lowe-McConnell. Ro, as everyone knew her, was a central figure in cichlid biology throughout her long career. She was a Fellow of the Linnean Society of London, served as its Vice-President, was the first Editor of the Biological Journal of the Linnean Society, and was awarded the Linnean Medal of Zoology. The Linnean Society honored Ro in 2015 with a special evening devoted to her career. Ro epitomized everything that we all recognize as the highest personal and professional standards. She coupled that with personal grace, good humor, and eternal kindness to everyone. We had informed Ro of our idea to edit a book on cichlids and our intention to dedicate the “Cichlid Book” to her; and she had reacted with characteristic grace and enthusiasm.

Maria E. Abate
David L. G. Noakes

In Memoriam



David L. G. Noakes, Ph.D.
August 3, 1942–December 1, 2020

The passing of David L. G. Noakes deeply moved the community of fish biologists. David was a constant, embodying in one scholar the best of what a scientific community has to offer—high scientific productivity with a respect for the history of the field and an eye always to the future for integrating fields of study; a leader in facilitating the dissemination of scientific knowledge and engaging with the public about science's role in solving the problem at hand; and the place where you would be treated to superb teaching and dedicated mentoring and collegiality that fosters opportunities for all.

David was a Professor of Zoology (later Integrative Biology) at the University of Guelph for 33 years (Photo courtesy of Marie Thérèse Rush-Smyth), where he taught several courses including animal behavior, ecology, and ichthyology; and he served as a Director of the Axelrod Institute of Ichthyology for 8 years. In 2005, he moved to Oregon State University to become a Director of the Oregon Hatchery Research Center and a Professor in the Fisheries and Wildlife Department, where he continued to teach, most recently his course in Fish Conservation and Management at his youthful age of 77. At both institutions, his excellence as a teacher was recognized with awards. David's esteemed research career investigating the early life history of fish species worldwide included holding several visiting faculty appointments at universities in North America, Europe, and Asia; and he was recognized with several awards by professional societies ranging from local (e.g., Lifetime Achievement Award, Oregon Chapter of the American Fisheries Society) and national (e.g., Fellow and Award of Excellence, AFS; Fellow, American Institute of Fishery Research Biologists) to international (e.g., Fellow, The Linnean Society; Royal Geographic Society).

David's enthusiasm for editing this "Cichlid Book" was infused with the respect he shared for these "remarkable" fishes, the discoveries they have been at the center of, and their importance in continuing to reveal the intrinsic and extrinsic evolutionary mechanisms that influence phenotypic variation and diversification. He published several papers (e.g., Noakes 1973) on the ontogeny of behavior of Midas cichlids at a time most studies on cichlids were focused on the reproductive behavior of the parents and when far less was known about how the young interacted with them or how parents responded to the offspring behavior. His descriptive and experimental studies examined the causal and functional relationships of cichlid behavioral ontogeny. He studied the larvae's distinct offspring parent-contacting (glancing) activity using ethology as well as histology of the parent's skin to examine this specialized behavior in the context of imprinting and social group formation. David was the first to document that young cichlids performed glancing in nature and also examined its environmental correlates (Noakes and Barlow 1973).

David wrote reviews (e.g., Noakes 1991) in which he compared development and other traits between mouthbrooders and substrate guarding cichlids, including contributing a chapter to volume 2 in this book series on cichlids (Keenleyside 1991). Through arranging for multiple symposia and other means, most recently this volume, he remained committed to the study of cichlids and those who study them past and present to foster connections between the sub-disciplines for evolutionary studies in the field and lab, contributes to cichlid conservation, and broadens the informed use and welfare of cichlids as model organisms in the lab.

In an early review (Noakes 1978) that compared the behavioral ontogeny of cichlids and salmonids, David noted the difference in how these two taxa were studied (in lab versus in field) and why (for basic research versus economic fisheries yield). He became a pioneer in fusing these approaches together to conduct basic research on salmonids and determine the factors responsible for hatchery fish developing differently from wild individuals of the same species; so that the implications on management and conservation could be addressed to diminish the differences.

David's study of complex life histories of salmonids as well as several other types of fishes (e.g., killifish, stickleback, sturgeon) was vast and broad in subject, species, locale, and scientific collaboration. David published over 25 book chapters and more than 120 peer-reviewed publications since 1979 including 20 on 6 species in the last 6 years (according to Web of Science). In addition to the evolution of behavior and life histories, he researched genetics, physiology, reproduction, speciation, phenotypic plasticity, and many areas of ecology; including exciting discoveries he and his colleagues made about Pacific and Atlantic salmon being able to orient to geomagnetic cues (e.g., Putnam et al. 2014; Scanlon et al. 2018; Naisbett-Jones et al. 2020). As a Director of the OHRC, David was able to effectively engage with its many stakeholders (K-12 school groups, the public at large, anglers, government officials, scientists local and distant) for the public good. In both Ontario and Oregon, David was involved in research projects with Indigenous peoples to enhance their local fisheries, and he used his broad expertise to be a science-based advocate of fish conservation.

During an oral history interview (OSU 2015), David talked about how his passion for reading and interest in facts inspired him to read every nonfiction book in his home town library in Hensall, Ontario before he was old enough for high school. He shared his passion for typewriters with many others; and the scientific community has benefited greatly from David's love of the written word and books! David was the Editor of this Fish and Fisheries Series for 20 years beginning with volume 25 from Beveridge and McAndrew (2000) on tilapias until this volume 40. He was an exemplar colleague to the many people he actively partnered with over the years at Springer Nature. David had a critical eye for proposals that would be highly relevant, inclusive in content, and enduring as a reference. He did tremendous work behind the scenes, always valued his colleague's input, and was generous about acknowledging the books that had personally influenced him. Like this volume, David deliberately cultivated several book projects with worldwide contributors or themes including *Chinese Fishes* (Noakes et al. 2010). Simultaneously for the past 19 years, David was the Editor-in-Chief of Environmental Biology of Fishes. Under David's leadership, the journal grew from quarterly to monthly and became global in scope with authors contributing from 117 countries. During his tenure, EBFi published 2690 papers meaning that he read about twice that, beginning when the manuscripts came by mail!

David's impact on the scientific world extends far beyond the written word as mentor, colleague, and friend. In addition to the numerous students and post-docs he mentored who work in and outside academia in education, conservation, consulting, and other related fields, he always had his door open to help others with their professional development. He was ahead of his time in recognizing women scientists, wrote about their accomplishments (Balon et al. 1993), and promoted their professional development. For the past 35 years, David was largely responsible for organizing The Ecological and Evolutionary Ethology of Fishes (EEEF) Biennial Conference which was just one of the many ways he was dedicated to mentoring students and connecting colleagues. He wrote in the History of EEEF, "We try to make sure that the meeting moves around to different geographic locations, so that we enable a different group of local people to attend, to show off their research, and to let us see the places where they live and carry out their science."

The mixing of science and comradery was a mainstay of David's career. He led the "Loaves and Fishes" Seminar Series at U. Guelph that is still fondly remembered and organized OSU's Steam Team Seminar and the Friday morning coffee club so others could indulge in his baking while celebrating staff and Darwin's birthdays. The Noakes generosity extended well beyond the office with David and his wife Pat frequently opening their home to create wonderful memories for students and colleagues. With relatively few words infused by his wit and sprinkled with his dry humor, David was able to engage people around him and generate the most interesting discussions. His closing email salutations of "Charrs" or "Best fishes" were classic David. David's kindness behind the poker face nurtured all; and his genuine interest and respect for others and ways of bringing people together will be long remembered. Along with his legacy of work as esteemed scientist and professor, David leaves a strong sense of connection between those who knew him; this speaks volumes about the richness of David's life and the many good things he made happen, of which this in memoriam only begins to describe.

Boston, MA, USA Maria E. Abate

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Preface

This volume is personal for me. George Barlow gave me a copy of his cichlid book, autographed with the admonition, “Remember the cichlids!” In January 2019, I convened a special session during the annual Canadian Conference for Fisheries Research in London, Ontario, Canada, to bring together a number of former students to recognize the lifetime contributions of Miles Keenleyside, including his major book on cichlids. Miles and his wife Hilda were present for that session, together with a number of former students and associates, including several who worked on cichlids. This volume represents my continuing commitment to cichlids and to George and to Miles and all of the others in this field—and in addition, presents a peculiar task for me as both Editor of this series and Co-Editor of this volume.

This volume is only the most recent in a long line of publications devoted to these remarkable fishes. For example, a previous volume in this series was dedicated just to the major importance of tilapia (Beveridge and McAndrew 2000). Entire volumes have been published on the cichlids of the Great Lakes of Africa, or even individual lakes in Africa, and on the cichlid fishes of Nicaragua. Of course, there have been major syntheses published on the behavior, ecology, and evolution of cichlids that have in a very direct fashion laid the groundwork for this volume. This does not even attempt to account for the numerous books and articles in the aquarium literature dealing with cichlids as perhaps the most popular group of fishes for aquarium hobbyists.

In producing this volume, we were fortunate to have contributions from a large number of colleagues who have developed highly productive research programs on cichlids across the full spectrum of current biology. The contribution by Mathew McConnell is perhaps the most comprehensive summary of the study of cichlids from the perspective of an academic historian. The chapters by colleagues in Africa and South America are fundamentally important as they present the perspectives on cichlids from colleagues who study and manage them as part of the native fauna. The remarkable program of studies of Lake Tanganyika cichlids by Hiroya Kawanabe and his colleagues is perhaps our most comprehensive insight into the behavior and ecology of cichlid communities.

Without doubt, the application of molecular techniques to the full range of hypotheses about the behavior, ecology, and evolution of cichlid fishes is the major contribution in this volume. It is interesting to note that cichlid research has always been based upon clear hypotheses with strongly held theoretical opinions, usually directed to evolutionary explanations. We can point to examples as fundamental as the evolution of parental care, foraging behavior, mate choice, and speciation. From the earliest descriptions of African and South American cichlids, scientists realized that those fishes challenged almost every existing concept in ecology, natural history, and evolution—based mostly on studies of birds and mammals. Almost from the first taxonomic descriptions of cichlids, the pioneers of the study of cichlids took advantage of the enormous diversity of cichlids, using a variety of comparative techniques, mostly based upon classical taxonomy and systematics.

In this volume, we can see major consequences from that strong tradition in cichlid research. The incredible developments in molecular genetics have been applied to a number of existing hypotheses concerning cichlid behavior, ecology, and evolution. That has led to the resolution of some long-standing questions, especially in taxonomy, systematics, and evolution. The availability of these techniques has refined and clarified our thinking in other areas, and the chapters in this volume clearly show the way forward. Cichlids have now become model species in their own right because they provide a unique combination of extraordinary details of ecology and life history in their native habitats with the ready availability of almost any species for detailed experimental laboratory studies.

This will not be the last book on cichlid fishes. But it might be the last book that can include so much of the information on cichlids in a single volume. As such it would be the last volume to include so much of the history, systematics, behavior, ecology, and evolution in one volume. That broad inclusion exemplifies the study of cichlids, and those who study cichlids.

Corvallis, OR, USA

David L. G. Noakes
Series Editor
Fish & Fisheries

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Contents

Chance, Choice, and Cichlids

Maria E. Abate and David L. G. Noakes

Abstract The Cichlidae, one of the most diverse families of vertebrates, is the subject of the volume entitled "*The Behavior, Ecology and Evolution of Cichlid Fishes*" which we introduce here. Cichlids are major members of their communities. They are socioeconomically important in fisheries, aquaculture, and the ornamental trade. The immense number of cichlid diverse forms challenge researchers to integrate new tools to delineate species, construct phylogenies, and determine species diversity; and their detailed study has significantly contributed to evolution models. Cichlid researchers have a strong tradition of taking a comparative approach. This book reflects that tradition with 20 reviews written by internationally recognized experts providing an integrative sub-disciplinary perspective, often including molecular studies. This volume is broad in scope, beginning with a review of the history of cichlid studies over two centuries. Next, four reviews examine cichlid diversification at different scales in African and Neotropical lakes and rivers; followed by four on conservation and management including species delimitation tools. The midsection, covering cichlid behavioral adaptations and their underlying mechanisms and effects, concerns the senses, parental care, sociality, and neurobiology. The last part of the book includes reviews on cichlid ecology, plasticity and evo-devo and closes with an examination of cichlids as models for biomedicine.

Keywords Cichlidae diversification · Cichlid study history · Model species · Social behavior · Brain and sensory systems · Ecomorphology · Anthropogenic disturbance · Invasive species

This volume is the fulfillment of a long-standing personal and scientific obligation to contribute to the history of studies of cichlid fishes. Noakes (herein "DLGN") was

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M. E. Abate (✉)
Department of Biology, Simmons University, Boston, MA, USA
e-mail: abate.maria.e@gmail.com

D. L. G. Noakes
Fisheries & Wildlife Department, Oregon State University, Corvallis, OR, USA

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personally involved in laboratory and fieldwork with cichlid fishes during his graduate studies on fish behavior (Noakes and Barlow 1973). Abate (herein "MEA") has had the pleasure of studying cichlids (Abate et al. 2010) joined by many undergraduate researchers who were turned into cichlidophiles by the beauty and social complexity of these fish, even during their first unruly encounters with experimental design.

Chance often plays a role in what people come to appreciate in life as is the case for each of us when it comes to cichlids. For MEA, it was a random encounter one day outside of the Museum of Comparative Zoology, home to the Thayer Expedition's vast collection of cichlid specimens from Brazil (see McConnell, this volume). There she struck up a conversation with Les Kaufman who introduced her to Karel Liem, cichlids, and phenotypic plasticity (Kaufman and Liem 1982). The coincidence of chance also brought DNLG to Halifax, Nova Scotia, Canada in December 2017 for the memorial service for Derek Iles, and the service itself made the cold of the season there less onerous. Anyone who knows anything about cichlids will be familiar with "*Cichlid Fishes of the Great Lakes of Africa*" by Geoffrey Fryer and Derek Iles (Fryer and Iles 1972). Their book was not the first word on cichlid fishes of African Great Lakes—but it certainly established those fishes on the international scientific stage. Their book was notable for several reasons. It combined detailed practical observations with strong theoretical insights. It was synthetic and progressive. They considered the broad scale of African Great Lakes (AGLs), and the even broader scale of species diversity, complexity, and evolution within those lakes. As they intended, their book drew attention to the incredible diversity of cichlid fishes in African Great Lakes, and the question of their evolution.

Descriptions of African cichlid fish species had accumulated in the major museums of England and Europe since the nineteenth century (Bloch 1801; Regan and Trewavas 1928; Trewavas 1928, 1946; Lowe 1955). There was a long history of discovery and descriptions of African cichlid fishes that increasingly drew attempts to account for the ecological and evolutionary mechanisms that might have produced such an extravagant example of speciation (Goldschmidt 1996). Standard evolutionary textbooks, mostly based on experience with ornithology (Mayr 1963), suggested rather dramatic geological cycles of changes in lake levels to account for what were clearly examples that did not conform to models of allopatric speciation. Sympatric speciation was anathema—history has had a lot to say about this. In the face of overwhelming ecological and genetic evidence, Ernst Mayr (2001, p. 181) eventually conceded that sympatric speciation did occur in cichlids in the African crater lakes.

This volume provides new interpretations of cichlid evolution from continental to regional scales in Africa and the Neotropics by using molecular genetics and genomics to understand the interplay of genomic structure and ecological factors (chapters by Wagner; Stiassny and Alter; Lopez-Fernandez; Torres-Dowdall and Meyer, this volume). The stunning polymorphism (e.g., Midas cichlid, see Fig. 2 of Torres-Dowdall and Meyer in this volume; Fig. 1) that we find so attractive has at the same time required a combination of new tools (van Rijssel et al.; Nyingi et al., this volume) to better distinguish species and assess species richness for more realistic

Fig. 1 Collection of cichlids in Nicaragua, 1969: how many species? (photo by Gerald Meral)

models of evolution and conservation action plans. The melding of quantitative molecular and field monitoring techniques (Stiassny and Alter; Njingi et al., this volume) is now modeling the evolution of cichlid species far beyond what conventional morphometrics and meristics could have suggested.

Our personal contacts with cichlids have combined some elements of chance together with active choices, that led to remarkable opportunities and interactions with some of the most productive people in cichlid research. For MEA several of these encounters have been at cichlid symposia presented at EEEF, the biennial Ecological and Evolutionary Ethology Conference of Fishes (Fig. 2). We recognize and freely acknowledge our good fortune for all of this. Without exception, all the cichlid researchers that we have encountered over the years, including the many contributors to this volume from around the world, have been generous to a fault in sharing their time and insights into the behavior, ecology, and evolution of these incredible fishes.

DLGN has personally experienced the considerable progression of studies of cichlid fishes from the days when exploration, taxon discovery, and detailed description were the norm to the present day when cichlids have become some of the most significant model species for the study of fundamental processes in biology, particularly researching the evolution of parental behavior (Fig. 3) and other social behaviors (Balshine and Abate; Jordan et al.; Félix and Oliveira, this volume). The study of cichlid social behavior has been a long tradition (Noble and Curtis 1939); and now molecular genetics has increased the potential to identify the relative roles of natural, sexual, and kin selection in shaping the evolution of cichlid societies. It is worth noting that even Bill Hamilton, the greatest theoretical biologist of his era (Fig. 4), was attracted to the questions of the evolution of parental behavior in

Fig. 2 Miles Keenleyside (Invited Chair of the Cichlid Symposium) with David Noakes and student award winners, Naomi Gardiner and Camille Leblanc, at the 2008 EEEF meeting held at Boston University. (photo by Maria Abate)

Fig. 3 Spawning pair of rainbow cichlid, *Archocentrus multispinosus* (formerly *Herotilapia multispinosa*) in laboratory aquarium. (photo by Jeffrey Baylis)

Amazonian cichlids (Henderson 2005). One of DLGN's serious regrets (of a number) is that at the time when he knew Bill, he did not realize that Bill also had an earlier interest in cichlid fishes.

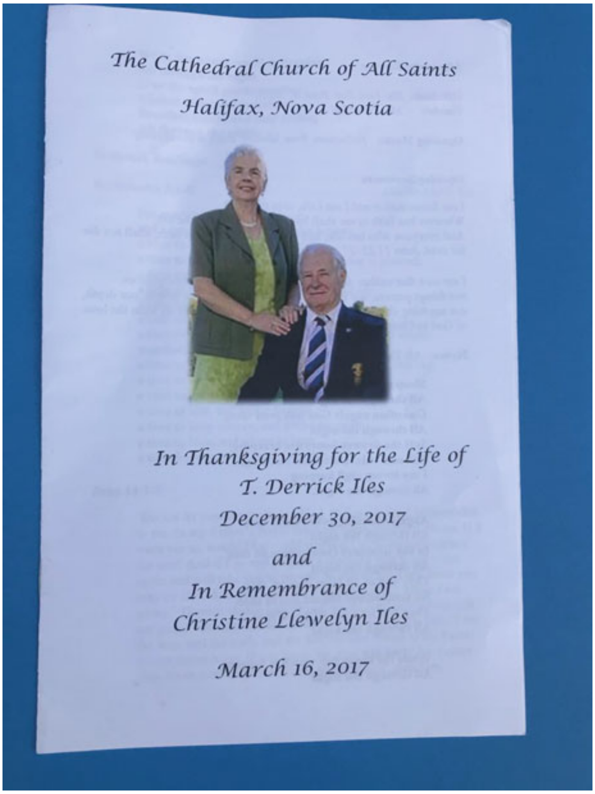
Cichlids also provide remarkable insights into the sensory world of fishes because of their tremendous diversity and ecological adaptations (Gray; Webb et al.; Lobel et al.; Schulz-Mirbach and Ladich; Félix and Oliveira, this volume.) In these chapters, behaviors of the signaler and the receiver are dissected in terms of their underlying mechanisms, including functional neurogenomics, and their consequences within a species and at the community level. Cichlids are best known in this regard for their coloration, visual displays, and as a model for vertebrate visual

Fig. 4 Bill Hamilton, October 1994. (photo by David Noakes)

ecology (Gray, this volume). Three chapters noted above are devoted to the study of mechanoreception and sound reception and production in cichlids as genomics, imaging techniques, acoustical research tools, and comparative studies have advanced their use for understanding the roles of the mechanosensory lateral line and auditory systems in mediating complex behaviors and how these sensory inputs influence evolution.

And yet the incredible ecological diversity of the cichlids continues to unfold as increasingly sophisticated theoretical approaches and analytical tools are focused on their evolution. We are pleased to include a chapter to summarize the long-term studies of Lake Tanganyika cichlids, pioneered by Hiroya Kawanabe (chapter by Takeyama, this volume), since the contributions of Japanese colleagues to cichlid field research have not been widely recognized. Our understanding of the ecology of cichlid fishes, particularly their respiratory ecology and trophic relationships, was built upon groundbreaking studies (e.g., Lowe-McConnell 1969; Fryer and Iles 1972). Contributions in this volume test some of the critical generalizations from those earlier studies on ecomorphology and take those areas of science in productive new directions to examine explanations involving trade-offs (chapter by Chapman) and feedback between internal and external drivers of variation (chapter by Hu and Albertson, this volume).

DLGN does not place any particular interpretation on the visit to Halifax and the memorial service for Derek Iles. It was the opportunity to meet members of his family and share their feelings about his remarkable life (Fig. 5). DLGN had known Derek for a number of years when he worked on marine fishes for the Department of Fisheries and Oceans Canada long after his work on cichlid fishes in Africa. But the coincidence of DLNG's contacts with cichlids and events over time seems to be ongoing. For example, during the 2019 presentations to recognize the 50th anniversary of the Apollo 11 landing on the moon, DLNG was reminded that unlike a great many people in different countries he did not see those events when they happened. Together with Jerry Meral ("JM"), another graduate student from George Barlow's laboratory, DLGN and JM were trapped in the "Soccer War" between El Salvador and Honduras during that week in 1969. Sitting in the airport in Tegucigalpa, Honduras and watching fighter aircraft take off to engage in the last aerial combat



The Cathedral Church of All Saints
Halifax, Nova Scotia

In Thanksgiving for the Life of
T. Derrick Iles
December 30, 2017
and
In Remembrance of
Christine Llewelyn Iles
March 16, 2017

Fig. 5 Memorial service for Derek Iles, Halifax, Nova Scotia. (photo by David Noakes)

between piston-engine aircraft (Fig. 6), while two men walked on the moon. Driving from Berkeley, California to field sites in Nicaragua and just happening to be in the wrong place at the wrong time. Of course, eventually reaching Nicaragua and spending an incredible field season watching cichlid behavior in the crater lakes (Thorson 1976). It did take some time, however, before DLNG and JM became accustomed to seeing cichlids for sale in the local markets—and to eating cichlids in the restaurant in the hotel—after spending so much time in the research laboratory keeping fish alive and healthy as valuable research specimens (Fig. 1). For MEA, the chance of being in the wrong place at the wrong time in Nicaragua came in the middle of the night when lodgings in a forest reserve caught on fire (Fig. 7). It was a reminder of how fragile every day can be for the people who live in these remote places and make the field study of cichlids possible for those who come from afar.

One of the fondest cichlid memories for DLGN is November 1980, sitting with ET, Ro, and Melanie in the British Museum, surrounded by bottles of museum specimens of cichlids and the proofs of ET's monumental book on cichlids (Trewavas 1983) while having tea and chocolate (in the form of the number 80) to celebrate ET's birthday. DLGN was truly fortunate to share time with ET and Ro at the international tilapia conference in Bellagio and hear them recount their wealth of personal observations of cichlids in Africa (Pullin and Lowe-McConnell 1982; Lowe-McConnell 2006).

Fig. 6 Salvadoran Air Force Corsair aircraft that took part in the 1969 "Soccer War", subsequently painted in USA color pattern. (photo by David Noakes)

In this volume, we have brought together people and their ideas that we think acknowledge the history and contributions of researchers who have studied cichlids and at the same time demonstrate the continued dynamic approaches and insights in this field. Of course, our debts to the major books by Baerends and Baerends-van Roon (1950), Greenwood (1974), ET (Trewavas 1983), Keenleyside (1991), and Barlow (2000) on cichlid fishes are obvious. The study of cichlids has progressed from the initial descriptive phase of discovery of new species and the documentation of the incredible diversity within this family to the most detailed analyses of molecular genetics. We are fortunate indeed to have the monumental historical contribution from Matthew McConnell to set the scene for our volume. We are especially pleased that we have contributions from colleagues in South America and Africa who bring very different perspectives on cichlids as native species (Natugonza et al.; Nyingi et al.; Agostinho et al., this volume).

The applications of molecular genetics to the study of almost every aspect of cichlid biology have at once revolutionized our understanding of cichlids and at the same time has led to new hypotheses to account for their behavior and evolution. Cichlids have now become model species, in their own right, for research on topics as diverse as neurobiology, sensory physiology, and environmental physiology. But we cannot ignore the increasing threats to native cichlids from their long history of being overfished (e.g., Lowe 1952) and the many other human activities that have disrupted habitat over the past few decades (chapters by Natugonza et al., Nyingi et al., this volume). Nor can we overlook the new threats of some cichlids themselves (Figs. 8 and 9) as invasive species often far beyond their native ranges (chapter by Agostinho et al., this volume).

Fig. 7 Lodgings ablaze in forest reserve, Nicaragua. (photo by Maria Abate)

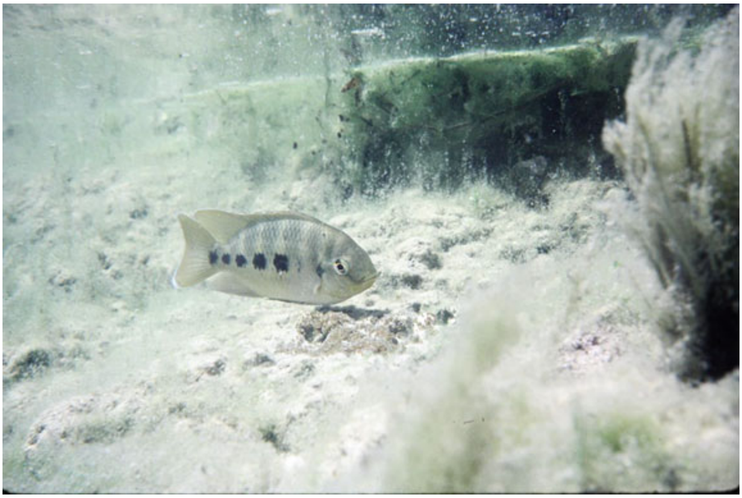


Fig. 8 Female spotted tilapia, *Pelmatolapia mariae* (formerly *Tilapia mariae*), in a Florida canal. (photo by Jeffrey Baylis)

Fig. 9 Female Mossambique tilapia, *Oreochromis mossambicus* (formerly *Tilapia mossambica*), retrieving free-swimming young back into her buccal cavity, in a Florida canal. (photo by Jeffrey Baylis)

As readers will note, the styles of the chapters in this volume are quite different, a welcome consequence of the diversity of the authors as well as differences in the stories they present. Readers will no doubt also notice our dilemma in what remains a fundamental task for anyone studying cichlid fishes. How do we deal with the ever-changing taxonomy, systematics and scientific nomenclature (or should we even consider common names) in a volume that includes references that span decades? In most cases, there are no connections between publications and voucher specimens deposited in museum collections, so it would not be possible to resolve the questions with certainty.

Along with the species name as it appeared in the original reference, several chapters in this volume also included the updated valid name. In some cases, the most widely referenced species name or well known common name (e.g., convict cichlid) was used to clarify which species was being referenced. Hence, readers will find that the name of a particular species that was extracted from the contributed chapters for the volume's *subject index* may be listed under its common, former or current name. While our approach to taxonomy was imperfect, we hope the volume is also useful for compiling findings for individual cichlid species over many years under its various names, which are summarized online in Eschmeyer's Catalogue of Fishes (Fricke at al. 2020) with a cross-link from FishBase (Froese and Pauly 2020) where common names can be searched.

This volume includes many insights about the exciting and promising future of cichlid studies. It has been emphasized for at least 20 years that cichlids are model organisms for the study of evolution (e.g., Kornfield and Smith 2000); and now, with sequenced genomes and the recognition of different mechanisms underlying their highly varied phenotypes, some cichlids have also become model species for biomedical research. Compared to the typical lab rat or lab fish, the in-depth knowledge we have of cichlids in nature makes them a far more powerful model when it comes to understanding how gene–environment interactions influence the development of vertebrate traits including social behavior. With new molecular and imaging tools being used for cichlid studies, we not only have the opportunity to learn a lot more about cichlids but even some things about ourselves. This book will not be the last word on cichlids, but it certainly sets out what the next words will be for further discoveries of the mechanisms responsible for their complex traits and remarkable phenotypic variation (Parsons et al., this volume).

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Frontiers in Cichlid Research: A History of Scientific Advancement

Matthew McConnell

Abstract This chapter summarizes 200 years of the study of cichlid fishes, ranging from the first descriptions of South American and African species in early natural histories to the work of twentieth-century biologists. The rise and influence of evolutionary theory and the development of new knowledge and techniques in the study of genetics are considered central influences in a variety of fields of research involving cichlids, including ecology, ethology, aquaculture, and fisheries. Significant developments and their historical context are considered in relation to the current state of a variety of cichlid research programs, showcasing the extent to which cichlids have become both model species in evolutionary biology and a crucial species in global food production.

Keywords Natural history · Modern science · Colonial science · British imperialism · Darwinian synthesis · Environmental history · Tilapia fisheries management · Biological species · Allopatric speciation · International science

1 Cichlids in Natural History

> To have more Aristotles, more Alexanders were needed. Positive Natural History requires work and expense that a private person without patronage cannot afford.—Georges Cuvier

For much of their history as objects of scientific inquiry, cichlid taxonomy has been in question. Today, cichlids are classified as teleosts, an ancient class of ray-finned, "true bone" fishes that account for 95% of extant fish species (Barlow 2000). The family Cichlidae, traditionally belonging to the Perciformes suborder of Labroidei, is most recently classified as a member of the order Cichliformes and includes over 1700 species (Nelson et al. 2016; Fricke et al. 2020). With some

M. McConnell (✉)
School of History, Philosophy, and Religion, Oregon State University, Corvallis, OR, USA

Department of American Studies, University of Hawaii, Manoa, HI, USA
e-mail: mjmcconn@hawaii.edu

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estimates as high as 3000 species, cichlids are not only representative of 10% of teleost fishes, they are one of the most diverse families of extant vertebrates (Helfman et al. 2009). Cichlids are believed to have evolved around 160 million years ago (Barlow 2000). During this time, Gondwanaland, the supercontinent composed of present-day Africa and South America, broke up and the southern Atlantic opened, separating founding populations of cichlids that radiated extensively.

The greatest cichlid biodiversity is found in The Great Lakes of East Africa. With estimates on its initial basin formation ranging between 9 and 12 million years before present, Lake Tanganyika is the oldest of the African Great Lakes. It is home to 24 fish families, more than any other lake, with 18 occurring in the tributaries and marshes around the lake. Malawi, between 1 and 2 million years old, is home to over 500 species (possibly as many as 1000 or more). Lake Victoria—the second largest lake on earth and roughly the size of Switzerland—is around 400,000 years old and has dried out completely at least three times over that period. Its basin is believed to have refilled from one such drought a mere 14,700 years ago. Since that time, it has become home to at least 400 species, although it is difficult to say in the wake of recent ecological disasters how many cichlids once existed there or how many now remain (Barlow 2000). Cichlids also inhabit lakes, marshes, floodplains, many river systems in central and northern Africa and Madagascar. Only 20,000 years ago, the Kalahari Desert was an enormous lake called Makgadikgadi. Throughout the Pleistocene, a rapidly evolving radiation of cichlids comparable in morphological diversity to the extant African Great Lakes thrived there (Joyce et al. 2005). Among these were the serranochromine cichlids, and it is now believed that when the lake dried up around 10,000 years ago, the major river systems of Southern Africa were “seeded” with serranochromines (Lowe-McConnell 2006).

In Southeast Asia, and Central and South America, cichlids are predominantly of the riverine variety. In each of these unique locations and environments, species are equipped with a dazzling array of biological variation in coloration, diet, mating, and parental behaviors. This astounding diversity is likely the driver for their popularity among aquarists. It is also the root of a great question surrounding these amazing animals: How have they evolved so quickly? Humans have only recently endeavored to answer this question, but the history between humans and cichlids is far older.

The Nile, with its headwaters at Lake Victoria, is home to tilapiine cichlids, and Egyptians farmed Nile Tilapia as long ago as the third millennium BCE. Ancient Egyptians called the fish Bolti, and revered it as a symbol of rebirth (tilapias recur in Egyptian art with lotus blossoms emerging from their mouths and are thought to signify resurrection). Humans have long treated cichlids as a valuable food source. Ranging from Central Africa to Israel and Jordan, *S. galilaeus* has historically supplied the fisheries of the Jordan Valley (Barlow 2000). The species is called “St. Peter’s Fish” after a miracle in the Book of Matthew, wherein Peter (following his teacher’s instruction) catches one of the fish, reaches into the tilapia’s buccal cavity (where one might normally find a school of young), and retrieves a coin to pay the temple tax. Tilapias have also supported fisheries carried out by Africans using homemade seines and palm leaf ropes since at least 1865 when David Livingstone documented the practice (Lowe-McConnell 2006). Subsistence fisheries in Africa remain crucial today. For example, Malawi fish provided 75% of the animal protein consumed in Malawi as of 1994 (Barlow, 2000). At the same time, tilapia have become the leading fish for aquaculture in the world in the twenty-first century, with Tel Aviv University in Israel remaining a leading center of tilapia culture research (Beveridge and McAndrew 2000). Cichlid fisheries are both ancient and ongoing practices.

Fishes were often neglected as subjects of natural histories until the middle of the sixteenth century, and descriptions of specific cichlid species do not appear for another two centuries (Cuvier 1828). The first scientific classifications occurred in the late eighteenth and nineteenth centuries when colonial expansion reached its zenith. During this time, the Americas and Africa were explored, mapped, and evaluated as resources. In this new, global arena of research, a naturalist tradition that had been rekindled centuries earlier grew wildly popular among amateurs and professionals alike, bringing the stunning biodiversity of cichlids from both sides of the Atlantic to the attention of the Western scientific world.

1.1 Traditions in Taxonomy: 1750–1800

Until the end of the 1790s, most natural history collections were in personal cabinets containing shells, minerals, ancient coins, and books; they were considered fashionable possessions, every bit as aesthetic as they were scientific (Farber 2000). When the classification of animal specimens became popular, collections were often gathered by medical students who had anatomic knowledge valuable for description. The interest of university scholars in natural specimens, combined with the aristocratic implications of such collections, conveyed social status on owners of such cabinets of curiosities. Royalty, such as the King and Queen of Sweden, had their own cabinets, and in 1751, Carl Linnaeus studied these royal collections (Fernholm and Wheeler 1983). As the first curator of the Swedish Museum of Natural History (known at the time as The Academy Zoological Collection), Linnaeus acquired many descriptions of species and specimens for The Ichthyological Collection Building—founded 1739—through his “apostles” on their journeys abroad. Aside from his more educated volunteers, Linnaeus and other renowned natural historians were aided by enthusiasts who attempted classifications of animals, plants, and minerals using Linnaean binomial taxonomy (Farber 2000). Often, collections were produced by naval officers performing other functions on board their ship (frequently surgeons). Such collections were returned home to the care of wealthy private collectors, and many were given as gifts to royal families or other members of the social elite.

In his 1758 10th edition of *Systema Naturae,* Linnaeus described the North African *Oreochromis niloticus* (currently the aquaculture tilapia of choice) and *S. galilaeus*. He also described the South American *Cichlasoma bimaculatum* under the genus *Labrus,* the first species of *Cichlasoma* ever to be described. The same species was described as if it were a new species altogether—*Chromys punctate*—by Marcus Elieser Bloch, who from 1782 through 1795 classified various

South American, Asian, and African species based on collections sent to Berlin. Misappropriations and errors in systematics were characteristic of taxonomic work involving cichlids in the late eighteenth and the nineteenth centuries. Their remarkably recent speciation, along with frequent cases of convergent evolution, made this family an especially challenging subject in an era in which the concepts of evolution, as well as the disciplines of biology and ichthyology, were just taking shape.

Adolf Frederick and Louise Ulrika of Sweden were not the only royalty to support the growth of Natural History. In 1793, the Royal Garden at Paris was reorganized and renamed the National Museum d'histoire Naturelle under the direction of George-Louis Leclerc Comte de Buffon. It contained collections of fishes formerly of the King's Cabinet, which was composed of specimens acquired on voyages around the world, including fishes brought back from the Egyptian expedition (1798–1799) of Francois Peron and Charles Lesueur during Nicolas Baudin's voyage around the world (1800–1804). From 1798 through 1803, Bernard Germain de Lacépède authored *Histoire naturelle des poisons* (a continuation of Buffon's volumes of natural history), describing cichlid species of South America, Africa, and Asia. In 1799, Alexander Von Humboldt (considered one of the founders of biogeography, and a profound influence on Charles Darwin and Alfred Russel Wallace) sailed for South America, and his *Voyage de Humboldt et Bonpland, Observations de Zoologie* (1834) identified several species of *Cichla*. By establishing a state-sponsored program that offered professorships to trained naturalists and their staff, France had set a new standard (Farber 2000). The Museum of Natural History was a national collection, evidencing the colonial prowess and exploratory accomplishments of an entire nation, and collections grew rapidly in this atmosphere due to the cooperation between museum staff, naval officers, and colonial explorers (Bauchot et al. 1997).

1.2 The Golden Age of Natural History: 1800–1900

By the end of the Napoleonic Wars, the scale of European states' colonial activities had increased significantly, and in most Western nations, museums were increasingly controlled by municipal governments and associated with the research of renowned universities (Farber 2000). In 1819, the French museum established a program to train traveling naturalists, setting a trend of professionalization of natural history in other countries that coincided with a precipitous rise of naturalists in the field between 1750 and 1850. This can be seen as an important development in the expansion of specific branches of natural history such as zoology (and by the mid-nineteenth century, ichthyology), and it is near the end of this period that the family name Cichlidae first appears, in 1850 (Barlow 2000).

Over the course of the nineteenth century, naturalists from many countries came into contact with cichlid species. Those to describe or classify the most were French, Dutch, German, British, and American. This period marks a general increase in international cooperation between researchers in the effort to establish complete, standardized classifications for species, with trips abroad and contact with other ichthyologists often resulting in loans of interesting specimens, exchanges, and generous gifts to museums (Bauchot et al. 1997). The resulting works were some of the great accomplishments of the naturalist era: Georges Cuvier's *Histoire Naturelle des Poissons* (22 volumes published from 1828 to 1849), described over 4000 fish species, fewer than half of which were previously known to science.

One of the first aides at the museum in Paris, and a traveling naturalist, was Cuvier's student Achillie Valenciennes. In Berlin, Cuvier and Valenciennes studied and described several American cichlid species collected by Bloch and Johann Gottlob Theaenus Schneider, the first to apply the genus *Cichla* for a group of cichlids native to South America (Bloch and Schneider 1801, Johann Friedrich Hennig edited, expanded, and republished his original work, *Systema Ichthyologiae iconibus cx illustratum*). The genus name *Cichla* was based on the Greek "Kichle" for sea fishes like wrasses. In 1829, Valenciennes described Central American cichlids among a collection of Mexican fishes from Ferdinand Depp and Marcus Bloch and in 1831, Cuvier and Valenciennes described additional Asian and South and Central American species. In London, Edward Turner Bennett gave Cuvier access to the collections of the Zoological Society he had described in 1827, as well as the new acquisitions of the British Museum and the Zoological Society. He had identified some South American cichlids himself in 1830. Cuvier also worked alongside the keeper of Zoology at the British Museum of Natural History, John Edward Gray, and Dutch naturalist Laurence Theodore Gronow (also at the British museum) who together collaborated on a catalogue of specimens that included several species of South American cichlids (Gronow 1854).

The Koninklijk Instituut (forerunner of the Royal Netherlands Academy of Sciences) and the Kabinet des Konings were founded in the Netherlands 1806 under Napoleonic rule. After the battle of Waterloo, some natural history collections, confiscated by France during the short-lived government of the French Directory, were returned to Holland and presented to Leiden University by King William in 1815 (Boeseman 1997). Here, Coenraad J. Temminck conceived of an Imperial Dutch Museum that would unite his private collection with the university and royal collection, and in 1820, the Rijksmuseum in Leiden was formed with Temminck as its first director. In 1820, the new museum was named the National or Rijksmuseum van Natuurlijke Historie, and 4 years later, Temminck was on good working terms with Valenciennes, whom he gave access to collections in Leiden. From 1858 on, Pieter Bleeker was responsible for many of these collections (often sent from the East Indies). A Dutch medical doctor for Dutch East Indies Trading Company, Bleeker was a practicing ichthyologist and herpetologist and provided specimens of cichlids from East Asia (1868) and Madagascar (1862–1877). In British East India, cichlids were collected and classified by natural historians and officers of the crown alike, depicted in carefully illustrated panels (e.g., Fig. 1), as in the Orange Chromide depicted below (first classified by Bloch in 1795), found in Sir Francis Day's 1888 work on the fauna of British East India.

Women interested in learning the trade skills of natural illustration, taxidermy, and the classification and cataloguing of natural history specimens found assistant opportunities in museums. Here, they were able to conduct research that universities would have seldom allowed (while some universities offered women undergraduate

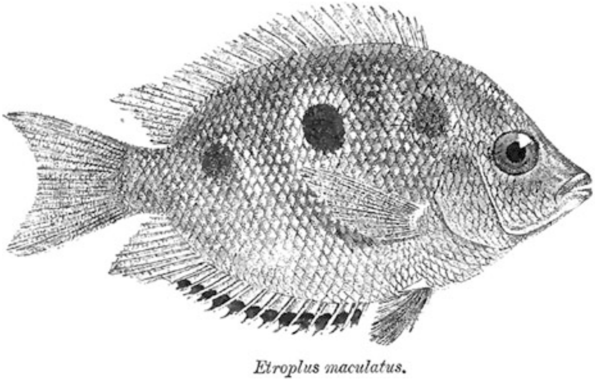

Fig. 1 An Orange Chromide. (Reproduced from Day 1888)

and graduate degrees in zoology, academic positions were rare). Yet, even in museums where women could contribute to their field, the work was usually considered voluntary; women often received little or no pay (Brown 1994). It was in the Museum of Zoology at the University of Utrecht that Louise Schilthuis, one of the first female ichthyologists, became curatrix and identified species of cichlids in her *Collection of fishes from the Congo; with description of some new species.*

In 1806, Emperor Franz I opted to enlarge and systematize Germany's natural history collections, and several large collections of fishes were incorporated. Johann Natterer, assistant at the natural history museum in Vienna, returned from an 1817 expedition to Brazil and recruited the Austrian, Johann Jakob Heckel for museum taxidermy (Herzig-Straschil 1997). Heckel curated the fish collection from 1835, during which time it grew considerably. Heckel remained at Vienna where he catalogued incoming cichlid specimens from the Americas; his extensive paper on *Cichlidae* in 1840 was based on Natterer's collections from Brazil.

In 1885, the German government granted Carl Peters, entrepreneur and explorer, an imperial charter to establish a protectorate in the African Great Lakes region (Fig. 2). The colony of East Africa divided Lake Victoria in half and bordered lakes Tanganyika and Malawi (In 1892, the Njassa Sea). The result was the collection and classification of African Lake species of cichlids; In 1888 by F.M. Hilgendorf, in 1893 by Georg Johann Pfeffer, curator of the Natural History Museum at Hamburg (destroyed during World War II), and in 1897 by Max Wilhelm Carl Weber, German professor of anatomy and physiology at University of Amsterdam from 1883. In 1885, Tanzania, Rwanda, and Burundi were placed under the rule of the Imperial German Government, but they were not without competition. Britain had established a colonial administration at Cape Colony in 1807 during the Napoleonic Wars, and Port Elizabeth and Grahamstown received settlers in 1820. In 1858, searching for the source of the Nile, John H. Speke found the headwaters and discovered the southern shore of what local Arabs called "Ukerewe" and the Basuba of Kenya called "Nyanja" (or Nyanza). As the first European to see the lake, he named it in honor

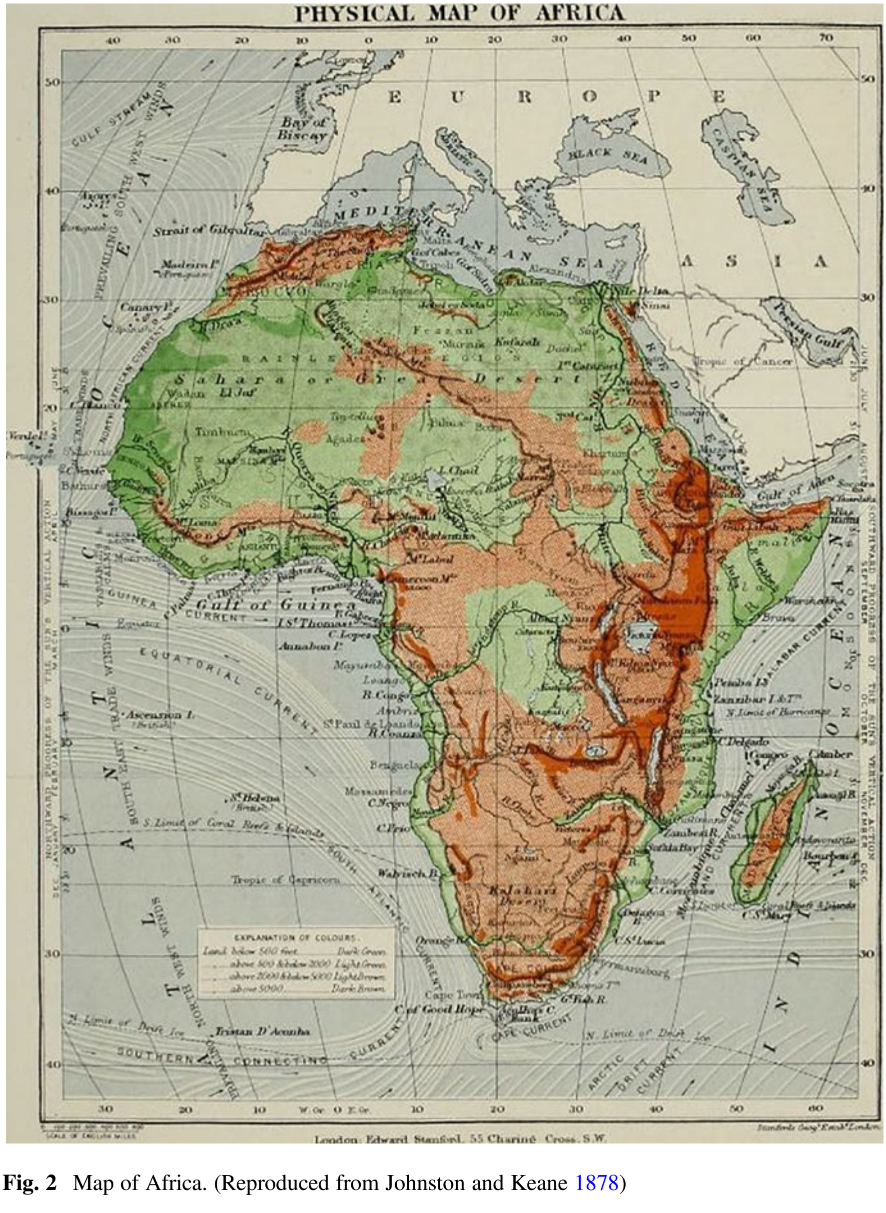

Fig. 2 Map of Africa. (Reproduced from Johnston and Keane 1878)

of Victoria, Queen of England. In 1875, the American journalist Henry M. Stanley circumnavigated the lake and popularized the name Speke had given it in the Western world (Awange and Ong'ang'a 2006). Soon, Lake Victoria was frequented by missionaries, soldiers, and traders.

Explorations of the other African Great Lakes and central Africa were also underway. In 1859, David Livingstone reached what he called Lake Nyassa (now Malawi), and in 1894, biologist and explorer John Edmund Sharrock Moore led the British Tanganyika Expedition. In the 1890s, Great Britain colonized Kenya and Uganda, followed by Germany's colonization of the Tanzanian mainland in 1899. The Imperial German Government maintained control over Tanzania, Rwanda, and Burundi until after the First World War, when Tanzania was placed under the British mandate and Rwanda and Burundi came under Belgian rule.

During this time, there were many British and German discoveries of new cichlid species in Africa. From 1834 through 1836, Sir Andrew Smith led a scientific expedition into the interior of South Africa, where many riparian or riverine species of cichlid would be found (Smith 1849). A surgeon and ethnologist, Smith had been ordered to Cape Colony where he met and was inspired by Charles Darwin, who was traveling onboard the H.M.S. Beagle. Darwin himself obtained specimens of several species of South American cichlids during his voyage, which were later classified by Leonard Jenyns in 1842 (an English naturalist who had been offered Darwin's position on the Beagle first, but apparently turned the opportunity down for health and personal reasons). Considered the father of zoology in South Africa, Andrew Smith's 1837 work, written upon his return from the colony, was the first to classify cichlids according to the genus *Tilapia*. Smith was also first superintendent of the South African Natural History Museum at Cape Town, which opened in the 1820s (Gon and Skelton 1997). It is presumed that Smith, who met the Lord Somerset, Governor of the Cape, in 1825 and proposed the museum, had produced his own collection from his time in Grahamstown, which became the museum. By 1840, the museum was essentially derelict, its remaining collections passed to the South African College. Governor Sir George Grey hired E.L. Layard in 1854 to maintain the museum, which was reinstated in the 1850s (Gon and Skelton 1997). Many cichlid specimens were sent to George Albert Boulenger in London, who classified them in 1898. Boulenger had been invited to the British Museum of Natural History by its keeper of zoology, Albert Günther, whose 1864 *Descriptions of new species of Batrachians from West Africa* was the first description of the Midas cichlid. Both men classified and catalogued a great number of cichlid species from South America, Africa (Fig. 3), and Madagascar in the late nineteenth century.

South African museums developed out of a need to raise public and official financial support, often creating opportunities for local involvement. The Albany museum for example—which opened 1855—declared that any man in the eastern province could be admitted as a member, the goal being the creation a local scientific research society (Gon and Skelton 1997). However, it was not a man of science, but one Miss Mary Glanville in 1882 who was the first paid curatrix of the Albany Museum. Her hope was that the fisheries increasing on the coast of Port Alfred would drive collections of fish and marine mammals. With the exception of the Albany Museum's self-trained J.L.B. Smith, no ichthyologists were working in museums as curators or researchers from 1895 to 1950, but the South African Government saw aquatic research as increasingly valuable. Thus, from 1896, the Marine Biological Survey, now called Sea Fisheries Research Institute, was created

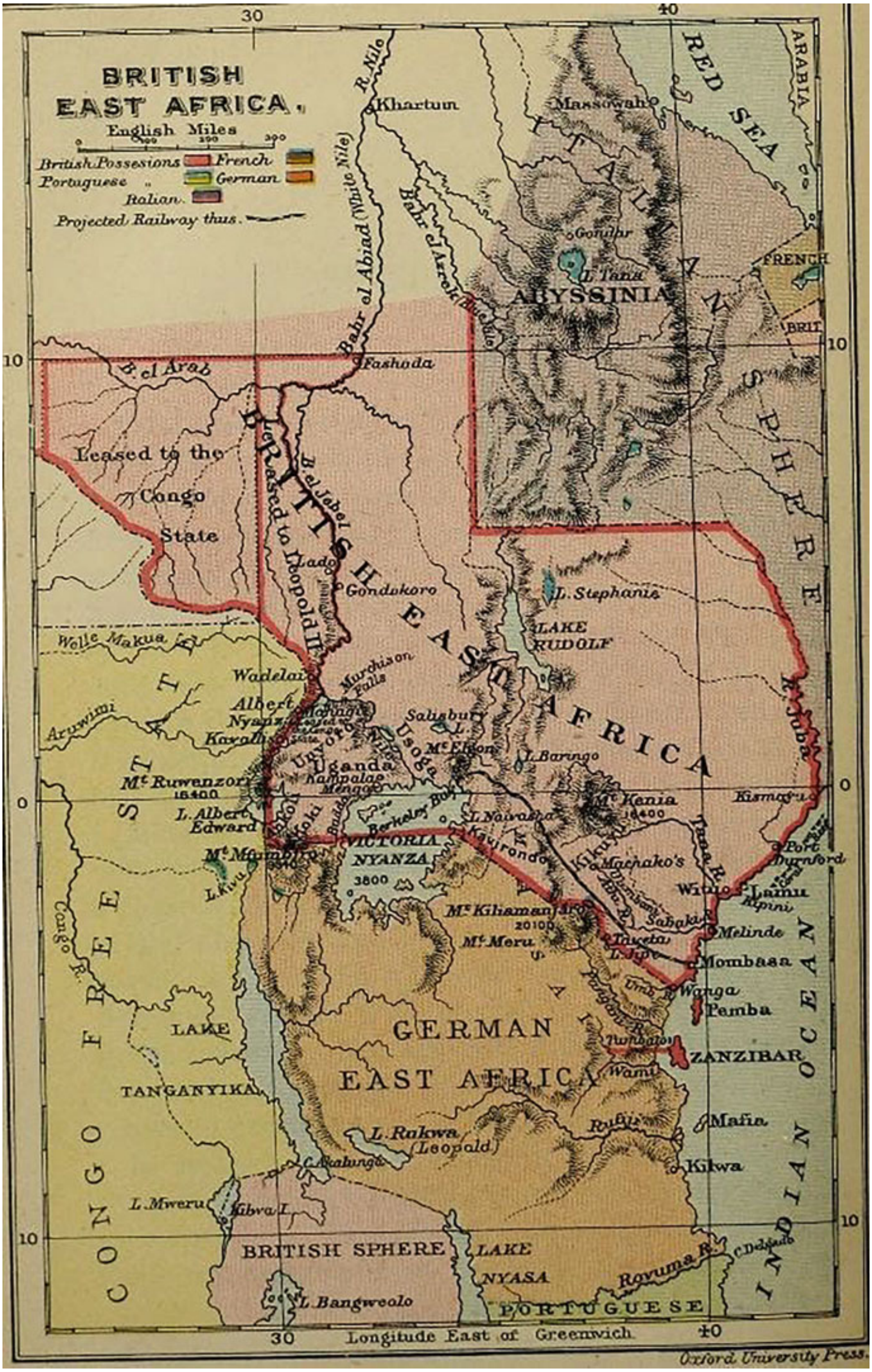

Fig. 3 British and German East African colonial holdings. (Reproduced from Lucas 1897)

and run by John D. F. Gilchrist, chair of the Department of Zoology at the South African College, and Honorary Keeper at the South African Museum. He enlisted Boulenger in London to help with species identifications, and many specimens sent by Gilchrist were used for Boulenger's and Johnston's catalogues (Johnston 1916) of African freshwater fishes (Gon and Skelton 1997).

On the other side of the Atlantic, cichlids from Central and South America (Fig. 4) remained by far the most represented in collections, and by mid-century, naturalists in Massachusetts, Philadelphia, and Washington all possessed specimens. In 1859, Jean Louis Agassiz, a biologist and geologist who studied with Cuvier and Humboldt in Paris, founded the Museum of Comparative Zoology at Harvard. Austrian zoologist Franz Steidachner visited Agassiz at Harvard to work on South American fishes from the Thayer Expedition in 1869, and collected additional species on a trip to South America with Agassiz in 1871 (Herzig-Straschil 1997).

Down the coast at the Academy in Philadelphia, Theodore Gill was wildly prolific. In 1862, his *Remarks on the relations of the genera and other groups of Cuban fishes* identified cichlids in the Caribbean, and in 1877, having moved to the Smithsonian Institution in Washington, DC, Gill and Bransford described central American cichlids in their *Synopsis of the fishes of Lake Nicaragua* as part of the Panama Canal Surveys then ongoing through the US government. After he left Philadelphia, a personal museum sprang up in Gill's absence maintained by Edward Drinker Cope. Cope's work bankrupted him, but he amassed the largest collection of fishes at the Academy in Philadelphia ever; until, that is, Henry Weed Fowler became curator of cold-blooded vertebrates at the Academy of Natural Sciences, Philadelphia and vastly increased the institution's collection and ichthyological research (Smith-Vaniz and McCracken Peck 1997). Cope's *Contribution to the ichthyology of the Marañon* 1869 detailed South American cichlid species. Both men were students of David Starr Jordan.

During his time at Cornell, Cope befriended Jordan, now considered the father of American Ichthyology. Jordan had studied under Agassiz during summer session at his Penikese Island field school in Massachusetts, and worked with Albert Günther before starting his own Ichthyology program at Stanford in 1891 (Brittan 1997). In 1899, along with J.O. Snyder, he identified cichlids from the Americas. Jordan had many prominent students, including Carl Eigenmann, and his wife Rosa Smith Eigennmen, considered the first woman in ichthyology in the United States (Brown 1994). After marrying, the pair left for Harvard to work on Agassiz's mostly unstudied collections from Brazil. Together, they described many fishes in the Americas, including cichlids, and especially those discovered on a trip to British Guiana funded by the Carnegie Museum (1894). Both Carl and Rosa had studied underneath Jordan at Indiana University; most of the early students of ichthyology in North America were either resident or corresponding members of the academy sharing their knowledge (if not always their specimens) with their fellows (Smith-Vaniz and McCracken Peck 1997).

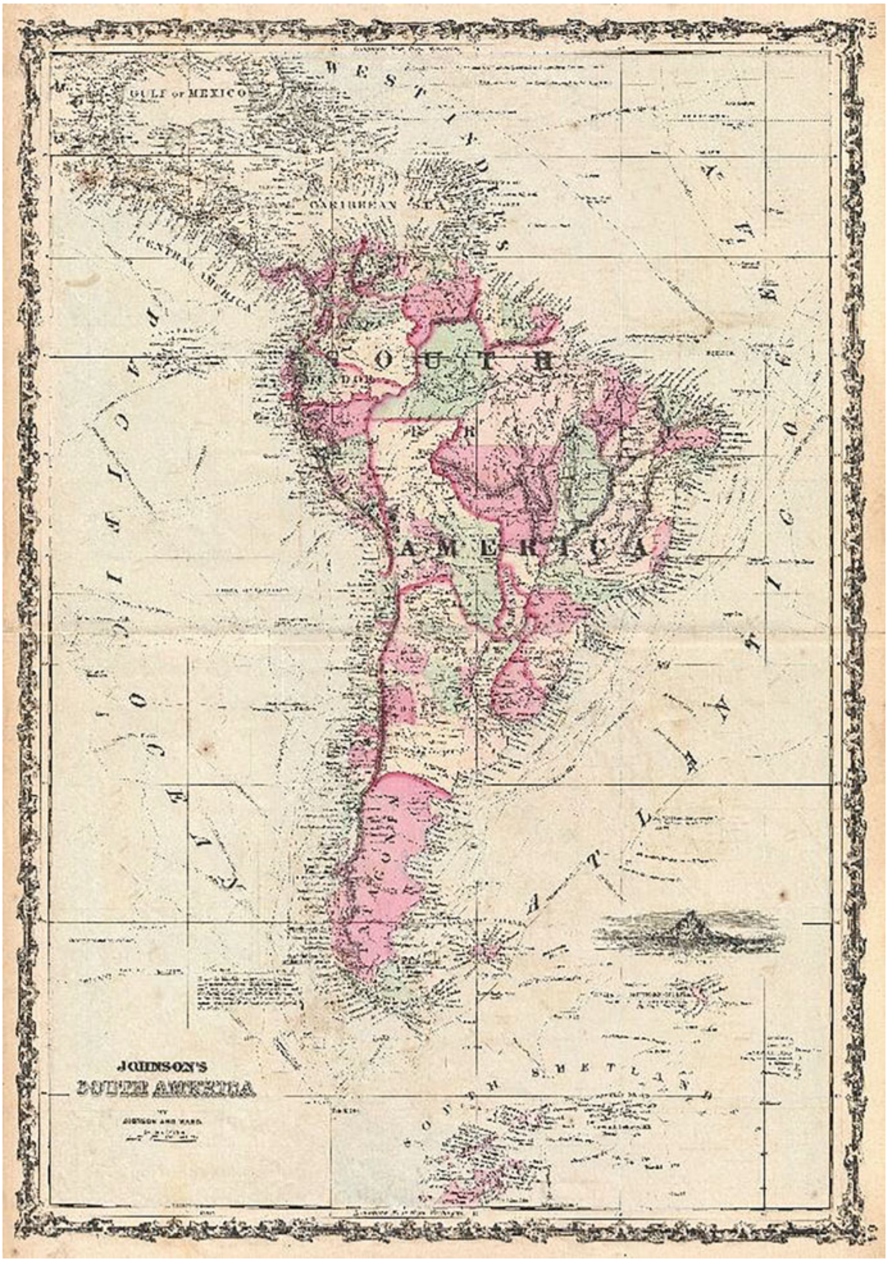

Fig. 4 Map of South America. (Reproduced from Johnson 1862)

The natural history museum was an important academic center of this expanding intellectual exchange, both in America and abroad. By 1900, Germany had 150 natural history museums, Great Britain 250, France 300, and the United States 250. Cape Town, São Paulo, and Buenos Aires opened museums that built on local collections and purchased specimens from commercial houses in Europe (Farber 2000). Many of these museums contained cichlid specimens, and each relied on the work of countless naturalists who classified and discovered species all over the globe during the golden age of naturalism. While some names stand out in the history of the taxonomic tradition coming out of centers of learning such as Paris, Berlin, London, or Massachusetts, they are joined by so many contributing amateurs and professionals that to list them all here is impossible. It is difficult to imagine the conditions under which the voyages of 200 years ago were carried out by such individuals. To circumnavigate the world took years and involved travel to locations that had been hitherto entirely unknown. Collections work in natural history had become increasingly scientific, but the motivations for a scientist to go exploring often remained as romantic as they were intellectual.

2 Pioneers of Cichlid Research

> Today, when a young scientist can leap into a plane and arrive at a well-equipped laboratory, complete with modern sampling devices and computers, to study some aspect of a specialist subject, it is difficult to realize what was then involved in such a prototype enterprise.—Rosemary Lowe-McConnell

By the turn of the century, natural history was being replaced in academia by biology. This was largely due to the work of Thomas Henry Huxley, who proposed in the late nineteenth century that the science of biology not be restricted to physiology, but should encompass the entire study of life, from the cell to evolution of the organism. This influenced the rise of biology departments offering graduate training in laboratory work with both physiology and morphology, previously the purview of natural history (Farber 2000). Huxley was also popular for his defense of natural selection, which by 1900 was generally accepted as the mechanism of evolutionary change (even if the heritability of this change was not well understood). By this time, ichthyologists interested in evolutionary biology were aware of the biodiversity of the African Great Lakes cichlids, and focus began to shift from African and New World riverine species to those in the Great Lakes (Barlow 2000).

Journeys to and from research locations in Africa could require months of travel time and might expose the traveler to malaria and other tropical diseases; a sleeping sickness epidemic in the Lake George region, for example, prevented cichlid research from 1931 to the late 1940s (Lowe-McConnell 2006). These dangers, along with the occasional need to shoot a crocodile with an elephant gun, made the study of cichlids in the African Great Lakes somewhat prohibitive. Yet, the naturalist penchant for exploration remained, even as natural history as a field was transforming. The ways in which specialized areas of cichlid research were involved in a larger scientific conversation concerning the nature of speciation will be treated in subsequent chapters. Here, we will examine the context in which those pioneering cichlid scientists operated—in this case—often under the aegis of increasing fisheries and aquaculture of tropical species, both in Africa and in Central and South America.

2.1 The Shift from Natural History and the Legacy of The Crown: 1900–1930

Many ichthyologists interested in the study of cichlids retained strong ties to prominent research museums and continued to contribute to classification. Axel Lönnberg, head of the Vertebrate Department of the Swedish Natural History Museum, described cichlid species from Africa in 1903 and would go on an expedition to Africa in 1910. Jacques Pellegrin, who was the Chair of Herpetology and Ichthyology at the Museum d'histoire naturelle in Paris, produced a treatment of cichlids over 3 years beginning in 1903 that described species from Central and South America as well as Madagascar and Africa (Pellegrin 1904). Pellegrin was a prodigious ichthyologist discovering and classifying hundreds of species, many from the family *Cichlidae.* His work *Contribution to the anatomical, biological and taxonomic study of fish of the family Cichlidae* constituted the most complete phylogenetic assessment of the family in his time, and was the first major revision to the taxonomy, just ahead of Regan's in 1905.

Christoph Gustav Ernst Ahl, the Director of the Department of Ichthyology and Herpetology at the Museum fur Naturkunde, Berlin, also classified African and South American species (in his 1927 work), and German zoologist Hermann von Ihering traveled to Brazil in 1880 to take a position at the National Museum of Rio de Janeiro and in 1894 founded the Museu Paulista in São Paulo. His work in 1914, just 6 years before he would leave Brazil forever, identified new species of South American cichlids. Four years later. Alipio de Miranda-Ribeiro, a Brazilian herpetologist and ichthyologist and Director of the Department of Zoology at the National Museum of Brazil, classified several specimens that had been held at von Ihering's museum in Paulista (Ribeiro 1918). As the focus of research moved from the museum and the crown to the professional in the academy, museums formed ties with higher academic institutions, and some of them—like the Departmento de Zoologia, São Paulo—would eventually begin teaching and supervising graduate students in addition to their research and curatorial activities (Naérico et al. 1997).

During the transitional period between the museum and the lab in the early to mid-1900s, a school of British cichlid study developed. The two earliest figures in this group were Boulenger, and Charles Tate Regan, ichthyologist and Keeper of Zoology at the Natural History Museum in London. Regan and Boulenger did not exactly see eye to eye on the best way to classify these confusing fish. In 1905, Regan's *A revision of the fishes of the American cichlid genus "Cichlasoma" and of the allied genera* provided the first comprehensive review of the entire neo-tropical cichlid fauna, assuming relationships based on importance of the anal spine as a primary grouping trait (the first comprehensive catalogue of known African Cichlids was developed around the same time by G.D.F. Gilchrist and W.W. Thompson in South Africa from 1913 to 1917). In his seminal work, Regan isolated *Cichla* as a sister group to the remaining neo-tropical assemblage. However, in Boulenger's 1915, *Catalogue of the fresh-water fishes of Africa in the British Museum (Natural History)* three central genera were instead suggested: *Tilapia*, *Paratilapia*, and *Pelmatochromis*. Regan countered in 1920 and extended his argument to the African Great Lakes in 1922 with *The Cichlid Fishes of Lake Victoria.* This second work effectively overturned Boulenger's phylogenetic assignments, replacing them with two lineages (*Haplochromis* and *Tilapia*), a system that endured for the next 50 years.

Another significant figure with direct connections to this early British school of cichlid study was Ethelwynn Trewavas, who began her work with African cichlids as an assistant to Regan in 1928 when he was made Director of the British Museum, joining officially as an Assistant Keeper in 1935. The same year Trewavas became Assistant Keeper, she joined a research expedition with K. Ricardo-Bertram and H.J. Borley who conducted a fishery survey of Lake Malawi (Noakes 1994). Specializing in freshwater fishes of Africa, almost every collection examined caused Trewavas to revise the current understanding of cichlid classification (Trewavas 1935). Her first revision of the cichlid genus was published in 1931 (Trewavas 1931), with her major work on cichlids coming much later.

Prominent groups of ichthyologists with works focusing on cichlids had also been developing in the United States. In 1903, Eigenmann and Clarence Hamilton Kennedy wrote *On a collection of fishes from Paraguay, with a synopsis of the American genera of cichlids.* Eigenmann continued his contribution to the future study of cichlids with his 1912 work, *The freshwater fishes of British Guiana, including a study of the ecological grouping of species*. In it, he laid the foundation for ecological work providing an identification key to some 300 species of South American fishes. While the American shift of focus in cichlid research focus to Africa is not dramatic, it began in this period. In 1917, ichthyologists John Treadwell Nichols and Ludlow Griscom were describing African species (Nichols et al. 1917), while only 6 years prior, ichthyologist J.D. Haseman (1911) described his difficulty in distinguishing between two closely related species of cichlid he had collected on an expedition throughout "Bahia" (Brazil).

By 1929, American Museum of Natural History Collectors R. and L. Boulton visited Lake Malawi, helping to bring attention to the diversity of the African Great Lakes cichlids to the United States where most specimens had previously been from Central and South America. Public interest was also on the rise following the 1935 publication of William T. Innes's *Handbook of Exotic Fishes* for aquarists, setting the stage for veterans flooding back into universities a decade later when the Second World War ended to grow the cichlid research community substantially, many of them seeking education in biology or fisheries and aquaculture (Brittan 1997).

2.2 *Tropical Fisheries and the Growth of Cichlid Research: 1930–1960*

In the United States and Great Britain, specialized researchers studying specific aspects of cichlid behavior and biology often emerged from the traditional systematics background of the museum setting described above. Their work was supported by the state largely in connection with the expansion of tropical fisheries (especially in Africa), which grew rapidly in the 1940s (Lowe-McConnell 2006). As scientists directly involved in fisheries struggled to measure and predict the population dynamics of riverine and limnologic systems, this work often brought them head to head with the riddle of cichlid speciation. E. Barton Worthington, for example, concluded based on his biogeography and ecology of the African Lakes that present and past barrier conditions to fish movement led to isolation and speciation, and that when geographical isolation was complete, the degree of differentiation also depended on the organisms concerned. Cichlids, he thought, tended to differentiate based on ecological opportunity wherever they were isolated, whereas lungfish, *Protopterus* species, did not.

Worthington was a pioneer in studying the ecology and biogeography of the East African lakes and fishes; however, Worthington's prime directive was not to unravel the evolutionary secrets of cichlids. Rather, he was on assignment from the Crown to survey the Koki Lakes, drainage basins between lakes Victoria and Edward. In this survey, Worthington found no tilapia, which he recommended be introduced. This was done in 1939 to the detriment of the cichlid haplochromine stocks that existed there (Lowe-McConnell 2006).

The history of cichlid research in Africa has been driven in many ways by large-scale fisheries operations. In 1908, the Belgian Congo became a colony, bordering Lake Albert. In 1918, the German protectorate of East Africa, which bordered all three African Great Lakes, was divided between Britain and Belgium and organized as a League of Nations mandate. Each of these Lakes contained valuable stocks of cichlid fauna. In 1929, the Colonial Office Report on the Fish and Fisheries of Lake Victoria by Michael Graham of Lowestoft Laboratory, England, recommended the creation of an East African Fisheries Research Station at the already established Lake Victoria Fisheries Service in order to appropriately manage the resources of Lake Victoria and of the surrounding British territories of Kenya, Uganda and Tanzania. This idea was kept alive by Worthington, who led the first exploratory fishery surveys of many of the East African Lakes and visited in 1944 to discuss proposed plans with representatives from the three territories sharing Victoria's waters. The Colonial Office of the British government requested that he prepare a memorandum for research and management of freshwater fisheries communities in East Africa in 1944. It was also mandated that for the three territories of Kenya, Tanganyika, and Uganda, a fisheries station would be set up on Lake Victoria at Jinja, Uganda and a Lake Victoria Fisheries Board would be financed and formed by the Colonial Development and Welfare Fund.

British Fisheries efforts overseas were limited in the 1930s due to the development of concerning political conditions on the European continent following the rise of Nazi Germany. Nonetheless, several important surveys and studies were undertaken during this time. In 1936, Kate Ricardo and Janet Owen of Cambridge explored Lake Rukwa and the Bangweulu Swamps, producing a Crown Agent Fisheries Report in 1939, and 2 years later, Ricardo was part of the Lake Nyasa Fishery Survey under Dr. B.S. Platt, which aimed to find methods of improving health and standards of living for the African population. One year after Ricardo's visit, The Lake Nyasa Survey produced a 178-species outline detailing the cichlid food web, finding along the way that the "one" main commercial tilapia species was in fact three or four closely related tilapias (Bertram and Trant 1991).

Along with Ricardo, Ethylwynn Trewavas was a leading member of the British Colonial Department of World Food Supplies and ichthyologist at the British Museum of Natural History. Her 1935 *A Synopsis of the Cichlid Fishes of Lake Nyasa* and related works emphasized the variation among the mbuna species flocks of Lake Malawi (then Nyasa), describing both the number of species and their diverse coloration and adaptations. The Second World War interrupted further plans to study the biology of commercial tilapia in Central and East Africa (Lowe-McConnell 2006). From the 1940s through the 1960s, pond culture of tilapia also increased, especially among Belgians living in the Congo and Rwanda who relied on the fish as a food source. At the experimental Fish Culture Research Station in Katanga at Elizabethville (Lubumbashi), Belgians experimented with *T. melanopleura.*

As the Second World War drew to a close in 1945, Rosemary Lowe-McConnell spent several months at the British Museum's fish section with Trewavas learning to identify fishes of Lake Nyasa using collections of preserved fishes in the Museum. Through 1947, in a survey commencing just after the Allied victory in Europe, Lowe-McConnell headed to Africa to survey for potential fisheries and aquaculture development (Lowe-McConnell 2006). One year later, she became a member of the newly created United Kingdom Overseas Research Service, overseeing the ichthyological research operating out of the East African Freshwater Fisheries Research Organization (EAFFRO), where entomologists, hydrologists, algologists, and ichthyologists worked together to understand the lakes in a complete sense, including chemical and physical properties that might affect production rates of different species of fishes and fisheries prospects to take pressure off two endemic tilapia species (Lowe-McConnell 2006). During the same period, Trewavas, who 5 years earlier had produced *The cichlid fishes of Syria and Palestine* concerning tilapias valuable to aquaculture (Trewavas 1942), continued to be an important figure in African aquaculture and fisheries. She was appointed a member of the Fisheries Advisory Committee to the Secretary of State for the Colonies in 1945, and in 1947, she spent 2 months in Nigeria attached to the Fisheries Development unit, working with Mr. Dowsan, the Fisheries Officer (Noakes 1994). The same year, she observed scale eating behavior in Malawi, hypothesizing that *Corematodus shiranus* with colors mimicking those of *Tilapia squamippinis* could get close enough to tear the scales off another cichlid and eat them (Barlow 2000).

The end of the war allowed for the construction of fisheries management institutions in Africa that had been delayed for years. The first EAFFRO lab had been built at Lake Victoria in 1946, funded by the British Office of Colonial Development and Welfare. Upon arriving at the intended site, Bobby Beauchamp found that city fathers had placed it in an area designated for "offensive trades." Construction commenced on the spot previously intended for the houses instead, and was completed in 1949. EAFFRO was formally opened by government of Uganda in 1950, the same year Humphrey Greenwood arrived at the lab (Lowe-McConnell 2006). It was part of a larger scale increase in interest in African fisheries. By 1949, The Uganda Fish Marketing Corporation (TUFMAC) had been built at Lake George, setting up a gillnet fishery to supply dried tilapia by road to mines and other centers. John Barley organized African recorders to provide valuable fisheries statistics; between 1941 and 1943, there was no strict differentiation between commercial and domestic fishermen (Lowe-McConnell 2006). By 1955, a fishmeal plant was established to convert TUFMAC's fish scrap to cattle food. From 1950 to 1959, annual reports of the Uganda game and fisheries department showed an average catch of over 3 million tilapia a year. Lake George was producing one of the highest yields per unit area recorded for any natural body of water.

In 1954, under the direction of Peter Jackson, Nkata Bay became the headquarters of the Joint Fisheries Research Organization survey of Northern Lake Malawi (where Geoffrey Fryer would conduct his classic study of mbuna cichlids and Derek Iles would study the biology of Utaka cichlids). In the early 1950s, fish farms were set up by the Fishery Departments in all three East African territories to distribute small tilapia and explore the best conditions for culture in pond complexes (Lowe-McConnell 2006). This occurred on both sides of the Atlantic, with the British Guiana Fisheries Division establishing breeding ponds for imported *T. mossambica* around the same time. Many of these endeavors were fraught with ill consequences. For example, when Kariba (in Zambezi) was stocked with *O. macrochir* from Lake Mweru in 1959, Chilanga fish farm fingerlings were used. However, these fingerlings were Kafue river stock, later identified as a different species, and their introduction constituted a spectacular failure (the fingerlings were immediately devoured by predators). This underscored the value of taxonomic work in fisheries.

In the 1950s, the importance of Rosemary Lowe-McConnell's work in the study of tilapia cannot be overstated (Fig. 5). In 1952, Lowe-McConnell found that in Lake Bunyoni, populations of *O. niger* and *O. esculentus* had disappeared, replaced by or hybridizing with *O. niloticus*. She determined that size at maturity varies from lake to lagoon, with lake species at Albert maturing at and growing to a larger size. In 1955, Lowe-McConnell, adding much to our knowledge of tilapiines in African lakes from Turkana in northern Kenya to Jipe in Tanzania, went on a trip that began

Fig. 5 Lowe-McConnell in Guyana in the 1950s. (Reproduced from Stiassny and Kaufman (2015) by permission from Springer Nature)

with a visit to TUFMAC in an attempt to determine if Lakes George and Edwards' tilapia populations were distinct and where they bred. No evidence of movement between lakes was found (Lowe-McConnell 2006). However, Lowe-McConnell and Peggy Brown found several undescribed species of tilapia related to *O. mossambicus* at Lake Jipe and the Pangani system at Korogwe, Tanganyika. In the course of their work, it became clear that these species were all part of an interrelated group separate from other East African tilapias. The pair visited tilapia culture experiments in progress at the Kenya Government Experimental Fish Farm in Sagana, but with the onset of the Mau Rebellion, research was halted at RRDC and the associated fish culture unit until 1955 (Lowe-McConnell 2006).

Traveling to South America, where she lived in British Guiana from 1957 to 1962 with her husband (involved in an ongoing geological survey), Rosemary Lowe-McConnell contributed to the growth of aquaculture and fisheries. While on the continent, she worked for the Fisheries Division of the Department of Agriculture, noting that this work was carried out "at the princely sum of $1 a year. . .as wives could not be 'gainfully employed'" (Lowe-McConnell 2006). While in this capacity, Lowe-McConnell nonetheless worked to establish breeding ponds for imported *Tilapia mossambica* and catalogued countless tropical fish species, pondering as she did so the evolutionary history of cichlids in the Americas in her work *Land of Waters*. In it, Lowe-McConnell considered the separation of South America and Africa during the breakup of Gondwanaland and subsequent geological events as providing a valuable case of comparative evolutionary biology on both sides of the Atlantic. This work prefigured the growth of cichlid studies in Central and South America in the 1970s, when evolutionary studies would begin to focus on the Great Lakes of Nicaragua alongside the Great Lakes of East Africa as part of valuable comparative studies in an effort to understand the mechanisms of cichlid evolution. Much like in East Africa, this reevaluation of the cichlids as objects of valuable scientific inquiry would sometimes come into conflict with fishing industry interests concerned first and foremost for the economic productivity of the lakes, even as many of the scientists studying cichlids (Lowe-McConnell included) were conducting research in the hopes of informing best practices in fishery management.

In the United States, the study of cichlids was less focused on the aquaculture or fisheries of cichlids than on the taxonomy of American species, but the connection between the two areas of study certainly existed. George S. Myers of Stanford University was both Head of Fishes at United States National Museum and Advisor to the US Fish and Wildlife Service, as well as the fisheries of the Brazilian government. He was the scientific consultant on Innes's *Exotic Aquarium Fishes*, which helped to popularize exotic cichlid species in the aquarium trade, species that Myers had in many cases classified himself from South America (Myers 1935). Interest in cichlids stemming from the aquarium trade would receive another boon with the founding of the *Tropical Fish* Hobbyist magazine by Herbert Axelrod, an aquarium enthusiast who received his doctorate at New York University and for decades strove to produce the most exhaustive aquarium literature available. With regard to cichlids, this endeavor culminated in *The Most Complete Lexicon of Cichlids* in 1993.

It should be mentioned that the aquarium trade and its corresponding literature, while existing contemporaneously with the growth of cichlid research writ large and contributing to public interest in cichlids, have often proved to be both a valuable resource and a source of great consternation for the scientific community. While prominent importers continued to distribute cichlids to enthusiasts from major centers in America, Germany, and Japan, thousands of people received and circulated often conflicting and confusing information concerning naming, classification, and priority in cichlid identifications. At the same time, liaisons between the industry and academics conducting cichlid studies were not infrequent, with Axelrod and Myers as just two examples. Myers in particular, coming from the strong tradition of ichthyology at Indiana University where he worked as a curator for Carl Eigenmann, was greatly influential at Stanford (where he arrive in 1926), where he contributed to the rise of many prominent researchers (Brown 1994).

Since the early twentieth century, academic positions in US universities and colleges required earning a doctorate. Many women earned doctorates in zoology between 1896 and 1930, but the plight of women in the field of ichthyology had not improved significantly from the late nineteenth to the early twentieth century. Most of the highly credentialed women scientists who chose to remain in higher education could find positions only in women's colleges or in public schools, none of which were institutions that could afford research (Brown 1994). It is noteworthy that some of the earliest American cichlid research to go beyond the traditional naturalist approach was that of G. K. Noble. In 1939, Noble, at the American Museum of Natural History, investigated sexual identification in the jewelfish with Brian Curtis. By examining the role of visual cues such as the development of the nuchal hump in reproductive behavior, they found that in individual recognition, lifelike movement and facial markings were particularly important. Noble and Curtis also hypothesized that cichlids would fixate on the first young they encountered, an area of study ahead of its time that would later be known as parental imprinting. Their theory was disproved; in fact, many cichlids were found to accept foreign young regardless of previous experience. Nonetheless, Noble and Curtis stand out in this era as pioneers in research concerning cichlid sexual selection.

2.3 Decolonization and the Struggle for Sustainable Fisheries: 1960–1980

From 1945, nationalist movements surrounding Lake Victoria, paired with the political and economic consequences of World War II in Europe, weakened Western domination in Africa. In 1961, Tanzania became independent followed by Uganda, Rwanda, and Burundi in 1962, while Kenya gained independence in 1963. At the same time, there was an increase in manmade lakes (and their ecological study) as dams for hydroelectric power became increasingly common. This occurred behind African dams in Zambezi, and the lower Volta River, Ghana, and Lake Nasser-Nubia. Tilapias flourished in these lakes, thus providing an interest in continued business relations between Western companies and the associations that now controlled regions in which they had established valuable industries (Lowe-McConnell 2006). The legacy of colonial rule over the people of the region had brought with it resource management structures that removed the power from traditional leaders to the central governments of newly sovereign nations such as Kenya, Uganda, and Tanganyika. This meant that the continuing management responsibilities of lake fisheries, often in collaboration with state and private business from Western nations, had been entirely removed from the subsistence fishermen whose families had relied on catches in these lakes for hundreds of years (Awange and Ong'ang'a 2006).

A prime example of this arrangement can be seen at EAFFRO, which continued to operate from Jinja, Uganda through the 1960s. In 1954, to boost tilapia catches, *T. zillii* (a macrophyte-feeder present in Lake Albert) was introduced to Lake Victoria. With it came *O. leucostictus*, *O. niloticus*, and finally, *L. niloticus* (Lowe-McConnell 2006). Geoffrey Fryer opposed the introduction of the Nile

Perch in particular, and in 1960 published an article on the potential disastrous consequences (Fryer 1960a). Nonetheless, Nile perch were officially introduced in 1962 (Goldschmidt 1996). Robin Welcomme studied Lake Victoria ecology in 1963 as a member of the EAFFRO staff, concluding that indigenous species were being extinguished, especially by *O. niloticus* and *L. niloticus*. Yet, after a lake-wide survey in the late 1960s showed total fish populations of the lake to be 80% haplochromine, a fishmeal plant became operational in Mwanza in 1976 to take advantage of this available resource. By the end of 1970s, about 10 trawlers were working the Mwanza area, and while the highest yields of haplochromines were recorded in 1977, within a decade, the area showed signs of overfishing.

The International Biological Program was launched for the decade from 1964 to 1974, stimulated by the International Geophysical Year from 1957 to 1958, and intending to study biological productivity and human welfare (the implications of ecological studies for resources use now rapidly gaining acceptance in biological and zoological communities). The Freshwater Productivity section had its headquarters in London with Worthington as Scientific Director. Julian Rzóska, a hydrobiologist who fled Poland during the World War II and arrived at Oxford to continue his research, coordinated the Productivity of Freshwaters section's 232 ongoing projects from 42 countries by 1969 (Lowe-McConnell 2006). Setting out to obtain internationally comparable observations of basic biological parameters in order to coordinate suitable methods for measuring productivity in natural ecosystems, the *Handbook of Freshwater Fish Production* was completed by 1968.

In the mid-1960s, Lowe-McConnell and the Uganda International Biological Program team found maturational and full size of catches diminishing due to intensive fishing. Some of these results were published in Welcomme's (1966), *Recent Changes in the Stocks of Tilapia in Lake Victoria*. In 1966, the British Royal Society began a 5-year biological study of Lake George, Uganda under Mary Burgis, Lesley McGowna, Tony Viner, Ian Dunn, and George Ganf. The study later included the work of Christine and David Moriarty, Johanna Darlington, Mike Tevlin, and James Gwahaba. Their base of operations was a derelict Uganda Fish Marketing Corporation building at Kasenyi on the lake, damaged by an earthquake, where they proceeded to begin building their lab and accommodations from scratch in collaboration with Makerere University staff. By 1971, a comprehensive ecological picture was in hand, including the discovery (by Dave and Chris Moriarty) that *T. nilotica* were able to digest cyanobacteria, which had global application for tilapia aquaculture.

Stocking areas in the Americas and Asia (e.g., Fig. 6) resulted in problems as well. The completion of the Panama Canal in 1914 had resulted the creation of the artificial Lake Gatun, quickly colonized by South American fishes (Zaret and Paine 1973). In one notable incident, Peacock cichlids (*Cichla ocellaris*) introduced into a dammed portion of a Panamanian creek escaped their man-made environment in 1966 when the dam overflowed. The piscivorous *C. ocellaris* spread into Lake Gatun and surrounding river systems, eventually leading to the extinction of several local species.

Time-table of the travels of T. mossambica

Introduced in	Coming from	Year	Manner of Introduction into open waters
Java*	East Africa(?)	1939(?)	
Sumatra	Java	1939	
Bali, Indonesia	,,	1941	
Lombok,	,,	1941	
Malaya*	,,	1943	Escape
The Celebes	,,	1944	
Taiwan (Formosa)*	,,	1944	Escape
The Moluccas	,,	1949	
St. Lucia*	Malaya	1949	Direct release
Thailand*	,,	1949	Direct release
Trinidad	St. Lucia	1949	
Grenada	,,	1949	Direct release
West Borneo	Java	1950	
East Borneo	,,	1950	
Amboina, Moluccas	,,	1950	
Banka, Indonesia	,,	1950	
The Philippines*	Thailand	1950	Direct release
Jamaica*	St. Lucia	1950	Escape
Barbados	,,	1950	
Dominica	,,	1950	
Martinique	,,	1950	
Sabang, Pakistan	Java	1951	Direct release
Ceylon*	Malaya	1951	Direct release
Haiti*	Jamaica	1951	
North Borneo	Malaya	1951	
Hawaii	,,	1952	
Dominican Republic	Haiti	1953	
Travancore-Cochin, India	Malaya	1953	
Guinea, Br.	Haiti	1954	
Egypt	Thailand	1954	
Fiji	Singapore	1954	
Japan	Thailand	1954	
Cook Islands	Fiji	1955	
Guam	Philippines	1955	
Laos	Thailand	1955	
New Caledonia	Fiji	1955	
Saipan (Micronesia)	Philippines	1955	
South Korea	Thailand	1955	Direct release
Guatemala	Haiti	1958	
El Salvador	Guatemala	1958	
Nicaragua	El Salvador	1959	Direct release

Fig. 6 Chronicling the spread of *Tilapia mossambica*. (Reproduced from Riedel (1965) by permission of Springer Nature))

Around the same time tilapia appeared in South East Asia that may have originated from an aquarium shipment to Hong Kong prior to WWII, Peter and Henny Davies relocated cichlids between different parts of the African Great Lakes for their collection business's convenience (Oliver 2013). As the aquarium trade increased, businesses arrived to collect on the lakes. Stuart Grant was licensed to operate from Malawi in 1973 and the company Aquarist Tropical Fish Ltd. (managed by Eric Fleet) arrived around the same time (Herlong 1999). After several years of a government-sponsored investigation of fish exportation Tony Ribbink recommended that the Davies' former pilot Norman Edwards, who had transported fishes to Blantyre international airport, be licensed to run the operation at Malawi in 1980 (Herlong 1999). Edwards was licensed to operate the Cape Maclear area following their departure. Until relatively recently, when efforts to reintroduce species and ensure sustainable catch rates gained traction, the aquarium industry joined fisheries and aquaculture in the tropics as a potential threat to biodiversity and ecosystem health.

During the 1970s, expanding African fisheries encountered a variety of problems including transportation demands and increased poaching (Lowe-McConnell 2006). For example, the Ferguson's Gulf site at Lake Rudolph, Turkana, failed because environmental constraints prevented production from maintaining commercial levels. Fisheries that flourished often did so to the detriment of local subsistence fishermen, who were no longer able to feed themselves or their families from native waters.

In most Great African Lakes where mechanized fishing occurred ecosystems changed significantly throughout the seventies. Of demersal fish in Malawi, 20% of 140 species trawled disappeared from catches within 6 years (Turner 1977). This prompted concern for the lakes' ecosystems for fisheries and conservation reasons. Anthony Ribbink of Rhodes University, South Africa was sponsored by the JLB Smith Institute of Ichthyology to work toward ensuring national park status for Lake Malawi (Ribbink later became CEO of the Sustainable Seas Trust). In 1972, the Dutch Haplochromis Ecology Survey Team (HEST) from the University of Leiden set up a research station near Mwanza in Tanzania to determine the long-term current status of, and long-term effects of fisheries on lake biodiversity (Goldschmidt 1996). The same year two International Biological Program meetings held in Poland and Reading were almost exclusively limnological (Le Cren and Lowe-McConnell 1980). Their results concerned the effects of physical variables on freshwater production, lake ecology, and stock productivity estimates. Researchers in evolutionary biology and aquaculture and fisheries were becoming increasingly aware of the problems associated with the introduction of new species into fragile ecosystems.

3 A Model Species in Evolutionary Biology

> If Darwin had gone not to the Galapagos Islands but to the East African Great Lakes perhaps he would have stumbled on the role played by sexual selection in the origin of species. Perhaps he would have discovered that females, by being fussy in their mate choice, could

> initiate the origin of species. Perhaps we would have a different theory of evolution today.—Tijs Goldschmidt

Throughout the mid to late twentieth century, cichlid research shifted considerably from the naturalist tradition, growing from a group of ichthyologists interested in taxonomy to a professionally diverse group of scientists with particular interests in social and reproductive behavior, geographic distribution, anatomy, and physiology (Bauchot et al. 1997). At the same time that this expansion and specialization was occurring, random mutation, recombination, and sexual as well as natural selection became foundational to understanding the evolutionary process. Huxley's vision of a "biology" extending from the smallest components of the cell to the advent of new species became a reality in this half century (Farber 2000). The stage was set for an inquiry into the process of evolution using cichlids as model organisms. Scientists devoted to studying biology, developmental ontology, and lake ecology for the purposes of fisheries science confronted questions of cichlid diversity that had now grown beyond the scope of systematics alone, incorporating evidence from diverse new areas of study to suggest possible evolutionary histories. Sometimes, the work of evolutionary biologists challenged the established taxonomy of the previous generation of naturalists, such as when Wolfgang Wickler challenged Regan's cichlid phylogeny (Wickler 1963). The new ethological school of cichlid research was critiquing and hoping to refine the systematics of earlier naturalists who did not incorporate behavioral considerations into their determinations of evolutionary histories. In the following sections, the focus will turn to these new types of research and the diverging views they fostered concerning the mechanisms at work in cichlid evolution.

3.1 *The Evolutionary Synthesis and Specialization in Cichlid Research: 1930–1970*

Lake Malawi, largely by virtue of its cichlid species flocks, contains more species than any other lake on Earth. Indeed, the cichlids of Lake Malawi represent a wider range of niches filled, with less physical variation, than any other vertebrate group (Turner 1994). The high variability of lake levels, and the potential for this to isolate and then recombine groups of cichlids over long periods of time, has been considered one possible explanation for the incredible amount of cichlid diversity. In 1390, Lake Malawi's water level was about 120–150 meters below current measurements. When the Ngonde King took Mapunda of the neighboring Mwela region as his bride between 1815 and 1835, the water level was so low he was able to walk across the north of the lake for the ceremony (Barlow 2000). By 1860, the water level had risen by approximately 100 meters. Cichlids that inhabited rocky islands in 1869 would have suffocated when those areas were exposed only 30 years prior. This seems to indicate color forms and biological diversification over a period of only a few hundred years (Goldschmidt 1996). Less extreme but of potential importance are more recent changes in water level. For example, between 1914 and 1928, Rodney Wood described breeding locations of both *T. squamipinnis* and *T. saka*. In 1945, when Rosemary Lowe McConnell recorded spawning in the lake, it was 10–15 feet deeper.

Although the shift toward evolutionary biology began earlier in the twentieth century, it was not widely seen as compatible with the study of genetics and heredity until the 1930s, when the idea that Darwinian selection and Mendelian inheritance were not mutually exclusive gained acceptance. In 1930, Sir Ronald Aylmer Fisher's *The Genetical Theory of Natural Selection* had posed the possibility of "runaway" natural selection; the idea that evolution of sexual preference could establish an effective reproductive isolation between two differentiated parts of a species, even when geographical or other factors were not favorable for such separation. The full importance of this concept would not become commonly agreed upon until the early 1940s, by which point, an understanding of the genetic basis of evolution by natural selection was better understood. Theodosius Dobzhansky (1937) published a milestone work in this synthesis that would come to define modern evolutionary biology: *Genetics and the Origin of Species*. Alongside him, Julian Huxley strove to bring the fragmented fields of ecology, genetics, paleontology, population genetics, embryology, systematics, comparative physiology, and anatomy under one framework. His 1940 *The New Systematics* focused on how spatial isolation required for allopatric speciation was achieved, and he published the seminal work *Evolution: The Modern Synthesis* in 1942. Ernst Mayr is said to have completed the evolutionary synthesis in his *Systematics and the Origin of Species* of the same year (Mayr 1942). In it, he gave new life to the importance of reproduction as a critical force in evolutionary biology, an approach that embraced interactions between the organism and the environment such as reproductive isolation by sympatric means. This premise served as the main framework for understanding speciation in cichlids via interspecific isolating mechanisms throughout most of the twentieth century, guiding the debate as to the intralacustrine origins of the Great Lakes Cichlids in Malawi, Tanganyika, and Victoria, for which evidence has been consistently sought to confirm either an allopatric (perhaps a micro-allopatric) or a truly sympatric, stasipatric origin (Greenwood 1991).

Interest in the study of cichlid evolutionary biology increased considerably following J. L. Brooks' 1950 *Speciation in Ancient Lakes,* which discussed cichlids as models of sympatric speciation. This was the first time researchers began to systematically examine the mechanisms of cichlid speciation in the Great Lakes of Africa, questioning how so many species could coexist in the same lakes in the absence of clear geographic barriers. Cichlids posed what George Barlow (2000) would call a "morphological paradox:" their anatomy from one species to the next was similar, and yet, the differences between species in terms of their environment, diet, reproductive and parental behavior, communication, and coloration were distinct. In 1941, the Dutch biologist Gerard Baerends' Behavioral Working Group was one of the first teams to address such questions. Working as Niko Tinbergen's assistant at the University of Leiden Lab from the 1950s, Baerends helped to establish cichlids as a valuable subject of behavioral study, arguing that color and phenotype could be used to assess behavioral or physiological status, and that monogamy was synonymous with substrate guarding.

By this time, ethology and ecology had emerged as important disciplines. Zoogeographic and ecological contributions joined taxonomic and anatomical studies of cichlids to indicate how resource utilization occurred and intralacustrine allopatric speciation took place (Ribbink 1991). There was a growing realization that paleontology, the study most used to determine evolutionary histories, could not provide information on behavior, color, soft tissues, and interrelations between species in their own ecosystems crucial to understanding speciation (Goldschmidt 1996). At Stanford University, George Myers was one of the founders of the Biosystematists: a group of researchers in fields from botany to herpetology and ichthyology who wanted to address common problems in paleontology, biology, and systematics to explain evolutionary problems. Konrad Lorenz's ethological work throughout the 1960s and 1970s on pair bonding can be seen as a milestone in ushering in the behavioral era of evolutionary biology, laying the groundwork for his 2002 *On Aggression*. Calling behavior for young was largely classified by Baerands and Baerands van Roon (1950), who detailed "jolting" and "pelvic fin flicking." They categorized basic cichlid body signals such as lateral and frontal display, aggression inhibition, quivering, and leading. Later, other researchers continued this work, describing fanning, mouthing, churning, leaf lifting, fin digging, and micronipping (Keenleyside 1991). Baerands and Baerands-van Roon also described six systems of chromatophores, describing their color patterns and meaning (especially with regard to reproduction). From 1950 to 1970, investigations of the phenomenon of cichlid speciation expanded to include social behavior (Barlow 1983), bioacoustics revealed a rich vocal repertoire in cichlids including threat behavior in defense of territory (Myrberg et al. 1965; Rodman 1966), and the geographic distribution of species (Poll and Matthes 1962).

Within a decade of Mayr's crowning work in the evolutionary synthesis, Watson and Crick made their groundbreaking discovery determining the physical structure of DNA, and the study of evolution expanded accordingly to include the genetic factors in phenotypic diversity and the relationship between reproductive behavior and selection of heritable traits (Watson and Crick 1953). As Dobzhansksy (1973) put it, nothing in biology makes sense except in light of evolution. But cichlids presented problems for traditional understandings of natural selection. One problem in explaining the organism (rather than the gene) as the object of selection was the existence of apparently disadvantageous physical traits: extreme characteristics, often coloration, that would attract the attention of predators or in some other way make an organism less capable of surviving in the wild. The question of such "handicaps" became pertinent to the study of cichlid speciation since many Great Lakes cichlids—especially the mbuna of Lake Malawi—possessed a dramatic array of colors and physical forms.

Fischer's "runaway sexual selection" explained such phenomenon, arguing that traits developed to signal fitness are selected for by the opposite sex, leading to an exaggeration of these traits, leading to the evolution of new forms which might not confer actual fitness on the organism, continually reinforced in the population by sexual selection. The idea that females might influence evolution simply by their mate selection preferences, called the “sexy son” hypothesis, was held to drive such Fisherian runaway (Fisher 1930). A competing model, called the “good genes” hypothesis, stated that in fact handicap traits were biologically affordable for males because of so many positive counterbalances that increased fitness. Thus, no explanation admitting to these males’ lack of real fitness was necessary. Another explanation was sensory bias or sensory exploitation, which—in keeping with the sexy son hypothesis—held that the ability to draw a female’s attention was a greater selective driver than actual fitness.

In 1954 and 1956, Peter H. Greenwood published two works on cichlids, believing the morphology of Lake Victoria cichlids ideal for the study of evolution, and in 1965, he studied coloration and mating behavior as attributes of adaptive radiation in Lake Nabugabo (a satellite lake to Victoria). In 1966, Greenwood’s *The Fishes of Uganda* was published (an early milestone in his lifelong study of haplochromines), by which point the reproductive behavior of cichlids in Victoria was of interest to scientists around the world in the study of evolution (Lowe-McConnell 2006).

In an effort to understand this process, cichlid reproductive behavior was studied extensively. In many species, such as *S. melanotheron* and *S. occidentalis* investigated by Evelyn S. Shaw and Lester R. Aronson (1954), it was not known how long if at all a male would stay with its young in the field, or how long a female required to produce a second clutch of eggs (Aronson 1945, 1949). In 1953, Rosa Kirchshofer—at the Wilhelminberg Biological Station—found that anal fin spots on some species seemed to mimic eggs. In 1965, Wolfgang Wickler found that males presenting these imposter eggs to females would, upon the female’s attempt to gather the extra eggs, orally inseminate the eggs already carried in the female’s buccal cavity. Wickler argued that predation on young might have selected for monogamous behavior among previously haremic males in the open bottom dwelling lamprologines of Lake Tanganyika. However, not all cichlids were found to be monogamous. *Apistogramma* were found to sometimes “sneak” during reproduction (Loiselle 1985), and both haremic of monogamous behavior depending on environmental conditions (Burchard 1965). In general, mating systems on both sides of the Atlantic have proved to be remarkably plastic. In 1963, George Barlow concluded that the evolution of mating systems in cichlids proceeded from monogamy with bi-parental care to polygamy with maternal care.

One of the earliest explanations for cichlid variation focused on cichlid exploitation of dietary options in the environment, allowing for trophic niches to develop and speciation to occur due to resource competition (Barlow 2000). From 1952 to 1955, N. LeLeup and George Marlier, director of the Belgian research station at Uvira, Lake Tanganyika, observed scale eating behavior; a particularly strange example of this kind of specialization (Marlier and Leleup 1954). Fryer’s 1956 *New species of cichlid fishes from Lake Nyasa* and 1959 *Some aspects of evolution in Lake Nyasa* pioneered work in the ecology of cichlids, studying the mbuna of Malawi and relating dentition and jaw structure to feeding behavior. Criticized by Myers (1960), Fryer (1959, 1960b) responded in kind by further demonstrating both habitat stenotopy and specialized feeding mechanisms. Supporting his view, George W. Coulter found in 1967 that the ecological separation of deep-water demersal cichlids in Lake Tanganyika was more likely to be based on diet than habitat preference. One year later, D.J. Randall and Harman showed that South American cichlids ate sponges (highly indigestible to most fish), as well as fruit or seeds that fall into the water. The same year, Albrecht asserted that herbivory evolved as a dietary specialization recently in tropical cichlids, with almost all these species' young initially eating tiny animals and later switching to other material. Piscivorous adult cichlids were also known. In 1961, Matthes reported hunting behavior for *B. microlepis* juveniles that followed shoals of clupeids, herding them into shallow bays where adults caught them. Although it was no certainly known to be a driver of speciation, the diversity of cichlid diets was certainly a compelling place to look.

To study cichlid behavior in more detail, new techniques were employed, and the rise of underwater photography became a commonplace research tool to this end. By the 1960s, scuba had revolutionized underwater observations of fish behavior and ecology in clear lakes, pioneered in particular by Hiroya Kawanabe's studies of freshwater fishes in streams while at Kyoto University, including later studies in Lake Tanganyika (Yuma and Harada 1998; Kawanabe and Nagoshi 1997). The description of new species occurred increasingly as an unintended result, rather than the object, of these scientific studies. Another aid to the discovery of new species was the expanding aquarium trade. From 1950, the aquarium trade for cichlids grew significantly, with Peter and Henry Davies establishing cichlid collection stations (with Cape Maclear as the main station) in the early to mid-1960s, with mbuna from Lake Malawi arriving at fish stores in the United States by 1966. This aided in taxonomic revision by virtue of dedicated aquarists. In 1965, J.E. Burchard pointed out that it was aquarists who discovered that many substrate-guarding *Apistogramma* species of South America are polygynous, forming harems in which sexual dimorphism is often extreme. Finally, the growth of fisheries also aided in the discovery of new species (e.g., The Belgian Hydrobiological Expedition, ending 1954, which gathered a large collection of Tanganyikan cichlids).

3.2 Sexual Selection and the Curious Adaptive Radiation of Cichlids: 1970–1980

The specialized areas of cichlid research that emerged in the previous 50 years grew significantly in the 1970s. Conceptual shifts in evolutionary biology throughout this decade challenged earlier theories of niche selection in which competition for resources was seen as the primary driver (Goldschmidt 1996). In 1977, Frederick Sanger's development of DNA sequencing afforded new tools to examine molecular biology and the details of natural selection at the genetic level. Although notable studies with implications for cichlid evolution in the Americas occurred in the late twentieth century—for example, Martin's (1972) study of the biogeography of the freshwater fishes of Honduras—from 1970 through 1980, the focus in cichlid research moved largely to Africa.

By the end of the decade, most studies in speciation sought to answer two basic questions. The first was whether or not sympatric speciation had occurred in cichlids. If it had, then new species arose in the absence of geographic barriers. Suspicion that cichlids had radiated in a manner unfamiliar to scientists existed since at least 1972, when Trewavas, J. Green, and S.A. Corbet authored *Ecological studies on crater lakes in West Cameroon. Fishes of Barombi Mbo* commenting on the unusual speciation in cichlids (Trewavas et al. 1972). The same year, Fryer and T.D. Iles' groundbreaking *The Cichlid Fishes of the Great Lakes of Africa: Their Biology and Evolution* described "speciation gone wild," comparing the species of Tanganyika, Malawi, and Victoria.

The second major question in cichlid research followed logically: If sympatric speciation had occurred, then how? This question led to many hypotheses, which fall broadly into two categories. One explanation was that there was a physical driver, something about cichlid anatomy or their ecological niche, together with competition for resources within the seemingly borderless space they inhabited that promoted selection. The second explanation was that the selective force was behavioral, the prime candidate being mate selection. A great deal of study combined aspects of both possibilities, and to date, there appears to be evidence supporting multiple positions on the matter. Not all researchers have maintained one position over the other, and many find cichlids to be such a complicated case that they opt not to take sides.

Studies of anatomy and ecology revealed many unique cichlid characteristics in the 1970s. In 1971, Regnier studied chemical signals between cichlids, termed semiochemicals, and in 1974, Bardach and Villars found taste receptors to be distributed all over cichlid bodies. Two years later, McKaye and Barlow found that parents recognize their young by chemical cues in *C. citrinellum*, and Meyer, Fernald, and Michael Herzog from Göttingen (an aquarist) sent Barlow evidence that Midas cichlids can change sex, a phenomenon later growing into a significant field of study (Barlow 2000). D. Ohm first documented protogyny in cichlids in the dwarf South American species *Crenicara punctulata*, 1978. Fernald and Hirata 1979 measured the speed with which male coloration could change the year after. Lanzing and Bower (1974) found that color patterns in a variety of different species used the same 14 units, showing that coloration could be used to determine phylogenetic relationships between species. Voss (1980) compared the color patterns of 20 African species and found that they could be used to discriminate individual species as well as genera and, at the phylogenetic level, discerned different lines of evolution leading to different specializations: display of invariably colored structures in different species, and specializations in quick pattern changes. Supporting the importance of color in behavior and mate selection, Levine and MacNichol demonstrated that cichlids could see color in 1979.

Much of this research was crucial in the quest to unravel the riddle of cichlid speciation. If sufficient physical barriers of some kind had existed, then allopatric speciation must have occurred in a very short window of geological history. If sympatric speciation had occurred, then some physical or behavioral traits unique to cichlids must have played a role in their radiation. Investigations as to what this unique trait might have been frequently focused on diet or feeding. Keenleyside classified three general types of herbivorous fishes: grazers, browsers, and phytoplanktivores (1979). Many cichlids are also piscivorous, some being specialized to consume the young of other cichlids, or even cichlid scales in particular. In 1973, Barlow and Noakes found that young regularly fed from their parents' bodies, consuming mucus their parents secreted. This was termed "contacting" (Noakes 1979; Noakes and Barlow 1973). In 1970, Knöppel found evidence that central Amazonian cichlids ate ants, plants, bug larvae, algae, and fish. Fryer and Iles thought that the spatulate teeth of *E. cyanostictus* were used for extracting small insects and crustaceans from algal coverings on rocks. This diversity posed an ecological dilemma. Many cichlid species sharing similar foods coexisted, but in the 1970s, as this was becoming increasingly clear, it had been widely accepted in evolutionary theory that related species with similar diets should not share overlapping environments (Yamaoka 1991).

In their comparison of many African Great Lakes cichlids, Fryer and Iles had detailed cichlid outer jaws (which are particularly dexterous and adaptable) and the pharyngeal jaws (e.g., Fig. 7), which with relatively minor changes can be adapted to many different food types. Cichlids were categorized as feeding by suction, ram feeding, or biting (Liem 1991). In 1978, Greenwood and Karel Liem independently provided evidence based on lab experimentation that the Great Lakes taxa most specialized phylogenetically and morphologically were also "jacks of all trades" when it came to feeding repertoires (Liem 1979). Greenwood studied the size and shape of pharyngeal apophysis in 1978, and one year later, Liem studied feeding in cichlids using X-rays, determining that they could move their outer jaws in a variety of ways to manipulate different food items, allowing the jaws to "take on the properties of a simple hand" (Liem used the term aquatic or hydraulic tongue for this ability). This seemingly paradoxical view contradicted the alternative that the most morphologically specialized taxa were remarkable specialists for particular feeding habits.

Cichlid feeding morphology was found to be so variable that it was said to represent a diversification unparalleled in any other vertebrate family (Liem 1991). As a consequence, it was so well studied that it is now better understood in cichlids than in any other teleost family. In 1973, Liem and Greenwood claimed that the cichlid bauplan provided a unique substrate for rapid anatomical change, especially in the evolution of different feeding mechanisms. In 1975, Waddington showed that ecophenotypically induced plasticity existed and argued that its role in speciation was significant, especially if changes were environmentally induced, since potentially reversible morphological changes could then be incorporated into the genome through some form of assimilation. This sentiment was echoed in 1978 by Rosenzweig's idea of competitive speciation, asserting that the mechanism driving evolution in cichlids was the establishment of niche diets due to trophic resource limitations.

In the previous two decades, a strict focus on genetics in evolutionary biology had been seen as narrow-minded by many ecologists and ethologists. In the 1970s, the synthesis of evolutionary mechanisms at both the micro and macro environmental

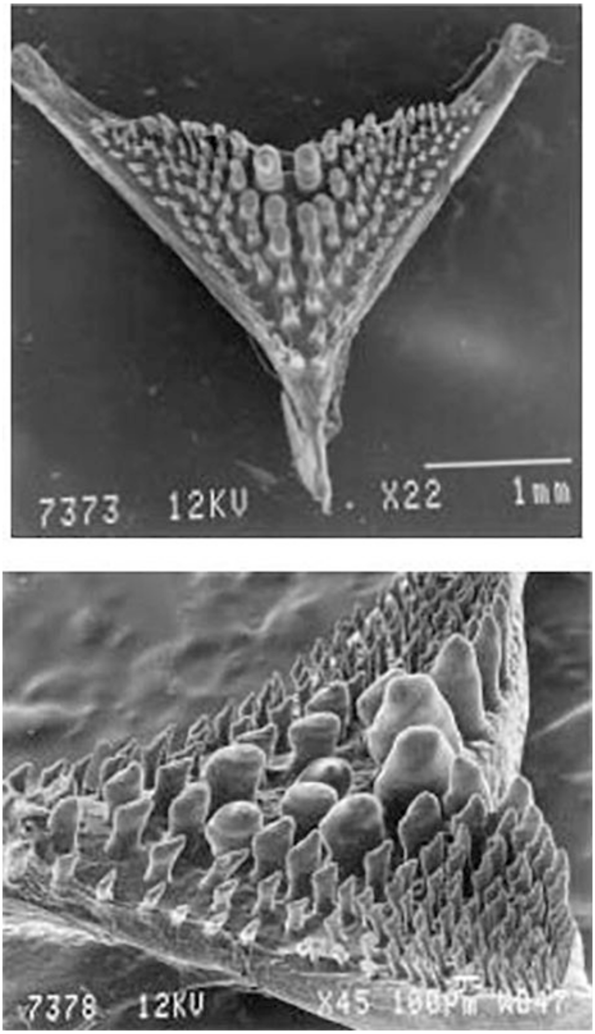

Fig. 7 Two views of the lower pharyngeal bone of a male *Lamprologus ornatipinnis*, showing the high degree of specialization of this well-adapted aspect of cichlid morphology. (Reproduced from Gordon and Bills (1999) by permission of Springer Nature)

levels allowed for cichlid research to serve as a bridge between these two worlds of scientific inquiry on the question of speciation. In this era, Irving Kornfield (who, along with Echelle, would support Rosenzweig's idea of competitive speciation in 1984) laid the foundation for the genetic study of cichlid phylogenies. His *The cichlid fishes of Lake Victoria, East Africa: The Biology and evolution of a species* in 1975 and his co-authored work with Koehn the same year, *Genetic variation and evolution in some New World cichlids*, tackled the issue (Kornfield and Koehn 1975). The work continued in 1978 when Kornfield's *Evidence for rapid speciation in African cichlid fishes* demonstrated extremely low genetic distance among morphologically divergent cichlid lineages within Lake Malawi, while studies in Tanganyika showed significant differences. Many ecological and ethological studies also directly concerned cichlid taxonomy. Fryer and Iles' studies led them to challenge Regan's phylogeny, which had no serious contenders since its establishment in the 1950s. Additional challenges to Regan's phylogeny came from Heinrich Scheuermann in, *A partial revision of the genus "Limnochromis" Regan 1920*, 1977 and Greenwood's 1974 studies of pharyngeal jaws concluded that species from separate Great Lakes (previously believed to be closely related) were, in fact, examples of convergent evolution.

Biogeography and ecology continued to be powerful tools in elucidating cichlid evolutionary history and speciation. Sage and Selander (1975) argued that taxonomic analyses needed to be reconsidered on the grounds that ecophenotypic polymorphism existed in cichlids, and Cichocki's 1976 study of morphology, ecology, and historical biogeography supported the theory of a monophyletic African radiation. Anthony J. Ribbink and B.J. Hill (1979) found from experimental and field data that cichlid fishes were extant to a depth of 200 meters in Lake Malawi, but that depth distribution was restricted by swimbladder physiology. The same year, Hiroya Kawanabe and a group of Zairean scientists began studies in Lake Tanganyika. Believing as the British ecologist Charles Eton did that communities must be viewed as whole of interactions among organisms, Kawanabe and Nagoshi (1997) sought to uncover the complexity of biotic interactions promoting high species diversity. These underwater studies, lasting into the early twenty-first century, focused on the ecology and ethology of littoral cichlids and revealed much about resource partitioning (Yuma and Harada 1998).

Many studies of cichlid physiology or morphology had important implications for behavior, and from the early 1970s, some studies incorporated aspects of both approaches. Behavioral ontogeny and developmental biology are prime examples. In 1966, Lev Fishelson had found that one significant difference among *T. nilotica* and *macrocephala* was the respiratory network of blood vessels in embryos. He suggested that early movements of pectoral fins and whole body "wriggling" produced water currents across these respiratory networks, and found that embryos of guarders had a transitional respiratory network of blood vessels on the anal fin fold, while embryos of bearers have a comparable respiratory network on the surface of the yolk sac. Almost a decade later, in 1975, Hanon found that one species described as intermediate between bearer and guarder had both types of transitional respiratory network. Among a number of alternative suggestions, Balon proposed his terminology for the development of cichlid young: period, phase, and stage (Balon 1975).

Jones (1972) had recently determined that hatching could occur at different stages of development within a species depending on a variety of intrinsic and extrinsic factors, and thus could not be taken as a fixed reference point for either definition or description of normal stages of development. Noakes added to Jones' assertion that young in guarder species (as opposed to bearer species) hatched at markedly different stages in development. Noakes and Balon would further find in 1982 that embryonic and larval development differed significantly, since—in fact—bearers did not have a larval period in their ontogeny (Noakes and Balon 1982a, b). The physical aspects of such research often entailed the study of biological development in the two groups ("bearers" and "guarders"), which Noakes and Barlow termed precocial (young that begin exogenous feeding when large and with a well-developed sensory and motor control), and altricial (young that begin feeding with a less developed alimentary canal, typically consisting of a simple, straight tube). Bearer young were found to be in a fully formed juvenile state when released, whereas guarder young begin swimming as incompletely differentiated larvae. These differences in size, mobility, and digestive capacity were the purview of physiology and anatomy, but carried important implications for behavior. Noakes and Barlow (1976) investigated an array of issues concerning parent–young behavioral interactions previously unanswered, including the recognition of parents and young by each other. Here, they concluded that in *C. citrinellum,* parents learned to recognize their young during each parental cycle, but that this memory was somewhat short term, and that parents would accept conspecific young younger than or the same age as their own dry, but not older.

While many behavioral studies simply sought a deeper understanding of the species in question, more often than not, they were concerned with the relationship between speciation and reproduction. This inquiry drew attention to the process of breeding in cichlids, which was discovered to be remarkably diverse across species. In 1972, Keenleyside found that reproductively mature males sometimes possessed female or juvenile coloration, enabling them to steal fertilizations during the reproduction of others. John Maynard Smith applied game theory to such biological phenomena in 1979, arguing the tendency to "cheat" as well as fighting has an important reproductive role as both imply greater fitness in animals. At the same time, Amotz Zahavi argued that natural selection should favor signals that could *not* be cheated since the existence of "cheatable" signals allowed inferior contestants to succeed, whereas they should find the biological costs too great to bear and fail since they are not, in fact, the fittest (i.e., handicaps should only work if the male is also higher quality).

Through the 1970s, attention was increasingly drawn to the cichlid species of Central and South America as valuable objects of evolutionary biological study. In particular, the cichlids of the Great Lakes of Nicaragua, where McKaye and Barlow (1976a, b) found that *C. citrinellum* at Lake Jiloá were size dimorphic according to color morphs "gold" and "gray," with golds pairing and breeding at smaller sizes than grays, and more successfully at greater depths, while grays mated more successfully at lower depths. In a similar investigation, published the same year, Barlow and John Munsey found introgressive hybridization between *C. labiatum* and *C. citrinellum* in Lakes Masaya and Jiloá. Studies with the potential to examine incipient speciation events and apparent cross-species hybridization brought these Nicaraguan lakes to the fore, alongside those in Africa, as valuable study sites (Barlow and Munsey 1976). In 1976, Jeffrey Baylis called for a renewed endeavor to examine New World as well as Old World species for their interest to ethologists in his own study of the complex social behavior of *H. multispinosa* (Baylis 1976a, b). Gerald Meral found female cichlids in Nicaragua competed for nest sites and courted passing males, a very unusual situation in the animal kingdom, and certainly among fishes, and George Myers outlined the ways in which South

American and African species were similar, rooting his analysis in the geological history of continental drift and of the area from the Isthmus of Tehuantepec to eastern Panama dating back to the Tertiary period (Myers 1966). Future work examining the species of Nicaraguan lakes would continue in this tradition (see Torres-Dowdall and Meyer 2021).

As with the work being conducted in Nicaragua, work in East Africa continued to focus on sexual selection in cichlids, finding that, on both continents, cichlids display a diverse range of mating types. In polygyny, one male fertilizes eggs of more than one female. In polygynandry, each male fertilizes eggs of more than one female and each female has eggs fertilized by more than one male. In polyandry, one female reproduces with multiple males, while each male reproduces with only that female. Almost all cichlids have biparental care of young, unusual, since in fish usually childcare is male dominated (Barlow 2000). In 1972, Trivers found that biparental care effectively removed both parents from further reproduction during care, and argued that each parent should therefore be tempted to desert in order to invest in additional matings (Trivers 2002). Yet, parents observed in field were persistently monogamous despite communal brooding, and despite the fact that the female invests more in the egg than the male does in the sperm (Ward and Wyman 1977). There were, of course, exceptions. In the presumably primitive *Etroplinae*, such as the Orange Chromide, males were found to sometimes invest equal time in care of eggs as compared to females (Ward and Samarakoon 1981).

The parental systems of cichlids have been particularly well studied in search of an explanation of cichlid diversity via sexual selection, and fall broadly into two categories: those of mouth brooders and of substrate brooders. It was once supposed that mouth brooding was causally related to buccal morphology (Fryer and Iles 1972). However, mouthbrooders of Malawi and Tanganyika were found to have radically different diets and feeding morphology, complicating this view (Barlow 1991). Anthony J. Ribbink found that for maternal mouthbrooders (almost all species in Lake Malawi), maturing young were released at a safe site and recalled into the mouth during danger (Ribbink et al. 1980). After several days, the young no longer responded to recall signals. It was found that in general, the female concentrated on activities directly with brood while males guarded or patrolled territory (Barlow and Munsey 1976; Keenleyside 1983), although in *S. melanotheron,* it is the male that provides parental mouthbrooding (Pauly 1976).

Although cichlid parents usually guard their young ferociously, some species pass parental duties onto other cichlids. Ward (1975) found creching, the pooling of young in large schools in which they are cared for communally. Sjölander thought that the adopting of foreign young (sometimes of different species) might be a response to young-eating predation pressure (Sjölander and Fernö 1973). McKaye found in Lake Xiloá, Nicaragua, that altruistic males guarding foreign (interspecific) brood (sometimes more than one) would drive away approaching predators (McKaye and Barlow 1976a, b). This allowed mothers to spend less time defending and resulted in higher reproduction success rates. This phenomenon, known as the dilution effect, explained voluntary incorporation of foreign young into a parent's brood as increasing the chances of survival for the parent's offspring by extension.

McKaye also observed that in creching among Central American cichlids, foreign young were not always just accepted into another brood, they were sometimes kidnapped (McKaye and McKaye 1977). Experimental manipulations in the lab and field produced the generalization that adults caring for young would accept conspecific young from other broods into their own if the sizes matched. These findings were supported by observations from other researchers (Noakes and Barlow 1973; Myrberg 1975).

In Darwinian selection, individuals compete for food and refuge. In sexual selection, no other species are involved in the competition: males compete for access to female eggs. When lekking was discovered in cichlids, it became an area of focus for this problem. In lekking, males display in an arena (or lek) and females view the performance at a distance and select their preferred mate. This practice granted researchers an opportunity for direct observation of the runaway sexual selection that was held to lead to such rapid speciation. The good genes hypothesis stated that female choice was indicative of real fitness. In the lek, then, males on display were selected for their overall high genetic quality. But this was a problematic premise. If it were true, why would unsuccessful males remain? For the lek to evolve, the number of females attracted per male had to be higher than those lured to a solitary male. Direct observations show no such advantage. Assuming good genes hypothesis was correct, lekking seemed great for females, but bad for most males (Barlow 2000). So why should it persist?

The curious adaptive radiation of cichlids is a stark contrast to Darwin's finches, which constituted 14 species all on separate islands. In the Great Lakes of Africa, hundreds of cichlid species existed (many of which still thrive), mating and acquiring a variety of resources in overlapping territories lacking obvious geographic barriers. If sexual selection was driving this mysterious diversity, then the question—simply put—was how do females choose and why? There was still no consensus on an explanation in the late seventies. This era of inquiry into cichlid evolution—marked by ecology, ethology, and physiology—now saw something new on the horizon, a field of research that has changed and continues to change the life sciences in profound ways; genetics.

4 The Future of Cichlid Research

> I am by nature a cheerful and optimistic person. Growing up in the age of atomic weapons, I learned to practice denial, which was essential for mental health.—George Barlow

Keenleyside argued that genetic research involving cichlids could be broken into three general, but often overlapping, categories: Descriptive studies characterizing attributes of the family or groups of taxa, studies examining genetics as they bear on systematic problems (e.g., phylogeny or taxonomy), and studies exploiting genetics to examine the processes of evolution (Keenleyside 1991). Since accurate evolutionary histories required knowledge from each area of study, and since speciation could not be understood without phylogenetic history, the central roles of the men and women researching genetics in these areas were interconnected (Kornfield 1991). From the late twentieth into the early twenty-first century, the diversity of opinion on the issue of cichlid evolutionary history—and the ways in which it was studied—radiated so significantly that any simple classification becomes misleading. As one example, studies in physiology became crucial to understanding behavior, since studies found chemical cues that prime sexual behavior also aid in species or sex recognition in mate selection (Barlow 2000).

Cichlid research had never existed in particularly well-defined categories, but in this period, interdisciplinary studies became the rule rather than a common exception. In spite of this diversity of study, the importance of genetic studies became a common element in almost all these allied fields, seeming to unify previously disparate groups under the same programmatic end result: verification from genetic evidence.

4.1 The Gene and Cichlid Research: 1980–1990

From the 1980s onwards, cichlid research was increasingly the work of an active and diverse network of men and women whose subjects of study became inextricably interrelated even as they continued to provide different and specialized solutions to the same basic problems. One such problem was the continuing debate between allopatric and sympatric explanations of cichlid radiation. Since the 1950s, it had been suggested that cichlids represented some type of speciation different than the classical sort, possibly due to runaway sexual selection. Some supported the argument that geographical limits to species distribution alone drove speciation (Witte 1984). Others argued for the importance of sexual selection in speciation, a framework that would largely endure until the early 1990s (Dominey 1984).

Lande supported the latter premise, arguing that runaway sexual selection would heavily modify male traits such as size, color, and courtship behavior (Lande 1976). Lande’s polygenic model considered genetic change of a continuous character in a population in which variation could be produced both by several genes and by the environment (Lande 1980, 1981); such a character could be the color or form of a cichlid nest (known as a “bower”). However, many researchers preferred to posit both sorts of speciation as mechanisms in cichlid evolution. McKaye and Gray (1984) suggested that despite Malawi’s historical lack of geographic barriers, geologically brief pond formation around the lake edge could drive classical, allopatric speciation. Seismic surveys of sediments showed that Lake Tanganyika was in fact once three distinct lakes, seeming to support a wider application of this explanation (Scholz et al. 2003). However, McKaye and co-authors also agreed with the basic premise that runaway sexual selection could explain the diversity of Malawi (McKaye et al. 1984).

If sexual selection was in fact the driving force behind speciation, then the most obvious place to look for evidence of this would be in the behavior of spawning and breeding cichlids. From 1980 to 1983, McKaye described cichlid leks in Lake

Malawi, which are the largest among vertebrates in the world, with 5000 to 50,000 males in a 4-km long stretch of shore constituting the mating "arena" (McKaye et al. 1990). A bower is built by the male and is the indicator of fitness on display. McKaye and colleagues studied the reproductive ecology of 50 Haplochromines in Malawi, finding that bowers could be divided into ten types, supporting the conclusion that bowers arose from a common ancestor dividing into rapidly evolving species in which local ecological conditions were not the driving evolutionary force in bower form. McKaye (1984) also observed that among mbuna males of *P. williamsi,* defense of transient territories was common, but of 70 species that spawned over sand, two did not establish territories; the transient spawning territories of these Malawi cichlids were considered unique. Knowledge of the stunning variety of spawning sites among cichlids by species continued to grow. It was found that, in the case of some dimorphic species too large to enter the nest—or in the case of females that spawn in small snail shells—the male could only approach the threshold and hope to fertilize the eggs from beyond (a fact observed by Meek as early as 1907). For South American convict cichlids (*Cichlasoma nigrofasciatum*), however, eggs were attached to the ceiling or sides of a cave (Lavery 1991), with some species in Tanganyika doing the same in the lake bottom (as is also the case in Lake Gatun, Panama, where algae is known to be used as a substrate). Such apparent cases of similar traits and behaviors prompted continuing investigation to elucidate evolutionary relationships between species.

Parental behavior among cichlids is also extremely varied and served as another significant line of inquiry on the issue of speciation. Wittenberger (1981), for example, studied different mating systems and found that they often derive from differences in feeding habits. Townshend and Wootton (1984) added to this position, comparing fecundity and size of *C. nigrofasciatum* in captivity and in Nicaraguan lake, fish were smaller and less fecund, discovering that food resource availability constrained reproductive behavior. Aquarists found that South American earth eaters (*Geophagus brasiliensis*) showed a wealth of mating types in captivity extending from monogamous through haremic to open polygamous and from substrate guarding through primitive and advanced mouthbrooding (Barlow 2000). Schwanck (1987) found monogamy to be uncommon in African mouthbrooders, probably because maternal mouthbrooding provides the opportunity for males to abandon their mates. According to Keenleyside, monogamous male cichlids tended to flee and females to remain with the young when danger threatened (Keenleyside et al. 1990). In general, males spent more time away from the brood than females. Keenleyside (1983) found that in experimental ponds with a female-biased sex ratio, the tendency of *H. multispinosa* males to desert their first mate to get a second increased along with the number of surplus females, and that most of these males spawned within six days of deserting. Evidence accumulated during this time for a tendency to desert among males of many presumably monogamous species, with studies on desertion and polygamy carried out separately by Carlisle, and by Townshend and Wootton (Carlisle 1985; Townshend and Wootton 1985a, b).

Some links between parental behavior and evolutionary history were pointed to by Loiselle (1985), who found that transitional South American mouth brooding species showed a progression from monogamy to polygyny with the deciding factor appearing to be how long the eggs stuck to their substrate. Further elucidating this phenomenon, Trewavas (1983) reported on comparative studies indicating a progression from a delay in taking the eggs into the mouth to picking them up instantly across species. Kuwamura et al. (1989) also described parallel behavior among the haremic lamprologines of Lake Tanganyika, ranking 17 species on a gradient from biparental to maternal care, showing that more maternal species' young tended to become benthic rather than nektonic. In another comparative study by Kuwamura (1986), 28 of 35 species examined were found to be maternal mouthbrooders, while seven others had delayed or some other variation on mouth brooding. Yanagisawa and Nshombo (1983) found that in mouthbrooders (which predominate in the lakes of Africa), scale eaters immediately shelter non-adhesive eggs in their mouth after spawning. In most polygynous mouth brooders, the male would drive the female away, but in this case, the parents become a monogamous pair, jointly sheltering the young when they are spit out one week later.

In addition to the ability of the eggs to adhere to different substrate, Loiselle (1985) found that predation on young has been a primary selective force for monogamous behavior among previously haremic males in the open bottom dwelling lamprologines of Lake Tanganyika. According to the evolutionary theory of parental investment, offspring become increasingly valuable as they reach maturation (Dawkins 1976). However, it was argued by Loiselle, Lavery and others that in some species—such as convict cichlids—it was not age, but vulnerability to predation, that was the best indicator of parental investment (Barlow 2000). Around this time, it was also shown that when a clutch is too large and there are too many young, the fitness of individual young is diminished (Lavery and Keenleyside 1990a, b). However, optimal clutch size for different cichlids and how this might be determined remain unknown. Ward and Samarakoon (1981) reported species differences in the defense of young with some parents alternating care to take time to feed and, in other cases, found that both parents remain with the young constantly. Tamsie Carlisle (1985) in Panama showed that a greater number of young led to greater defensive behavior in parents. Yanagisawa (1986) found that in some species, the female broods the eggs and the embryos, and the pair of parents jointly defends the young. Yanagisawa's observations led him to believe that two parents were in fact not required to protect the young, but that male care was favored because it permitted the female to feed at a normal rate and shorten the interval between broods. Shine (1978) had outlined a principle based on a similar phenomenon, referred to as the "safe harbor." In many species, newly mobile cichlids were found to stay near the spawning site requiring protection, usually from both parents, rather than disperse and search for food (as do the young of most species with male-only care).

Regardless of its relationship to monogamy, polygamy, or polygyny, mouthbrooding has been of enduring interest to evolutionary biologists. Despite the increasing evidence that categorizing species as mouthbrooders or substrate brooders was an over-simplistic dichotomy, emphasis remained on these reproductive methods as crucial to understanding evolution in cichlids (Kuwamura 1986). A behavior of special interest was intra- and interspecific mouth brooding, in which a species might carry young in its mouth from another parent, or even from another parent of a different species entirely, a phenomenon called creching, which was described by Ribbink et al. (1980) in females of several species, including African tilapiine cichlids. Tetsu Sato (1986) in Tanganyika showed that mouth brooders would even carry young catfish. McKaye described reliable interspecific creching in mouth brooding African cichlids that mix their young with those of catfish around the same time (McKaye 1985). It was suggested that kidnapping another animal's brood might be an effective anti-predator adaptation, increasing young size to increase a single offspring's odds of survival. However, Pitcher (1986) argued that this dilution effect could only work if predation did not increase with brood size. The exact evolutionary origins and function of creching remained unclear.

With increasing emphasis placed on cichlid broods themselves, two areas of study concerning the reproduction of cichlids that gained traction in the mid to late 1980s were behavioral ontogeny and developmental biology, which focused on growth from the larval state. The issue of conspecific recognition emerged as a critical question in the study of speciation. Shaw and Innes (1980) worked with *A. pulcher* and implied that parental recognition of foster young depended on the behavior of the young, as well as chemical and visual cues, and that young might be capable of learning simple responses. The question of sexual imprinting had bearing on how new species of cichlids originated, since learned species recognition would be an important factor in adult sexual selection. This recognition was found to occur in cases where species in overlapping physical areas had no overt differences in shape or coloration. Russock and Schein had investigated the effects of early social experience on filial and subsequent adult social preferences in *S. mossambicus* as early as 1977, and through 1986 found that although young had an initial predisposition to respond to the general characteristics of their mother, they would respond similarly to a range of objects.

The question of whether early imprinting affected later social behavior was concluded to concern only the mechanism at work (Noakes 1991), and researchers focused on this since these effects could reveal how cichlids came to show their usual social reference as a consequence of early experience. Such factors were also considered of potential significance in cases where young were reared by foster parents of their own or other species. Recognition or association between cichlids was also implicated in the phenomenon of "helping" by Taborsky (1984), who found that members of successive broods might be found together in a territory since helpers from an older brood often remained behind to assist with the new. The behavioral consequences of early social experience attracted much interest, but the physiological conditions and changes in ontogeny related to cichlid development were found to be equally important avenues of study. Crapon de Caprona (1982) found that at least some of the early chemical and visual signals of *H. burtoni* influenced social responses, and social interactions among juveniles were shown to affect growth rate. Such studies also had implications for mating style, diet, and evolutionary history, as in the case of Noakes and Balon (1982a, b) who report that bearer species do not have a larval period in their development. The issue of sex change during development was also of special interest. This phenomenon could be employed strategically in aquaculture production since small male fish are excluded by large males during reproduction, but small females are just as viable (Barlow and Munsey 1976).

When a large female could hold more eggs, however, the size situation was found to be reversed. For years, the plasticity of hermaphroditism was thought to be confined mostly to marine fishes, demonstrated in only a few freshwater species (Cole 2010). However, Richard Francis (1992) showed that many fishes are protogynous, starting life as a female and then staying female or becoming male. Water pH and temperature were found to be important factors; for dwarf cichlids in *Apistogramma*, for example, higher temperatures produced more males (Heiliginberg 1965). Francis and Barlow found that in some cichlids, growth rate determines sex change, with slower rates leading to female development. Size was also found to be related to dominance and territorial holdings for the purpose of reproduction, with dominance behavior, neuronal changes, and hormones contributing to the development of testes in dominant males (Francis and Barlow 1993). Brem (1988) found that, as with tilapias, sex reversal in haplochromines could be induced by hormonal treatment early in development.

While many researchers maintained that rapid speciation must have occurred due to runaway sexual selection (Dominey 1984), the most significant competing explanation was still viewed by many to be the argument from feeding morphology (since expanded upon) of Liem and Greenwood (1981). They argued that the cichlid “bauplan” provided a uniquely adaptable system capable of rapid change in diet and behavior that, under competitive resource pressure, allowed for niche selection. Throughout the 1980s, diet, feeding behavior, and morphology all remained significant areas of study. Focusing on cichlid diet, McKaye, McKenzie, and Kocher in 1982 and 1983 discovered at least three species of paedophages in Malawi, and McKaye and Marsh (1983) showed that zooplankton would be favored as a food source when abundant. Heinz Bremer and Ulrich Walter (1986) discovered secretocytes in some species, specialized cells in the mucus eaten by young, potentially to acquire valuable gut flora. The fact that young feed on different food types for the first 8.5 months prompted Meyer (1989) to propose the heterochronic model, accounting for the fact that young also differ from the adult form morphologically, especially in head measurements reminiscent of different feeding behavior phenotypes. Meyer (1987) manipulated the diet of *C. managuense* from Nicaragua and quantified changes in head morphology that resulted during development. Diet was also found to impact coloration, demonstrated by Barlow (1983).

While some researchers studied cichlid diet, others focused on the adaptability of feeding behavior. Barel (1983) proposed that feeding behavior in cichlids has two morphotypes, biters and suckers (though others showed these to be nonrigid categories). Van Oijen (1982) found piscivores to be the most speciose group in Lake Victoria (accounting for up to 40% of all species), and Hori (1983) found that hunting either nocturnally or diurnally in piscivores involved turning over stones and pursuit or ambush tactics. But while much research was still devoted to specialized diets, others began to suspect that feeding behavior alone could not explain the extent of cichlid speciation. Between 1980 and 1983, Barel, Galis and

Hoogerhound argued that, in contrast to prior opinions that adaptive radiation mainly concerned the feeding apparatus, more recent research suggested that all anatomical systems (gills, eyes, ovaries, etc.) were involved.

Cichlid functional design had long been held to allow specialization into trophic and ecological niches, but there were problems with this explanation. More accurate phylogenetic assignments were required to clarify persistent issues in questions of cichlid evolutionary history pertinent to speciation, and the taxonomy remained confounding even as genetic research advanced by leaps and bounds. Kocher and Meyer established the first estimates of divergence between New World and Old World fauna, but McKaye (1980) followed by Liem and Kaufman (1984) found that South American cichlids presented problems for hypotheses based on studies of African cichlids. Kullander (1988) pointed out that *Crenicichla* cichlids had specializations similar to those in African rheophilic cichlids, but that this did not necessarily indicate historical evolutionary relationships accurately. Stiassny (1982) found South American *Cichla* to be a morphologically aberrant taxon, with their closest relatives in fact being the neo-tropical pike-cichlids of the genus *Renicichla*. Morphological markers of taxonomic relationships were continually debated, with Kullander (1982) rejecting Regan's "three spines vs more than three spine" dichotomy, positing instead that *Cichla* resembled distant percoid relatives because of an ancient unchanged lineage. Stiassny (1987) found that the presence of six rather than seven lateralis canal foramina in the preoperculum was a grouping characteristic that conflicted with Kullander's 1983–1988 descriptions of characters shared by *Crenicichla*, and not found in *Cichla*.

Meanwhile, the taxonomy in Africa was also hotly debated. From 1981 to 1984, Stiassny, Zihler, and Gaemers (among others in their field) worked to establish that the family Cichlidae was monophyletic (Gaemers 1983). Oliver supported the monophyly of African radiation with a morphological feature study (1984), and recognized the Zairean genus *Heterochromis* as a taxon removed from remaining African types, a major advance in understanding high-level relationships. Greenwood joined a growing group of researchers challenging Regan's preeminent phylogeny. To get around errors and ambiguities associated with the less accurate process of protein electrophoresis, Dorit (1986) applied restriction enzyme analysis of mtDNA to questions in systematics concerning fauna in Lake Victoria, demonstrating heterogeneity of mtDNA phenotype frequencies in several species that supported Greenwood's taxonomic revisions. Greenwood's major revision of the haplochromines taxonomic system based on the shape of the skull, teeth, and mouth and several other characteristics, reflected his belief that the species flocks in the Great African lakes in fact formed a superflock (Goldschmidt 1996).

Tijs Goldschmidt, too, began to consider the possibility that the cichlids of Victoria might represent one huge species with "hundreds of masks" behind which one genome was "hiding," an assertion akin to the superflock that Greenwood imagined (Goldschmidt 1996). Researchers were beginning to question the basic premise that some form of physical adaptability had allowed niche selection in cichlids; now they wondered whether or not resource partitioning or competition was even involved at all. Goldschmidt (1989) argued that the number of resources a species might exploit was limited by the compatibility of the anatomical requirement for coping with these resources. It was a common ecological assumption that competition must have occurred in the distant past. However, in the course of his investigation, Goldschmidt found no evidence of such competition in Furu species at Lake Victoria (Goldschmidt 1996). Similarly, Hori (1987) had found that mutualism in Tanganyika could be studied from the viewpoint that it raised species richness in each feeding habit group *without* resource partitioning. If behavior in cichlids could diverge by virtue of the connections among three kinds of interspecific relationships in feeding, commensalism, mutualism and competition in ecological communities within tropical ecosystems, then this might circumvent the need for resource partitioning as a driver of speciation, but do so without discounting that speciation had, in fact, occurred. However, if specimens classified as belonging to different taxonomic species did not interbreed in nature, and if there were no barriers to interbreeding between these organisms, then the taxonomic and population-genetic species would coincide, suggesting the possibility of a superflock.

For Liem and Greenwood (1981), this was the case. He held that similarities in the patterns of diversity of cichlids—like the Hawaiian honeycreepers and Darwin's finches—were more apparent than real. Therefore, complex ecosystems of cichlids could develop in the absence of geographical borders without initially violating the basic premises of classical evolution. The unique combinations of diet, feeding behavior, and habitat found by Van Oijen (1982) in Lake Victoria piscivorous haplochromines, or the commensal and mutualistic relationships in Tanganyikan rocky shore groups between predatory and epilithic algal-feeding cichlids found by Takamura and Hori (1983), might then be entirely superficial indicators of speciation. Ribbink reawakened the controversy over the very concept of "species," with a review in 1986 critiquing several controversial points concerning speciation. Kornfield et al. (1982) found that different trophic morphs in Mexico were actually members of the same species, and Sultan (1987) found, contrary to what had been previously accepted about cichlid adaptability driving speciation, that plasticity might be a form of "inertia" *against* speciation. This position was later taken up by Meyer, who began to question the role of trophic polymorphism in speciation from at least 1989. Despite recent origins and close affinities, it was now clear that similarities between many Victoria and Malawi species were due to convergence and perhaps largely superficial. When it came to cichlid evolutionary history, anything seemed possible.

At the same time that evidence from genetics and morphology was suggesting that cichlid species were more apparent than real, evidence was mounting from biogeography to show that these species were not only real but had emerged by allopatric mechanisms. In Tanganyika and Malawi, cichlids restricted to shallower coastal areas due to water depths greater than 200 meters—which lacked enough dissolved oxygen—were contrasted with species in the shallower waters of Victoria where more diversity had developed over a comparatively shorter geological timespan. From 1981 to 1987, Kawabata, Mihigo, and Yamaoka found communities distributed according to depth and lake-bottom physiography showing similar general trends in resource partitioning (Kawabata and Mihigo 1982). Lewis and Van

Oijen (1980, 1981) showed a sharp contrast between Lakes Malawi and Tanganyika in terms of habitat distribution, with Victoria habitats usually lake-wide. Goudswaard and Witte (1984) showed that demersal cichlid species' composition was strongly influenced by water depth and the nature of nearby substrates (many researchers supported this premise with similar findings). Similarly, Bell-Cross and Minshull (1988) found that the occurrence and abundance of *Serranochromis* species was determined by preference for shallow reedy lakes or swamps.

Sharp and Marsh had already found that mbuna existed where water was well oxygenated, and that their territorial requirements were species-specific. In a 1983 study that involved 121 stations in 14 regions, 196 mbuna species were identified with only two lithophilic species occurring in every study region, showing simply that the smaller a rocky "island" or pinnacle is, the fewer species it supports (Marsh et al. 1983). Species were found to occur in a depth range of 3–10 m where well-oxygenated water and high algal productivity were present. The distribution of other species was more difficult to explain, since species inhabiting similar northern and southern habitats were, for unclear reasons, not present in similar habitats in central regions. Variation within populations at particular sites was small, but across a series of habitats, changes in colors and size were obvious.

The argument that resource partitioning or physical separation drove cichlid speciation, although formed in previous decades as an antipode to the suggestion that sexual selection might drive sympatric speciation, seemed now inextricably linked with behavior and reproduction. Similarly, sexual selection and ontogenetic development had been found to connect intimately with environment, diet, and other physical factors. Ringler (1983) found that feeding preferences and specializations could develop either as a result of experience or through maturational changes, and Ribbink (1984) found that *Docimodus evelynae* developed into a scale eater from a juvenile "cleaner." Similarly, Gottfried (1986) showed that Midas cichlids changed from suckers as juveniles to biters as adults. Noakes and Balon (1982a, b) suggested mouth brooders and substrate brooders as alternative styles of life history and ontogeny, guarders being altricial and bearers being precocial. The complexities of these studies were nicely encapsulated by the works of Nagoshi (1983), in which spawning and parental care were found to contribute an additional dimension to the utilization of space and other resources behavioral differences associated with alternative methods of pair formation (Brichard 1978).

The general conclusion of the wide array of work done in the 1980s was that the process of natural selection in cichlids must be complicated and defies explanation according to any single factor. Selection operates with respect to different colorations and mating systems, environmental change, diet, morphology and developmental biology, territoriality, and other behavior, and these variables do not affect selection independently. In particular, a recent speciation or inability to discriminate other species, kidnapping and ability to recognize individuals and sexual dimorphism (or lack of) are crucial and interrelated factors in sexual selection (Barlow 2000). These aspects of the organism are deeply interconnected, and they have been found to demand interdisciplinary approaches if any understanding of the complexities of their roles in speciation is to be gained.

4.2 The Tragedy and Promise of Fisheries and Aquaculture: 1980–2000

While the use of new technology and research in genetics clearly aided a variety of research programs related to evolutionary biology, these advances were also directly applicable to fisheries and aquaculture for commercial production. At the end of the 1970s, Ramshaw et al. had found that standard starch gel electrophoresis underestimated within-taxon variation by 30% or more (because co-migrating bands may not be identical or buffer systems may not resolve slight differences in net charge), and Takezaki and Nei (1996) argued that estimations concerning genetic divergence were highly dependent on the number and identity of loci examined. Similarly, Hillis (1987) found that small sample sizes might significantly bias estimates of variation and reduce the ability to detect alleles. These technical problems and inaccuracies would have to be surmounted for considerable progress to be made in areas related to genetic study. A significant step forward was the development of the Polymerase Chain Reaction (PCR) by Kary B. Mullis (1994), which allowed for advancement beyond earlier technological limits to genetic study.

Advances made in genetics have had important benefits for the aquaculture of tilapias since 1983. Gjedrem (1985) showed the value of genetics for selection in aquaculture, and Seyoum (1989) conducted mtDNA characterizations of tilapias from East Africa and distinguished seven subspecies clearly, with direct applicability for defining wild and cultured stocks. Much research aimed at increasing the efficiency of aquaculture production through better control of breeding and the maximization of yield, whether genetic in nature or not. Lowe- McConnell, as well as Noakes and Balon, considered mixed-sex, freely-breeding tilapia populations kept in confined spaces and found that under these circumstances, tilapia mature early and breed prolifically, overpopulating the pond with undersized fish and thus undercutting the maximum economic return (Pullin and Lowe-McConnell 1982).

Another problem in aquaculture was the ratio of male-to-female production. Maximizing economic yield requires more males, since male tilapia grow to a larger size, with more metabolic energy channeled directly to growth. Females direct energy into ovarian growth, which is considerably greater than testicular growth. Avtalion and Don (1990) found that females tended to occur in monosex systems because autosomal genes contribute to sex determination. While alleles at supposed sex determining loci could be manipulated by hybridization, simple crosses might not control for these additional sources of allelic variation, confounding attempts to maximize yield (Avtalion 1982). Further complicating this issue, Scott et al. (1989) found that spontaneous sex reversal in tilapias, while infrequent, was common to all commercial stocks. It was also found that YY “supermales” could occur if a phenotypic female (a genetic XY male) mated with a male (in fact, this phenomenon was discovered accidentally).

Genetic studies were not merely a means of understanding how to best maximize the output of farmed tilapias, it was a means of actively manipulating the genetic code to achieve this goal. Only 2 years after the International Center for Living

Aquatic Resource Management (ICLARM) 1980 conference on *The Biology and Culture of Tilapias,* Philippart and Ruwet (1982) collated an immense amount of information available on ecology and distribution of tilapias, Lovshin provided a review of tilapia breeding and hybridization in Brazil and elsewhere, and the textbook *The Biology and Culture of Tilapias* appeared (Pullin and Lowe-McConnell 1982). Two years later, Trewavas summarized the distinguishing features of tilapiini (Trewavas 1983, 1982). In 1989, the ICLARM officially recommended tilapias and carps as species of focus for the Consultative Group on International Agricultural Research. It was in accordance with this goal that the maximization of commercial tilapia stocks was sought by means of genetic manipulation. Wolters (1982) found that in polyploids, gonadal development might be suppressed so that additional energy could be channeled into increased physical growth. Chourrout and Itskovich (1983) produced triploid tilapias through cold and heat shocks. Myers (1986) induced tetraploidy in tilapias using thermal and pressure shocks, and Brem (1988) demonstrated the expression of human growth hormone in tilapias microinjected with DNA early in development. Kocher et al. (1989) produced universal mtDNA primers for cichlid PCR studies, just one year after Wachtel argued that the identification of sex specific regulatory loci in cichlids could, and should, progress rapidly if findings in other vertebrate systems were exploited. The ICLARM was, by this time, a world leader in fostering research to support genetic objectives in tilapia (Kornfield 1991).

As the species of cichlid first to appear in written human history and in early depictions of controlled breeding—Nile tilapia (*Oreochromis niloticus*)—quickly became the most popular fish for modern aquaculture methods in the world, with its exponential production commencing by the end of the 1980s (Teletchea 2018, and see Fig. 8). In cichlid rich lakes, wild fisheries castatrophes were becoming more commonplace, seemingly providing all the more reason to raise commercial stocks of tilapias in isolation from fragile ecosystems. In the late 1980s, in response to dangerous changes in African Lake ecology, Lowe-McConnell and Fritz Roest of the Fish Section of the International Agricultural Centre at Wageningen Netherlands organized a symposium on Resource Use and Conservation of the African Great Lakes at University of Burundi in Bujumbura, 1989 (Lowe-McConnell et al. 1992). Recommendations from the symposium were used to apply for international funds for fisheries and diversity projects on African lakes. Yet, even as concern over lake ecologies mounted, officials in Bujumbura consulted with a Swiss firm to determine a building site for a pipeline and town authorities in Burundi consulted with an Austrian university concerning the building of a sewage outfall pipe, both of which would pollute valuable freshwater fisheries. Similarly, it was amid concerns of oil drilling in Lake Tanganyika that the International Limnological Association formed the African Great Lakes Group (also convened by Lowe-McConnell, this time in New Zealand, 1987). Lake Victoria and Tanganyika were not the only lakes threatened, and by the early 1990s, Lake Malawi's history was recounted by Tweddle (1991), showing that the use of beach seines since the 1970s—leading to reduced catches in the 1980s—finally expanded to such an enterprise that in the early 1990s, fish stocks in the southeastern arm of the

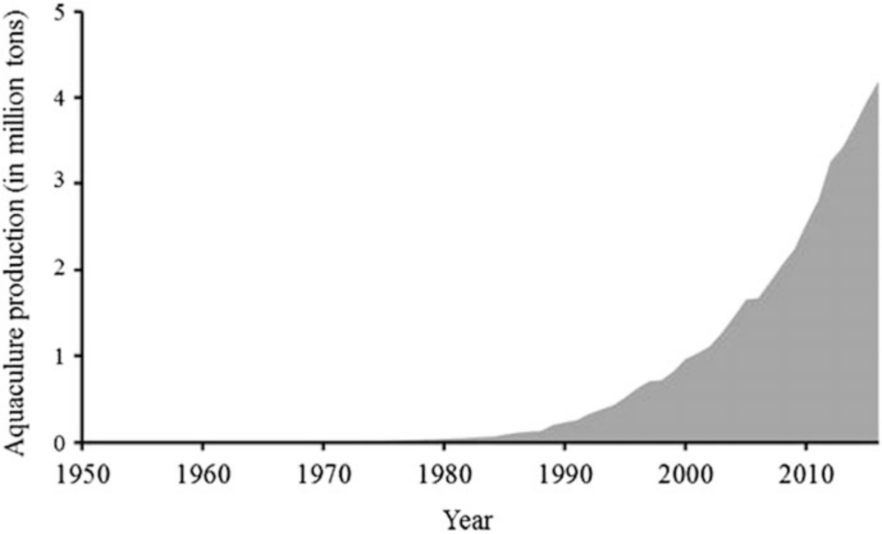

Fig. 8 Global aquaculture production (in million metric tons) from 1950 to 2016 of the Nile tilapia *Oreochromis niloticus;* data from the FAO database. (Reproduced from Teletchea 2018, licensed under CC by 3.0)

lake and those of Lake Malombe collapsed. By 1996, Malawi Fishery Department records showed a decline in endemic tilapia catches to negligible amounts, and today, beach seines are rare in the South east Arm of Lake Malawi not because local authorities have enforced strict regulations, but simply because so few fish remain to be caught (Lowe-McConnell 2006).

Of the tales of fishery collapse on the African Lakes, none is as poignant as Lake Victoria. After 1980, annual fish catches in Lake Victoria consisted of 80% Nile perch (Barlow 2000). This noticeably affected catches of native cichlid species by 1987, species that had been the primary food source of Nile perch in the Mwanza area (Barel et al. 1991). From 1977 to 1983, the University of Leiden HEST team caught occasional Nile perch, but the populations seemed low enough that they were not alarmed. By 1985, the situation had changed considerably, with Tijs Goldschmidt finding that normally common species were entirely missing from catches (Goldschmidt 1996). Haplochromine stocks at Victoria were almost entirely obliterated by 1987, and the same year, benthic prawn and cyprinid fishes replaced these cichlids as the main food source for *L. niloticus*, completely changing the ecology of the lake (Barel et al. 1991). Although cichlid stocks at Lake Victoria served as a crucial resource to local populations for hundreds of years, by the twenty-first century, it was the exotic Nile perch that drove the economies of the surrounding nations (Awange and Ong'ang'a 2006). Since the 1970s, total catches increased between four- and five-folds, making Victoria the world's largest freshwater fishery, and the number of fish harvested at Lake Victoria peaked between 1991 and 1992 (Awange and Ong'ang'a 2006).

Over 3 million people depend on the fishery at Lake Victoria for their livelihood in Tanzania alone, and in Uganda, fishing is an important source of high-quality food, employment revenue, and has led to development of infrastructure, and is currently the second most important export commodity next to coffee (Awange and Ong'ang'a 2006). Yet, Lowe-McConnell and others noted that as of 1995, many locals were no longer able to provide fish for their families; cichlid catches were no longer substantial, or legally attained (Lowe-McConnell 2006). Surrounded by five countries forming one of the densest and poorest rural populations in the world, the Lake Victoria basin had a population of approximately 26 million in 1999 with a growth rate of about 3% annually (Awange and Ong'ang'a 2006). Increasing pollution pressures on Lake Victoria and pollution impact by municipal and industrial discharges became visible in some of the rivers feeding the Lake and along the shoreline; small-scale gold mining increased in part of the Tanzanian catchment area, leading to mercury contamination of the waterway (Awange and Ong'ang'a 2006). Continued commercial overfishing in the south drove many cichlid species to extinction and left many rare or endangered.

Phosphorous and nitrogen concentrations rose, and algal growth increased five-fold from the 1960s to the 1990s (Awange and Ong'ang'a 2006). This algal growth was exacerbated by the extinction of local species that once consumed it. Artisanal fishing by lakeshore villagers also became a significant threat in some areas, very long and fine-meshed nets that catch even juvenile cichlids in large numbers now being widely used. Intensive fishing of furu cichlids was no longer possible, as the Nile perch introduced to Victoria had decimated their populations, also consuming the catfish that had once been the furu's main predator, and thus removing over one hundred species from the ecosystem. Following the disappearance of the furu cichlids that consumed them, prawn populations increased and Nile Perch began to feed intensively on prawn (Goldschmidt 1996). However, the prawn had replaced detritus eating furu cichlids, and small sardines had taken the place of zooplankton eating furu cichlids. Species capable of keeping the algae levels of the lake in check effectively vanished from the food chain. In turn, massive increases in blue-green algae were left to be decomposed by oxygen consuming bacteria. By the late nineties, 50–70% of the lake was deoxygenated year-round, making it unlivable for any fish species, including haplochromine cichlids and the Nile perch that had driven many of them to extinction (Goldschmidt 1996).

The fisheries of Lake Victoria have not yet collapsed, but the threat is imminent: ecosystems that have been greatly simplified by humans are often only productive for a short period (Goldschmidt 1996). The decline is already noticeable—the biomass and abundance of Nile perch decreased from 790,000 tons in 1999 to 530,000 tons in 2001 (Awange and Ong'ang'a 2006). It has been argued that enforcing a regional fishing ban would cost industry stakeholders, fish processors, traders, exporters, and transporters billions of dollars. It is also estimated that export losses would be significant. Any ban, however ecologically reasonable, would cause considerable economic turmoil—an outcome that may be inevitable, given the fishery's impending decline. In response to this dilemma, the Lake Victoria Fish Processors Association of Tanzania volunteered to cease fishing for 4 months of breeding to allow the Nile Perch populations to recover. The firm is currently demanding that similar moves be undertaken by Kenya and Uganda. However, such a proposal would bring 32,000 small fishermen into conflict with Lake Patrols preventing subsistence fisheries (Awange and Ong'ang'a 2006).

Recently, there has been an effort in each of the three East African Countries to pursue sustainable fisheries. A Convention for the Establishment of the Lake Victoria Fisheries Organization (LVFO), currently supported by the EU through the Lake Victoria Fisheries Research Project, drafted with FAO assistance was signed by Kenya, Uganda, and Tanzania in 1994. It intends to promote better fisheries management and conservation. More recently, three of the East African countries collaborated through the support of the Food and Agriculture Organization (FAO) Committee for Inland Fisheries in Africa (CIFA), Sub-Committee for Lake Victoria.

Witte et al. found in 1991 that 300 species had apparently gone extinct in Victoria. This reality was rendered even more tragic by Johnson and Scholz's geological work in 1996, which showed that the biodiversity of Lake Victoria was likely only 12,400 years old. The fish in this lake represented the most diverse, most rapidly radiating group of living animals known to man, and in a few short decades, the opportunity to study this phenomenon was almost entirely destroyed. In the late twentieth and early twenty-first centuries, evidence of these changes has continued to garner some helpful responses. A growing number of biologists, limnologists, and anthropologists became actively involved in trying to conserve Lake Victoria and its biological diversity. The furu were included in the book of endangered species of the International Union for the Conservation of Nature, and a Captive Breeding Program was launched. Some 40 species were sent to Europe and the United States, each fish packed in a plastic bag where they were housed in US and European zoos and bred.

A great deal of research, both based at Lake Victoria and abroad, has aimed to better understand and resolve issues of ecological overexploitation. The Lake Victoria Research and Conservation Team, which included the HEST group from Leiden, contributed significantly to this project. The Lake Tanganyika Research Project of Osse Lindqvist's team at University Kuopio, Finland from 1992 to 1998 on production and optimal management of pelagic fisheries, as well as the UNDP/GEF Lake Tanganyika Biodiversity Project (through 2000), aimed to deal with pollution control and protect biodiversity. Another long-term proponent of holistic ecological health in the biological sciences has been Hiroya Kawanabe. In 1991, Kawanabe founded the Center for Ecological Research at Kyoto University, and in 1992, Kawanabe organized the "SymBiosphere: ecological complexity for promoting biodiversity international" workshop there. Kawanabe also worked with the Organization for Tropical Sciences at Laselva, Costa Rica, and pushed for the Center for Ecological Research (CER), Kyoto, to start the "International summer seminar on the global environment and ecology."

As amateur enthusiasts and aquarists interested in cichlids became concerned, so too did the aquarium trade begin to organize events designed to bring about positive change. Michael Tlusty (2002), for example, promoted the aquaculture of cichlids for efficient aquarium trade production and for species conservation; the Species Survival Program of the American Zoological Association now manages 28 such captive populations of haplochromine species. It is hoped that this might relieve pressure placed on local populations by hobbyists or aquarists, especially for desirable rare or newly discovered species. However, even ornamental fish breeders rely on fresh wild stock periodically, and as a result, the benefit to wild populations may be minimal except in cases of extreme population loss (as has occurred at Lake Victoria). An example of successful reintroduction of species based on this model is the work conducted by Larry Johnson (a cichlid enthusiast who discovered an interesting feeding behavior in *Sciaenaochromis fryeri* and photographed a new species of *Lethrinops* for the first time), Ad Konings, and associates through the Stuart M. Grant Conservation Fund. Together, they returned *P. saulosi* to Taiwanee Reef, Lake Malawi. These fish were produced by Stuart M. Grant Limited that operates the largest cichlid export facility on Lake Malawi. This procedure was repeated in 2014 and was planned again for 2015 (Konings 2013).

As fisheries around the world have encountered numerous ecological issues, the aquaculture of tilapia has continued to expand. By the 1990s, a consensus emerged that research into tilapia genetics should move away from all male hybridization and toward a systematic application of quantitative genetics in breeding. The tools available to genetic study were advancing significantly—exemplified by the technology and techniques necessary to sequence the human genome between 1990 and 2003—a task that has grown more efficient and accessible to researchers with each passing year. Such advances have continued to aid in the aquaculture of tilapia in a variety of ways, as can be seen in the 1994 work of Franck, Kornfield, and Wright concerning tilapia phylogeny, as well as that of Andreas R. Dunz and U.K. Schliewen (2013), whose molecular study re-classified and created a split in Smith's 1840 *Tilapia* genus.

4.3 The Continuing Role of Genetics in Cichlid Phylogeny: 1990–2000

In E.O. Wilson's (1998) *Biodiversity,* a species is regarded conceptually as a population or series of populations within which free gene flow occurs under natural conditions. This means that most individuals at a given time are capable of breeding with members of the same species, or at least that they are capable of being linked genetically to them through chains of other breeding individuals. By definition, they do not breed freely with members of other species. However, this creates a dilemma when observing a species: Which is the more relevant grouping feature, morphology of reproductive isolation? Demonstrating the genetic relationship between organisms is without a doubt the most powerful modern tool available in the effort to unlock the complex and ever-changing riddle of how new species form. However, owing to Aristotelian notions of the function of organisms and the relationship of function to form, early natural philosophers believed form to follow logically from function. Thus, in the mind of most learned men prior to the late nineteenth century, morphology could be thought of as the ideal design to meet the intended purpose of physiology. As a result, the tradition of classification within natural history has long been rooted in observable morphology and anatomy rather than the reproductive relationship between large groups of individual organisms.

Throughout the late twentieth century, genetic evidence mounted to overturn taxonomic assumptions based primarily on outward appearances. Using the HENNIG86 program, Stiassny (1991); Stiassny and De Pinna 1994 used the outgroup method of phylogenetic analysis to produce a cladogram of the Neotropical lineages with three trees, and later proposed *Retroculus* to be the most basal cichlid in South America. Kullander (1998) supported this idea with genetic analysis. Pairing this with morphology, Stiassny found evidence that the ethmovomerine region of the neurocranium shared by the Neotropical assemblage might serve as a grouping feature, finally offering a stable substitution for Regan's phylogeny, which had been repeatedly challenged since the 1950s.

In many cases, the search for "stable" phylogenies meant confronting and accounting for apparent incidents of interspecific breeding. Meyer et al. (1990) determined a monophyletic origin of species in Lake Victoria, concluding that the species of Lake Victoria are a genuine species flock and overturning Greenwood's polyphyletic model. Martin et al. (2006) found "introgression," or gene flow between species in the lakes, or in the past between different lake (and even river) populations. Oppen et al. (1997) showed that in four species of mbuna, there was small but measurable gene flow between intraspecific populations, which were genetically distinct, in a sympatric situation. This seemed to argue against the conclusion that cichlids were in fact many species, or at least against the fact that sympatric speciation occurred.

On the other hand, Fabrice Duponchelle and Tony Ribbink, now the Director of SADC/GEF Lake Malawi/Nyasa Biodiversity Conservation Project, worked to determine cichlid evolutionary relationships using mbuna DNA samples and found that the results indicated a paraphyletic lineage. The presence of a well-differentiated mtDNA polymorphism confounded cladistic analysis (two divergent and statistically distinct mtDNA lineages being present). This pattern suggested lineage sorting, the random fixation of ancestral mtDNA clones within isolated populations characteristic of classical, allopatric speciation. Additionally, some endemic non-mbuna haplochromines were found to possess distinctive mtDNA profiles identical to members of the mbuna. This indicated that as currently defined, mbuna were a paraphyletic group. However, McKaye et al. 1993) found that genetic analysis could not discriminate unambiguously among species of mbuna (although they cautioned against assuming too much from this based on the fact that biological species may have identical cleavage profiles).

Evidence of cichlid introgression and the existence of geographic isolation seemed to undermine the conclusion that sympatric speciation (especially via the popular mechanism of sexual selection or reproductive isolation) played a role in cichlid radiation; yet, there was also evidence to support the conclusion that sympatric mechanisms were at work in addition to traditional allopatric means. In Turelli et al.'s (2001) *Theory and Speciation*, a convincing general model of sympatric speciation delimiting testable or observable conditions is called for to specify how the process can and cannot occur, especially in the case of reproductive divergence despite continual (but limited) gene flow. Much work in cichlid research in the 1990s and beyond attempted to answer this call, particularly by examining sexual selection and reproductive isolation mechanisms.

Many studies focused on the issue of recognition in sexual selection, since any system of recognition of a proto-species might contribute to speciation and reduce interspecific breeding. Jennifer Holder (1991) argued that the high possibility of hybridization due to overlapping physical regions in cichlids should encourage behavior that distinguishes between species. She showed that in monogamous cichlids, visual and chemical cues are needed to recognize species in the absence of behavioral cues, supporting Baylis' "multiplicity of cues" hypothesis. Similarly, Kenji Karino (1997) showed that the size of the castle/bower does not matter in mate selection, implying that different bower types function as cues in species recognition for reproduction. Supporting the idea that mate selection is cued by a variety of factors, Phillip Lobel (1998) found that Malawi lekking cichlids use vocalizations to approach females but their exact role in communication or mate assessment is still unknown. Balshine-Earn and Lotem (1998) found that *N. pulcher* from Tanganyika recognized a video image of her mate (1998). Paterson (1993) proposed the specific mate recognition system (SMRS) for conspecific reproduction as a solution to this problem.

The strongest evidence for sympatric speciation comes from examples of incipient speciation involving sexual selection. Adaptation of sensory and signaling systems to local environmental signal transmission conditions can cause speciation when the sensory or signaling systems affect mate choice, a phenomenon known as "Sensory drive speciation." Seehausen et al. (1998) demonstrated that sympatric populations living at different water depths evolved different male breeding coloration, undergoing divergent evolution in visual pigments and adapting to local light. Mairi E. Knight and George F. Turner (2004) found that lab mating trials indicate incipient speciation by sexual selection among *P. zebra*, in which females show preference for different male courtship colors that are indicative of their own geographic region. Elisabeth Martin and Michael Taborsky (1997) found that *P. pulcher* red males are monogamous or haremic, while yellow males are only monogamous, a contrast in mating style accompanied by behavioral differences in territoriality. Red males were found to produce three times the offspring, while yellow "satellite" males might occasionally equal "Red" fitness by sneaking (the first time for any animal a reproductive equivalency of fitness has been shown for sneaking compared to conventional means). Despite these examples of incipient speciation, color may not always be a key factor. By contrast, Barlow (1998) showed that coloration played little role in speciation among substrate brooding species in Central America.

Morphology, physiology, behavior, and genetics are all important factors in identifying a species and determining its evolutionary relationship to other organisms. Once the theory of evolution gained sufficient acceptance, all these traits could be seen as randomly varying within a population, with selective pressures determining how alterations in form over time might allow organisms to function in new and adaptive ways, thus driving reproductive isolation and speciation. The late twentieth century generally continued to see the study of relationships between cichlid species shift to molecular genetics, but our modern endeavors to classify organisms have never entirely caught up to this shift. Researchers continue to grapple with the possibility that, if we are observing evolution in action rather than a static set of species as would have been assumed in the early years of the naturalist tradition, we may be confounding pattern with process. At the same time that genetic studies were ascendant in cichlid systematics (i.e., from the late twentieth century on), an emerging body of work conducted in Iceland tackled the problem from outside the world of cichlids by examining polymorphisms (phenotypic diversity such as different morphs of forms) within a single species: the Arctic charr, *Salvelinus alpinus* (Jonsson et al. 1988). This approach reduces the analysis to the ultimate contrast with African Great Lake cichlids by selecting Icelandic lakes with only a single model species. The hypothesis is that if we can understand the origin of sympatric polymorphism in Arctic charr, then we can extend that mechanism to the origin of cichlid species (Kapralova et al. 2011).

As many as four morphs of *S. alpinus* occupy different habitats in one landlocked lake, separated by trophic specializations and reproductively isolated from each other (Skúlason et al. 1996). These morphs differ substantially in appearance (especially with regard to the anatomy and physiology of feeding) but are conspecific by some definitions (Skulason et al. 1989). Life history differences among morphs appear to be partly genetically based (Skúlason et al. 1996), some differences possibly being controlled by a single locus, with phenotypic plasticity playing a proximate role (Smith and Skúlason 1996). Further, it has been shown that the four morphs exist at differing levels of phenotypic and genotypic segregation, with one morph completely reproductively isolated despite all morphs in question sharing an intralacustrine origin (Gislason et al. 1999).

It has been suggested that the evolution of resource-based polymorphisms is driven by flexible behavior (especially related to trophic adaptations) in the early phases with morphological divergence occurring as speciation advances. Studies have shown that in some fish species the evolution of sympatric morphs occurs locally, following postglacial invasions of common ancestors (Snorrason and Skúlason 2004; Kristjánsson et al. 2011, 2012). Evidence has mounted in favor of sympatric trophic polymorphism as a viable explanation for this diversity (Noakes 2008).

Contemporary and recent patterns of restricted gene flow have apparently been conducive to the evolution and maintenance of adaptive genetic variation of *S. alpinus* (Kristjánsson et al. 2011). These and other similar studies have added to the argument that, in cases where phenotypic diversity seems related specifically to resource acquisition in the absence of clear physical barriers (as is the case with many African cichlids), different trophic conditions might be driving speciation within a population, visible first as the increasing diversification of resource polymorphisms (i.e., stable phenotypes sensitive to environmental selective forces) within a species. The broader application and interpretation of these hypotheses of intraspecific polymorphism and speciation appear to be a likely area for our understanding of cichlid evolution.

4.4 Looking Back and Moving Forward

The field of cichlid research has changed dramatically in the more than 250 years since the family's first appearance in Linnaean taxonomies. Whereas the 1880s saw fisheries operations in colonial holdings such as Africa take root, the 1980s saw those enterprises at the height of a drastic expansion that changed both the lakes and surrounding areas. In 1880, national natural history museums devoted kingly sums to collecting and categorizing species that were entirely new to the Western science, and by 1982, Kullander determined in his revision of South American cichlasomines that, in fact, some of these groups had existed since at least the Tertiary Period. At the same time that they were discovered to be ancient in South America, cichlids were discovered to be startlingly young in Africa; in 1982, Cromie suggested that Lake Malawi could be only 100,000 years old.

We continue to live in a time of great discovery in cichlid research. About 400 species have been described from Malawi, and between 450 and 500 additional suspected species have been collected, photographed underwater, or both, but remain undescribed. Visits to any remote, rocky shore still produce new discoveries, as do deep-water trawls in unsampled areas. In 1996, Ole Seehausen discovered that, despite its ecological devastation, Lake Victoria still retains a previously unknown group of rock reef cichlids that evaded the extensive predation of Nile perch. Seehausen produced a book on the ecology of this recently discovered flock of nearly 100 colorful rock-dwelling "Mpipi" cichlid species in Victoria, a diversity rivaling the mbuna of Malawi. Many river systems are still unexplored and information on little known cichlids is scattered in aquarium literature, reports, and collections made over a wide area.

Just as surely as many species remain to be discovered even in the twenty-first century, there are many avenues of research just opening up for exploration. Cues like olfaction and sound were left largely unexamined even in the 1990s, with Barlow's study of the effects of acoustic signals between cichlids being the first to catalogue the relatively rich sonic repertoire of some cichlids from a young age. Another line of inquiry concerns interspecific dominance hierarchies, examined by Andries and Nelissen (1990), a new area of research emerging in the late 1980s. The study of energetics in relation to mating systems is yet another research program that is still in its infancy and might be expanded.

Cichlids have been increasingly hailed as model species for the study of evolutionary biology (Kornfield and Smith 2000). However, despite the current importance of developmental biology, there are few programs using cichlids, though their availability (depending on species), great diversity, and ease of raising and observing make them ideal candidates. Significant advances in the understanding of cichlid taxonomy and systematics could be combined with ontogenetic study and life history. Comparative behavioral studies in development could have implications for the role of behavioral ontogeny in evolution writ large. Even though much work has been done on the subject of cichlid speciation, each species has a unique combination of ecological attributes that might serve a variety of functions in speciation, and the precise mechanisms by which these have allowed for niche segregation in the Great Lakes of East Africa remain unknown. On the other hand, the problem of distinguishing between known species continues to require more attention. In contrast to significant efforts on cichlid supraspecific classification, for example, very little has been published on the technical problems of haplochromine species distinction. Possibly in response to this inadequacy, there has been a return to the collections tradition in modern cichlid fieldwork. Researchers like Ad Konings (2011) have exhumed the original museum collections specimens from centuries past to reclassify known species and reconsider existing phylogenies according to new knowledge of these animals, some of which are now extinct. Neither is it the case that the "old ways" ever entirely left us. Indeed, the connection between cichlid research and ichthyology in the more traditional sense (systematics and specimen collection) has been retained in many ways, perhaps due to the ongoing central importance of cichlid classification in the study of this family of fishes. Melanie Stiassny, as just one example, continues to act as Curatrix of Ichthyology at the American Museum of Natural History.

Although much has changed in 200 years of cichlid study, those who pioneered it and those who study cichlids today have a great deal in common. Separated by vast amounts of time they are nonetheless bound together by a common interest to determine the place of things—a sense for the "order" of organisms, so critical to natural history—a question that remains despite the myriad scientific discoveries and advances of our present day. It is a question that is unanswered not because the study of cichlids has failed to progress, but because with each question answered, ever more curiosities arose. Inquiries into the deceptively simple question of cichlid history are branching and radiating, like the specializing fields of cichlid research that endeavor to arrive at a solution. Like the rapidly evolving cichlids themselves, they are multiplying—spreading out, changing, adapting and becoming unique—yet they remain inextricably related. It is because the subjects of cichlid research are so diverse, complex, and fascinating that they have taken us centuries to scratch the surface. Our understanding of their behavior and biology now fills volumes, yet the origin of so many species in a span of time so short remains a mystery.

One is struck by the sensibility of the dilemma. If the answers were easy, we would have them already! The complexities of biological evolution—genetic, behavioral, and environmental—demand a more holistic, yet simultaneously a more precise, understanding. This is a combination we still find elusive. In time, as we continue to watch cichlids evolve, perhaps they will enter the history books as another scientific triumph (a chapter easily closed). Or perhaps not. Perhaps new species will still be found. Perhaps aquarists at home will call scientists at universities and reveal tidbits of cichlid behavior that are still surprising. Perhaps it will require hundred more years of work with these animals only to realize what we are just beginning to learn: That we are still standing on the frontier, and the pioneers of cichlid research are not consigned to dusty tomes. They are remembered, they are in the field and in the lab, and they are preparing a new generation to embark on voyages of discovery that have not yet been written.

Acknowledgments Regrettably, much valuable information is left out of a brief history spanning over two centuries. To adequately cover the work of the professional men and women and supporters outside academia who have been instrumental to the advancement of cichlid studies would be a much larger project. It is my hope that this introduction might serve as a resource for future endeavors. Without the guidance and help of Michael Osborne, Anita Guerrini, David Noakes, Maria Abate, and Tori Spence, this would not have been possible.

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Ecological Opportunity, Genetic Variation, and the Origins of African Cichlid Radiations

Catherine E. Wagner

Abstract Genetic and genomic data for African cichlids have accumulated over the past decades along with an increase in data available on the composition and species richness of cichlid communities in African lakes. Increasing availability of both of these kinds of data allows us to begin asking questions about macroevolutionary drivers of repeated cichlid adaptive radiation, about the factors that influence the diversity of cichlids that coexist within lake communities, and about the genetic underpinnings of adaptive radiation as a process and the ecological conditions conducive to it. I here survey what is currently known in both the genetic and the ecological realm, and point to key unanswered questions that should remain a focus of research in the coming decades as we seek to integrate genomic work with the ecology of cichlid adaptive radiation.

Keywords Adaptive radiation · Speciation · Hybridization · Diversity-dependent diversification · Genomics · Species richness

1 Introduction

The large cichlid radiations of the East African Great Lakes Tanganyika, Victoria, and Malawi have long been the primary focus of cichlid research (Fryer and Iles 1972). The sheer number of species described from these lakes, plus the remarkable convergent evolution of specialized ecological phenotypes across independent radiations, has drawn scientists to study these fishes since their discovery. However, the past decade has seen tremendous growth in studies that move beyond the diversity and biology of the Great Lakes radiations. Studies have sought to understand the origins of the large radiations in the context of their ancestry and relatedness to riverine fish (Genner and Turner 2012; Joyce et al. 2010; Meier et al. 2017), and

C. E. Wagner (✉)
Department of Botany, University of Wyoming, Laramie, WY, USA
e-mail: catherine.wagner@uwyo.edu

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have examined larger-scale patterns of cichlid diversity in lakes across the African continent (Wagner et al. 2012, 2014). Coincident with this work has been a revolutionary change in the genomic resources available for cichlids (Brawand et al. 2014), the nature and scale of genetic data we are using to address questions about the history of species and radiations (e.g., Keller et al. 2013; Wagner et al. 2013; Malinsky et al. 2015; Poelstra et al. 2018; Meier et al. 2018), and the analytical approaches available to analyze rich genomic data. These resources and tools have opened vast new windows into details of the history of these fishes that were previously unattainable, and these technical advances are continuing with great rapidity.

I here review the developments of recent work on the history and diversity of African cichlid radiations, with a focus on the factors that have come to the forefront as the primary predictors of African cichlid diversity, and the evolutionary processes that have been implicated in producing those patterns. I follow that with a discussion of genetic and genomic work illuminating the history of cichlid radiations, and the history of species within these radiations, with greater clarity than has previously been possible. The role of spatial genetic structure has a long history of discussion in the context of cichlid speciation, and I discuss current knowledge pertinent to understanding links between microevolutionary patterns within species and diversity at macroevolutionary scales. I conclude with a discussion about integrating the ecological and genomic aspects of cichlid diversification for a holistic view.

2 What Predicts Cichlid Adaptive Radiation and Diversity?

Along with the large (200–500 species) adaptive radiations of Lake Tanganyika, Malawi and Victoria, cichlids have undergone endemic diversification in many lakes across Africa, ranging from the sister species pairs in crater Lake Guinas in Namibia, to the radiations in West African crater lakes (Stiassny et al. 1992; Dunz and Schliewen 2010). Additionally, many cichlid species have failed to speciate and diversify within lakes after successful colonization (Wagner et al. 2012; Seehausen 2006). This has produced a mosaic pattern of cichlid diversity in freshwater lakes across Africa, some of which have no in situ diversification, others of which have multiple lineages of cichlids that have diversified together within the same lake (Fig. 1).

Wagner et al. (2012) took data on the presence or absence of cichlid diversification across a large set of lakes to ask what extrinsic (environmental) and intrinsic (trait-based) factors predict whether or not cichlid adaptive radiations happen. Three predictors of cichlid radiation were consistent across a variety of analytical approaches: lake depth, energy (measured as net solar radiation), and the presence or absence of sexual dichromatism (Wagner et al. 2012). This broad-scale predictive approach is useful for both placing our previous knowledge of the factors important to cichlid speciation on a broader macroevolutionary scale, and also for generating new hypotheses about factors influencing speciation and diversification. In this way,

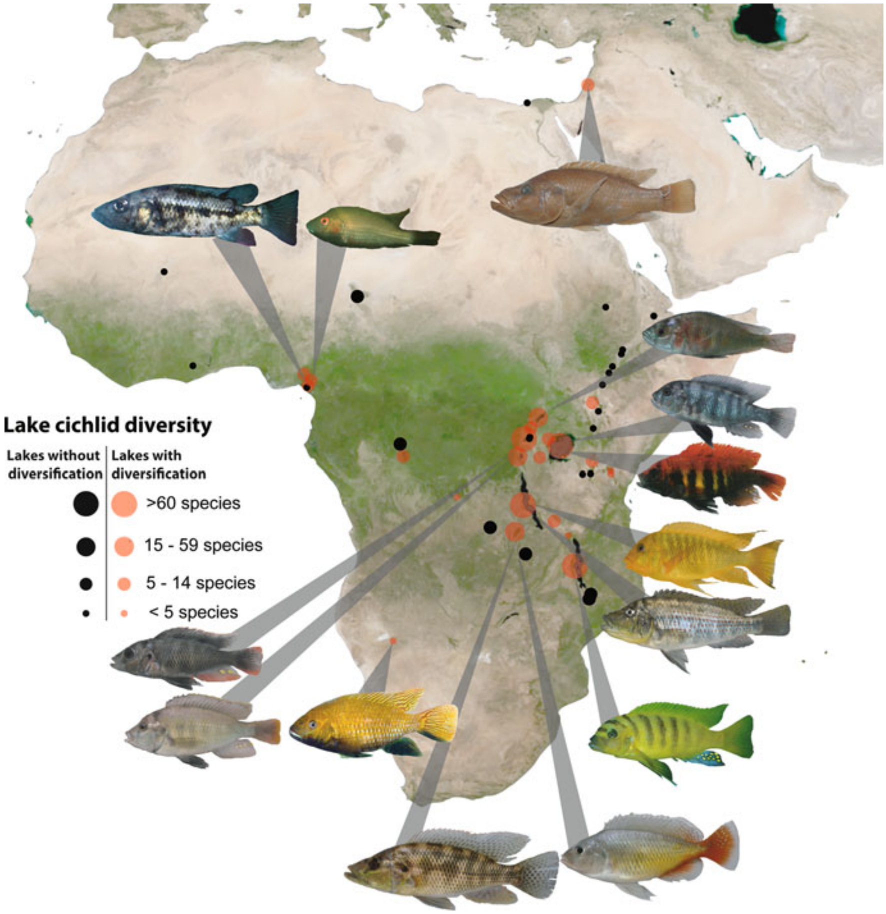

Fig. 1 Cichlid diversification and species richness across African lakes. Lakes vary tremendously in species richness, and whether or not in situ diversification has occurred. Photo credits to O. Seehausen, U. Schliewen, J. Jenson, O. Rittner, and the author

we move closer to understanding mechanisms underlying broad-scale diversity patterns. However, in many ways, this work is a first step, and a greater understanding of the predictability of cichlid radiations will come from studying exceptions to these "rules" of diversification, and to more deeply examining the mechanisms underlying these results. A key part of this additional examination is seeking to understand links between macroevolutionary patterns and speciation mechanisms.

2.1 Making Links to Speciation Mechanisms

For both lake depth and sexual dichromatism, there are strong links between these factors and well-known mechanisms of speciation. Sensory drive is a well-studied mechanism in cichlids wherein sensory bias leads to coupling between natural and sexual selection that can result in speciation (Seehausen et al. 2008; Maan et al. 2006; Kawata et al. 2007). In cichlids, this mechanism relies on depth-driven light gradients that influence the detectability of certain wavelengths. Sensory drive speciation is well studied in Lake Victoria, but its relevance across other lakes is less well established. In particular, the light environment along depth gradients in Lakes Tanganyika and Malawi differs substantially from Lake Victoria, wherein the latter waters are comparatively turbid due to high amounts of dissolved organic material (Levring and Fish 1956). In contrast, Lakes Tanganyika and Malawi have exceptionally clear waters, which has led to skepticism about the efficacy of sensory drive as a mechanism of divergence in Lake Malawi (Smith et al. 2012), an argument that could be extended to Lake Tanganyika due to similarities in water clarity in this lake. Additional studies evaluating the role of light and depth gradients on cichlid coloration and selection gradients in a variety of lake environments are needed. Although sensory drive is one mechanism of speciation linked to water depth, it is not the only plausible mechanism through which depth-adaptation may be important in fostering cichlid diversification. Indeed, the depth-structured distribution of many closely related taxa in a broad range of lakes speaks to the general importance of depth gradients in generating and maintaining cichlid diversity (e.g., Hata and Ochi 2016; Ribbink et al. 1983). In addition to selection gradients related to the light environment, depth-specific physiological adaptations are often necessary because of the physiological challenges associated with pressure changes with water depth (Seehausen and Wagner 2014). Although this has received little study in cichlids (but see Ribbink and Hill 1979), it may well be an important feature leading to selection gradients and speciation. Developing resolved species-level phylogenies of cichlid adaptive radiations will facilitate work examining how often depth transitions happen with speciation, and more broadly within and among clades during intralacustrine cichlid diversification.

In addition to water depth's link to gradients in natural selection that may be linked to speciation, depth may function as a proxy for lake stability because deeper lakes are longer-lived. This stability may then, in turn, foster conditions more suitable for adaptive radiation, or simply allow more time to allow radiations to occur. Lake depth and age are highly correlated across African lakes, making distinguishing between the effects of these factors difficult (Wagner et al. 2012). Although depth better predicts radiation than lake age in data subsets where these factors are not correlated (see supplemental material, Wagner et al. 2012), this does not discount the possibility that older lakes may also be more likely to foster adaptive radiations simply because there has been more time for them to occur. The clearest example of a lake where time has been a crucial contributor to diversity is Lake Tanganyika, which is the second oldest lake in the world at 9–12 million years in age

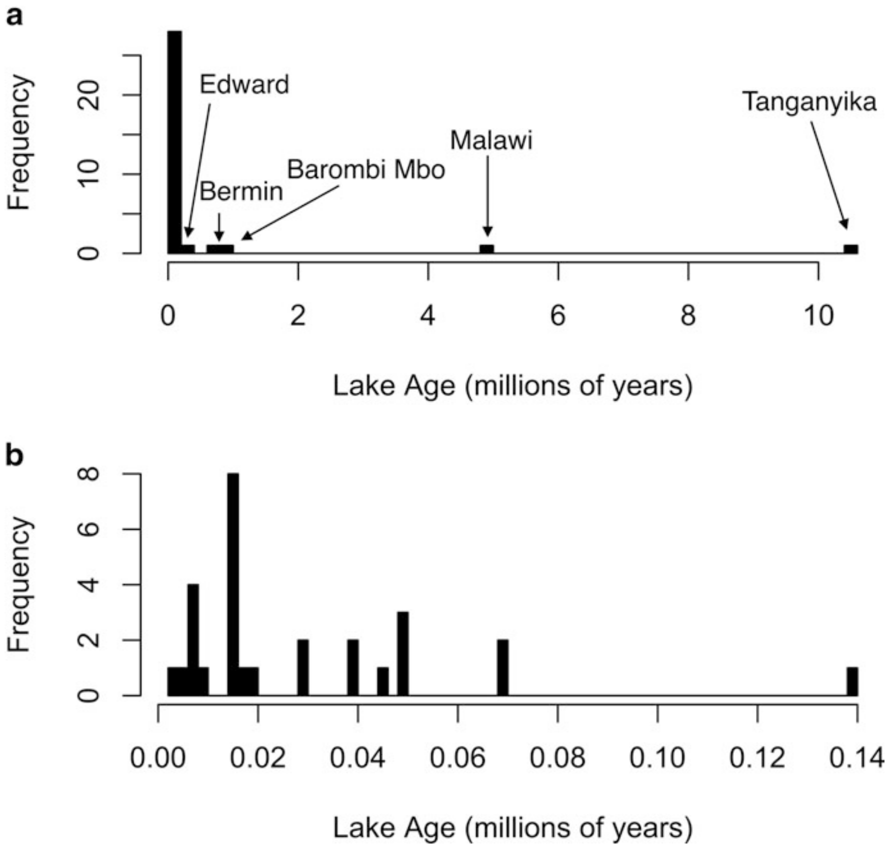

Fig. 2 The vast majority of African lakes in which cichlids live are young. (**a**) Only a handful of lakes, including Lake Tanganyika, Lake Malawi, and Lake Edward (deep lakes in the Western Rift), and Lake Bermin and Lake Barombi Mbo in Cameroon (deep crater lakes), are older than 250,000 years in age, (**b**) whereas the majority of African lake are much younger

(Cohen et al. 1993). Lake Tanganyika's cichlid diversity is much more phylogenetically diverse than most African lakes, with independent radiations in multiple tribes within the lake (Salzburger et al. 2005; Meyer et al. 2015, 2017; Irisarri et al. 2018). This translates into much larger morphospace occupation (i.e., the multivariate space gleaned through analysis of geometric morphometric data that radiations occupy) than Lakes Malawi or Victoria, despite greater species richness in both of these lakes than in Lake Tanganyika (Young et al. 2009). In general, it is important to recognize that the vast majority of lakes are young (Fig. 2). Only a handful of lakes, including Lake Tanganyika, Lake Malawi, and Lake Edward (deep lakes in the Western Rift), and Lake Bermin and Lake Barombi Mbo in Cameroon (deep crater lakes), are older than 250,000 years in age. This age distribution differs markedly from terrestrial environments, where well-known island archipelagos that are home to substantial endemic diversity are generally much older (Galapagos: ~4–0.7 million years;

Hawaii: ~5–0.4 million years). This may imply generally that in comparison to most terrestrial systems, lacustrine cichlids are able to diversify exceptionally rapidly, and time may frequently not act as a constraint on diversity in these systems.

Energy is not a factor that has been considered as a driver of cichlid diversification previously, and its importance in the models in Wagner et al. (2012) allows us to make new hypotheses about why these relationships might exist. Energy is widely studied as an important predictor of macroecological patterns in species richness (Evans et al. 2005; Fine 2015), and the relationship between energy and resource abundances may have important influences on population evolutionary dynamics and speciation (Hurlbert and Stegen 2014). Understanding these links requires additional work. Furthermore, there are large gaps in our understanding of how net solar radiation (as a proxy for energy) actually translates into productivity and/or resource abundance in these lake environments. In some cases, the highest productivity translates into decreases in fish diversity due to the increased turbidity of the water that results (e.g., Seehausen et al. 1997). In other cases, African lakes are capable of paradoxically high productivity despite high water clarity through exceptional rates of benthic primary production (e.g., Tanganyika; Coulter 1991). Because of the complex and diverse limnology of these lakes, further research linking general patterns of solar radiation to influences on the resource environment are needed.

It is also interesting to consider factors included in the Wagner et al. (2012) study that did not produce consistent positive effects but are thought to be important in cichlid adaptive radiation. One of these is the lake area. Abundant evidence exists for speciation mechanisms involving geographic divergence within large lakes. This includes frequent allopatric distributions of closely related taxa in large lakes (Genner et al. 2004; Koblmüller et al. 2011; Egger et al. 2007), as well as strong spatial genetic divergence over short geographic scales in many cichlid species, particularly rock-dwelling species in large lakes (e.g., Wagner and Mccune 2009; Sefc et al. 2007; Danley et al. 2000; Arnegard et al. 1999) (see Sect. 3.3 below). However, increased lake size does not positively influence the probability of cichlid radiation (Wagner et al. 2012). This is clear evidence that cichlid speciation mechanisms can operate at very small scales, and that large geographic areas are not a prerequisite to adaptive radiation the way they are in other adaptive radiations (Losos and Parent 2010; Losos and Schluter 2000). This makes cichlids an exception among most adaptively radiating taxa.

2.2 *Predictors of Species Richness of African Lake Cichlid Assemblages*

A full understanding of cichlid diversification would involve understanding both the mechanisms underlying the formation of new species and how these speciation mechanisms contributed to broad-scale patterns in diversity. Because species persistence and extinction, in addition to speciation, also contribute to realized patterns of species richness (Rosenblum et al. 2012), the extent to which understanding speciation mechanisms may help us to understand patterns in species richness is an open question. One important point is that the primary predictor of species richness in cichlids in African lakes is surface area (Wagner et al. 2014), a factor which was generally not predictive of whether or not cichlid adaptive radiations occurred (discussed above; Wagner et al. 2012). This underscores the point that factors related to the origins of adaptive radiation may be fundamentally different from those determining how many species evolve in an adaptive radiation.

Wagner et al. (2014) studied species richness in African lakes and found a positive and nonlinear species–area relationship (Fig. 3a), similar in form to what had previously been documented in *Anolis* lizard assemblages on Caribbean islands (Losos and Schluter 2000). Evolutionary species–area relationships may be driven by two distinct evolutionary processes: (1) the positive relationship between area and species richness could result from a relationship between diversification rate and area; (2) area could be a limit to the number of species that evolve, thus creating a relationship between species richness and area that is independent of diversification rate. Unlike in *Anolis*, the positive and nonlinear species–area relationship in cichlids is not driven by the onset of speciation in lakes of large geographic areas, because cichlids form endemic species even in very small lakes. In addition, there is no clear relationship between diversification rate, as calculated from clade age and species richness, and lake surface area (Fig. 3b), indicating that the species–area relationship is not driven simply by increased diversification rates in larger lakes.

Diversity-dependent diversification models posit that the diversification of a clade is dependent on diversity already present in that clade. If the form of diversity dependence is negative, where speciation rates slow as species accumulate, this will lead to a slowdown in diversification rates through time. The concept of diversity-dependent diversification presents a problem for commonly used estimates of diversification rate that assume that rates are constant through time. If rates vary through time and this variation is related to clade age, the rates we measure while assuming that diversification rates are constant will be wrong (Rabosky 2009).

Whether diversification is commonly diversity-dependent or not, and what mechanisms might drive these relationships, has been a subject of frequent debate in recent years (Rabosky and Hurlbert 2015; Harmon and Harrison 2015). Although many disagree with the concept of diversity-dependent diversification because it necessitates assuming a "limit" or clade-level carrying capacity to diversification, what is less frequently appreciated is that equilibrium in these models reflects a balance between speciation and extinction, which is distinct from the carrying capacities assumed by these models. This speciation–extinction balance may lie well below the carrying capacity (Fig. 3c), particularly when extinction is non-zero. Thus, although the existence of a carrying capacity influences the change of speciation and/or extinction rates as species richness of the clade increases, this carrying capacity does not necessarily set the equilibrium species richness in the system. Cichlids are an intriguing example for which to consider diversity-dependent diversification as a process influencing the evolution of species richness, because

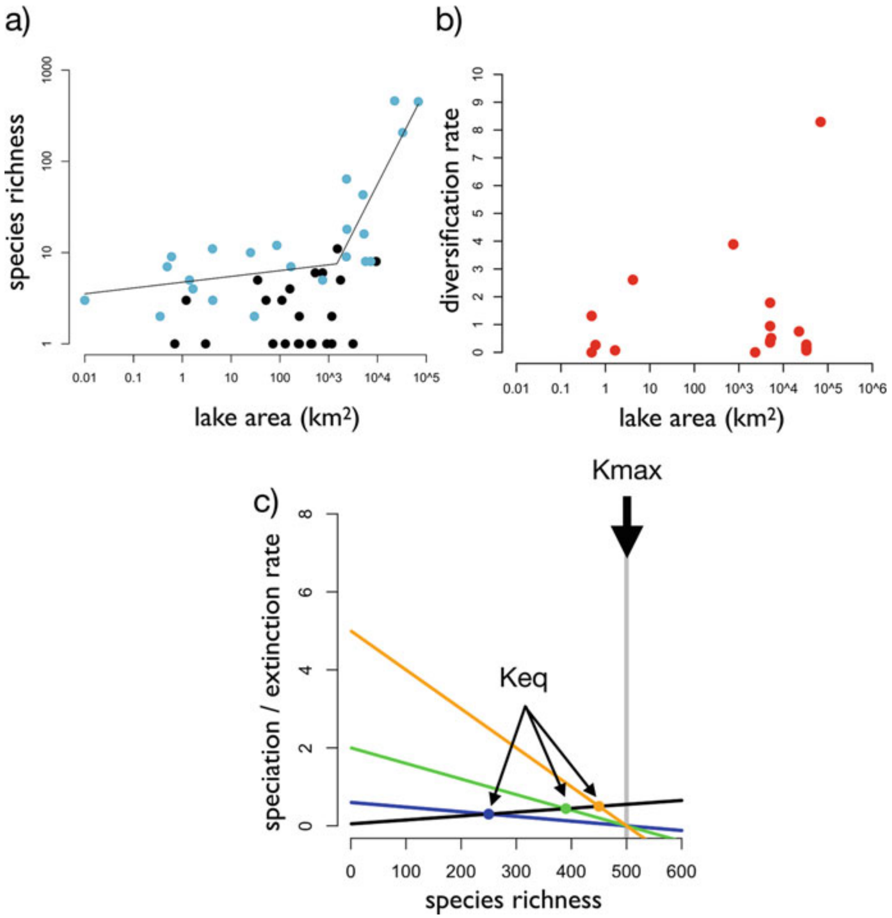

Fig. 3 The species–area relationship for cichlids in African lakes is strongly impacted by in situ speciation (**a**), where blue dots indicate lakes with in situ speciation and black dots indicate those lakes assembled only by dispersal. Despite this positive relationship between species richness and lake surface area, there is no relationship between diversification rate and area (**b**), indicating that the positive species–area relationship cannot be explained by differences in diversification rate in lakes of different areas. Although this finding is consistent with expectations for diversity-dependent diversification, it is important to recognize that diversity dependence reflects a balance between speciation and extinction (K_{eq}, (**c**)), and does not necessitate that clades are at a theoretical carrying capacity ($K_{\max}$, (**c**)). Panel (**c**) depicts three hypothetical diversity-dependent speciation rates (orange, green, blue) and one hypothetical extinction rate (black)

diversification rates vary dramatically across clades and lakes (Fig. 3b), and yet species richness is predictable by area (Fig. 3a).

Future work should continue to examine cichlid diversity in light of predictions of diversity-dependent models. As species-level phylogenies become available with the increasing ability of genomic data to resolve such relationships, explicit phylogenetic tests of diversity dependence will become possible (e.g., Etienne et al. 2012).

Cichlids are a case, however, where particular attention needs to be paid to the community context of diversification and how this may influence the assumptions of such models. The focus of these tests is on a single clade, whereas our predictions based on species richness patterns in African cichlids would lead us to hypothesize that clade diversification dynamics are dependent not only on the focal clade's diversity but also on the diversity of other sympatric cichlid lineages. A limitation of current phylogenetic models, and phylogenetic comparative methods in general, is the difficulty of fitting models involving interactions among multiple clades (Weber et al. 2017).

One recent development in understanding details of the community context for cichlid diversification is using fossils in lake sediment cores to understand when different cichlid lineages colonized Lake Victoria (Muschick et al. 2018). This work shows that although haplochromine cichlids are the only group to have dramatically diversified within the lake (Wagner et al. 2012), other lineages were present in the earliest sediment records from the lake's history. Specifically, there are tilapiine cichlids in these early records from just after the lake's refilling post-desiccation 15,000 years ago, as well as cyprinids (Muschick et al. 2018), yet neither of these groups has diversified in Lake Victoria, even though both of these groups have formed species flocks elsewhere in Africa. Although this finding does not negate a potential role of species interactions and priority effects influencing cichlid diversification, it clarifies that the clear dominance of haplochromines in diversification rate is not simply due to lack of competition from these other lineages.

3 The Origins and Maintenance of Genetic Variation in African Cichlids

A major challenge in evolutionary biology is to link our understanding of processes at macroevolutionary scales with processes at microevolutionary scales. Although this is an easily stated goal, it is an incredible challenge due to the fundamentally different scales at which we typically study these processes. In macroevolution, we focus on broad-scale patterns across clades and regions; in microevolution, the focus is typically on one or at most a few species. The thought of collecting sufficient microevolutionary data, for example, intraspecific population genetic data, to make inferences about how these processes influence whole clades and radiations, is daunting, and until recently, frankly impossible—it was not possible to collect sufficient microevolutionary data to fully inform macroevolutionary questions. However, the advent of new DNA sequencing technologies over the past ~10 years (e.g., Baird et al. 2008; Davey et al. 2011) has fundamentally changed the landscape of possibilities as we are able to readily collect enormous amounts of genomic data for many hundreds of individuals. These new technologies open new possibilities for bridging work in micro- and macroevolution that have previously been unattainable.

3.1 Genomic Data Facilitate Major Advances in Understanding Cichlid Evolutionary History

Due to the limitations of large-scale comparative analyses, Wagner et al. (2012) exclude many factors that undoubtedly influence cichlid adaptive radiation. One major area that is not addressed is emerging data on the genetic underpinnings of cichlid radiation. The details of cichlid evolutionary history have proven difficult to study using traditional genetic markers due to the rapidity of evolution in many clades. Early work using mitochondrial DNA data was foundational in establishing the monophyly of cichlid radiations, thus demonstrating that these groups were formed in situ within lakes rather than through complex dispersal processes among lakes (Meyer 1993; Meyer et al. 1990). However, mitochondrial DNA, or even a number of nuclear loci, is not useful for resolving relationships among species in rapid cichlid radiations (Streelman et al. 1998; Nagl et al. 1998; Koblmüller et al. 2010).

The attainability of genome-wide DNA sequence data has revolutionized the kinds of analyses possible in these rapid adaptive radiations. An early example of the utility of large numbers of genome-wide data came from reduced-representation genome sequencing approaches (e.g., RADseq; Baird et al. 2008) in Lake Victoria cichlids. Wagner et al. (2013) showed that when using large numbers of genomic loci (2–6 million base pairs of data, including invariant sites), Lake Victoria cichlid species form strongly supported monophyletic groups, and internal branches also have strong support. Importantly, the focal individuals in the study were all collected at a single geographic site (Makobe Island), making it clear that the genetic differences observed were not due to geographic divergence alone. These analyses simply used concatenated sequence data, and phylogenetic analyses which assume a bifurcating evolutionary history; it is unclear whether the reconstructed topologies primarily reflect evolutionary history or other processes known to influence phylogenetic reconstruction (e.g., introgression, selection). However, these results make clear the power that large amounts of genomic sequence data hold to address complex questions involving the evolutionary history of rapid adaptive radiations.

An increasing number of cichlid studies are using genomic data to address questions about details of the history of particular cichlid adaptive radiations. Studies using genomic data have been facilitated greatly by the publication of five annotated cichlid reference genomes spanning the African cichlid phylogeny (Brawand et al. 2014), and subsequent work improving these assemblies has made these resources even more valuable (Feulner et al. 2018; Conte et al. 2017, 2019; Conte and Kocher 2015). These reference genomes have enabled work using whole-genome resequencing data, and work linking patterns of genomic divergence to functional genomic information. For example, Malinsky et al. (2015) studied divergence between two haplochromine ecomorphs in crater Lake Massoko in Tanzania using whole-genome data from 146 individuals, and identified candidate genes with functions they hypothesize are linked to incipient divergence in regions of the genome that are differentiated between the ecomorphs. Likewise, Meier et al.

(2018), Poelstra et al. (2018), and Richards et al. (2018) used whole-genome data from Lake Victoria *Pundamilia,* Lake Ejagham *Coptodon*, and Barombi Mbo cichlids, respectively, and identified genomic regions that have been involved in divergence among closely related species. Additionally, Malinsky et al. (2018) studied whole genomes from 73 Malawi cichlid species and found low levels of genomic divergence and evidence for relatively extensive gene flow throughout much of the history of diversification of this group, and evidence for both parallel and unique selection on genes thought to underlie adaptation to deep water. Detailed studies of early stages of species divergence are a model for understanding genomics of the speciation process. Furthermore, as whole-genome sequence data accumulates, we are increasingly able to study questions of genomic divergence at the scale of entire cichlid radiations, and thereby dig much deeper into the history and ancestry of these groups. Genomic data are allowing us to study these processes more readily than ever before.

3.2 The Maintenance of Genetic Variation During Adaptive Radiation

One long-standing paradox in the theory of adaptive radiation is how genetic variation is maintained in the face of the strong natural selection that would be expected during adaptive radiation. If selection continually depletes genetic variation, how could speciation happen in such rapid succession from a single common ancestor? Particularly for cichlids, in which some adaptive radiations have truly exceptional diversification rates (Rabosky et al. 2013), how is it possible to evolve so many species so quickly without genetic variation being depleted to such an extent that further diversification is not possible?

In response to this paradox, one hypothesis for cichlids was that exceptionally fast mutation rates might increase genetic variation and facilitate more rapid diversification relative to other taxa (Salzburger 2018). However, genomic data clearly show that mutation rates for cichlids are not exceptionally fast, nor do they have other genomic properties that clearly predispose them to exceptional evolution (Brawand et al. 2014; Salzburger 2018).

3.2.1 Hybridization and Adaptive Radiation

A second hypothesis to address the paradox of how adaptive radiation proceeds without depleting genetic variation involves hybridization. Although the concept that hybrid ancestry might contribute to the rapidity and extent of adaptive radiation is not new (Seehausen 2004), new genomic tools are allowing tests of these hypotheses that have much greater power than was allowable before genomic data became readily available. Hybridization and subsequent introgression may contribute to adaptive radiation in two distinct ways, through "hybrid swarm origins," where hybridization prior to adaptive radiation influences its occurrence and outcome, and through the "syngameon hypothesis," where hybridization between members of a radiation facilitates speciation (Seehausen 2004). Both of these ways in which hybridization may contribute to adaptive radiation have now been documented in cichlids and increasingly these processes are being invoked as a key mechanism in understanding cichlid diversification. In addition to simply infusing new genetic variation into populations, hybridization may function as a facilitator of adaptive radiation because these variants have already been initially "screened" by selection when they arose and thus strongly deleterious mutations have been purged, they occur in higher frequency than new mutations and thus are less likely to be lost to drift, and they may occur in linkage disequilibrium with other variants that could facilitate large jumps in fitness when arriving in a new genomic context (Marques et al. 2019). Given that many cichlids can produce viable and fertile hybrids in species that are up to 10 million years divergent (Stelkens et al. 2010), hybridization may have been an important feature of cichlid evolution and diversification in general. As cichlid lineages have been separated and reunited as the hydrology of Africa has shifted over the past millions of years, there have been many opportunities for contact between divergent lineages.

One recent example of hybrid swarm origins of adaptive radiation is particularly intriguing for making a case that hybridization has been crucial in providing functional genetic variation that facilitated adaptive radiation. Meier et al. (2017) show that the radiations in the Lake Victoria region (the Lake Victoria Region Superflock, or LVRS) originate from an admixed ancestral lineage composed of both Nilotic and Congolese cichlid origin. Although showing hybridization prior to the onset of radiation is a first step toward testing a hybrid swarm origins hypothesis, a complete test of this hypothesis requires evidence that the variation attained from the hybridization event is functionally relevant and important to diversification in the adaptive radiation. Meier et al. (2017) show that SNPs (single nucleotide polymorphisms) derived from the hybridization event are more likely to show evidence for selection when examining evidence for selection on SNPs across the genome. In addition, LWS opsin, a well-studied gene underlying visual acuity in different light environments (Seehausen et al. 2008), shows evidence that two major allele clades present in the LVRS are derived from the hybridization of the two divergent lineages prior to adaptive radiation (Meier et al. 2017). This clearly links hybridization with its functional consequences in cichlid adaptive radiation.

Other cases with evidence for hybridization prior to the origin of cichlid adaptive radiations include evidence in both Nicaraguan crater lake cichlids (Kautt et al. 2016) and West African tilapiine cichlids (Poelstra et al. 2018) that intermittent admixture with the lineage that initially colonized the lake provided genetic variation to the emerging radiation. Additionally, evidence from Tanganyikan cichlids shows several major episodes of introgression between divergent tribes present in the lake (Irisarri et al. 2018; Weiss et al. 2015; Meyer et al. 2017), and between riverine lineages and early-radiating Tanganyikan tribes (Irisarri et al. 2018). However, in all of these cases further work is required to show that this admixture provided functionally relevant variation to the radiation. Poelstra et al. (2018) provided evidence that alleles related to olfactory function were derived from this introgression event, hinting at the possibility that the introgression did have functional consequences. Likewise, Irisarri et al. (2018) showed that introgression involved several interesting candidate genes, and other analyses show evidence for positive selection on classes of genes associated with vision and jaw development, yet it remains unclear in how many cases strong signals of introgression coincide with evidence for positive selection on those genes. Irisarri et al. (2018) also relied on a panel of candidate genes rather than conducting their analyses on whole-genome data; these patterns will be fascinating to test with whole genomes.

There is also clear evidence for hybridization among species within an adaptive radiation, including some evidence that these episodes of introgression may facilitate evolution as predicted by the syngameon hypothesis. This facilitation may be through the transfer of adaptive alleles to facilitate subsequent adaptive evolution that leads to speciation, or it could be through the occurrence of hybrid speciation directly, where a hybrid breeds endogenously and become a new species through reproductive isolation from the parental lineages (Schumer et al. 2014; Buerkle et al. 2000). Some evidence exists for both of these mechanisms in cichlids. Meier et al. (2017) show that in Lake Victoria's *Pundamilia,* red-blue species pairs that were previously thought to be geographical replicates of the same two species are actually a case of repeated divergence into red and blue forms, facilitated by introgression. Specifically, demographic modeling shows evidence that the red species from the first island was admixed with the blue species from the second island, prior to the divergence of the population at the second island into blue and red species. Additional work looking at patterns of divergence across the genome confirms the highly distinct evolutionary histories of these two species pairs, despite their morphological similarities (Meier et al. 2018). Alleles derived from introgression are likely to have been instrumental in the ability of the second red species to rapidly diverge. This case is an excellent example of how genomic data, and the evolutionary inferences that these data make possible, is fundamentally changing our understanding of cichlid diversity.

Recent evidence of introgression among major divergent lineages within adaptive radiations also suggests a role for hybridization in facilitating adaptive diversification. Such patterns have been noted in the major radiations in Lakes Malawi and Tanganyika (e.g., Irisarri et al. 2018; Meyer et al. 2017; Weiss et al. 2015; Genner and Turner 2012; Malinsky et al. 2018), as well as in smaller radiations, like the tilapiine radiation of hypersaline Lake Natron (Ford et al. 2015). Although introgression is clear from phylogenetic and population genetic work in these systems, additional work is needed to show the functional consequences of these within-radiation introgression events. Furthermore, better localizing these hybridization events using newly available genomic methods will be important to understand their impacts on diversity and diversification trajectories.

Hybrid speciation has frequently been suggested in cichlids, with evidence for this process in some examples (Salzburger et al. 2002; Keller et al. 2013; Schliewen and Klee 2004; Sefc et al. 2017). Experiments with behavioral mate choice in Lake

Victoria cichlids demonstrate the possibility for assortative mating among hybrids under some circumstances (Selz et al. 2013), which might provide a mechanism for reproductive isolation of hybrid lineages despite sympatry with one or both parental lineages. In addition, transgressive segregation is common in hybrid cichlids (Albertson and Kocher 2005; Stelkens et al. 2008, 2009), and more extreme in more phenotypically divergent crosses (Stelkens and Seehausen 2009). If transgressive hybrids also have ecologies that are divergent from parental species, this may facilitate coexistence among them, when reproductive barriers are also present (Kagawa and Takimoto 2017; Seehausen 2013). In other cases, strong barriers to dispersal might act to physically separate hybrids from the parental species (Sefc et al. 2017); however, in this case, reproductive barriers would have to evolve in order for the hybrid taxa to return to sympatry with parental taxa and build sympatric diversity. Many other examples of hybridization among extant members of cichlid adaptive radiations exist (Streelman et al. 2004; Egger et al. 2012; Seehausen et al. 1997; Nevado et al. 2011), but there is limited clear evidence that these hybridization events played a functional role in cichlid diversification. Indeed, most examples of hybridization are thought to be detrimental to species integrity, and can lead to lineage extinction and decreases in species diversity, and this may well be the case for most instances of hybridization in cichlids (Seehausen et al. 1997). Investigating how often hybridization with cichlid adaptive radiations might be facilitative, relative to how frequently it erodes species diversity, should be a focus of ongoing research.

3.2.2 Incomplete Lineage Sorting

Although abundant evidence now exists demonstrating historical introgression in cichlids, and invoking introgression as an important means of maintaining genetic variation, we know little about when evolution in cichlids is truly constrained by limited genetic variation. Incomplete lineage sorting (ILS), where lineages share polymorphisms inherited from common ancestry long after divergence, also contributes to patterns of allelic sharing among species, particularly in situations where speciation has happened in rapid succession (Degnan and Rosenberg 2009), as in many cichlid adaptive radiations. Brawand et al. (2014) showed that for the three haplochromine cichlid species sequenced as part of the cichlid genome project, more than half of the sites supported topologies that conflict with the well-accepted species tree. It is important to note that the focal species in this study, *Pundamilia nyererei*, *Metriaclima zebra*, and *Astatotilapia burtoni*, are not part of the same cichlid adaptive radiation, and are millions of years divergent from each other. Although this analysis (done using the program coalHMM; Hobolth et al. 2007) does not explicitly account for introgression as a force maintaining genetic variation, the disparate geographic distributions of these species make recent gene flow impossible, and the result underscores the point that accounting for allele sharing due to ILS is crucial for understanding cichlid evolutionary history. Similarly, high ILS was found using a smaller set of SNPs and a larger number of taxa by Loh et al. (2013), although their modeling work largely attributes allele sharing to gene flow rather than to ILS. Nonetheless, large effective population sizes are expected to maintain high levels of standing genetic variation, and if many cichlid species have large populations, it may be possible for cichlid radiations to maintain genetic variation over long timescales despite episodes of strong natural selection. This might especially be the case if hybrid ancestry caused an influx of additional genetic variation prior to the origin of the clade. Adaptation from standing genetic variation may be a common form of repeated adaptation in many systems (Barrett and Schluter 2008), and maintenance of variation due to ILS may facilitate this in cichlids in addition to hybridization and introgression. Also, variation derived from ILS may be important to speciation and diversification in some of the same ways that make variants derived from hybridization particularly beneficial for adaptation: strongly deleterious mutations have already been purged, and these alleles will be in higher frequency than new mutations and therefore less likely lost due to drift (Marques et al. 2019).

Recently developed population genetic methods for detecting historical introgression explicitly account for ILS (Patterson et al. 2012; Durand et al. 2011). These methods include “ABBA/BABA” tests, also known as D-statistics, use counts or frequencies of allelic histories that conflict with the species history to understand if this conflict can be attributed to introgression or to incomplete lineage sorting. These tests have spawned a number of expanded tests with related assumptions that attempt to infer the directionality of introgression (Eaton and Ree 2013; Pease and Hahn 2015). These new methods present an important development in distinguishing ILS from historical introgression, which can be difficult, particularly in rapid radiations (e.g., Degnan and Rosenberg 2009). In a phylogenetic context, much previous work on cichlids has not explicitly tested for ILS versus introgression as sources of phylogenetic incongruence (Koblmüller et al. 2010; Meyer et al. 2015), although recent work has begun to address this using new analytical approaches (Meyer et al. 2017; Irisarri et al. 2018; Meier et al. 2017). Distinguishing these processes is crucial for accurately interpreting the evolutionary history of cichlid clades.

It is important to remember that the vast majority of African cichlid diversity is found in lakes, that lake-adapted phenotypes are rarely able to persist in rivers (Seehausen 2015). However, although the vast majority of current lakes are young (Fig. 2), many lakes existed in Africa that are no longer present (Salzburger et al. 2014; Danley et al. 2012), and these paleolakes likely held cichlid diversity that may persist in current lineages in the form of genetic variation that arose in these paleolake environments. One example is cichlids of southern African rivers, which have contributions to their diversity from species formerly present in paleolake Makgadikgadi (Joyce et al. 2005), a large paleolake that existed in southern Africa during the Pleistocene. Although this lake is now gone, southern African rivers remain unusually morphologically and genetically diverse, and this diversity has been introduced to all major southern African rivers as a result (Joyce et al. 2005). Likewise, a paleolake, Obweruka, in the Lake Victoria region (Danley et al. 2012, Salzburger et al. 2014) is hypothesized to be the site in which Congolese and Nilotic lineages met to produce the admixed lineage which would later go on to form the Lake Victoria Region Superflock (Meier et al. 2017). The diversification that happened in this large paleolake that existed until the late Pliocene may have had dramatic impacts on the diversity in the Lake Victoria region today.

3.3 Spatial Genetic Structure and the Origin of Cichlid Species

Cichlids have long been of interest in speciation research because of their ability to speciate within lakes which lack clear physical barriers to gene flow (Coyne and Orr 2004). However, even early verbal models of cichlid speciation recognized the importance of geographic structure within lakes on cichlid speciation (Trewavas 1947; Fryer and Iles 1972; Fryer 1959). With substrate-specialized littoral species, the lake environment forms a linear strip of suitable habitat patches around the perimeter of the lake. Lake level fluctuations cause these patches to merge and subdivide, at each instance challenging species barriers with gene flow between divergent neighbor populations. This model depends crucially on the spatial scale and extent of divergence among neighboring populations.

The initial focus in studying geographic genetic patterns in cichlids was large-scale phylogeographic studies that investigated the impacts of lake subdivision in Lake Tanganyika's history (Sturmbauer et al. 2001; Sturmbauer and Meyer 1992). Although some lineages appear to exhibit genetic structure coinciding with this history of basin subdivision, there are two reasons that these subdivision events are unlikely to generally be important in cichlid diversification. First, most lakes do not have a geomorphological structure such that they would have experienced periods of subdivision, thus this mechanism is not generalizable to other lakes. Second, in Lake Tanganyika, subdivision would only have happened rarely in the history of the lake, thus episodes of basin isolation cannot explain the origin of the lake's 200+ endemic species, most of which did not evolve during lake low stands. Population isolation in satellite lakes is a similar mechanism to the subbasin isolation hypothesis, invoking clear physical barriers to gene flow, that has been proposed for cichlid speciation (e.g., Greenwood 1965). However, evidence for this is rare (but see Genner et al. 2007), and it is hard to imagine that this mechanism would be so frequent as to contribute substantially to cichlid diversity in any species-rich adaptive radiation.

Many studies have now shown that some cichlid lineages are strongly geographically divergent at small spatial scales in Lakes Malawi and Tanganyika (tens of kilometers; e.g., Koblmüller et al. 2011; Duftner et al. 2006; Taylor et al. 2001; Arnegard et al. 1999; Van Oppen et al. 1997; Danley et al. 2000; Markert et al. 1999) (Table 1). Other studies have shown that this pattern is not universal: some lineages have very little genetic structure over large spatial scales in these lakes (e.g., Wagner and Mccune 2009; Sefc et al. 2007) (Table 1). Furthermore, in Lake Victoria, geographic differentiation among incipient species appears to be rare compared to differentiation among incipient species in sympatry (Seehausen and Magalhaes 2010). This suggests that speciation mechanisms that operate within a single patch (e.g., along depth gradients; Seehausen et al. 2008) appear to be the more important axes for species formation than geographic structure in Lake Victoria haplochromines. Likewise, such non-geographic speciation mechanisms must operate for cichlids in crater lakes that are too small for geographic structure to play a role

Table 1 Studies using microsatellite data to assess geographic population genetic structure

Species	Lake	km studied	Fst	Genus/tribe	Genus richness	Source
Pseudotropheus zebra	Malawi	60	0.025	*Pseudotropheus*	25	Rico et al. (2003)
Pseudotropheus callainos	Malawi	60	0.077	*Pseudotropheus*	25	Rico et al. (2003)
Metriaclima zebra	Malawi	42	0.041	*Maylandia*	35	Danley et al. (2000)
Metriaclima sandaracinos	Malawi	42	0.017	*Maylandia*	35	Danley et al. (2000)
Tropheops sp. “mauve”	Malawi	60	0.106	*Tropheops*	8	Rico et al. (2003)
Tropheops sp. “olive”	Malawi	60	0.067	*Tropheops*	8	Rico et al. (2003)
Melanochromis auratus	Malawi	42	0.151	*Melanochromis*	15	Markert et al. (1999)
Labeotropheus fuelleborni	Malawi	42	0.079	*Labeotropheus*	2	Arnegard et al. (1999)
Protomelas taeniolatus	Malawi	280	0.026	*Protomelas*	15	Pereyra et al. (2004)
Protomelas fenestratus	Malawi	280	0.012	*Protomelas*	15	Pereyra et al. (2004)
Protomelas similis	Malawi	20	0.001	*Protomelas*	15	Pereyra et al. (2004)
Copadichromis sp.	Malawi	400	0.004	*Copadichromis*	25	Taylor et al. (2001)
Diplotaxodon macrops	Malawi	75	0.001	*Diplotaxodon*	7	Shaw et al. (2000)
Diplotaxodon sp. “offshore”	Malawi	175	0.001	*Diplotaxodon*	7	Shaw et al. (2000)
Diplotaxodon limnothrissa	Malawi	460	0.001	*Diplotaxodon*	7	Shaw et al. (2000)
Eretmodus cyanostictus	Tanganyika	40	0.098	Eretmodini	5	Taylor et al. (2001)
Simochromis diagramma	Tanganyika	60	0.006	*Simochromis* + *Pseudosimochromis*	5	Wagner and McCune (2009)
Petrochromis sp. “moshi”	Tanganyika	60	0.157	*Petrochromis*	8	Wagner and McCune (2009)
Petrochromis sp. “kazumbe”	Tanganyika	60	0.073	*Petrochromis*	8	Wagner and McCune (2009)
Eretmodus cyanostictus	Tanganyika	21	0.060	Eretmodini	5	Sefc et al. (2007)
Tropheus moorii	Tanganyika	21	0.053	*Tropheus*	6	Sefc et al. (2007)
Ophthalmotilapia ventraiis	Tanganyika	21	0.009	*Ophthalmotilapia*	4	Sefc et al. (2007)
Variabilichromis moorii	Tanganyika	62.5	0.128	*Variabilichromis*	1	Duftner et al. (2006)

For each study, the table denotes the geographic scale of the study and the pairwise Fst value associated with the maximum geographic distance between sites in the study. Genus richness is drawn from FishBase as the total number of valid species names per genus or tribe (as indicated in the table) in species differentiation (Schliewen et al. 2006; Barluenga et al. 2006; Kautt et al. 2016; Poelstra et al. 2018). Thus, current work suggests that geographic speciation mechanisms may be more important in some cichlid faunas than in others.

If scales of geographic divergence were a consistent predictor of the frequency of speciation, such lineages would be predicted to have higher speciation rates than lineages lacking strong geographic structure. Although cichlid phylogenies are not sufficiently resolved at the species level to strongly test this hypothesis yet, one course approximation of this idea would be to test for a relationship between clade richness and scale of geographic population structure (e.g., Wagner and McCune 2009; Harvey et al. 2017). Given available data, this does not seem to be the case. Table 1 is a compilation of studies measuring geographic genetic divergence in Lake Malawi and Lake Tanganyika cichlid species using microsatellite data. I restricted this list to include only studies using microsatellites to avoid marker-based differences in the detection of geographic structure. To generate a comparable measure of genetic divergence at the various geographic scales of these studies, I divided the pairwise Fst value observed from the most distant sites in the study by the geographic scale of the study to generate a "relative Fst" value that was comparable across studies at different spatial scales. Although this approach assumes a linear relationship between Fst and geographic distance, this is consistent with IBD relationships observed in the studies where such relationships were reported. For genera which were represented by more than one species, I calculated the median relative Fst value across all studies. Genus-level richness data is derived from information in Fishbase (Froese and Pauly 2014), where I took the number of currently valid species belonging to the genus that occur in the Fishbase database. Neither in Tanganyika ($r = 0.099$; $p = 0.857$) nor in Malawi ($r = -0.260$, $p = 0.534$) is there a significant correlation between genus-level richness and relative Fst (Fig. 4). Log transforming genus-level richness prior to analysis also does not produce any significant relationship. These are small sample sizes, and ideally one would not compare Fst values across studies without normalizing for differences in the variance of microsatellite datasets (e.g., Meirmans 2006). However, such normalization is beyond the scope of this analysis, for a course approximation of geographic divergence as a predictor of speciation frequency.

Despite these caveats, there does not seem to be a clear relationship between genus-level richness and scale of population geographic structure, indicating that species with highly geographically structured populations do not tend to form more species within the radiations of Lakes Tanganyika and Malawi. Several factors might explain this, even if geographic structure is important in the speciation process. First, extinction rates might also be higher in strongly geographically structured species, making diversification rates equivocal despite a real difference in speciation rates among highly structured and little structured lineages. Second, if persistence of species is limited at a higher level, such as in a diversity-dependent diversification type model (Rabosky 2009), the community context and/or the ecology of the incipient species may influence their persistence, and thus speciation rates and patterns of species richness might be decoupled. Both of the two above scenarios consider situations in which speciation rates per se do not predict species richness

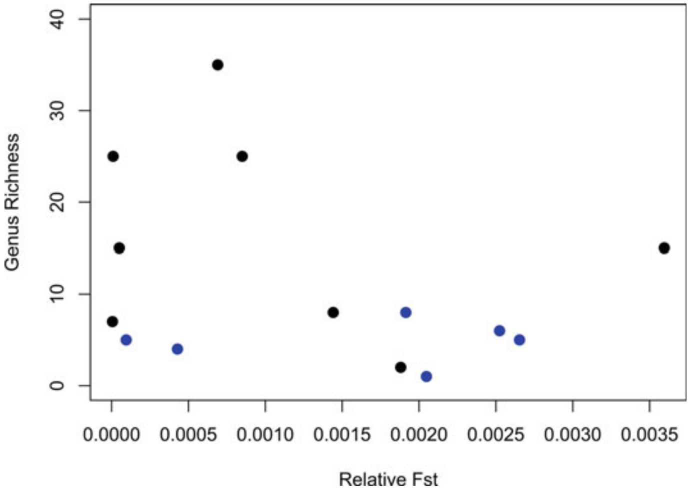

Fig. 4 The relationship between genus-level species richness and population structure in Malawi (black) and Tanganyikan (blue) cichlids. There is no clear relationship between the degree of population genetic structure, as measured from microsatellite data, and genus-level species richness, suggesting that species with stronger population genetic structure do not contribute more to the buildup of species richness. Pairwise Fsts were normalized over the geographic scale of the study

patterns, consistent with results at broader macroevolutionary scales (Wagner et al. 2014). Additional work should focus on understanding links between microevolutionary processes and macroevolutionary patterns within cichlid adaptive radiations.

For macroevolutionary work examining patterns of species richness, it is crucial that the species being considered are defined and delimited in consistent ways across the dataset being considered. For cichlids, this poses a challenge because different lakes and even different clades within lakes have received different amounts of taxonomic study, and there are different traditions of splitting versus lumping taxa based on their geographic distributions. For example, in some cases, allopatric populations that differ in phenotype have been split into multiple species, whereas in other situations allopatric color variants are recognized but not given species status (e.g., Pauers 2010; Koblmüller et al. 2011). To address this inconsistency, Genner et al. (2004) used taxon co-occurrence data (i.e., whether taxa are found together in sympatry or not) to standardize richness estimates for species complexes in Lakes Malawi, Victoria and Tanganyika. Adding these estimates to those from complexes that they did not include in the study, Genner et al. (2004) conclude that lower and upper estimates for Lake Malawi, Victoria, and Tanganyika, are, respectively, 451–600, 447–535, and 162–184 species. These are notably different estimates than are frequently discussed in the literature, particularly for Lake Malawi, which is often cited as having more than 800 species (e.g., Genner and Turner 2012). It is imperative that we recognize that such numbers are not directly comparable across lakes and that these high estimates include the splitting of many allopatric populations. In order to conduct comparative work that has consistency across radiations, approaches like that of Genner et al. (2004) are crucial. Additional careful work examining the within-lake geographic distribution of species diversity is needed for cichlids, and efforts to connect such work across lakes will be valuable in efforts to compare diversity patterns across lakes.

Thus, it is clear that strong spatial genetic structure, particularly in rock-associated cichlids, may be an important ingredient to speciation for cichlids in large lakes, yet it is also clear that this pattern is not universal, and speciation mechanisms which do not require geographic genetic structure also operate. It is possible that interaction between modes of speciation that require geographic subdivision, and modes of speciation lacking this requirement, interact to produce interesting larger-scale patterns in biodiversity. Wagner et al. (2014) suggest that this may explain the nonlinear species–area relationship for cichlids, where richness increases at a faster rate with area in larger lakes (see Sect. 3.2.2 above). As more case studies of cichlid speciation accumulate, we should continue to strive to understand what modes and mechanisms of speciation are most common, and whether these characteristics are predictable given the cichlid lineage and its traits, or the lake environment, in question.

4 Conclusion: Ecological Opportunity and Adaptive Radiation

It is now clear that cichlid adaptive radiation depends on both intrinsic factors and the environment. In this vein, we could view radiations as the intersection between key innovation and ecological opportunity: both need to be present in order for radiations to occur. This concept has been infrequently discussed in work on key innovations, where some researchers have pointed out that the origin of a key innovation may long precede diversification, even if diversification is strongly contingent on that trait (Weber and Agrawal 2014; De Queiroz 2002). This view emphasizes the contingency on which any innovation depends to impact diversification. Taken in the context of cichlid diversification, one classic example of cichlid key innovation is the pharyngeal jaw. Although phylogenetic evidence clearly shows that the origin of this trait is not linked to increased diversification in the contexts in which it has been studied in the teleost phylogeny (Alfaro et al. 2009), we know that cichlid pharyngeal jaws are crucial for a wide range of trophic ecologies these fishes evolve within radiations. Thus, perhaps we should view pharyngeal jaws as a contingent key innovation: when coupled with ecological opportunity in the form of freshwater lakes with an abundant and diverse resource base, this trait becomes an important innovation for the diversification of cichlids. Meaningful discussion of both key innovations and ecological opportunity requires that we think about their reciprocal influences on each other.

In this framework, we might view a number of traits as intrinsic factors important to cichlid diversification—which arguably, are key innovations. We now have abundant evidence for the importance of sexual selection in cichlid speciation (e.g., Maan et al. 2010; Seehausen and Van Alphen 1999) and in predicting whether or not lineages diversify (Wagner et al. 2012) (see Sect. 3.2.1 above). Traits linked to sexual selection, like sexual dichromatism, could thus be considered key innovations for cichlids, and ones that have evolved and been lost multiple times across the cichlid tree. It is also increasingly clear that hybridization can play a major role in the onset of adaptive radiations (e.g., Meier et al. 2017; Poelstra et al. 2018; Irisarri et al. 2018) and in the speciation process as adaptive radiations proceed (Meier et al. 2016; Selz et al. 2013) (see 3.2.2 above). Although hybridization is not a trait per se, it is certainly an intrinsic feature that should be considered a key factor in understanding cichlid adaptive radiation.

All of these key innovations and intrinsic factors are dependent upon environmental context. For example, the interaction of sexually selected phenotypes with environmental conditions is crucial to their functioning (Maan and Seehausen 2011). Also, the paleoenvironmental context through which divergent lineages are brought together is required for hybridization to be possible, as well as for other species interactions that might impact diversification (Salzburger et al. 2014; Muschick et al. 2018). These contingencies of historical geography strongly influence what lineages will seed new lake environments as they appear. Such features will have profound effects on evolutionary outcomes. Additionally, as cichlid assemblage richness is predicted by environmental variables, although evolution is an important ingredient in creating these species, the environment could be argued to be an even more important determinant of diversity (see Sect. 3.2.2 above). When viewed through this lens, it is clear that there is an enormous amount of contingency on which diversification outcomes depend.

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Evolution in the Fast Lane: Diversity, Ecology, and Speciation of Cichlids in the Lower Congo River

Melanie L. J. Stiassny and S. Elizabeth Alter

Abstract More than 40 years ago in their compendium of fish diversity in the lower Congo River (LCR), T. R. Roberts and D. J. Stewart posed the question, “Why does the LCR harbor so many cichlids?” Here we seek an answer through a synthesis of the last 40+ years of research on cichlid diversity, ecology, and speciation. Our review suggests a key role for the unique geomorphology and hydrology of the river itself and its history of connectivity to other African freshwater ecosystems. In contrast to the river upstream of Pool Malebo, the LCR channel is entirely bedrock, and littoral habitats are mostly rocky and rock-strewn. In situ measurements have recorded dramatic changes in channel topology, fluctuating bed bathymetry, and regions of extreme depth. A combination of high annual discharge, steep elevational decline, and fluctuating channel width and depth result in extraordinarily high-energy flow regimes throughout the LCR. In-stream hydraulics and bathymetry appear to play a key role in isolating cichlid populations and are likely powerful drivers for micro-allopatric isolation and speciation, often over remarkably small geographical scales. Moreover, this hydrologically extreme environment is the evolutionary backdrop for an unusual array of cichlid morphologies, including the only known blind cichlid (*Lamprologus lethops*).

Keywords Congo basin · Geomorphology · Flow dynamics · Diversification · Micro-allopatry

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M. L. J. Stiassny (✉)
Department of Ichthyology, American Museum of Natural History, New York, NY, USA
e-mail: mljs@amnh.org

S. E. Alter
Department of Ichthyology, American Museum of Natural History, New York, NY, USA

The Graduate Center, City University of New York, New York, NY, USA

Biology and Chemistry Department, California State University, Monterey Bay, Seaside, CA, USA
e-mail: ealter@csumb.edu

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1 Introduction

Sprawling across 4370 km of equatorial Africa, from Lake Tanganyika in the east to the mouth of the Atlantic Ocean in the west, the Congo River drains some 3.68 million km^2, including the largest remaining expanse of intact rainforest on the continent. Zaire, the former name for the Congo River, is said to be a corruption of the word "Nzere," meaning "*the river that swallows all rivers*"—surely an apt descriptor of this largest of all African river basins. Perhaps not surprisingly, given its complex and extensive drainage network, the Congo basin (CB) harbors an exceptionally rich fish fauna. Estimates of species richness for the CB vary but converge on a number close to 1270 species (Winemiller et al. 2016). However, as numerous new species are discovered each year, that number is likely a significant underestimate. In contrast, cichlid diversity, excluding the hyperdiverse faunas of the Lake Tanganyika basin, is relatively muted. With only around 120 named (if not all formally described) species across the entire basin (Table 1), Congo cichlids conform to a pattern of relative paucity in African rivers compared with their predominance in the lacustrine systems of the continent. However, looking at species distributions and broad-scale patterns of endemism across the CB (Fig. 1), it is evident that cichlid diversity is not evenly partitioned. Remarkably, given an area of less than 2% of the entire basin, the lower Congo (LC), with a representation of 30% of cichlid species present in the entire basin and with 78% of those endemic to the LC, is an obvious outlier (Fig. 1), and clearly a hotspot of cichlid richness and endemism. This is not a novel observation: in their seminal paper on fishes of lower Congo River (LCR), Roberts and Stewart (1976:240) wrote:

> Perhaps the most striking aspect of the taxonomic composition of the Zairean rapids fishes is the preponderance of Cichlidae" and that "Such predominance of Cichlidae is a noteworthy contrast to the situation in rich riverine faunas everywhere else in Africa, including low gradient rivers in the Zaire basin, where cichlid species, endemic or not, are always few in number and seldom contribute substantially to the numbers of individuals present.

Roberts and Stewart's study was published more than four decades ago and since then new surveys and taxonomic revisions, and a number of molecular-based investigations, have revealed even greater diversity (Table 1). These studies have begun to illuminate the complex evolutionary histories of many LCR cichlids as well as of the river itself. However, the question implicitly posed by Roberts and Stewart—why does the LCR harbor so many cichlids?—remains unanswered. In this chapter, we seek to investigate this question through a synthesis of the last 40+ years of research on cichlid diversity, ecology, and speciation, as well as in the context of recent findings that suggest a key role for the unique geomorphology and hydrology of this extraordinary system.

Table 1 List of cichlid species present in the Congo River basin (exclusive of Lake Tanganyika and associated Malagarasi River)

Genus	Species	Taxonomic Authority/ relevant literature	Regional occurrence
Chromidotilapia	*schoutedeni*	Poll and Thys van den Audenaerde, 1967 (see Schwarzer et al. 2015)	CC, UC
Congochromis	*sabinae*	(Lamboj, 2005)	CC (+LG)
Congochromis	*squamiceps*	(Boulenger, 1902)	UC
Congochromis	*dimidiatus*	(Pellegrin, 1900)	CC (+LG)
Congochromis	*pugnatus*	Stiassny and Schliewen, 2007	UC
Congolapia	*bilineata*	(Pellegrin, 1900)	CC
Congolapia	*crassa*	(Pellegrin, 1903)	CC
Congolapia	*louna*	Dunz, Vreven & Schliewen, 2012	CC
Coptodon	*congica*	(Poll and Thys van den Audenaerde, 1960) (see Dunz and Schliewen 2013)	CC
Coptodon	*rendalli*	(Boulenger, 1897) (see Dunz and Schliewen 2013)	ZC, UC, Ka (+SA)
Coptodon	***tholloni***	(Sauvage, 1884) (see Dunz and Schliewen 2013)	**LC, CC (+ LG)**
Ctenochochromis	*oligacanthus*	(Regan, 1922)	Ub
Ctenonochromis	***polli***	(Thys van den Audenaerde, 1964)	**LC, CC**
Cyclopharynx	*fwae*	Poll, 1948	CC*
Cyclopharynx	*schwetzi*	Poll, 1948	CC*
Haplochromis	***snoeksi****	Wamuini Lunkayilakio and Vreven, 2010	**LC**
Hemichromis	*cerasogaster*	(Boulenger, 1899)	CC*
Hemichromis	***elongatus***	(Guichenot, 1861)	**LC, CC, Ka, Ub, UC (+LG +SA)**
Hemichromis	*lifalili*	Loiselle, 1979	CC?
Hemichromis	***stellifer***	Loiselle, 1979	**LC (+LG)**
Heterochromis	*multidens*	(Pellegrin, 1900)	CC
Lamprologus	*congoensis*	Schilthuis, 1891	CC, Ka
Lamprologus	***lethops****	Roberts and Stewart, 1976	**LC**
Lamprologus	*mocquardi*	Pellegrin, 1903	CC, Ub, UC
Lamprologus	*symoensis*	Poll, 1976	UC
Lamprologus	***teugelsi****	Schelly and Stiassny, 2004	**LC**
Lamprologus	***tigripictilis****	Schelly and Stiassny, 2004	**LC**
Lamprologus	*tumbanus*	Boulenger, 1899	CC*
Lamprologus	***werneri****	Poll, 1959	**LC**
Lamprologus	***markerti****	Tougas and Stiassny, 2014	**LC**
Nanochromis	***consortus****	Roberts and Stewart, 1976	**LC**

(continued)

Table 1 (continued)

Genus	Species	Taxonomic Authority/ relevant literature	Regional occurrence
Nanochromis	***minor****	Roberts and Stewart, 1976	**LC**
Nanochromis	*nudiceps*	(Boulenger, 1899)	Ka
Nanochromis	***parilus***	Roberts and Stewart, 1976	**LC, CC**
Nanochromis	***splendens****	Roberts and Stewart, 1976	**LC**
Nanochromis	*teugelsi*	Lamboj and Schelly, 2006	Ka, CC
Nanochromis	*transvestitus*	Stewart and Roberts, 1984	Ka*
Nanochromis	*wickleri*	Schliewen and Stiassny, 2006	Ka*
Nanochromis	*sp. "mbandaka"*	see Schwarzer et al. (2011)	CC
Nanochromis	*sp. "ndongo"*	see Schwarzer et al. (2011)	CC
Oreochromis	***lepidurus****	(Boulenger, 1899)	**LC**
Oreochromis	*mweruensis*	Trewavas, 1983	ZC
Oreochromis	*upembae*	(Thys van den Audenaerde, 1964)	UC
Oreochromis	*salinicola*	(Poll 1948)	ZC
Orthochromis	*kalungwishiensis*	(Greenwood and Kullander, 1994)	ZC
Orthochromis	*luongoensis*	(Greenwood and Kullander, 1994)	ZC
Orthochromis	*polyacanthus*	(Boulenger, 1899) (see Salzburger et al. 2005; Schwarzer et al. 2012a)	UC, ZC
Orthochromis	***stormsi***	(Boulenger, 1902) (see Salzburger et al. 2005; Schwarzer et al. 2012a)	**LC, UC, ZC**
Orthochromis	*torrenticola*	(Thys van den Audenaerde, 1963)	ZC
Pelmatochromis	*nigrofasciatus*	(Pellegrin, 1900)	CC, UC
Pelmatochromis	*ocellifer*	Boulenger, 1899	CC
Pseudocrenilabrus	*nicholsi*	(Pellegrin, 1928)	UC
Pseudocrenilabrus	*philander*	(Weber, 1897)	Ka, UC, ZC (+SA)
Pseudocrenilabrus	*philander dispersus*	(Trewavas, 1936)	Ka, UC
Pterochromis	*congicus*	(Boulenger, 1897)	CC
Sargochromis	*mellandi*	(Boulenger, 1905)	Ka, UC, ZC
Sargochromis	*thysi*	(Poll, 1967)	Ka
Sarotherodon	***galilaeus boulengeri***	(Pellegrin, 1903)	**LC, CC, Ka**
Sarotherodon	***nigripinnis***	(Guichenot, 1861)	**LC (+LG)**
Schwetzochromis	*neodon*	Poll, 1948	Ka*
Serranochromis	*angusticeps*	(Boulenger, 1907)	ZC (+ SA)
Serranochromis	*macrocephalus*	(Boulenger, 1899)	ZC, Ka (+SA)
Serranochromis	*jallae*	(Boulenger, 1896)	ZC (+SA)

(continued)

Table 1 (continued)

Genus	Species	Taxonomic Authority/ relevant literature	Regional occurrence
Serranochromis	*spei*	Trewavas, 1964	Ka, UC
Serranochromis	*stappersi*	Trewavas, 1964	ZC (+SA)
Serranochromis	*thumbergi*	(Castelnau, 1861)	ZC, UC (+SA)
Serranochromis	*toddi*	(Boulenger, 1905)	Ka
Steatocranus	*bleheri*	Meyer, 1993	UC
Steatocranus	*bleheri*	see Schwarzer et al. (2011)	CC
Steatocranus	***casuarius****	Poll, 1939	**LC**
Steatocranus	***casuarius“brownpearl”****	see Schwarzer et al. (2011)	**LC**
Steatocranus	***gibbiceps****	Boulenger, 1899	**LC**
Steatocranus	***cf. gibbiceps****	see Schwarzer et al. (2011)	**LC**
Steatocranus	***glaber****	Roberts and Stewart, 1976	**LC**
Steatocranus	***mpozoensis****	Roberts and Stewart, 1976	**LC**
Steatocranus	*rouxi*	(Pellegrin, 1928)	Ka
Steatocranus	***tinanti****	(Poll, 1939)	**LC**
Steatocranus	***tinanti “ultraslender”****	see Schwarzer et al. (2011)	**LC**
Steatocranus	***tinanti “inga”****	see Schwarzer et al. (2011)	**LC**
Steatocranus	***tinanti “intermediate”****	see Schwarzer et al. (2011)	**LC**
Steatocranus	*ubanguiensis*	Roberts and Stewart, 1976	Ub
Steatocranus	*sp. “lefini”*	see Schwarzer et al. (2011)	CC
Steatocranus	*sp. “redeye”*	see Schwarzer et al. (2011)	Ka
Steatocranus	*sp. “Kwilu”*	see Schwarzer et al. (2011)	Ka
Steatocranus	*sp. “dwarf”*	see Schwarzer et al. (2011)	CC
Steatocranus	*sp. “bulkyhead”*	see Schwarzer et al. (2011)	CC
Steatocranus	*sp. “maluku”*	see Schwarzer et al. (2011)	CC
Steatocranus	*sp. “mbandaka”*	see Schwarzer et al. (2011)	CC
Steatocranus	*sp. “kisangani”*	see Schwarzer et al. (2011)	UC
Teleogramma	***brichardi****	Poll, 1959	**LC**
Teleogramma	***cf. brichardi****	see Alter et al. (2017)	**LC**
Teleogramma	***depressa****	Roberts and Stewart, 1976	**LC**
Teleogramma	***cf. depressa****	see Alter et al. (2017)	**LC**
Teleogramma	***gracile****	Boulenger, 1899	**LC**
Teleogramma	*monogramma*	(Pellegrin, 1927)	Ka
Teleogramma	*obamaorum*	Stiassny and Alter, 2015	CC
Thoracochochromis	***bakongo****	(Thys van den Audenaerde, 1964)	**LC**
Thoracochromis	*brauschi*	(Poll and Thys van den Audenaerde, 1965)	CC*
Thoracochromis	*callichromus*	(Poll, 1948)	CC*
Thoracochochromis	***demeusii****	(Boulenger, 1899)	**LC**
Thoracochochromis	***fasciatus****	(Perugia, 1892)	**LC**
Thoracochochromis	*luluae*	(Fowler, 1930)	Ka

(continued)

Table 1 (continued)

Genus	Species	Taxonomic Authority/ relevant literature	Regional occurrence
Thoracochochromis	*moeruensis*	(Boulenger, 1899)	ZC
Thoracochromis	*schwetzi*	(Poll, 1967)	Ka
Thoracochromis	*stigmatogenys*	(Boulenger, 1913)	Ka, ZC
Tilapia	*baloni*	Trewavas and Stewart, 1975	ZC
Tilapia	*ruweti*	(Poll and Thys van den Audenaerde, 1965)	ZC (+SA)
Tilapia	*sparrmanii*	Smith, 1840	Ka, UC (+SA)
Tylochromis	*aristoma*	Stiassny, 1989	CC
Tylochromis	*bangwelensis*	Regan, 1920	ZC
Tylochromis	*elongatus*	Stiassny, 1989	UC
Tylochromis	*labrodon*	Regan, 1920	CC, Ub, UC
Tylochromis	***lateralis***	(Boulenger 1898)	**LC, CC, Ka, Ub, UC**
Tylochromis	*microdon*	Regan, 1920	CC*
Tylochromis	*mylodon*	Regan, 1920	ZC*
Tylochromis	***praecox****	Stiassny, 1989	**LC**
Tylochromis	*pulcher*	Stiassny, 1989	CC
Tylochromis	*regani*	Stiassny, 1989	ZC, UC
Tylochromis	*robertsi*	Stiassny, 1989	Ub, CC, UC
Tylochromis	*variabilis*	Stiassny, 1989	CC, Ka, Ub, UC

Haplochromine generic assignments follows: Froese, R. and D. Pauly. Editors. 2020. FishBase. World Wide Web electronic publication. www.fishbase.org. Species indicated in bold are present in the LCR and those in bold underscored and marked with an asterisk are endemic to the LCR region. Column on far right indicates broad regional occurrence: LC (lower Congo), CC (central Congo), UC (upper Congo), Ka (Kasai drainage), Ub (Ubangi drainage), ZC (Zambian Congo). (+) Indicates distribution extends beyond the Congo basin: SA (southern Africa), LG (lower Guinea). Asterisks following regional occurrence indicate species restricted to lacustrine habitats. Broad geographical subdivision of the CB is as in Fig. 1

2 Characterization of the LCR: A Geo-hydrological Context for Cichlid Diversification

The important summary of Runge (2008) builds on the authoritative earlier studies of Veach (1935), Robert (1946), and Cahen (1954) to provide an excellent introduction to the physical geography and geomorphology of the present-day Congo basin. A number of recent reviews also provide additional useful information for the basin (O'Loughlin et al. 2013; Alsdorf et al. 2016; Harrison et al. 2016). Of most interest in the present context is the final course of the main stem of the Congo River as it flows out of Pool Malebo en route to the Atlantic some 450 km downstream (LCR, Fig. 2a, b). At the western edge of the CB, a sill formed at the eastern boundary of the Atlantic Rise (Western Escarpment), impeded the flow of the river, backing it up into a shallow lake-like expansion known as Pool Malebo

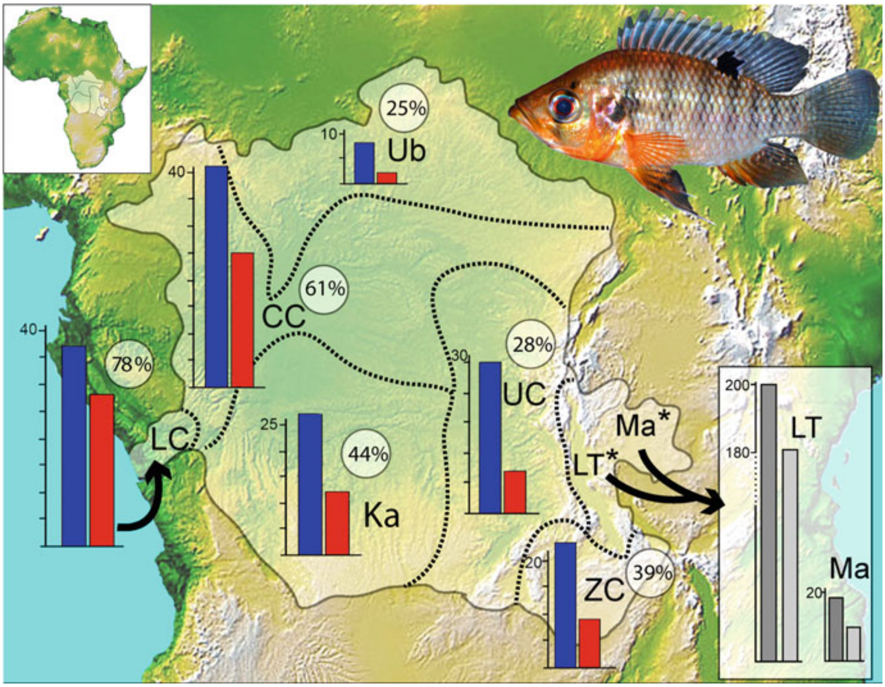

Fig. 1 Cichlids of the Congo Basin. Regionalization of the basin modified after Brooks et al. (2011): LC, lower Congo, CC, central Congo, Ka, Kasai, Ub, Ubangui, UC, upper Congo, ZC, Zambian Congo, LT, Lake Tanganyika, Ma, Malagarasi. Inset bar charts indicate estimates of regional species richness (blue) and endemism (red). Shaded circles indicate percentage endemism (excludes cichlids of LT* and Ma*). Species estimates for LT from Konings (2015), and for Ma from DeVos et al. (2001). Inset photograph of *Pterochromis congicus*, courtesy of P.V. Loiselle

(formerly Stanley Pool). Although the precise origin of the Pool is unclear, most authors consider it to be a remnant of a large, land-locked lake formed in the early Pliocene when repeated uplift of the Atlantic Rise last dammed the outflow of the Congo River (see below, and Runge 2008). Today, near the twin capitals of Kinshasa (Democratic Republic of Congo) and Brazzaville (Republic of Congo), the LCR spills over that rocky sill and plunges down a narrow gorge cut through the Crystal Mountains of the Atlantic Rise. From Pool Malebo, at an elevation of c. 280 m above sea level to the port town of Matadi 350 km downstream, the river drops 270 m in elevation as it flows through series of intermittently narrow (<0.2 km) and wide (>2 km) gorges in a channel that undergoes numerous and often rapid changes in direction, in response to a highly variable bedrock bathymetry. The average rate of discharge from the Pool is 46,200 m^3s^{-1} (Runge 2008), and this enormous volume of water flows down a rock-strewn, bedrock-constrained channel on a contorted route to the Atlantic.

Based on a combination of geomorphology and geology, Robert (1946) divided the "rapids section" from the Pool to Matadi into three regions of the LCR. The first,

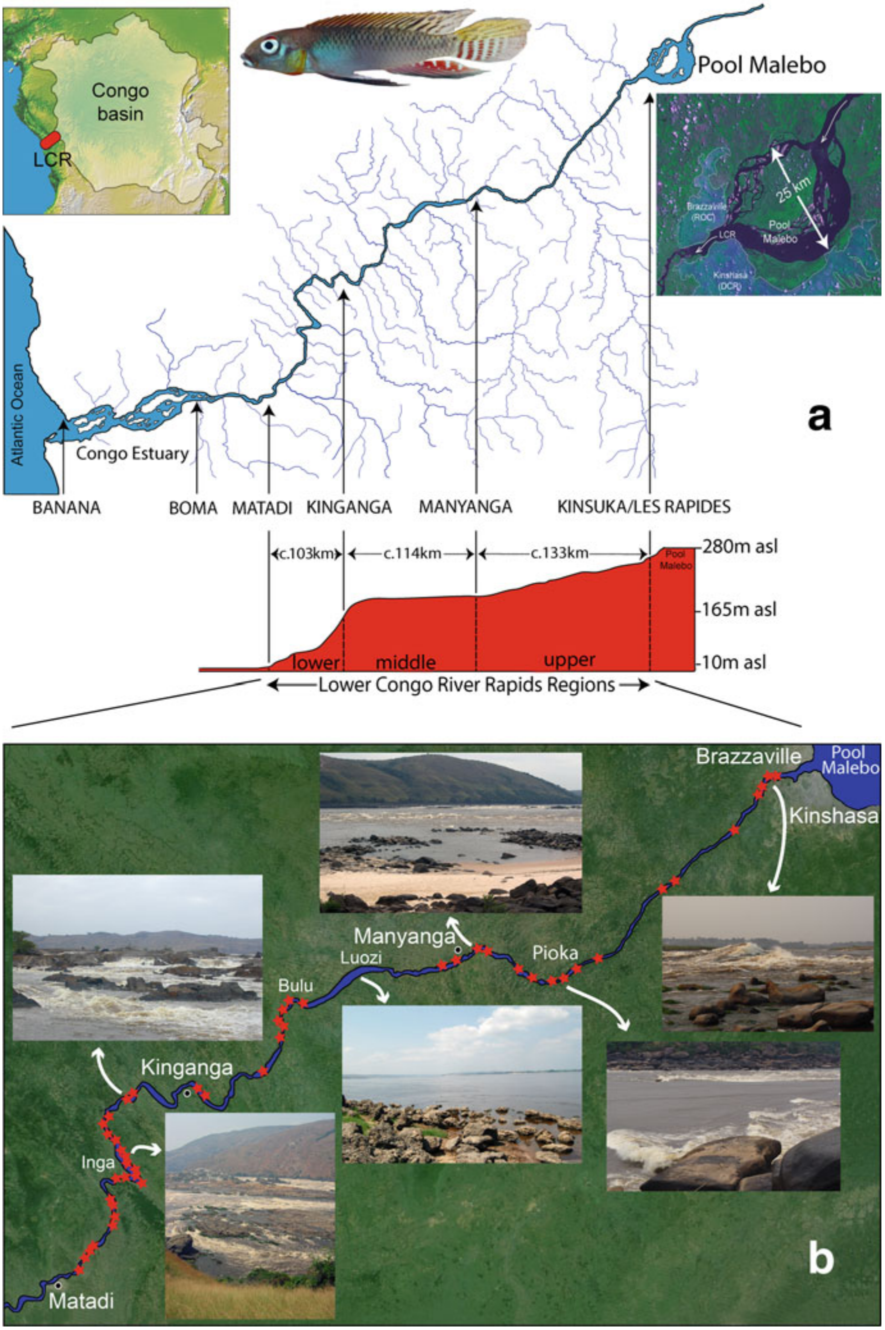

Fig. 2 Location and course of LCR from Pool Malebo to the Atlantic Ocean. (**a**) Broad regionalization of the LCR and elevation profile modified after Robert (1949). Inset photograph of *Nanochromis splendens*, courtesy of U. Schliewen. (**b**) Course of LCR "rapids regions" from Pool Malebo to Matadi. Red stars indicate approximate locations of major cross-channel rapids. Inset photographs show water surface and shoreline conditions at sites indicated by white arrows. Photographs courtesy of AMNH

uppermost region stretches 133 km from the Pool to Manyanga, over which the river drops more than 80 m resulting in numerous surface rapids, some of which span the channel. Between Manyanga and Kinganga, the middle (navigable) section spans about 114 km, and here the river is generally wider with a more gradual elevational drop of less than 20 m and few surface rapids, most of which are concentrated around and below the region of Bulu (Fig. 2b). Below Kinganga to Matadi the lower section extends for some 103 km over which the river drops nearly 170 m forming a series of massive rapids and cataracts, including the spectacular 15-km-long Inga Falls (Fig. 2b).

In order to better understand how channel bathymetry and hydraulic conditions within the LCR relate to patterns of fish diversity, hydrologists from the US Geological Survey and American Museum of Natural History (AMNH) conducted a series of in situ measurements. The surveys took place during July 2008 and July–August 2009, at the end of the main dry season and time of lowest water in the LCR. These studies included a series of cross-channel and short longitudinal transects and a 130 km single-line longitudinal bathymetric survey undertaken by a National Geographic Society-sponsored team of white water kayakers with kayaks outfitted with differential GPS and digital echo sounders (Fig. 3b). Short cross-channel transects were conducted from a motorized wooden pirogue with a digital echo sounder and a dGPS unit securely fastened to its hull (Fig. 3a). In addition, flow dynamics at depth and channel bathymetry were investigated using a four-beam acoustic Doppler current profiler (ADCP) in tandem with dGPS and echo sounders deployed from a large motorized wooden pirogue in reaches around Kinshasa, Manyanga, and Bulu (Fig. 4). Detailed methods of ADCP data collection and analysis and a series of preliminary findings are discussed by Oberg et al. (2009) and Jackson et al. (2009).

In marked contrast to the river upstream of Pool Malebo, the LCR channel is entirely bedrock (although some in-channel, alluvial deposits are present), and strong bedrock controls are clearly evident throughout the system. Littoral habitats are almost entirely rocky and rock-strewn (Fig. 2b), with some intermittent sandy, or occasionally grass fringed or muddy, shorelines. In situ measurements recorded dramatic changes in channel topology even over very short distances (Fig. 3a, b), and this highly irregular bed topography appears to have profound effects on flow dynamics even in the absence of rapids. In many stretches of deep, open water, large vortices, boils and suck holes are visible at the surface, formed as deep jets of water traveling at high velocities encounter towering rock columns and canyons. In addition to dramatic changes in bed bathymetry, regions of extreme depth were also recorded. For example, in the Bulu reach (Fig. 4a), ADCP deployment accurately recorded depths of up to 160 m (Fig. 4c), and during the single-line longitudinal bathymetric survey kayakers recorded depths of greater than 220 m (Fig. 3b). While that depth trace is not corrected for pitch and roll of the kayaks, there can be little doubt that the LCR is, in places, among the world's deepest rivers. But perhaps even more striking is the observation that these deep canyons, pools, and trenches are located in close proximity to, and interspersed between, regions of extremely shallow water where massive whitewater rapids span the entire channel (Fig. 2b).

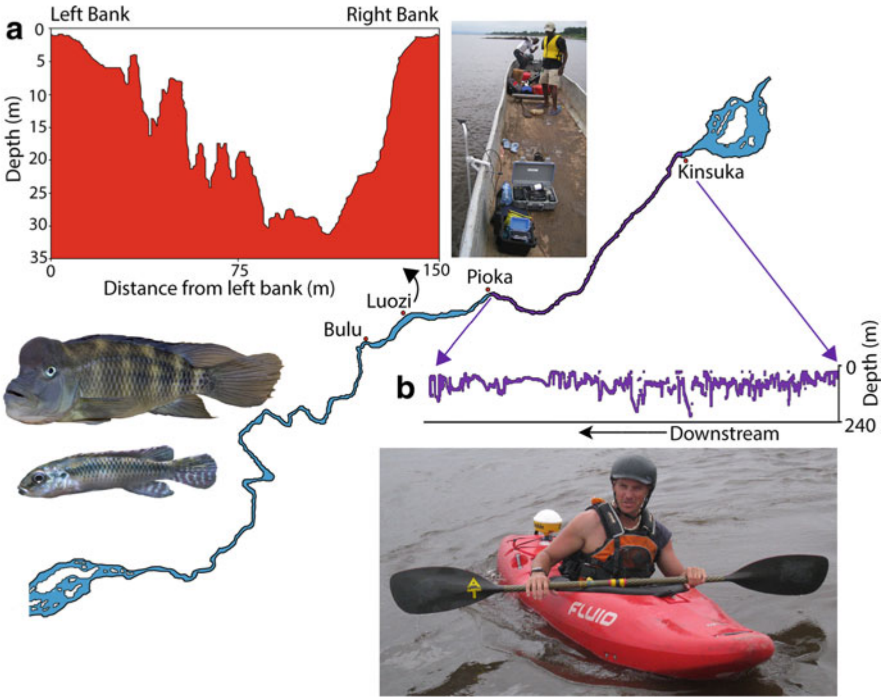

Fig. 3 Bathymetry at sites along the LCR. (**a**) Cross-channel profile near Luozi with photograph of wooden pirogue from which digital echo sounder and dGPS were deployed during repeated bank to bank transects across the channel. (**b**) 130 km single-line longitudinal depth trace made by kayakers between Kinsuka and Pioka (trace uncorrected for pitch and roll). Kayaks (inset) were outfitted with base-mounted echo sounders and rear-mounted dGPS receivers. Inset photographs of *Steatocranus casuarius* and *Nanochromis minor*, courtesy of O. Lucanus

The combination of high annual discharge, steep elevational incline, and fluctuating thalweg and channel width result in extremely complex flow regimes throughout much of the LCR. To better record and visualize these hydrological features, the 2008–2009 surveys employed ADCPs linked with dGPS to gather detailed measurements of water velocity profiles, backscatter, and channel depth. Most effort was expended in the Bulu reach (Fig. 4a), as this was the region from which specimens of the enigmatic blind cichlid, *Lamprologus lethops* had been found, suggestive that this region may harbor deepwater habitats (see below). Examination of individual transects and depth-averaged velocities indicate that, in much of the sampled area, coherent bank-to-bank flow structures are entirely absent. For example, a transect made while entering bend 1 at Bulu (Fig. 4b) shows that regions of low flow velocity (blue and green) near the banks are completely isolated from those at the opposite bank by a high shear zone of flow separation vertically spanning the entire water column. A high-velocity downstream core (red) exceeds 4 m/s, while secondary flow structures (arrows) appear as persistent large vortices, and significant recirculation of water flowing *upstream* at the banks with velocities exceeding 2 m/s is recorded. In

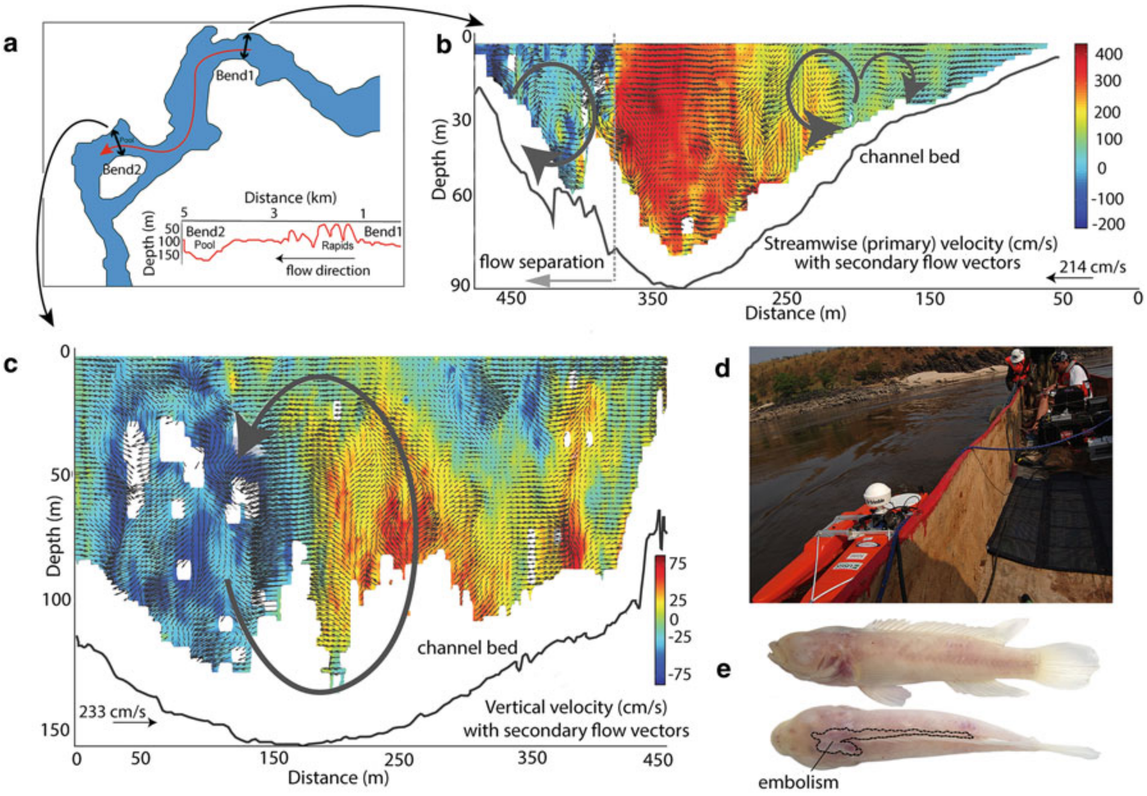

Fig. 4 Flow dynamics and bathymetry at additional sites along the LCR. (**a**) Map of Bulu reach with sampled sites indicated. (**b**) ADCP data visualization of primary (colors) and secondary (arrows) velocities of cross-channel section at Bend 1. Interference limits data acquisition near bed (white). (**c**) ADCP data visualization of vertical (color) and secondary (arrows) at cross-section of "pool" at Bend 2. Interference and intense turbulence limit data acquisition (white) (**b**, **c** modified after Jackson et al. 2009). (**d**) Wooden pirogue with ADCPs and dGPS deployed from a tethered trimiran, a digital echo sounder is located on the pirogue opposite the trimiran. (**e**) *Lamprologus lethops* (AMNH 248124, 56.2 mm SL), photographed immediately post-mortem. Black outline indicates the surface location of gas bubble embolism

regions of much greater depth (Fig. 4c), coherent vertical structures span the full 160 m depth, and large persistent cells of upwelling (yellow) and downwelling (blue) water coexist with vertical jets (red) that rapidly transport water between the bed and the surface.

3 Geological Context of the LCR

Current understanding of the complex history and manner of formation of the present-day Congo River network is incomplete. However, recent studies synthesizing seismic data (Kadima et al. 2011), and evidence from terrigenous depositional studies, regional geomorphological analyses, and phylogeography provide a compelling reconstruction of the Neogene evolution of the basin (Flügel et al. 2015). In the western CB, sedimentary studies along the coastal zone suggest a protracted history of shifting and intermittent outflow of the CB into the Atlantic. The first capture of a previously endorheic basin is thought to have occurred late in the Cretaceous, near the site of the present-day Ogowe River, with progressive southward migration taking place through to the mid Cenozoic. Although a final consensus has yet to be reached, interpretation of palaeosedimentological data and analyses of present-day river topology indicates that by the mid to late Miocene the main depocenter of sedimentation from the CB was in the vicinity of the Kouilou-Niari River, located to the north of the outflow of the present-day LCR. Although mechanisms are unclear, sediment loading and flexural uplift of the interior basin may have played a role in the migration of the Congo outlet, while tectonic activity associated with Miocene reactivation of the west African orogen appears to have initiated the final capture of the entire CB by the LCR. The formation of the current outlet—the LCR—is likely the result of ongoing tectonic activity causing the reactivation of an antecedent LCR valley ("Bas Congo" aulocogen, Gioan et al. 1989). A single high-energy capture event draining an inland Pliocene lake is now generally considered to have occurred around the Miocene–Pliocene transition, resulting in the formation of the present-day LCR and the remaining Congo River network. While an earlier proto-LCR, persistent as a small Atlantic coastal drainage, likely occupied some unknown extent of the preexisting valley, the current high-energy, high-flow regime of the present-day LCR is recent and was not fully established until sometime between 2 and 5 myr. In addition, studies of terrigenous dust flux from marine sediments indicate cycles of aridity across the African continent over the late Pliocene and Pleistocene, indicating that the LCR may have undergone significant fluctuations in water level with low discharge periods occurring ~2.8, 1.7, and 1 Mya (deMenocal 2004; Takemoto et al. 2015).

Regardless of the precise mechanisms of its origin, the present-day LCR is clearly a highly unusual riverine system. In many respects, it better resembles a high-gradient, headwater mountain stream—albeit one with an extraordinarily large discharge—than the lower reaches of any more typical large tropical river. Its rocky shorelines, heterogeneous bed topology, and extreme hydraulics generate a complex array of flow regimes and habitats, and these features potentially play a key role in isolating fish populations by inhibiting both cross-channel and upstream–downstream movement. Such features, whether torrential whitewater rapids, deep canyons, or turbulent high-energy in-stream flows, likely present effective barriers for the small-bodied, predominantly lithophilic cichlid fishes so characteristic of the LCR system. Our findings suggest that the river itself may be a powerful driver of micro-allopatric isolation, actively facilitating phenotypic and ecological divergence, often over remarkably small geographical scales, through processes of natural selection, sexual selection, and genetic drift (Alter et al. 2017; Markert et al. 2010; Schwarzer et al. 2011).

4 Living on the Edge: *Lamprologus lethops*

Of all LCR cichlids, none is more intriguing than the so-called “blind cichlid” of Bulu. Described in 1976 by Roberts and Stewart, *Lamprologus lethops*, is the only cichlid that is cryptophthalmic and fully depigmented. Specimens are primarily known from a short stretch of the LCR centered around Bulu, although a few individuals have reportedly been recovered near Luozi less than 20 km upstream, and a single individual was recently found entrained in a circulating current alongside a rocky outcrop at Tadi, some 30 km downstream of Bulu. The highly derived, seemingly troglomorphic morphology of *L. lethops* (Figs. 5a and 6a) is strikingly divergent from that of the sympatric *L. tigripictilis* (Figs. 5d and 6b) or other congeners. While *L. tigripictilis* is found in large numbers in inshore habitats throughout the region, *L. lethops* is only found dead or moribund at the water surface in a condition of strong positive buoyancy. According to local fishermen, dead or dying *L. lethops* are found entrained among flotsam or wedged under rocks along the shorelines, but source population(s) are unknown. During five field visits totaling approximately 60 days AMNH ichthyologists, aided by local fishermen, recovered over 50 specimens ranging in size from 125.4 mm SL to 32.2 mm SL, but despite intensive efforts found no evidence of surface-dwelling populations, nor any nearby cave systems. In individuals of less than 40 mm SL small, dorsally positioned, optic globes are often clearly visible beneath expansive frontal bones (Fig. 5a), while in all larger specimens the optic globes are not externally visible being deeply recessed under heavily ossified frontals covered by a substantial epaxial musculature that has migrated anteriorly over the entire orbital region. Schobert et al. (2012) provide a detailed comparative ocular anatomy of *L. lethops* and *L. tigripictilis* and describe a series of “degenerative” features of the eyes in *L. lethops*. These include greatly foreshortened optic globes, a decreased number of neuronal layers in the retina, and the absence of extraocular muscles and a rete mirabile. Based on these, and other features, Schobert et al. (2012) concluded that the eyes of *L. lethops* are not capable of image formation but may potentially be functional as light-sensing organs. This capability appears most likely in juveniles, in which optic globes are exposed

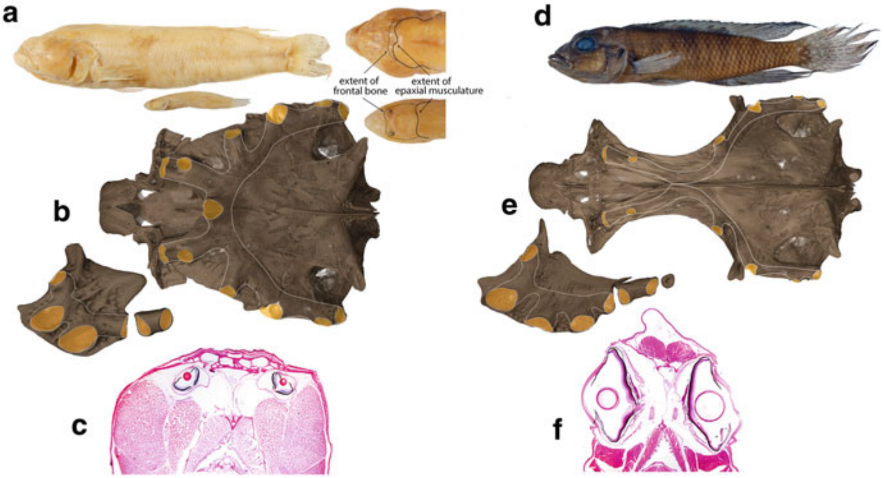

Fig. 5 (**a**) *Lamprologus lethops* AMNH 247885, 125.4 mm SL and AMNH 251325, 32.2 mm SL, with inset showing extent of epaxial musculature. (**b**) MicroCT segmentation of neurocranium (dorsal view) and infraorbital series with laterosensory canals and pores highlighted. (**c**) Transverse section through cranium and eyes (hematoxylin and eosin stained). (**d**) *L. tigripictilis* (AMNH 247252, 119.5 mm SL). (**e**) MicroCT segmentation of neurocranium (dorsal view) and infraorbital series with laterosensory canals and pores highlighted. (**f**) Transverse section through cranium and eyes (hematoxylin and eosin stained)

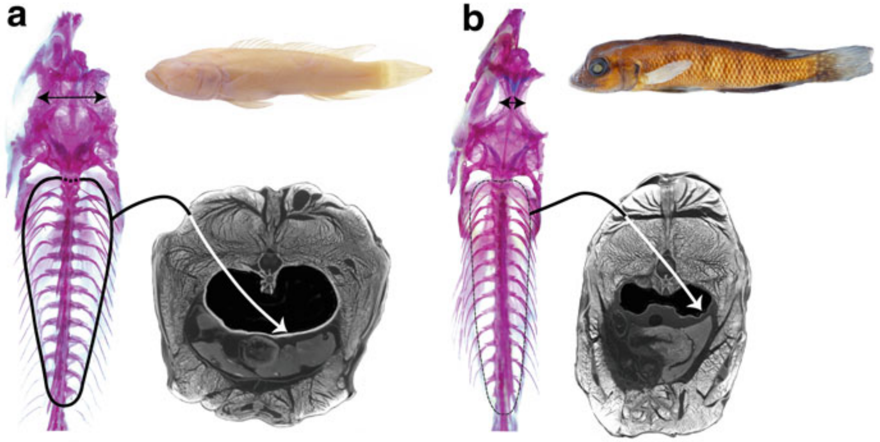

Fig. 6 (**a**) Cleared and stained *L. lethops* (AMNH 247962) in dorsal view, extent of gas bladder outlined. (**b**) Cleared and stained *L. tigripictilis* (AMNH 240906) in dorsal view, extent of gas bladder outlined. Both with transverse section through gas bladder (microCT scan after incubation in phosphotungstic acid). Double-headed arrows in (**a**, **b**) indicate width of frontal bones over orbit

beneath weakly ossified frontal bones. They also posited that the extreme dorsal positioning of optic globes is suggestive of a benthic lifestyle.

The serendipitous recovery of a single living individual found by fishermen from the shoreline at Bulu in 2007 provided a key observation. That specimen (Fig. 4e) exhibited some endothelial lesions when first retrieved, but was otherwise apparently undamaged. However, within a short time, numerous subcutaneous gas bubbles formed over its head, dorsum, and closer examination revealed numerous gas bubbles accumulated beneath the operculum and over the gills. The fish appeared to be suffering from gas-bubble disease, with resulting symptoms of catastrophic decompression syndrome (CDS) (Bouck 1980; Rummer and Bennett 2005) and died shortly after the onset of symptoms. In the absence of any nearby source of natural or human-mediated supersaturation of water (Weitkamp and Katz 1980), it seemed possible that the observed CDS was the result of the rapid transport of a depth-acclimatized fish to the surface. This was the first, albeit inferential, indication that in addition to rapids there may be deep water in the LCR.

The ADCP data illustrated in Fig. 4 not only reveals the presence of extremely deep water in the region but also suggests a potential mechanism for rapid vertical transport from the benthic zone. The large “pool” at bend 2 (Fig. 4c) is located below a sheer rock face about 3 km downstream of the village of Bulu and is a site where fishermen reported frequently finding dead *L. lethops*. In this pool, hydrologists recorded the presence of vertical jets that rapidly transport water between the deep rocky bed and the surface (Fig. 4c). If individuals of *L. lethops* living at, or close to, the rocky bottom were to become entrained in one of these jets they would be subjected to rapid and likely irreversible, upward transport. Such a scenario would result in their catastrophic decompression and death at the water surface.

While speculative, the supposition that populations of *L. lethops* live at extreme depths in one or more of the canyons in the Tadi–Bulu–Luozi region is supported by several anatomical and genomic singularities of the species when compared to its surface-dwelling congener, *L. tigripictilis* (Fig. 5d) and other cichlids. Consistent with reduction of eye size and image formation abilities, *L. lethops* possess markedly inflated laterosensory canals and pores (Fig. 5b), features associated with enhanced sensory acuity in diverse deepwater lineages of lake cichlids (Fryer and Iles 1972; Webb et al. 2014). But perhaps most suggestive of a depth association is the condition of the gas bladder in *L. lethops*. All cichlids are physoclistous and, although efficiently maneuverable within equilibrated depth ranges, are generally highly sensitive to rapid depth/pressure change. Most have limited compensatory abilities with slow equilibration rates—in experimental conditions in the range of just a few meters over 12 h periods (Ribbink and Hill 1979). The typically thin-walled tunica externa of the cichlid gas bladder (e.g., Fig. 6b) apparently contributes to low decompression and pressure equilibration rates and poor ability to rapidly move vertically through the water column. Given the extreme hydraulic conditions potentially exposing benthic fishes to upward transport and rapid decompression, it would be reasonable to anticipate that a reduced, or absent, gas bladder would be adaptive for such a benthic species. While uncommon, gas bladder reduction and loss is known to occur in other LCR cichlids, such as the rapids-adapted genus

Teleogramma (Stiassny and Alter 2015). However, this is not the case in *L. lethops* where, in contrast, the gas bladder is enlarged, encased by a greatly thickened tunica externa, and constrained within a hypertrophied rib cage (Fig. 6a); both attributes that would limit gas bladder expansion. Such a reinforced anatomy would potentially serve to increase the depth range over which *L. lethops* is able to resist positive buoyancy, possibly allowing it to maneuver over and above rocks and crevices, perhaps among pockets of calm or downwelling water. Occasionally, depth equilibrated individuals, or groups of individuals, must be swept out of that "pressure safe" zone above which positive buoyancy would exceed downward swimming abilities, and with an expanding gas bladder, they ascend rapidly to the surface—buoyant and exhibiting symptoms of CDS.

Whether individuals are able to recover from CDS, and/or persist in shallow water habitats has been controversial. We note here that many, but not all, specimens examined have ruptured gas bladders, evident as an anteriorly located tear or hole in the bladder wall. Clearly, such individuals would be unable to recover after ascent, and we suspect that even with intact gas bladders, if untreated, the effects of CDS would either kill the fishes outright or render them vulnerable to predation. However, with intensive human intervention specimens have been revived and a few survived in captivity. Lucanus (2013, p. 8) documents the process as follows:

> The fish showed some distress via gas bubbles and were pierced with a needle to relieve the pressure. For the next two weeks the fish lay on their sides and would not eat, in individual aquariums without decor, but eventually recovered. Of all animals caught, eighty percent would die in the first minutes after capture, another fifteen percent in the next day.

In addition to anatomical and physiological evidence, new genomic data support the hypothesis that *L. lethops* lives in a light-free or extremely low-light environment in the LCR. An analysis of genome-wide variation in *L. lethops* shows that, in addition to loss-of-function mutations in many genes related to eye development and pigmentation, disabling mutations also occur in the gene DDB2, related to repairing DNA damaged by UV light (Aardema et al. 2020). The loss of a functional spexin gene also suggests that *L. lethops* may have altered appetite or satiety as an adaptation to a low-food environment, a phenomenon also observed in Mexican cavefish (e.g., Riddle et al. 2018).

Clearly much remains to be learned about the ecology, evolutionary history, habitat, and population dynamics of this highly unusual LCR cichlid. Ongoing comparative genomic studies of *L. lethops* and related species, informed by the genomic resources currently available for its sympatric congener *L. tigripictilis* (Aardema et al. 2020), and the related Lake Tanganyikan species, *Neolamprologus brichardi* (Brawand et al. 2013), will further illuminate aspects of the genetic underpinnings of the unusual anatomy and physiology of *L. lethops*—perhaps the first known example of persistent, hydrology-driven, mortality in a natural system.

5 Molecular Phylogenetics: Patterns of Colonization and Radiation in the LCR

New molecular techniques can yield insights into the diversity and evolutionary histories of cichlid fishes that were difficult or impossible with the methods available to Roberts and Stewart. Numerous LCR cichlid lineages have since been identified with molecular data (Markert et al. 2010; Schwarzer et al. 2011; Alter et al. 2017; see also Table 1) and, in most cases, where subsequent morphological reexamination has been undertaken, these assessments have been corroborated and new species formally described (e.g., Schelly and Stiassny 2004; Wamuini Lunkayilakio and Vreven 2010; Tougas and Stiassny 2014; Stiassny and Alter 2015). As more refined molecular analyses continue to aid in focusing morphological studies, the tally of LCR endemics will undoubtedly rise further (Lowenstein et al. 2011).

Molecular approaches can now also be used to investigate when and how these diversification events occurred, elucidate patterns of hybridization and introgression, the genomic basis of morphological change and evolutionary innovations, and provide enhanced ecological insights through isotopic studies of food webs and dietary specialization. Though such methods hold great potential for a deeper understanding of the evolutionary history of Congo cichlids, to date only a handful of studies have used these tools to resolve phylogenetic relationships among LCR cichlid lineages or estimate patterns and timing of their diversification. Although relatively few compared to the burgeoning number of molecular investigations of African lake cichlids, these studies have utilized a diversity of approaches, including amplified fragment length polymorphisms (AFLPs), Sanger sequencing of mitochondrial and nuclear genes, microsatellite analysis, and genome-wide single nucleotide polymorphism (SNP) based approaches (double-digest restriction-associated DNA sequencing, or ddRAD-Seq). Most recently studies utilizing genome-wide ultraconserved elements (UCEs) have been initiated (Stiassny et al. 2016). For cichlids, these earlier efforts were advanced by the pioneering work of Julia Schwarzer, Ulrich Schliewen, and colleagues, with molecular studies focused on the numerous LCR endemics in the diverse genera *Steatocranus* and *Nanochromis*. Here we review these and other studies, highlighting areas where similar patterns across groups can be identified and common underlying processes invoked.

Recent molecular studies suggest a rather narrow time frame for colonization of the LCR by cichlids and other fishes and support the idea that colonization occurred at least twice in many clades. With calibrated divergence times for endemic LCR clades ranging from several thousand to ~5 Myr, these findings are consistent with the hypothesis that modern flow conditions in the contemporary LCR have been in place no longer than the last several million years (see Sect. 3 above).

Schwarzer et al. (2011) examined diversification patterns and timing of LCR colonization by *Steatocranus* and *Nanochromis*, using AFLPs and the mitochondrial marker, ND2. Their findings are broadly consistent with the estimated age of the LCR (2–5 Myr) and suggest that at least two temporally distinct colonization events occurred in each genus, followed by in situ diversification. Their phylogenetic reconstruction indicates that endemic LCR species in *Nanochromis* and *Steatocranus* do not comprise single, monophyletic clades, but rather fall into two independent lineages, indicating that the ancestors of these genera arrived in at least two events. Schwarzer et al. (2011) inferred the ages of the two endemic LCR *Nanochromis* clades as 2.67 (1.5–3.9) Myr and 1.6 (0.7–2.5) Myr. Likewise, they identified two clades of *Steatocranus* with age estimates of 4.48 (3.3–5.8) Myr and 0.94 (0.3–1.7) Myr. In addition, in both genera, younger taxa have a distribution limited to the upper and middle LCR, further supporting a hypothesis of two episodes of colonization, since in a single-colonization scenario followed by downstream diversification, the youngest species is expected to be distributed furthest down river.

Results from our own studies using mitochondrial and genome-wide SNP data for the genus *Teleogramma* are broadly consistent with the findings for *Nanochromis* and *Steatocranus* in both timing and spatial patterns. Our data indicate that the oldest mitochondrial lineage found in the LCR, represented by the endemic *T. brichardi*, dates to 4.7 (1.7–7.6) Myr and that the majority of LCR endemic mitochondrial lineages diversified some 0.77 (0.25–1.4) Myr (Alter et al. 2017). Moreover, nuclear SNP data also suggest two episodes of colonization, with *T. gracile* resolved as sister to the other LCR *Teleogramma* species, despite a distribution in the middle of the ranges of these other species (Fig. 7a). Interestingly, a recent study focusing on LCR spiny eels (*Mastacembelus*) found a similar pattern of two independent colonizations and subsequent diversification within a timeframe of ~4 Myr and ~0.5 Myr, respectively (Alter et al. 2015). Such common observations across diverse lineages lend support to the idea that geological, hydrological, and/or ecological conditions facilitated the colonization of the LCR at least twice during the past several million years.

Inferring the biogeographic origins of endemic LCR cichlids is fraught due to undersampling in many of the potential source areas including the Congo basin, but examining the ranges of putative sister taxa provides evidence that the CB and LCR gained and lost connections to several African ecoregions at different times during periods of hydrological reorganization of African river networks. For example, based on a study of the age and potential origins of several chromidotilapiine genera including *Teleogramma*, *Congochromis,* and *Nanochromis*, Schwarzer et al. (2015) propose an ancient connection between the northern CB, the northern part of Lower Guinea, and the Ghanaen–Eburneo region around the late Oligocene/early Miocene. These inferences are based on the ranges of the sister clades to *Congochromis* + *Nanochromis* (including *Chromidotilapia schoutedeni* found in the middle Congo/Lualaba; and *Limbochromis robertsi* found in Ghana). Divergence of these groups in the Oligocene/early Miocene appears to have occurred in allopatry. Biogeographic links between the CB and West Africa/Lower Guinea are also observed in some non-cichlid fishes including *Synodontis* (Day et al. 2013), and *Epiplatys* killifishes (Collier et al. 2009). These patterns provide support for the suggestion, based on sedimentary studies along the Atlantic coastal zone (see

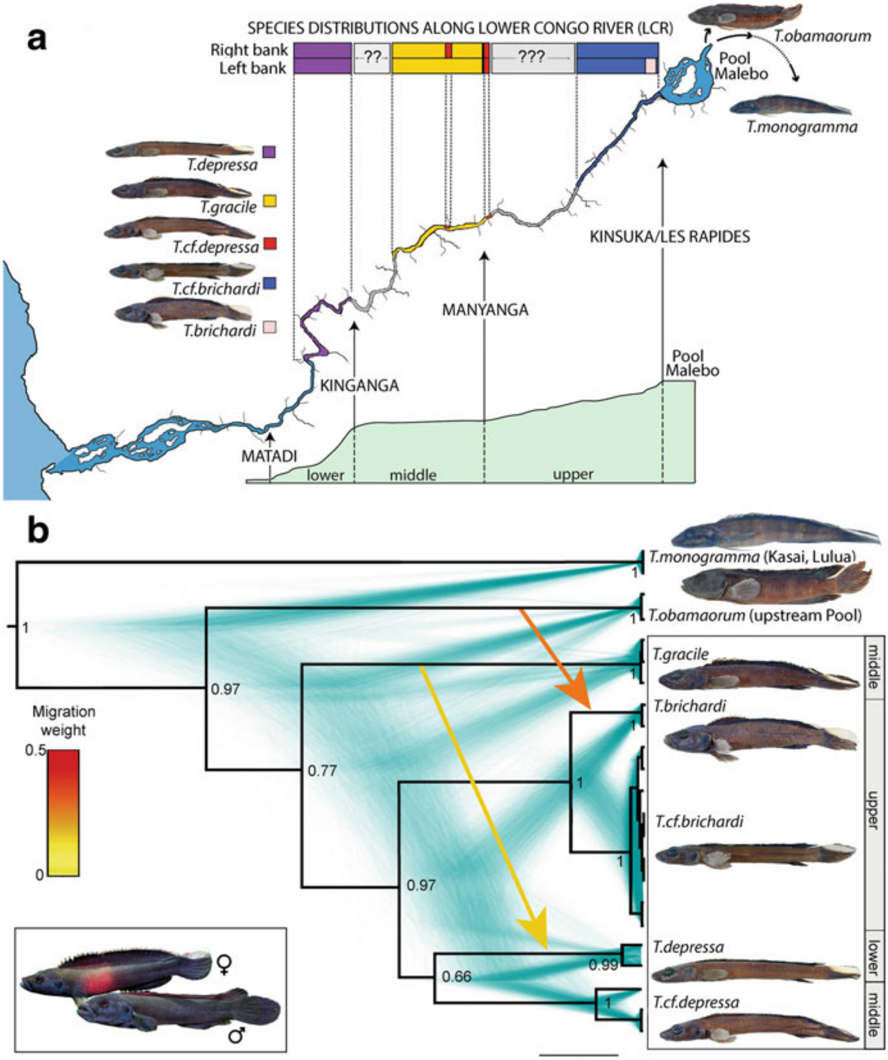

Fig. 7 (**a**) Distributional ranges of *Teleogramma* species along the LCR color coded and schematically represented by offset colored blocks. Regions where no sampling has been possible indicated in gray. (**b**) Phylogenetic relationships estimated from 37,826 SNPs using a multispecies coalescent analysis with the SNAPP program (Bryant et al. 2012). Posterior probabilities are indicated at nodes. Underlying tree cloud (in turquoise) indicates the range of tree topologies recovered. Arrows indicate possible introgression events detected based on the discordance between mitochondrial and nuclear phylogenies. Modified after Alter et al. (2017)

above), that the outflow of a proto-Congo may have initially drained west in the region of the present-day Ogowe Valley.

Haplochromines present evidence of another biogeographic connection. The phylogenetic reconstruction of Schwarzer et al. (2012a), which included the LCR species *Thoracochromis fasciatus, T. demeusi, T. bakongo, Haplochromis snoeksi, Ctenochromis polli,* and *Orthochromis stormsi* suggests that dynamic watershed rearrangements driven by Neogene tectonism (late Miocene/Pliocene boundary) caused multiple instances of introgression and potential hybrid speciation in this group. Mitochondrial and nuclear data in these taxa indicate ancient connections between Congolian and eastern African drainage systems as well as southern Congo–Zambezi connections (Schwarzer et al. 2012a).

Finally, phylogenetic relationships among lamprologine cichlids suggest a recent biogeographic connection between the LCR and Lake Tanganikya, a finding concordant with the pattern found in a clade of spiny eels (*Mastacembelus*) (Alter et al. 2015; Day et al. 2017) and in the cichlid genus *Oreochromis* (Ford et al. 2019). Although based mainly on mitochondrial data, most molecular studies suggest that riverine lamprologines are nested within the Lake Tanganyika radiation (Clabaut et al. 2005; Day et al. 2007; Schedel et al. 2019). Sturmbauer et al. (2010) used mtDNA and AFLPs to reconstruct the phylogenetic history of Lamprologini and, assuming the most recent connection between the Congo and Lake Tanganikya via the Lukuga River occurred in a window between 1.1 and 3.5 Mya, they estimate the split between riverine and lake lamprologines at ~1.7 Mya. Schedel et al. (2019) identify an mtDNA-based clade of central and lower Congo drainage lamprologines that diverged from Lake Tanganyika lamprologines 4.31–9.49 Mya; their analysis supports seeding of the Congo from Lake Tanganyika. While these studies have used a limited set of markers and very few representatives of riverine lamprologines, a recent analysis utilizing over 270 UCEs (151,727 bp) and including multiple individuals of all Congo River species also strongly supports a nested placement of a wholly riverine clade within the Lake Tanganyika radiation (Stiassny et al. 2016 and in prep.).

Taken together, these studies suggest that cichlid clades from different regions of the African continent gained access to the Congo or proto-Congo, and ultimately the LCR, during several distinct periods of connectivity, with chromidotilapines arriving first during the Oligocene/early Miocene, followed by a range of haplotilapiines during connections with east African and Zambezi drainages in the late Miocene/Pliocene, and most recently connections between Lake Tanganikya and Congo in the Quaternary (over the last ~1–2 Myr). Even within the relatively older chromidotilapiines, however, the ages of modern LCR endemics appear to be constrained to the last ~5 Myr, consistent with geological evidence suggesting contemporary hydrological conditions in the LCR are not likely to be much older. Additional data from other cichlid clades (Table 1) and fish families with LCR endemics are ongoing and will be essential for a more refined assessment of these biogeographic patterns and scenarios.

6 Biogeographic Divisions Within the LCR

Based on a series of geomorphological and geological features, three main biogeographic divisions have been recognized across the LCR “rapids region” (see above, and Robert 1946); these divisions are characterized not only by differences in habitat and hydrological attributes but also in patterns of local endemism and species assemblages. Not surprisingly, molecular studies have confirmed biogeographic breaks across a number of species, with the most dramatic break on either side (upstream/downstream) of the massive rapids at Inga (Fig. 2). For example, two clades of *Steatocranus* diversified on either side of the rapids roughly 3 Myr: (1) *S.* sp. aff. *tinanti* “Inga” found downstream of rapids versus *S.* cf. *tinanti* found upstream of rapids; (2) *S. glaber* and *S. mpozoensis* found downstream versus *S.* cf. *gibbiceps* found upstream (Schwarzer et al. 2011). Likewise, a split in *Nanochromis* of roughly the same age occurs between *N. consortus* (downstream) and *N. splendens* (upstream) (Schwarzer et al. 2011). In a study of *Lamprologus tigripictilis* sensu lato using microsatellite and mitochondrial markers, strong population structure was observed between populations upstream and downstream of the Inga rapids (Markert et al. 2010), and the downstream populations have since been described as a distinct, narrowly endemic species (Tougas and Stiassny 2014). These patterns are consistent with the “large Inga waterfall hypothesis” proposed by Schwarzer et al. (2011), suggesting that a waterfall once existed at Inga and isolated downstream lineages, followed by erosion of the falls into rapids allowing for subsequent upstream movement.

While no species of *Teleogramma* have been found below Inga, Markert et al. (2010) describe strong population structure across smaller rapids upstream of Inga in *T. depressa,* and Alter et al. (2017) highlight population structuring across the range of *T.* cf. *brichardi*. Moreover, the majority of lineages in *Teleogramma* (*T. brichardi*, *T. obamaorum*, *T. depressa*, *T.* cf. *depressa*, *T. gracile*) and many other LCR endemics (Schwarzer et al. 2011) have narrow geographic distributions broadly corresponding to hydrological features or habitat regions (Fig. 7a). In all, these studies demonstrate that high-energy in-stream flow structure, complex bathymetry, and the presence of numerous cross-channel rapids have likely played a major role in isolating upstream–downstream, and perhaps cross-channel, populations over extremely small geographical scales thus likely contributing to micro-allopatric speciation in several clades. Such hydrological controls are expected to be particularly effective for strongly lithophilic, small-bodied, physoclistous fishes such as the majority of cichlid species found in the LCR.

7 Hybridization and Reticulate Evolution

For many African cichlids, genetic data have revealed evidence of both recent and ancient gene flow across species boundaries (introgressive hybridization) resulting in repeated patterns of reticulate evolution (e.g., Salzburger et al. 2002; Smith et al.

2003; Koblmüller et al. 2007, 2010; Joyce et al. 2011; Schwarzer et al. 2012a, b; Wagner et al. 2013; Keller et al. 2013; Ford et al. 2015; Meyer et al. 2016). Interspecific gene flow has been hypothesized to play a generative role in diversification as well, for example through acquisition of novel traits and generating species of hybrid origin (Seehausen 2004). Hybridization is also evident across several clades of LCR cichlids and has been inferred via discordance between mitochondrial and nuclear phylogenies and other tests in *Steatocranus*, *Teleogramma*, and *Nanochromis*. Earlier work by Schwarzer et al. (2009) using mtDNA and AFLPs showed cytonuclear discordance in the placement of several taxa in both *Steatocranus* and *Nanonchromis*. A subsequent analysis by Schwarzer et al. (2012b) confirmed complex patterns of reticulation in *Steatocranus* by detecting conflicting phylogenetic signals. Their data support the hypothesis that the *Steatocranus* radiation represents an evolutionary network rather than a bifurcating tree, with one widespread species (*S.* cf. *gibbiceps*) serving as a "vector," connecting geographically distant lineages through gene flow. Similarly, Alter et al. (2017) found conflicting phylogenetic signal in the genus *Teleogramma*, with evidence for ancient but not ongoing introgressive hybridization between certain species (Fig. 7b). While the pattern of hybridization is not as complex as the one inferred for *Steatocranus* by Schwarzer et al. (2012b), it is notable that in both cases introgression appears to have occurred between species found on either side of Pool Malebo.

The apparent preponderance of strong mitonuclear discordance across these, and other, cichlid genera serve to emphasize the dangers of relying solely on mitochondrial genes for phylogenetic reconstruction of cichlids. These studies also demonstrate the potential importance of hybridization as a force shaping evolution and speciation in LCR cichlids, warranting closer study in other key LCR cichlids including those in the genus *Lamprologus*. Ancient hybridization has been postulated for lacustrine species of *Lamprologus* and *Neolamprologus* (see Gante et al. 2016 and references therein), including an instance of total mitochondrial replacement in *N. fasciatus* from *L. callipterus* (Nevado et al. 2009) and mitonuclear discordance in other Tanganikyan species (Koblmüller et al. 2007). Ongoing studies incorporating population-level sampling of all LCR and Congo River lamprologines targeting genome-wide UCEs will likely provide additional insights into potentially complex hybridization patterns in LCR lamprologines.

8 Conclusions and Future Studies

Since the publication of Roberts and Stewart's monograph in 1976, ongoing research has strengthened their proposition that, unlike the situation in most other African riverine systems, the LCR harbors a richly endemic and hyperdiverse cichlid fauna. We have attempted to summarize many of these new findings, particularly those related to the hydrology and geological history of the LCR, as well as evolutionary patterns revealed by molecular data. Overall, these studies indicate that the extreme hydrology and bathymetry of the river has shaped cichlid diversity through micro-allopatric processes, augmented by a series of ancient tectonic and hydrological changes that connected the paleo-Congo to various parts of southern, western and eastern Africa during diverse geological eras. With the relatively recent advent of extreme in-stream water velocities of the LCR, as it plunges from Pool Malebo toward the Atlantic, a pattern of downstream serial colonization and differentiation would be expected. However, molecular data indicate that the history of diversification has been more complex, with evidence for multiple episodes of colonization in several clades. Regardless, it is clear that this turbulent, high-energy system has exerted strong selective pressures on endemic cichlid species—most evident in unusual rheophilic morphologies that appear in *Steatocranus*, *Teleogramma*, and *Lamprologus*. The only known blind cichlid, *Lamprologus lethops*, represents the most extreme consequence of these selective pressures, though a deeper understanding of its evolutionary history awaits additional morphological, phylogenetic, and genomic analyses.

While enormous progress has been made in the last four decades in understanding cichlid evolution and ecology in the LCR, the studies summarized here have only scratched the surface of this exceptional system. New techniques in imaging including micro- and Dice-CT, and sophisticated new methods in 2D and 3D morphometrics, hydrological modeling, and next-generation sequencing have enormous potential to expand our knowledge about morphological diversification, and the timing and sources of speciation events, and the intrinsic and extrinsic drivers of those events. Most critically, more biological surveys are urgently needed, particularly in downstream areas such as Bulu, Tadi, and Inga where many of the most narrowly endemic and morphologically distinctive species have been discovered. Such surveys should also integrate geological and hydrological data collection to further our understanding of the physical context of evolutionary and ecological processes. Additional surveys to document the region's aquatic biodiversity have taken on increased urgency in light of the proposed development of a mega-dam (Grand Inga) that threatens to massively impact the flow regime of the LCR (Showers 2011; Oyewo et al. 2018).

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Neotropical Riverine Cichlids: Adaptive Radiation and Macroevolution at Continental Scales

Hernán López-Fernández

Abstract Neotropical cichlids include over 550 species from Central and South America and the Caribbean and are increasingly recognized as models for studying evolutionary diversification. Cichlinae's great morphological, ecological, and behavioral diversity is concentrated in the tribes Geophagini, Heroini, and Cichlasomatini. Feeding and swimming morphology broadly fit two gradients of ecomorphological differentiation: An "elongation axis" follows a ram–suction feeding gradient of deep-bodied fishes with diverse diets at one end and mostly predatory shallow-bodied taxa at the other end. Body and fin configurations correspond with habitats spanning open substrate to structured areas. A second gradient of morphology spans suction feeders and biters with benthic-feeding or complex three-dimensional habitats. Several body configurations reflect specializations to live in rapids. Rates of Cichlinae ecomorphological disparity and lineage diversification often showed early, rapid acceleration followed by a slowdown. Early divergence in South America was likely dominated by the radiation of Geophagini. Rapid geophagin diversification into new niches may have precluded divergence in other South American cichlids, particularly Heroini and Cichlasomatini. Further lineage and morphological divergence in Heroini increased after colonization of Central America. Cichlinae appear to have repeatedly radiated by taking advantage of ecological opportunity in novel environments across the Neotropics, resulting in widespread convergence.

Keywords Ecomorphology · Convergent evolution · Adaptive landscapes · Ecological opportunity · Geophagini · Heroini

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H. López-Fernández (✉)
Department of Natural History, Royal Ontario Museum, Toronto, ON, Canada

Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada

Current Address: Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA
e-mail: hlopezf@umich.edu

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1 Neotropical Cichlids Then and Now

Our knowledge of Neotropical cichlids has grown vastly since the publication of Keenleyside's (1991) edited volume. At the time, most work on South and Central American cichlids had been focused on taxonomy, ecology, and behavior, but little was known about phylogeny or the evolutionary biology of the group. Perhaps understandably eclipsed by the stunning diversity and breakneck speed of divergence of the East African radiations, Neotropical cichlids were not widely thought about as subjects of diversification studies. The decades since then have seen an enormous increase in interest on the evolution of Neotropical cichlids that is beginning to offer a valuable complement to the study of East African radiations.

In the first chapter of Keenleyside's book, Stiassny (1991) presented the first phylogeny for cichlids and established the reciprocal monophyly of the African and Neotropical clades. Her phylogeny set the stage for a flood of subsequent interest in reconstructing the relationships of cichlids, and the Neotropical clade in particular. A few years later Kullander (1998) and Farias et al. (1998), respectively, pioneered morphological and molecular phylogenetic analyses of Neotropical cichlids that eventually led to an increasingly solid base for studying the timing and mode of divergence in the clade. Also in the Keenleyside volume, Lowe-McConnell (1991) provided the only chapter dedicated to the riverine cichlids of the Neotropics and Africa: a brief summary of ecology that brought up the importance of studying the ecological and functional diversity of cichlids outside of the African Great Lakes. Lowe McConnell had pioneered the study of the ecology of riverine cichlids in both continents and published some of the first studies of South American cichlid ecology working in Guyana (1964, 1969). Her book "*Fish communities in tropical freshwaters*" set the stage for innumerable studies of fish ecology in the Neotropics and elsewhere (Lowe-McConnell 1975). By the 1980s and early 1990s, parallel but as yet separate advances in ecological and systematic studies started to converge through the emergence of comparative methods aimed at studying the evolution of ecological traits in a phylogenetic context (e.g., Felsenstein 1985; Grafen 1989; Harvey and Pagel 1991; Brooks and McLennan 1991). The first study linking ecology and an early expression of the phylogeny of cichlids looked at ecomorphology and convergent evolution in the Neotropics and Africa (Winemiller et al. 1995). Winemiller and colleagues used Stiassny's (1991) tree as a backbone and taxonomic classifications as a proxy for relationships; then they mapped an extensive dataset of morphometrics and diet on their tree. In that first comparative macroevolutionary study of riverine cichlids, they found extensive ecomorphological convergence between South and Central America, as well as convergence between Neotropical and African cichlid communities and taxa. Since then, extraordinary advances in molecular phylogenetics and an explosion of newly developed comparative methods have opened entirely new avenues for studying diversification and macroevolution.

The study of African lake cichlids consolidated the image of cichlids as classic examples of vertebrate "adaptive radiations" (e.g., Kornfield and Smith 2000;

Verheyen et al. 2003; Kocher 2004; Seehausen 2006; Salzburger et al. 2014). A concept originally defined by Simpson (1953), the modern "ecological theory of adaptive radiation" (Schluter 2000) studies a process by which the ancestor of a clade diversifies into a number of functionally distinct lineages. As new lineages emerge, ecological niches (together representing *ecological opportunity*, Schluter 2000; Yoder et al. 2010; Gavrilets and Losos 2009) are progressively occupied until eventually new lineages fail to become established due to the absence of further unfulfilled ecological opportunity. Adaptive radiation thus leaves a characteristic phylogenetic signature reflected in lineage and phenotypic divergence patterns (e.g., Gavrilets and Losos 2009; Glor 2010; Losos and Mahler 2010). Essentially, increasing diversity during adaptive radiation is evidenced by the rapid accumulation of lineages and of ecologically relevant (i.e., functional) phenotypic traits. This early increase or "early burst" of divergence is followed by a slowdown in rates of divergence as ecological opportunity wanes and lineages can no longer diversify into new niches. Simpson (1944, 1953) envisioned the niches occupied by successful, newly emerged lineages as *adaptive zones,* which together formed an *adaptive landscape* with peaks of high fitness and valleys of low fitness separating different lineages. Evolving lineages can invade new adaptive zones as they adapt to utilize niches within them. In this context, convergent evolution results from independent lineages being subject to similar selective pressures that drive them toward the same adaptive zone or *adaptive peak*. The concept of adaptive landscape allows envisioning the direction and strength of selection during macroevolutionary divergence as it would occur in adaptive radiation.

Until recently, the empirical study of adaptive radiations and adaptive landscapes was greatly limited by a lack of tools to analyze macroevolutionary patterns in a phylogenetic context. The rise of modern molecular phylogenetics and phylogenetic comparative methods has greatly expanded the study of adaptation and adaptive radiations at macroevolutionary scales. Comparative methods provide tools for two broad types of evolutionary inference: (1) establishing evolutionary correlations among characters (e.g., morphology, diet, habitat use) while accounting for lack of statistical independence due to common ancestry, and (2) fitting models of evolution to infer the processes under which diversity might have evolved (O'Meara 2012; Pennell and Harmon 2013). Both approaches use models of evolution, but while the former corrects for phylogeny (e.g., Felsenstein 1985) the latter uses phylogenetic patterns to delimit plausible hypotheses about the evolutionary process (e.g., Harmon et al. 2003; Rabosky and Lovette 2008; Mahler et al. 2010; Pennell and Harmon 2013; Slater and Pennell 2014). Emerging evolutionary models are also being developed to estimate the adaptive landscape of a clade by modeling selection on traits along the branches of a phylogeny (e.g., Beaulieu et al. 2012; Harmon 2018; Harmon et al. 2008; Ingram and Mahler 2013; Mahler et al. 2013; Mahler and Ingram 2014).

Until these new tools and increasingly strong hypotheses of phylogenetic relationships became available, the patterns of divergence and possible mechanisms that originated the functional and ecological diversity of Neotropical cichlids remained all but unknown. Recent work supports the idea that (1) functional divergence in

Neotropical cichlids is compatible with early adaptive radiations at continental scales, generally followed by stasis in functional and ecological innovation; (2) that convergence among clades has been extensive; and (3) that at least some of this convergence was driven by renewed ecological opportunity in novel environments. Further research is needed in determining whether and how the processes associated with the early adaptive radiations of tribes and genera may continue to play a role in more recent, species-level divergence. The exact timing and environmental context of Neotropical cichlid radiation still need much clarification. Nevertheless, the origin of Neotropical cichlid diversity is increasingly emerging as a continent-wide case of ecologically driven adaptive radiation that gave origin to the functionally and ecologically distinct lineages at the deeper levels of the phylogeny. Recent discoveries suggest that some Neotropical cichlids also have undergone radiations in geographically restricted riverine environments and relatively recent time frames (e.g., Burress et al. 2018; Piálek et al. 2018).

In this chapter, I attempt to offer a brief review of some of the recent advances in our understanding of Neotropical cichlid evolution. Due to space limitations and because I find them of particular interest, this review focuses on macroevolutionary patterns as perceived through the analysis of ecological, ecomorphological, and functional morphological data. I concentrate on describing the emerging understanding of patterns and possible mechanisms of higher-level adaptive diversification throughout South and Central America. Unfortunately, this focus requires leaving much of interest out from the chapter. I encourage readers interested in topics such as historical biogeography, behavior, or systematics to peruse the extensive literature available on those and related subjects.

2 The Riverine Neotropical Cichlid Fauna

Neotropical cichlids (subfamily Cichlinae) encompass over 550 described species plus an uncertain, but probably large, number that remain undescribed. Cichlid diversity in the Neotropics remains incompletely sampled, with new species being discovered frequently, either by reanalysis of previously established taxonomies (e.g., Maza-Benignos and Lozano-Vilano 2013; Schmitter-Soto 2007), study of established collection materials (Kullander and Varella 2015; Malabarba et al. 2015) or by field-based discovery, particularly in previously unexplored regions (e.g., López-Fernández et al. 2012a; Varella and Moreira 2013). Moreover, it is likely that our view of Neotropical cichlid diversity will continue to change as our understanding of geographic distributions and genetic variation increase (e.g., Amado et al. 2011; Colatreli et al. 2012; Willis et al. 2012, 2014; Willis 2017).

2.1 Taxonomic Diversity and Geographic Distribution

Neotropical cichlids are distributed from the southern United States where the Texas Cichlid (*Herichthys cyanoguttatus*) represents the northern-most lineage, to the northern edge of Patagonia in Argentina. Cichlids also naturally occur in the Pacific slopes of Colombia, Peru, and Ecuador, the Antillean islands of Cuba and Hispaniola, and the island of Trinidad (Fig. 1). Cichlinae diversity is not uniformly distributed either phylogenetically or geographically. Three monophyletic groups classified as tribes contain most taxa of Cichlinae: Geophagini, Heroini, and Cichlasomatini, with four additional tribes—Cichlini (1 genus, 16 described species), Retroculini (1, 4), Astronotini (1, 2), and Chaetobranchini (2, 4)—accounting for a much smaller but distinct number of taxa that occur only in South America east of the Andes.

The tribe Geophagini includes 16 genera and more than 260 described species at the time of this writing, and many more in need of description. Geophagini is the most species-rich Neotropical clade and ranges from southern Panama to northern Argentina, including the Pacific slope and Magdalena basin of Colombia, plus one drainage in the Guajira peninsula of Venezuela. Geophagin diversity reaches its peak in the Amazon and Orinoco basins, but the northwestern Andes, the Guiana Shield, and the Paraná basin also hold endemic genera or species with unique evolutionary and biogeographic significance (e.g., Burress et al. 2018; Kullander and Nijssen 1989; López-Fernández et al. 2012a; Piálek et al. 2012, 2018; Malabarba et al. 2015).

The tribe Cichlasomatini largely overlaps in distribution with Geophagini and includes 11 genera and 77 described species. Cichlasomatins are present further south on the Pacific slope of the Andes, reaching central Peru, but are most diverse in the lowlands of the Amazon and the Orinoco, as well as in the slopes of the eastern Andes (Kullander 1986; Musilová et al. 2008, 2009).

The only Neotropical cichlid clade broadly distributed in both South and Central America is Heroini, with a total of 183 described species in up to 38 named genera (Říčan et al. 2016). As a consequence of taxonomic revision of the genus *Cichlasoma* (Kullander 1983), to which most Heroini were once assigned, this group has remained in taxonomic flux for an extended period. Several lineages with long unrecognized generic status are now being assigned to either previously available or newly proposed names (e.g., Kullander 1983, 1996; Kullander and Hartel 1997; Schmitter-Soto 2007). Very recent work has made major revisions to heroin classification (McMahan et al. 2015; Říčan et al. 2016), but given the long history of taxonomic instability, it is likely that additional changes will occur as further taxonomic and phylogenetic understanding of Central American heroines continues to emerge. Phylogenetic analyses have revealed that several heroin genera with South American distributions have originated in Central America (e.g., Hulsey et al. 2004; Říčan et al. 2008; López-Fernández et al. 2010; McMahan et al. 2013; Říčan et al. 2016; Ilves et al. 2018) but our understanding of the historical biogeography linking South and Central American cichlids is far from definitive (e.g.,

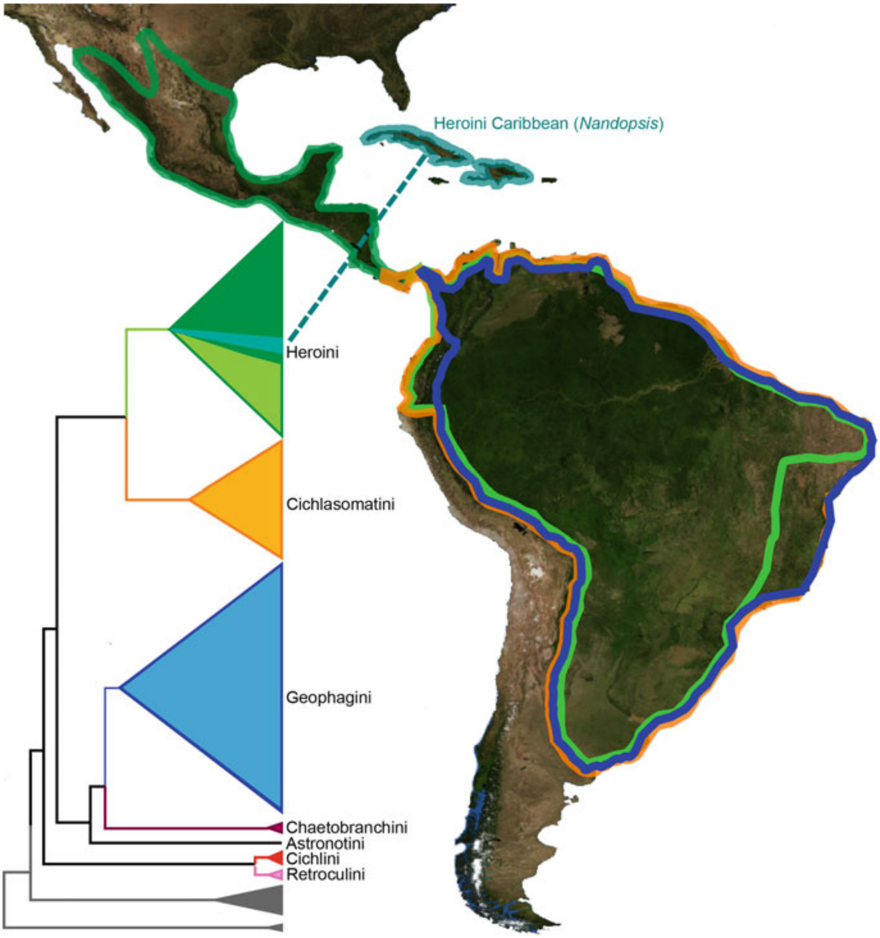

Fig. 1 Phylogeny and distribution of Neotropical cichlids (subfamily Cichlinae). A simplified version of the phylogeny of Cichlinae highlights each of the seven tribes, size of triangles represents approximate proportional species richness; see text for actual diversity. Heroini (Green, light green depicts taxa with South American distribution, dark green are taxa with Mesoamerican distribution, teal shows the genus *Nandopsis*, restricted to Cuba and Hispaniola in the Caribbean); Orange: Cichlasomatini; Blue: Geophagini; Purple: Chaetobranchini; Black: Astronotini; Red: Cichlini; Pink: Retroculini. Lineages in gray depict African, Malagasy, and Indian outgroups. Colored lines on the map represent the approximate distribution of the three main tribes in South and Central America. (Modified from López-Fernández et al. 2013; Satellite image courtesy of NASA: Neo Earth Observations)

Chakrabarty et al. 2011; Říčan et al. 2013; Tagliacollo et al. 2017; Ilves et al. 2018). South American heroines are comprised of two non-monophyletic sets of taxa: seven basal lineages which originated in South America (primary South American heroines, sensu Arbour and López-Fernández 2016, *Heros*, *Hoplarcus*, *Hypselecara*, *Mesonauta*, *Pterophyllum*, *Symphysodon,* and *Uaru*) and several others with South

American distributions but phylogenetically nested within the Central American clade (*Australoheros*, *Caquetaia*, *Heroina*, *Kronoheros* [= formerly *Caquetaia umbrifera*], and *Mesoheros*). Together, these two groups are broadly distributed in the Amazon, Orinoco, Paraná, and Pacific Andean basins from Colombia to northern Peru but are relatively species-poor—with the exception of *Australoheros* from the Paraná-La Plata. Finally, the only Caribbean cichlids belong in the genus *Nandopsis*, distributed in Cuba and Hispaniola with three described species and a putative fossil taxon (Chakrabarty 2006a, b).

2.2 Phylogeny, Times of Divergence, and Macroevolutionary Analyses

Neotropical cichlids (subfamily Cichlinae) are a monophyletic clade sister to a monophyletic African sister group (subfamily Pseudocrenilabrinae). In turn, the Neotropical-African clade is sister to a paraphyletic assembly of Indian and Malagasy taxa (Stiassny 1991; Kullander 1998; Farias et al. 2000; Sparks and Smith 2004; Smith et al. 2008). While species-level phylogenies are not established for most lineages and a few genus-level relationships remain elusive, relationships among the seven recognized Neotropical cichlid tribes and most genera within them are generally well established and supported (e.g., Hulsey et al. 2004, 2011; Říčan et al. 2008, 2016; López-Fernández et al. 2010; McMahan et al. 2013; Ilves et al. 2018, Fig. 1).

Relationships among most genera are reasonably well established within Cichlasomatini (Musilová et al. 2008, 2009, 2015; Smith et al. 2008; López-Fernández et al. 2010), and Geophagini (Kullander 1998; López-Fernández et al. 2005a, b, 2010; Ilves et al. 2018). The phylogenetic relationships among heroines are becoming increasingly resolved, particularly with the publication of recent phylogenomic analyses, but further study is needed to clarify some relationships (e.g., Říčan et al. 2008, 2013, 2016; López-Fernández et al. 2010; Hulsey et al. 2010; McMahan et al. 2015; Matschiner et al. 2017; Ilves et al. 2018). Basal heroins from South America form a paraphyletic arrangement sister to the rest of the clade. Whereas all studies find two large subclades among Middle American heroins, the exact composition of these groups and the relative position of some genera within them can vary depending on the analysis. This is particularly true of the relationships within the amphilophins clade; a clearly monophyletic group for which species assignment to different genera has been contentious due to often poorly resolved or ambiguously supported basal relationships. Even recent analyses based on extensive taxon sampling and genome-wide phylogenomic approaches still reveal some ambiguity in the relationships within amphilophins and a few other heroins (Říčan et al. 2016; Ilves et al. 2018). The position of the Antillean genus *Nandopsis* and of South American lineages within the Middle American phylogeny can also vary across studies. Due to such phylogenetic uncertainty, to differences in methods and to incongruence among age estimates, the historical biogeography of Middle American colonization and recolonization of South America by heroins remains an active area of study (e.g., Chakrabarty and Albert 2011; Hulsey et al. 2011; Říčan et al. 2013; Tagliacollo et al. 2017; Musilová et al. 2015, and see discussions in Matschiner 2018; Ilves et al. 2018).

Correctly estimating the age of cichlids affects much more than our understanding of Central American biogeography. The distribution of cichlids across the southern hemisphere coincides with that of many of the landmasses of Gondwana, making the family important in the study of historical biogeography of both fishes and other taxa. The age of cichlids also is critical in understanding the timeline of diversification and the environmental context in which Neotropical cichlids diversified. Despite the importance of having reliable estimates of cichlid ages, considerable debate persists, with current age estimates ranging from the early Cretaceous to the Eocene (e.g., Genner et al. 2007; Azuma et al. 2008; Friedman et al. 2013; López-Fernández et al. 2013; Říčan et al. 2013; Tagliacollo et al. 2017, and see the detailed review by Matschiner 2018). There are multiple reasons for such lack of consensus, including the limited information available from the fossil record, the varying sets of assumptions required to date molecular phylogenies, the molecular data used in different studies (e.g., nuclear vs. mitochondrial), and whether estimates come from analyses aimed at dating cichlids per se (e.g., Genner et al. 2007; López-Fernández et al. 2013; Tagliacollo et al. 2017; Matschiner et al. 2017; Irisarri et al. 2018) or from broader studies dating large clades of fishes that include cichlid taxa but may (Betancur-R et al. 2013, 2017b; Hughes et al. 2018) or may not include cichlid fossils (Near et al. 2012; Friedman et al. 2013).

Ultimately, the only way to reliably estimate the age of any clade is by using robust fossil calibrations. Although the cichlid fossil record is limited, there are some fossils with excellent preservation that should help accurately date cichlids. Particularly relevant in the context of this chapter are recently described fossils from the Eocene Lumbrera formation in Argentina. These fossils include the geophagin †*Gymnogeophagus eocenicus (the dagger symbol denotes a fossil taxon throughout the chapter)*, which phylogenetic analysis supports as part of the extant geophagin genus *Gymnogeophagus* (Malabarba et al. 2010; 2014). The Lumbrera fossils also include the putative heroin †*Plesioheros chauliodus* (Alano-Pérez et al. 2010) and the equivocally placed †*Proterocara argentina* (Malabarba et al. 2006). With an age of at least 40 Ma (del Papa et al. 2010; Malabarba et al. 2014), these fossils provide minimum ages for two of the main clades of Neotropical cichlids. The putative cichlasomatin †*Tremembichthys garciae* of Eocene–Oligocene age (Malabarba 2008; Alano-Pérez et al. 2010) may provide a minimum age for the third-largest clade of Cichlinae. A Miocene fossil assigned to the Antillean heroin genus *Nandopsis* is also available, although poorly preserved (Tee-Van 1935; Chakrabarty 2006a). Additionally, extraordinarily preserved African cichlid fossils in the genus †*Mahengechromis*, of Eocene age, are also available, but their phylogenetic placement is not clearly established (Murray 2001; Sparks 2004). Ongoing and future studies using expanded datasets and new methods for dating phylogenies have much to contribute to the currently controversial age of cichlids.

Despite the relatively poor state of our understanding of cichlid ages, using phylogenies for comparative analyses of Neotropical cichlid macroevolution is still a valid and powerful approach, especially when analyses focus on higher levels of divergence, such as tribes and genera. For the purposes of this chapter, whenever phylogenetic correction is used, most analyses are based on the phylogeny published by López-Fernández et al. (2010) and time-calibrated in López-Fernández et al. (2013). More recent analyses that have expanded both on numbers of loci and taxon sampling (e.g., Říčan et al. 2013, 2016) or used different molecular markers (e.g., Friedman et al. 2013) continue to support most of the higher-level relationships found in that study. Furthermore, the López-Fernández et al. (2010) phylogeny remains the most thoroughly sampled single analysis of Neotropical cichlid lineages throughout the subfamily. Recent exon-based phylogenomic analysis with comparable taxon sampling corroborated and strengthened most of the relationships found in that study (Ilves et al. 2018). Simulation analyses (Arbour and López-Fernández 2016) have shown that the macroevolutionary studies described in the rest of this chapter should remain robust to potential disagreements among phylogenetic hypotheses or potential identification problems pointed out elsewhere (e.g., Říčan et al. 2013 and see Ilves et al. 2018). When performing comparative analyses using phylogenies it is essential not to base all analyses on one tree, but rather to employ a distribution of trees that allows establishing credibility intervals and accounting for the possible biases introduced by phylogenetic uncertainty and branch length variation (e.g., Rabosky 2014; Slater and Pennell 2014). Time-calibration of phylogenies using Bayesian methods, as have been applied to Neotropical cichlids (e.g., López-Fernández et al. 2013; Říčan et al. 2013; McMahan et al. 2013; Tagliacollo et al. 2017), generate distributions of chronograms that span the range of variation in both phylogenetic relationships and in time estimates. These distributions of trees include ranges of age estimates with chronograms of correspondingly different total lengths (i.e., total ages). Meaningful statistical comparisons of trait evolution and distribution analyses among a sample of chronograms, however, are more easily obtained and interpreted if all trees have the same total length. This is achieved by adjusting all trees to an arbitrary total length, usually 1, which eliminates variation in tree length due to varying time estimates while keeping the proportionality of branch lengths among trees (e.g., López-Fernández et al. 2013). Such comparative analyses facilitate robust interpretations of evolutionary patterns along the distribution of trees, but due to the rescaling of tree length, they are based on "relative-time" and do not directly provide information regarding the absolute timing of evolutionary events. In an unexpected way, this is a fortunate circumstance because it allows for valid macroevolutionary analyses even in the presence of extensive disagreement in time estimates.

2.3 *Ecological and Morphological Diversity: Cichlinae Functional Morphospace*

Neotropical cichlids encompass a tremendous diversity of morphological, ecological, and behavioral adaptations. An extensive literature is available that includes ecological analyses, ecomorphological correlations, and functional morphological models that describe cichlid ecology. Trophic diversity in Neotropical cichlids is strongly associated with morphological variation. Ecomorphological and biomechanical studies have outlined the main axes of functional variation in trophic specialization and linked both ecomorphological and biomechanical traits with diet composition, prey attributes, or more rarely, foraging behavior (e.g., Burress 2016; Burress et al. 2013; Cochran-Biederman and Winemiller 2010; Hulsey and García De León 2005; López-Fernández et al. 2012b, 2014; Montaña and Winemiller 2013; Waltzek and Wainwright 2003; Winemiller et al. 1995). Despite all these studies, detailed dietary data are lacking for many taxa and their trophic preferences must often be inferred based on closely related but better-studied species or functional morphology (e.g., Arbour and López-Fernández 2014). Moreover, among existing analyses, units of measurement are often not comparable across studies (e.g., some use percent volume and others use frequency of occurrence of diet items), limiting our ability to integrate ecological and functional information on Neotropical cichlids.

Ecomorphological and functional convergence among clades of Cichlinae is widespread, in most cases making it difficult to constrain descriptions of trophic ecology to a particular clade. Cichlid communities generally share ecotypes across regions such that the functional groups present in a community are common across assemblages (e.g., Winemiller et al. 1995; Seehausen 2015). Most ecomorphological and behavioral diversity in Neotropical cichlids is concentrated in the three major clades, Geophagini, Heroini, and Cichlasomatini. Nevertheless, the smaller tribes encompass significant and sometimes unique sets of Cichlinae ecological specializations, most notably two specialized plankton-feeding genera in Chaetobranchini (*Chaetobranchus*, *Chaetobranchopsis*) and the exclusively piscivorous Cichlini (genus *Cichla*). Using phylogenetic corrections (see previous section for details), several recent studies of Cichlinae or Geophagini have summarized variation in ecologically meaningful external morphology (López-Fernández et al. 2012b, 2013; Feilich 2016), feeding biomechanics (Arbour and López-Fernández 2013, 2014), swimming functional morphology (Astudillo-Clavijo et al. 2015) and the lower pharyngeal jaw (Burress 2016). Other studies have directly correlated ecomorphology or functional morphology with stomach contents analyses in a phylogenetic context (Winemiller et al. 1995; López-Fernández et al. 2012b; Burress 2016). Because feeding and habitat use (related to swimming morphology) are among the most relevant axes of ecomorphological divergence in cichlids and other fishes (Collar et al. 2008; Price et al. 2011; Claverie and Wainwright 2014), these studies provide insight into some of the main drivers of Neotropical cichlid diversification within a generalized Cichlinae *functional morphospace* on which analyses and discussions of macroevolutionary patterns can be grounded.

With or without phylogenetic correction, Principal Components Analysis of external morphology, oral jaw mechanics and swimming attributes of Cichlinae result in two significant Principal Components (PC1, PC2) delimiting a two-dimensional morphospace dominated by variation in morphological traits associated with feeding and swimming (e.g., Montaña and Winemiller 2010; Cochran-Biederman and Winemiller 2010; López-Fernández et al. 2012b, 2013; Pease et al. 2012; Arbour and López-Fernández 2013, 2014; Astudillo-Clavijo et al. 2015). While not identical, the commonalities among morphospaces defined by these two axes allow them to be meaningfully joined into a diagrammatic representation that describes general patterns of ecomorphological specialization among Neotropical cichlids as we understand them today, particularly in regard to traits associated with feeding and swimming performance (Fig. 2). Variation in the pharyngeal jaws does not appear to follow the same pattern as this generalized space (Burress 2016), but this lack of correspondence adds to our understanding of cichlid trophic specialization and further supports the idea of a decoupling between oral and pharyngeal jaws in cichlid feeding biology (see below, and Liem 1973; Hulsey et al. 2006a, 2010).

2.3.1 Elongation or Ram–Suction Feeding Axis

Regardless of the variables analyzed, functional morphospace in Cichlinae is dominated by an “elongation axis” along PC1. This axis ranges between very elongate fishes with shallow bodies and heads and low positioned eyes (negative [left] end of horizontal axis on Fig. 2; e.g., the geophagin *Crenicichla*, and to a lesser degree *Cichla*, *Retroculus* and the heroins *Petenia* and *Parachromis*) versus taxa with deep bodies and heads and eyes displaced dorsally of which the most extreme examples are all within Heroini (positive [right] end of horizontal axis on Fig. 2, (e.g., *Symphysodon*, *Pterophyllum* and *Paraneetroplus* [= *Vieja* in recent taxonomic revisions]; throughout this chapter, I refer to the taxon names used in the original publications to facilitate the reading of earlier literature. Current generic names are given in brackets when pertinent). Functionally, the elongation axis represents a gradient between ram-feeding and suction or biting feeders. The ram-feeding end of the gradient (Fig. 2, left) includes lineages with highly protrusible oral jaws, fast opening and closing of lower jaws with even occlusion (gripping bite), relatively strong pharyngeal crushing potential and comparatively low suction force. These are attributes that generally characterize predatory fishes but can also include taxa specialized to living in rapids regardless of their feeding habits (e.g., *Teleocichla*, *Crenicichla*, *Theraps*, Arbour and López-Fernández 2013, 2014). This configuration allows both fast-start accelerations and turns associated with predation on elusive prey and maintaining position in high currents (Astudillo-Clavijo et al. 2015); often both are combined in various species of *Crenicichla* (Zuanon 1999).

Diet analyses show that many taxa in the elongate end of the axis are at least partially piscivorous and include the tribes Cichlini (Genus *Cichla*), Geophagini (*Crenicichla*), Cichlasomatini (*Acaronia*), and Heroini (*Petenia*, *Caquetaia*, *Parachromis*, and “*Cichlasoma*” (= *Mayaheros*] *urophthalmus*) (e.g., Winemiller

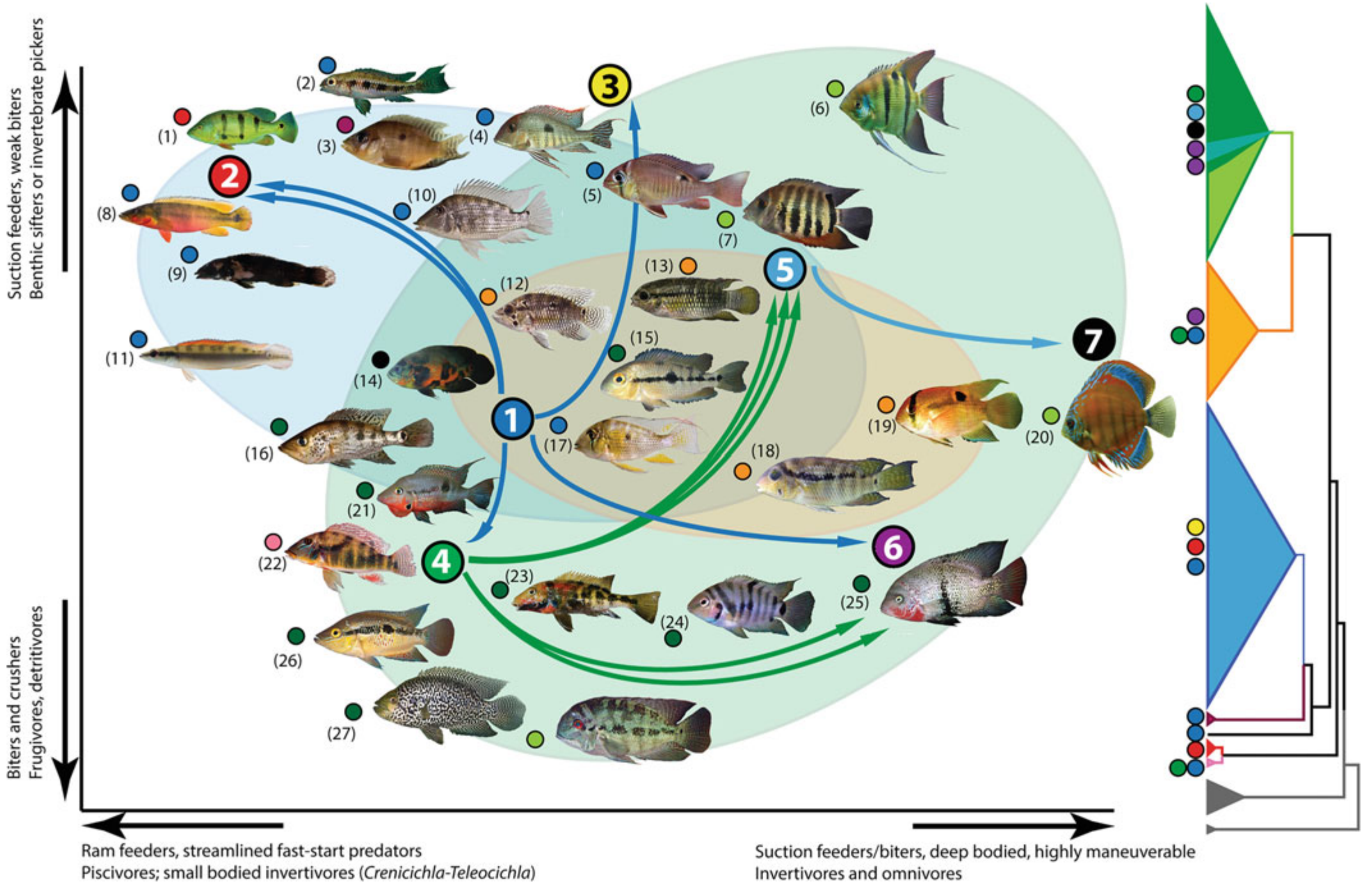

Fig. 2 Cichlinae functional morphospace and adaptive landscape—*Left*: A diagrammatic representation summarizes the ecomorphological and functional morphospace of Neotropical cichlids based on the first two axes of phylogeny-corrected Principal Components Analyses (see López-Fernández et al. 2013;

Arbour and López-Fernández 2014; Astudillo-Clavijo et al. 2015 for description of the original analyses and the actual PCA-based morphospaces). Ellipses depict generalized representations of morphospace for the main Cichlinae clades: Geophagini (blue), Heroini (light green: South America; dark green: Mesoamerica), and Cichlasomatini (orange). Numbered colored circles depict the approximate placement of feeding mechanics adaptive peaks (Arbour and López-Fernández 2014). Peak 1 (Blue) represents the most likely ancestral adaptive optimum for South American cichlids; Peak 4 (Green) is the most likely adaptive optimum for Central American cichlids. Arrows depict transitions between peeks; multiple arrows represent independent (convergent) moves between adaptive peaks. *Right*: Phylogeny showing the adaptive peaks (circles) detected for each of the Neotropical cichlid clades (triangles). Peak and clade colors in the phylogeny correspond to the peak and clade colors in the adjacent morphospace. Two peaks side by side (blue and green) represent an ambiguous reconstruction of the ancestral peak for a clade (i.e., blue and green for Cichlasomatini and Retroculini). Peak 6 (purple) evolved twice independently within Heroini; peak 2 (red) evolved independently in Cichlini and in the geophagine genus *Crenicichla*. See text and Arbour & López-Fernández for details and methods. Photographs depict representative genera/species and their approximate position in morphospace. See text for details of morphospace interpretation. Genera identification: (1) *Cichla*, (2) *Dicrossus*, (3) *Chaetobranchus*, (4) *Geophagus*, (5) *Biotodoma*, (6) *Pterophyllum*, (7) *Heros*, (8) *Crenicichla* (large, piscivores), (9) *Teleocichla*, (10) *Satanoperca*, (11) *Crenicichla* (small, invertivores), (12) *Acaronia*, (13) *Laetacara*, (14) *Astronotus*, (15) *Hypsophrys*, (16) *Petenia*, (17) *Acarichthys*, (18) *Bujurquina*, (19) *Cleithracara*, (20) *Symphysodon*, (21) *Thorichthys*, (22) *Retroculus*, (23) *Theraps*, (24) *Amatitlania*, (25) *Vieja*, (26) *Trichromis*, (27) *Parachromis*, (28) *Hoplarchus*. Species do not necessarily depict those utilized in the original analyses. Colored dots by each image depict the clade to which each genus belongs (and see Fig. 1): Blue = Geophagini, Orange = Cichlasomatini, Green = Heroini, Red = Cichlini, Black = Astronotini, Purple = Chaetobranchini, Pink = Retroculini (Photo credits: H. López-Fernández, J. Arbour, K. M. Alofs, M. H. Sabaj-Pérez)

1989; Winemiller et al. 1995; Montaña and Winemiller 2009, 2010; Cochran-Biederman and Winemiller 2010; Kullander and Ferreira 2006; López-Fernández et al. 2012b; Soria-Barreto et al. 2019). Despite having a diet dominated by fish, piscivory among Neotropical cichlids is achieved through a variety of functional configurations in different clades (see next section and Fig. 2). At the most elongate end of the gradient, the geophagin *Crenicichla* clade represents a unique set of functional and morphological configurations that is not found in any other clade of Neotropical cichlids (López-Fernández et al. 2013; Arbour and López-Fernández 2013, 2014; Astudillo-Clavijo et al. 2015). However, the highly specialized morphology of *Crenicichla* is not always associated with piscivorous diets or sit-and-wait predation, with some taxa having become benthic invertebrate feeders (e.g., Montaña and Winemiller 2009; López-Fernández et al. 2012b; Varella et al. 2016), frequently in association with body size reduction (Steele and López-Fernández 2014). The *Crenicichla* configuration is the most versatile of Neotropical cichlid morphologies and has been associated with its own adaptive zone. The only exception is the piscivorous genus *Cichla,* which has convergent feeding and swimming morphology with *Crenicichla* (Arbour and López-Fernández 2014; Astudillo-Clavijo et al. 2015). Another unique predatory configuration convergent among Neotropical cichlids is that of the "basket mouth" cichlids in the heroin genera *Petenia* and *Caquetaia* and the cichlasomatin *Acaronia*. These highly specialized predators combine ram attacks with extreme jaw protrusion, presumably as a way to increase closing speed when attacking elusive prey (Waltzek and Wainwright 2003).

The suction–biting end of the PC1 gradient (Fig. 2, right) includes taxa with strong but comparatively slower opening and closing of the oral jaws, uneven occlusion (quadrate offset resulting in "scissors"—like biting), and strong suction and/or biting ability. These taxa also tend to have larger caudal and pectoral fins as well as pelvic and unpaired fins placed comparatively far from the center of mass, resulting in elevated maneuverability presumably compatible with feeding on benthic or attached prey (Arbour and López-Fernández 2013, 2014; Astudillo-Clavijo et al. 2015). Diet among the suction–biting taxa includes invertebrates, plant material, fruits, detritus, and in some cases mollusks and other hard prey (e.g., Crampton 2008; Winemiller 1990; Winemiller et al. 1995; Cochran-Biederman and Winemiller 2010; López-Fernández et al. 2012b; Soria-Barreto et al. 2019).

The elongation gradient appears to be a widespread axis of morphological variation in fishes; for example, this gradient is very apparent among coral reef fishes (Claverie and Wainwright 2014). The strong functional morphological correlates of the gradient as described above in cichlids supports the idea that the association between the elongation axis and both swimming and feeding may be a major determinant of fish diversification. Interestingly, while the deep-bodied end of the axis in Cichlinae is consistent with findings in coral reef-fishes and supports interpretations of increased benthic habits and suction feeding, the elongated extreme of the gradient appears to diversify in less constrained ways and maybe more clade-specific (see Claverie and Wainwright 2014 for further discussion). In

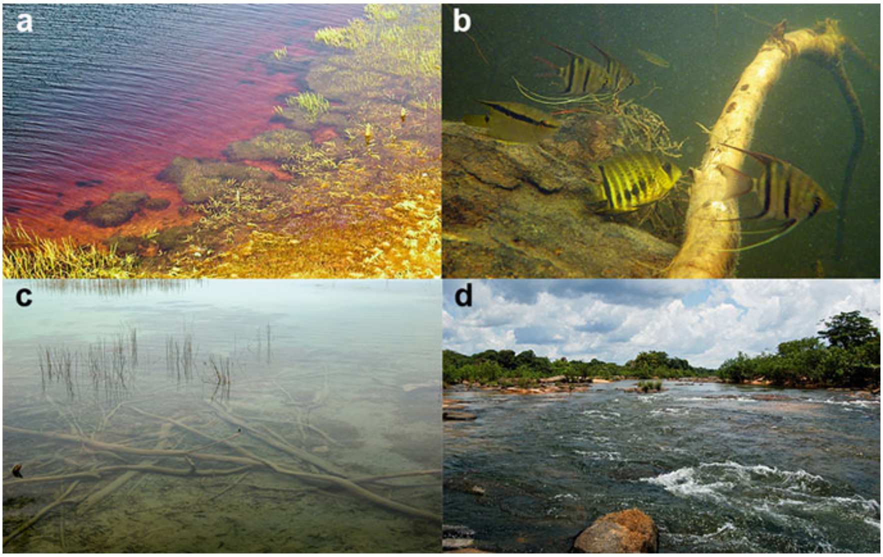

Fig. 3 (**a**) A black water stream with sandy bottom and some shoreline structure formed by vegetation and gallery forests (not visible in photograph) in the Venezuelan Orinoco River floodplain. These habitats tend to be dominated by substrate sifting Geophagini in *Geophagus*, *Satanoperca*, *Biotodoma*, *Apistogramma*, *Biotoecus* and predatory *Crenicichla* as well as the piscivorous Cichlini genus *Cichla*; Heroini genera *Heros*, *Hypselecara*, *Hoplarchus* and *Mesonauta* and the Cichlasomatini *Aequidens* and *Acaronia* are also present but are generally less abundant. (**b**) South American heroin taxa in a complex Amazonian habitat. The picture shows the Heroini genera *Pterophyllum*, *Mesonauta,* and *Heros* feeding among the branches of a fallen tree in a clear-water creek, Rio Negro basin, Brazil. Body shape in these genera, as well as *Symphysodon* and *Uaru*, do not overlap with any of those in the South American Geophagini and Cichlasomatini (López-Fernández et al. 2013). The South American Heroini includes some of the most extreme body shape, feeding, and swimming adaptations among Neotropical cichlids (Arbour and López-Fernández 2014; Astudillo-Clavijo et al. 2015). Presumably, competition limited the ability of Heroini to occupy niches already occupied during the early diversification of Geophagini, resulting in highly specialized South American heroin genera. Later invasion of Mesoamerica by heroins renewed ecological opportunity and triggered the diversification of Heroini into niches previously unavailable. See text for details. (**c**) A sandy bottom shore in the Usumacinta River basin in Mexico. Central American environments with sandy or muddy bottoms are frequently occupied by substrate sifting *Thorichthys*, *Astatheros,* and *Cribroheros* which are broadly convergent with South American geophagines; detritivorous lineages such as *Vieja* and *Cincelichthys* in Central America occupy niches not available to cichlids in South America, presumably due to the presence of detritivorous characiforms in families such as Prochilodontidae. (**d**) The Xingu River basin is rich in rapids where species of *Crenicichla*, *Teleocichla*, *Retroculus,* and others represent specialized rheophilic cichlid lineages. Convergent rheophilic Central American taxa include *Theraps*, *Wajpamheros,* and *Rheoheros* (Photo credits: (**a**, **c**, **d**) H. López-Fernández, (**b**) K. M. Alofs)

the case of cichlids, both locomotion and feeding correlates of elongation appear to be associated with an increasingly predatory lifestyle, and in some cases, with the evolution of rapids-adapted (rheophilic) lineages.

2.3.2 Suction–Biting and Maneuverability Axis

Variation along PC2 involves a gradient between suction feeders and biters, both frequently associated with feeding in or near the benthos, or in complex, highly three-dimensional habitats (Figs. 2 and 3). Taxa along this gradient share laterally compressed, deep bodies with relatively small mouths capable of generating strong, directed suction (Winemiller et al. 1995; Hulsey and García De León 2005; López-Fernández et al. 2012b, 2014; Arbour and López-Fernández 2013, 2014). Nevertheless, these adaptions encompass a wide variety of dietary specializations with an equally diverse combination of feeding mechanics involving suction and biting (Fig. 2). Although contrasts between extremes of the suction–biting gradient are not as strong as the elongation axis, PC2 separates largely substrate sifting taxa from species that feed on a variety of benthic or substrate-attached food items (e.g., algae, vegetation, or epibenthic invertebrates). Even though all taxa along axis 2 are to some extent suction feeders, it is clear that some employ biting or scraping in order to obtain food resources such as algae (*Hypsophrys*), fruits (*Tomocichla*), or detritus (e.g., *Paraneetroplus* [=*Vieja*]), whereas others extract benthic invertebrates from within the substrate or from its surface (substrate-sifting geophagins and heroins). These diverse feeding modes combine morphological attributes with behavioral components that are not reflected in morphological analyses (e.g., Hulsey and García De León 2005; López-Fernández et al. 2014; Weller et al. 2017). For example, substrate sifters ingest a mixture of inorganic substrate particles and food items (e.g., invertebrates, seeds) and methodically remove inedible particles through the gill openings by coordinated movements of the hyoid, the oral jaws, and the pharyngeal basket. This “winnowing” behavior separates food from debris, with the gill rakers acting like sieves directing food toward the esophagus and debris ejected through the gills. Although superficially similar to behavior in surfperches (Drucker and Jensen 1991), a pioneering biomechanical study recently showed winnowing is a functionally unique and underexplored axis of specialization among geophagins (Weller et al. 2017). Substrate sifting morphology is broadly similar but not identical across benthic-feeding taxa, which tend to have deep heads, large and dorsally placed eyes, wide mouth gapes, and longer snouts, but display an assortment of oral jaw mechanics that suggests a variety of functional configurations for food acquisition (Hulsey and García De León 2005; Arbour and López-Fernández 2014; López-Fernández et al. 2014; Weller et al. 2017). Consistent with their varied morphology, substrate sifters display a large diversity of diets (e.g., Winemiller et al. 1995; Hulsey and García De León 2005; Montaña and Winemiller 2009; Cochran-Biederman and Winemiller 2010; López-Fernández et al. 2012b; Soria-Barreto et al. 2019).

Analysis of the lower pharyngeal jaws in Neotropical cichlids revealed two different pharyngeal jaw configurations among substrate sifters, suggesting yet further diversification in prey manipulation modes (Burress 2016). The functional separation between the oral and pharyngeal jaw of cichlids has been long proposed as a key adaptive innovation (e.g., Liem 1973; Hulsey et al. 2006a, b, 2010; Burress 2016 and references therein). Among substrate sifters, this jaw independence may affect the efficiency of prey acquisition depending on the type of substrate (e.g., sand, mud, hard surfaces), location of food items with respect to the substrate (e.g., benthic infauna, epibenthic invertebrates, or detritus) or whether food items are attached or loose.

Most discussions of pharyngeal specialization tend to focus on dentition and force of the lower pharyngeal jaw (e.g., Hulsey et al. 2006b; Burress 2016), whereas comparatively little attention has been given to the functional role of broader pharyngeal variation on winnowing performance, prey capture, or prey selection (but see Galis and Drucker 1996; Burress 2016; Weller et al. 2017). Likewise, we know very little about the role of pharyngeal structures other than the potential influence of tooth plates on winnowing (but see Weller et al. 2017). In the case of Geophagini, it is possible that the "epibranchial lobe," an anteroventrally directed laminar expansion of the first epibranchial, could also be involved in enhancing the efficiency of substrate sifting or the evolution of mouthbrooding behavior (e.g., Lowe-McConnell 1991; López-Fernández et al. 2012b). Analogous structures to the epibranchial lobe of geophagins are present in the South American genus *Retroculus* and some African cichlids, but to the extent that I am aware, no functional analyses have been performed on the pharyngeal lobes of any of these groups. Given the ubiquity of winnowing and the functional diversity of oral jaws in sifting cichlids (particularly Geophagini), it would be interesting to explore associations between oral and pharyngeal jaws and consumption of benthic food. Such studies could enhance understanding of the functional morphology of the pharyngeal basket, discerning how different substrate-sifting taxa actually perform winnowing, and establishing whether differences in winnowing behavior and mechanics facilitate interspecific dietary divergence.

The functional complexity of the suction–biting axis is also reflected in the swimming attributes of suction feeders and biters. Within Geophagini variation along this axis suggests diversification in both habitat and swimming attributes associated with a benthic/epibenthic adaptive zone (Astudillo-Clavijo et al. 2015, and see below). Variation in swimming morphology is associated with divergence in fin size, shape, and position within the deep-bodied end of the elongation axis, which ecological studies suggest is congruent with variation in habitat preferences (e.g., Claverie and Wainwright 2014; Willis et al. 2005; Soria-Barreto and Rodiles-Hernández 2008; Cochran-Biederman and Winemiller 2010; Montaña and Winemiller 2010, 2013). Interpretation of this vertical axis suggests that substrate sifters (top end of axis, Fig. 2, e.g., *Geophagus*, *Satanoperca*) may have body and fin shapes optimized for hovering or maneuvering with precision while searching for, biting at, or scooping and winnowing food items on or within substrates. The negative end of the axis (center to bottom of Fig. 2, e.g., *Guianacara, Apistogramma, Teleocichla*) tends to be associated with fishes having paddle-like paired fins inserted relatively far from the center of mass that presumably enhance maneuverability within structurally complex habitats such as vegetation, rocky reefs, and submerged wood debris. Despite the distinctions made above, however, trait combinations that enhance maneuverability can be found all along axis 2, albeit some of them involve different aspects of locomotion. These swimming attributes are expected to relate to different habitat preferences, but further study is needed to test that assumption (Astudillo-Clavijo et al. 2015; Feilich 2016).

In summary, much of the functional morphological and ecological variation in Neotropical cichlids can be placed along two main axes of adaptive divergence. These axes are defined by functional trait combinations affecting feeding and swimming performance and indicate strong trade-offs between diet and habitat use. A dominant elongation axis is shared with most other fishes and represents a gradient between elongate, fast-swimming, or sit-and-wait predators that use ram feeding, and deeper-bodied fishes capable of maneuvering with precision while searching for and consuming food attached to or buried within substrates. All fishes along this gradient are capable of using a variety of habitats, from open water to structurally complex with variable current velocity, but rely on different strategies to maneuver through them and access food resources (Fig. 3). A second axis of functional variation describes further specialization between biting and substrate sifting taxa, and consumption of attached or buried prey. Neotropical cichlids exhibit specializations along the length of this suction–biting gradient, and diversity is impressive even just among substrate-sifting taxa.

2.3.3 Adaptive Landscape of Neotropical Cichlid Evolution

The axes of the Cichlinae functional morphospace, as currently understood, describe adaptive suites for distinct ecological roles (niches) and reveal repeated instances of ecomorphological convergence. Modeling selection on functional traits along the branches of the phylogeny allows inferring an *adaptive landscape*. Although methods continue to evolve and results must be read with caution, recent work based on 10 variables associated with feeding biomechanics and 75 species representing all Cichlinae tribes estimated an adaptive landscape with seven adaptive peaks and 11 regime shifts among peaks (Fig. 2). In this context, "peaks" represent ecomorphological configurations assumed to maximize fitness and to be favored by selection, whereas "adaptive shifts" represent ecomorphological changes from one peak to another via a novel ecomorphological configuration. Seven of these shifts correspond with convergence on the same three adaptive peaks (Fig. 2, peaks 2, 5, and 6). Two additional shifts correspond with the invasion of new, non-convergent adaptive zones restricted to one clade (Fig. 2, peaks 3 and 7 and see Arbour and López-Fernández 2014). Analyses of simulations without convergence and models that vary the regime shifts both indicated that some of the observed peaks could consist of multiple non-convergent peaks, suggesting that additional adaptive peaks may exist (Arbour and López-Fernández 2014).

Peaks 1–3 include all tribes except Cichlini and Heroini, with peak 1 estimated as the ancestral regime for Cichlinae (Fig. 2). Within Cichlasomatini, the genus *Cleithracara* is the only genus outside adaptive peak 1, as it has converged toward peak 6, a strong biting adaptive zone otherwise restricted to South American Heroini and possibly one Central American lineage. Within the ancestral peak 1, functional optimization tends toward improved oral jaw velocity transmission and reduced jaw opening and closing force, hypothesized to be associated with the substrate sifting behaviors of geophagins (see above, and Arbour and López-Fernández 2014). This view is congruent with the finding of a geophagin adaptive peak of swimming morphology optimized for maneuverability and associated with substrate sifting taxa (Astudillo-Clavijo et al. 2015). Despite their shared adaptive regime, there is a large variation in feeding modes among lineages in peak 1 (e.g., planktivory in Chaetobranchini, substrate sifting in Geophagini, omnivory in Cichlasomatini). Interestingly, a recent analysis of Cichlinae adaptive landscape as defined by pharyngeal jaw shape variation using the same phylogenetic context found a non-convergent regime within substrate sifting geophagines of the genera *Geophagus* sensu *lato* and *Gymnogeophagus* (Burress 2016) that was not detected in our analysis as different from peak 1. Likewise, the same analysis found a convergent peak in pharyngeal jaws that includes the piscivores *Cichla* and *Petenia* and the planktivorous *Chaetobranchus*, which in our analysis belong in three different adaptive peaks (see below, and Fig. 2). Given the likely functional decoupling of oral and pharyngeal jaws, the difference in estimated adaptive landscapes based on each set of jaws is not surprising and provides a broader understanding of the multidimensional nature of adaptive divergence in Neotropical cichlid early diverging lineages (i.e., recognized as tribes and genera, and see next section).

The geophagin clade *Crenicichla/Teleocichla* and the tribe Cichlini (genus *Cichla*) convergently occupy adaptive peak 2, which is jaw-velocity optimized and congruent with the predatory tendencies of many of these taxa. This feeding adaptive peak is consistent with a unique adaptive peak described by Astudillo-Clavijo et al. (2015) for the swimming morphology of Geophagini. Adaptive peak 3 includes *Biotodoma-Dicrossus-Crenicara* (although a less favored reconstruction included those genera plus *Geophagus* sensu lato and *Gymnogeophagus*). This latter peak includes several specialized benthic and epibenthic feeders in Geophagini that bite, suck, or scoop and sift for prey (López-Fernández et al. 2012b, 2014).

Adaptive peaks 4–7 are dominated by Heroini and tend to be optimized for high suction potential or strong biting force (i.e., toward the right portion of PC1 and the lower half of PC2 in ecomorphospace, Fig. 2). Peak 4 was reconstructed as the ancestral adaptive zone in Heroini, with the South American genera *Pterophyllum*, *Mesonauta*, *Uaru,* and *Heros* showing a convergent shift toward peak 5, and *Symphysodon* shifting uniquely toward peak 7 with the strongest suction potential of any Neotropical cichlid. Mesoamerican cichlids all remain within adaptive zone 4 except for the convergent *Herotilapia* and *Paraneetroplus* (= *Vieja*) which shifted toward peak 6, with strong biting forces and presumably associated with diets that include plant material and vegetative detritus (Winemiller et al. 1995).

Interestingly, South American Heroini are confined to their own adaptive zones (peaks 4, 5, and 7), and most Central American heroines diversified within adaptive zones 4 and 6. In contrast, geophagines diversified within the confines of peaks 1, 2, and 3, with cichlasomatins largely restricted to peak 1. This suggests that, despite the large convergence in morphospace occupation (Fig. 2) and diet, the adaptive regime shifts between South and Central American cichlids have been largely independent from each other, with their evolutionary trajectories following clade-specific paths.

This interpretation of the adaptive landscape is supported by ecomorphological and functional variables in morphospace, which suggest that both the timing of origin of Cichlinae tribes and the presence of non-cichlid clades contributed to shape the evolution of Neotropical cichlids. In the following section, I broadly discuss how the timing of divergence, ecology, and biogeographic shifts, by affecting ecological opportunity, may have influenced the evolution of the adaptive landscape and driven convergence among the main clades of Neotropical cichlids.

3 Neotropical Cichlids as Ancient, Continental Adaptive Radiations

Cichlids are among the most celebrated and studied adaptive radiations, mostly because of intense interest in the remarkable species flocks of the East African Great Lakes (Kornfield and Smith 2000; Verheyen et al. 2003; Kocher 2004; Seehausen 2006; Salzburger et al. 2014) and the smaller crater lakes radiations in Africa and Central America (Schliewen et al. 1994, 2001; Barluenga et al. 2006; Elmer et al. 2010; Martin et al. 2015). These lake radiations generally share a relatively recent origin of a few tens of thousands to a few million years (e.g., Seehausen 2002; Genner et al. 2007; Day et al. 2008; Elmer et al. 2010). In contrast, diversification of the much older, continentally distributed, river-dwelling cichlids of Africa and the Neotropics is much less understood. We have only recently started addressing the question of whether riverine cichlid divergence might follow processes analogous to the adaptive radiation paradigm widespread among their lake-dwelling kin. These studies increasingly suggest that diversification processes in Neotropical cichlid lineages have not been uniform through time or across the phyletic history of the clade. Rather, phylogenetic, comparative, and fossil evidence suggest that diversification of the modern Neotropical cichlid fauna is the result of accumulated episodes of evolution with potentially different drivers through evolutionary time. Moreover, at least in some cases, diversification of Neotropical riverine cichlids appears to have followed a pattern consistent with early adaptive radiations resulting in most of the modern functional and higher-level phylogenetic diversity, followed by a relative deceleration of adaptive diversification. Nevertheless, in at least two cases, it appears that pike cichlids in the genus *Crenicichla* may have diversified through much more recent riverine adaptive radiation.

3.1 Decoupled Divergence Patterns: Temporal and Phylogenetic Scale of Divergence in Neotropical Cichlids

We have referred to the earlier stages of Neotropical cichlid diversification as "ancient continental adaptive radiations" (López-Fernández and Albert 2011;

López-Fernández et al. 2013; Arbour and López-Fernández 2016), which appear to have given origin to most of the functionally and ecologically distinct lineages spanning modern Neotropical cichlids at the taxonomic levels of tribes and genera. This initial period of adaptive divergence generally appears to have been followed by widespread adaptive stasis, with lineage-level divergence dominated by speciation within genera and often resulting in high species richness but low ecomorphological divergence. Ecomorphological variation within living genera is often negligible compared to variation among genera (López-Fernández et al. 2012b), with the exception of *Crenicichla* and perhaps a few others (e.g., Kullander et al. 2009; Piálek et al. 2018; Burress et al. 2013; Burress et al. 2018). This proposed phenotypic stasis within genera is evident in at least one fossil cichlid, †*Gymnogeophagus eocenicus*, an Eocene taxon that can be unambiguously placed within a living genus (Malabarba et al. 2010, 2014). With few known exceptions such as species of *Amphilophus* in Central American crater lakes (e.g., Barluenga et al. 2006) and some *Crenicichla* in localized areas of the Uruguay and Paraná river basins (Burress et al. 2018; Piálek et al. 2018), recent or ongoing species-level diversification in Neotropical cichlids appears to be broadly driven by nonadaptive forces and biogeographic happenstance (e.g., Farias and Hrbek 2008; López-Fernández and Albert 2011; Argolo et al. 2020). Whether adaptive divergence plays a larger role in recent Neotropical cichlid divergence is poorly understood. In the following paragraphs, I describe recent analyses of the early origin of Neotropical cichlids at the tribe and genus level. Disparity among these older lineages encompasses the vast majority of the functional and ecological diversity of cichlids in modern South and Central American assemblages.

3.2 South America: Early Burst of Divergence in Lineages and Phenotypes

All clades of Neotropical cichlids originated in South America. Although the temporal framework of divergence of Cichlinae and its subclades remains unclear and controversial (see Sect. 1), the order in which clades originated is relatively well established by a number of phylogenetic analyses that include all tribes (e.g., Smith et al. 2008; López-Fernández et al. 2010; McMahan et al. 2013; Ilves et al. 2018). Patterns of lineage diversification based on Lineage Through Time analysis (LTT plots, Pybus and Harvey 2000) were compatible with early and rapid lineage diversification followed by a decrease in the rate of lineage accumulation in Geophagini, and to a lesser extent the entire Cichlinae (López-Fernández et al. 2013). A similar pattern in Cichlasomatini was statistically nonsignificant, and patterns in Heroini indicated linear accumulation of lineages. Further, the comparison of models with constant and variable rates of lineage accumulation favored processes with variable rates, including diversity-dependent models for Cichlasomatini and Geophagini. López-Fernández et al. (2013) interpreted these combined results as compatible with early, diversity-dependent lineage diversification in Geophagini, and evidence that the origin of geophagin genera is compatible with the ecological model of adaptive radiation. McMahan et al. (2013) found significantly fast rates of lineage accumulation in the African cichlid clade containing the East African radiations (Schwarzer et al. 2009), as well as some evidence of fast lineage accumulation in Heroini (contra Hulsey et al. 2010; López-Fernández et al. 2013), but not Geophagini. The studies, however, focused on different timelines of divergence: whereas López-Fernández et al. (2013) focused on the early two-thirds of the evolutionary history of the clade and genus-level divergence to account for incomplete species-level sampling, McMahan et al. (2013) interpreted the entire length of Cichlinae diversification, including modern diversity, making the two studies not directly comparable. Regardless, lineage diversification patterns are apparently compatible with early, diversity-dependent lineage diversification within Geophagini and possibly Heroini, a pattern theoretically congruent with adaptive radiation. These patterns need to be reexamined with more densely sampled phylogenies that span all times of divergence and more accurately reflect diversity across cichlid clades (and see Burress and Tan 2017).

In the ecological model of adaptive radiations, theory predicts that early bursts of lineage diversification should be paralleled by concomitant early bursts of phenotypic divergence (Gavrilets and Losos 2009; Glor 2010; Schluter 2000; Yoder et al. 2010). Analyses of phenotypic disparity through time (DTT plots, Harmon et al. 2003) using the axes of Cichlinae functional morphospace (see above, Fig. 2) with external ecomorphological characters (López-Fernández et al. 2013), feeding biomechanics (Arbour and López-Fernández 2013) and swimming functional morphology (Astudillo-Clavijo et al. 2015) all reveal a significant decline in phenotypic diversification through time for Geophagini. This pattern, however, is not found for diversification within Heroini or Cichlasomatini. In addition, Arbour and López-Fernández (2016) found declining feeding biomechanics disparity through time for all basal lineages of Cichlinae in South America, indicating early adaptive divergence and suggesting that divergence of lineages now recognized as tribes was also consistent with an adaptive radiation. Therefore, disparity through-time and lineage-through-time analyses coincide in finding an early burst in basal divergence of Neotropical cichlids. These results, particularly those based on morphological disparity, suggest that both the initial divergence of Neotropical cichlid tribes (Arbour and López-Fernández 2016) and subsequent diversification within Geophagini in South America are consistent with adaptive radiation (López-Fernández et al. 2013; Arbour and López-Fernández 2013; Astudillo-Clavijo et al. 2015). The pattern of early niche divergence followed by a reduced diversification rate suggests there was a progressive filling of adaptive zones and niche partitioning among ancestors of contemporary tribes and genera. We have interpreted these patterns as evidence of early ecological opportunity for cichlid diversification in South America.

Although evidence suggests all main lineages of Cichlinae may have diversified in an early adaptive burst involving the ancestral forms leading to the modern tribes, diversification within the tribes clearly did not occur at a uniform rate. Early divergence in South America was likely dominated by the radiation of Geophagini.

Rapid diversification into new niches by geophagins may have precluded divergence in other lineages of South American cichlids, particularly Heroini and Cichlasomatini, which did not undergo phyletic and functional diversification until later (e.g., Fig. 1, and see López-Fernández et al. 2013). Geophagins occupy a vast swath of South American cichlid functional morphospace (Fig. 2, and see López-Fernández et al. 2013; Arbour and López-Fernández 2014). Other tribes in South America tend to show little overlap with geophagins (Fig. 2, e.g., South American Heroini, Cichlasomatini, Retroculini, Cichlini), or when they do overlap, tend to do so toward the center of morphospace where both morphology and ecology tend to be generalized (e.g., most Cichlasomatini). This morpho-functional segregation is most notable among the basal South American heroin lineages *Pterophyllum*, *Symphysodon*, *Uaru*, *Heros,* and *Mesonauta*. These genera display extreme morphologies both for feeding and swimming (Fig. 2) and often (although not always) can be found coexisting with each other in structurally complex habitats where geophagins tend to be uncommon (e.g., Fig. 3b). Lineages of South American heroins may have been under selective pressure to move into adaptive zones unoccupied by geophagins (e.g., peaks 5 and 7, Fig. 2 and see above). These heroin zones are characterized by strong suction or biting forces and deep bodies optimized for complex habitats that are not broadly occupied by substrate sifting or predatory geophagins that occupy zones 1, 2, and 3 (Fig. 2). Available niches would have been further limited by the presence of a potentially high diversity of non-cichlid fishes (e.g., Winemiller et al. 1995; Albert and Reis 2011, and see Sects. 3.3 and 4), resulting in the highly specialized basal South American Heroini.

3.3 Central America: Renewed Ecological Opportunity and Convergence

Analysis of rates of phenotypic divergence (as opposite to the pattern of change in phenotypic disparity) among South and Central American lineages of Cichlinae, controlling for biogeographic origin, reveals an intriguing pattern. Using Node Height Tests (Freckleton and Harvey 2006; Slater and Pennell 2014) to correlate the rate of phenotypic divergence and time or branch lengths in a tree, Arbour and López-Fernández (2016) compared rates of phenotypic evolution between two groups formed by South and Central American lineages of Cichlinae, respectively. These analyses revealed a significant effect of biogeography on rates, showing a decrease in phenotypic divergence in South American cichlids on both PC1 and PC2 of feeding morphospace (Fig. 2). The Central American heroin lineages initially showed high morphological evolutionary rates followed by a decrease along PC1. Both the initial rate and the subsequent rate of decrease mirrored those for South American lineages along the ram–suction gradient of morphospace (Fig. 4). Likewise, the initial increase in evolutionary rates following the colonization of Central America suggests that Heroini experienced ecological release (i.e., renewed

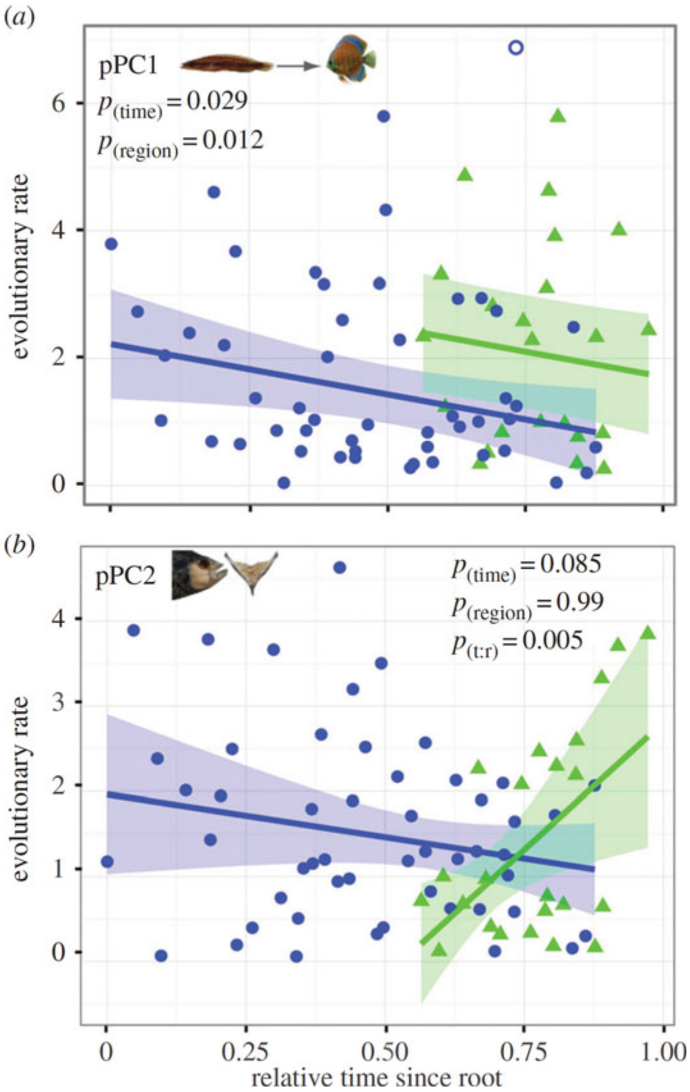

Fig. 4 Changes in evolutionary rates of ram–suction morphology in South and Central America (top row, PC1; bottom row, PC2) on a relative-time chronogram of 75 species of Neotropical cichlids based on López-Fernández et al. (2013). Evolutionary rate estimates (absolute value of standardized independent contrasts) through time for South American (blue, circles) and Central American (green, triangles) taxa, including the regression line (shaded region = 95% CI) from a Node Height Test using a robust regression of standardized independent contrasts against distance from the root for each node (Reproduced with permission from Arbour, J. H., & López-Fernández, H. (2016). Continental cichlid radiations: functional diversity reveals the role of changing ecological opportunity in the Neotropics. *Proceedings of the Royal Society B: Biological Sciences*, *283* (1836), 20160556)

ecological opportunity) in the absence of competitors. This conclusion is further supported by the extensive overlap between South American Geophagini and Central American Heroini morphospace (Fig. 2, López-Fernández et al. 2013; Arbour and López-Fernández 2014), suggesting that, once released from competition, heroins were able to diversify into similar morphospace and ecological niches as those of geophagins. Interestingly, divergence in ecomorphology was paralleled by increased rates of vision protein molecular evolution (Hauser et al. 2018). At the lineage level, these findings may also be congruent with the increased rate of divergence found by McMahan et al. (2013) within Heroini. A recent study analyzing purely lineage divergence suggests that diversification shifts across cichlids may be frequently related to renewed ecological opportunity after colonization of new biogeographic regions (Burress and Tan 2017).

It is important to highlight that the observed decline in evolutionary rates in Central America is not mirrored by an equivalent reduction in phenotypic disparity through time (see above). This suggests either that (a) Central American heroins may be undergoing an adaptive radiation that has not yet reached the point at which niches are saturated and therefore there is no evidence of a decline in the rate of functional diversification (e.g., Hulsey et al. 2010), (b) different processes drove functional divergence between South and Central America, or (c) either the methods or datasets yield insufficient statistical power to detect a decline in morphological differentiation among Central American heroins (and see Arbour and López-Fernández 2016).

While rates of evolution along PC1 for Central American lineages declined, rates started low and continually increased along PC2, the suction/biting gradient (Figs. 2 and 4). This result, fundamentally different from the observations in South American lineages, suggests that variation toward larger oral jaw muscles and pharyngeal tooth plates in Central American cichlids may be associated with access to biting/crushing adaptive zones not occupied by cichlids in South America (Arbour and López-Fernández 2014, 2016; Burress 2016). Variation in the suction/biting axis further highlights the expansion of the functional morphological and ecological repertoire of heroins in Central America. On the one hand, the clade invaded adaptive zones otherwise restricted to geophagins (e.g., piscivory, substrate sifting), but it also evolved into the use of entirely novel adaptive zones among Neotropical cichlids. This is particularly notable in the appearance of frugivorous and detritivorous niches, which in South American rivers are restricted to Characiformes, Siluriformes, and other non-cichlid fishes (e.g., Curimatidae, Prochilodontiade, Serrasalmidae, Loricariidae, Winemiller et al. 2006; Correa et al. 2007, 2015; Sidlauskas 2008; Lujan et al. 2012). Thus, evidence continues to accumulate supporting the idea that cichlid diversification in South America was limited by interactions among clades within the family (e.g., Geophagini) as well as non-cichlids (e.g., Characiformes). The increasing rates of evolution in Central American heroines along the suction/biting axis suggests that ecological release from these South American competitors may have played a large role in the functional expansion experienced by the clade (e.g., Winemiller et al. 1995; López-Fernández et al. 2013; Arbour and López-Fernández 2014, 2016; Burress 2016).

4 Divergence in Rivers and Lakes: Are Processes the Same?

Despite the current uncertainty regarding the age of cichlids, it is indisputable that Neotropical and most African riverine cichlid taxa belong to older lineages than those present in lake radiations of both Africa and Central America (e.g., Verheyen et al. 2003; Koblmüller et al. 2008; Elmer et al. 2009; Schwarzer et al. 2009, 2011; Betancur-R et al. 2017a; López-Fernández et al. 2013; McMahan et al. 2013; Friedman et al. 2013, Matschiner 2018). An obvious "null" hypothesis to explain the comparatively limited diversity of cichlids in rivers is that lineage and phenotypic divergence may have occurred at a constant rate over a long period of time, whereas diversity in the East African lakes resulted from a recent "explosion" of diversification. However, this constant-rate hypothesis is repeatedly rejected by comparative analyses of Neotropical cichlids, indicating more complex processes were involved in generating modern diversity. Ecological and functional diversity in riverine Cichlinae appears to have originated early in the South American divergence of cichlids, followed by a slowdown in phenotypic diversification (see Sect. 3). Such morphological stasis within the clade suggests that ecological selective pressures that shaped the early functional diversification of Neotropical cichlids have remained active for an extended period of time. In combination, comparative analyses point toward a clear division of the timeline into an early period of South American adaptive radiation that originated early diverging lineages (tribes and genera), followed by a more recent but prolonged period during which diversification appears to have been dominated by speciation within the ecomorphological boundaries of genera (Argolo et al. 2020). Phenotypic stasis in South America, however, has not been uniform across all clades, with some clearly undergoing much later adaptive diversification, particularly within *Crenicichla* (e.g., Burress et al. 2013, 2018; López-Fernández et al. 2013). A second major period of adaptive divergence resulted from renewed ecological opportunity following the invasion of Central America by heroins (Arbour and López-Fernández 2016; Hauser et al. 2018), but the phylogenetic signal of adaptive radiation is much less clear. It appears that this adaptive diversification process may be ongoing, at least in terms of further specialization along the suction–biting gradient. Clearly defining these different periods of divergence will be essential to circumscribe episodes in Neotropical cichlid evolution and to identify underlying forces that drove their divergence through the long and complex history of the Neotropical region.

With the exception of the incipient radiations of the heroin genus *Amphilophus* in Nicaraguan crater lakes (e.g., Barluenga et al. 2006; Elmer et al. 2010, and see Torres-Dowdall and Meyer 2021), the vast majority of modern Neotropical cichlids are adapted to live in rivers and floodplains. Therefore, beyond differences in age and tempo of evolution, the environmental and ecological "stage for evolution" in which the continental cichlid radiations unfolded may be essentially different from that provided by insular lakes. Lakes where recent cichlid radiations have evolved are generally island-like: they provide ecological opportunity within a restricted area and are largely, although not exclusively (e.g., Day et al. 2009), dominated by cichlids, with limited influence of other fish taxa. In that sense, the adaptive radiations of lacustrine cichlids are much more like those of Caribbean *Anolis* (Losos 2009) or Galápagos finches (Grant and Grant 2008). In contrast, Neotropical cichlids, particularly in South America, evolved largely within riverine systems with long-established non-cichlid fish communities and frequent environmental disturbances that reshaped the landscapes, fluvial connectivity, and ecological conditions over tens of millions of years. Much evidence suggests (see above) that the ecological roles played by non-cichlid taxa influenced ecological opportunities for cichlids (e.g., Winemiller et al. 1995; López-Fernández and Albert 2011; Albert and Carvalho 2011). Recent work has modeled cichlid radiations in lakes on the basis of spatial and ecological multidimensionality combined with the influence of sexual selection (e.g., Wagner et al. 2012; Aguilée et al. 2013; Seehausen 2015). Although multiple niche dimensions are involved in the diversification of cichlids in both lakes and fluvial systems, certain factors seem to be more influential in lakes and others in rivers. For example, depth and sexual selection play a dominant role in lake radiations (Seehausen et al. 2008; Wagner et al. 2012; Seehausen and Wagner 2014), whereas community assembly and species interactions seem to have strongly influenced fish evolution in the Neotropical fluvial systems (Albert and Reis 2011; Bower and Winemiller 2019).

Ecological opportunity, or lack thereof, for cichlid diversification in the Neotropics was undoubtedly shaped by abiotic elements such as sea-level changes, orography, and associated changes in hydrology and fluvial geomorphology in South and Central America. Unfortunately, the complexity of this history makes it difficult to ascertain the environmental context for early Neotropical cichlid diversification. In South America, for example, extensive paleo-lakes or mega-wetlands that persisted for prolonged periods of time (e.g., Paleo Amazonas-Orinoco, Lago Pebas, Lundberg et al. 1998, 2010; Hoorn et al. 2010; Albert and Reis 2011) undoubtedly influenced fish evolution. However, compared to present-day lakes containing cichlid species flocks, these ancient South American mega-wetland systems were less insular and with different environmental conditions than closed lakes; they received water from huge drainage basins and probably were more similar to the vast floodplains of the modern South American Pantanal and Llanos. Consequently, these systems were almost certainly much more dynamic than an African Rift Valley lake. From the late Cretaceous to the end of the Miocene, South American mega-wetlands shifted between riverine, shallow lacustrine, and estuarine conditions under the influence of climate change, marine incursions and transgressions, and tectonic activity (Lundberg et al. 1998; Hoorn and Wesselingh 2010; Albert and Reis 2011). Thus, even assuming the mega-wetlands were an important setting for Neotropical cichlid evolution, we must remember that they were part of even larger fluvial systems. In such a context, and given the vast time expanses involved, it may be impossible to determine whether processes affecting early cichlid evolution in the South American mega-wetlands were similar to those in modern lakes. Ultimately, understanding Neotropical cichlid diversification requires analyses of historical biogeography in the context of repeated reconfigurations of river drainage networks and the coevolution of large, complex assemblages of phylogenetically diverse fish species (e.g., Winemiller et al. 1995; Albert and Reis 2011).

The cichlid fossil record is, expectedly, moot on whether sexual selection or depth (both associated with coloration and visual cues, see Seehausen et al. 2008; Hauser et al. 2018) played a strong role in early Cichlinae divergence as they do in cichlid flocks within modern lakes. Most Neotropical rivers do not have major depth gradients, but rather are affected by dendritic spatial connectivity and dynamic responses to seasonal flow and flood regimes. Depth may be a major driver of cichlid divergence in lakes (Seehausen 2015), whereas, for river-dwelling cichlids, habitat fragmentation within fluvial networks promotes allopatric speciation (e.g., Dias et al. 2013 and see Seehausen and Wagner 2014). In riverine cichlids, the combined effects of hydrological disturbance (e.g., Albert et al. 2011; Crampton 2011), drainage capture (Ribeiro 2006; Albert et al. 2018), population fragmentation (e.g., Fagan 2002; Campbell Grant et al. 2007; Campbell Grant 2011), and river network architecture (e.g., Thomaz et al. 2016) are likely dominant elements influencing genetic structure and rates of speciation and extinction.

Several features of Neotropical cichlids suggest that sexual selection may be less influential when compared to its role in the evolution of cichlid species flocks in African lakes. Although sexual dimorphism is present in Cichlinae, it tends to be subtle and not as widespread as in African lake lineages. This may be a result of different light conditions in rivers compared to lakes. Vision-associated molecular evolution has been shown to be habitat-specific and is at least partially related to adaptation to dim light (e.g., Terai et al. 2006; Schott et al. 2014; Torres-Dowdall et al. 2015; Hauser et al. 2018). Although it seems indisputable that ecological and morphological specializations are prominent in cichlid evolution in both lakes and rivers, it is possible that ecological conditions in rivers limit the complementary role of sexual selection in adding to species diversity. It is perhaps telling that the two Neotropical genera with the greatest species richness, the geophagins *Apistogramma* and *Crenicichla*, each with about 100 species, show marked sexual dimorphism. Interestingly, while *Crenicichla* species display a considerable amount of functional diversity (e.g., Piálek et al. 2012, 2018; Burress et al. 2013, 2018; Arbour and López-Fernández 2014; Astudillo-Clavijo et al. 2015), *Apistogramma* seems to display much more limited morphological differentiation. It remains unclear whether sexual selection has a widespread role in speciation among these or other sexually dimorphic riverine Neotropical cichlids. For instance, Ready et al. (2006) demonstrated that color differences are associated with prezygotic reproductive isolation in populations of *Apistogramma caetei*, but the studied color forms were allopatric, suggesting that the principal driver of speciation was a response to local environments in allopatry rather than color-based assortative mating in sympatry as is the case in most lake cichlids (Ready et al. 2006; Seehausen et al. 2008).

Finally, despite the differences between lake and riverine environments, there is extensive convergence among cichlid assemblages in South American rivers and African rivers and lakes, which often harbor similar coexisting ecotypes or functional groups (e.g., Winemiller et al. 1995; Seehausen 2015). Seehausen (2015) suggested that the difference between lake and riverine cichlids in Africa often is one of species richness and not necessarily of functional diversity. Regardless of their phylogenetic relations or ecological circumstances, cichlids tend to repeatedly evolve into certain niches and assemble into communities that contain similar sets of functional groups. These patterns suggest that local species interactions may constrain community structure (Montaña et al. 2014) and possibly limit niche diversification in rivers (Winemiller et al. 1995; Seehausen 2015). Conversely, as more species assemble into local communities, species interactions could intensify and thereby promote niche diversification. This generalization, however, can only be taken so far because there is a non-trivial number of niches occupied by East African lake cichlids that, to my knowledge, are not present in riverine cichlids of any continent. These include specialized ecologies such as eye-biting [Lake Malawi's *Dimidiochromis compressiceps* (e.g., Fryer and Iles 1972)] or scale predation [Lake Tanganyika's *Perissodus* (e.g., Hori 1993; Kusche et al. 2012)], among others. The availability of these niches to cichlids may be determined by available ecological opportunity. For instance, fin-nipping and scale feeding in South America is observed in several piranhas (Serrasalmidae) that frequently coexist with cichlids, and detritivory and frugivory, although present in Central American cichlids, is absent from South American lineages presumably because these feeding habitats are widespread among characiforms (Winemiller et al. 1995, and see above). Unfortunately, these patterns of niche occupation and exclusion, while suggestive of a historical role for species interactions in adaptive divergence, cannot be easily linked to actual drivers of speciation.

In contrast to our emerging understanding of the interplay between ecology, morphology, sexual selection, and genomic structure in the evolution of lake cichlids (e.g., Kocher 2004; Santos and Salzburger 2012; Brawand et al. 2014; Seehausen 2015; Malinsky et al. 2015), our knowledge of the evolutionary forces driving divergence of cichlids in the older and more dynamic fluvial systems of South and Central America remains limited. Revealing the processes that originated the modern ecomorphological diversity of Neotropical cichlids requires integrating two major types of elements affecting their divergence. Firstly, we must clarify the timing and extent to which environmental and biogeographic events of continental and regional scale affected diversification. Secondly, we must assess the evolving historical role of ecological interactions among fish clades. Together, environmental transformation and ecological coexistence through time shaped ecological opportunity and modulated the adaptive diversification of cichlids and other fishes in the Neotropics.

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Sympatric and Allopatric Diversification in the Adaptive Radiations of Midas Cichlids in Nicaraguan Lakes

Julián Torres-Dowdall and Axel Meyer

Abstract The Nicaraguan Midas cichlid species complex is a natural experiment where fish from a large source population from turbid and shallow great lakes very recently (<20,000 years ago) colonized eight small crater lakes. The colonizers experienced completely novel environments in the clear and deep calderas. So far, 13 Midas cichlid species have been described, but more genetic clusters were identified. Although some of these species arose in allopatry, many more evolved in the absence of barriers to gene flow within two crater lakes. They contain small radiations of four and six endemics, respectively. These radiations constitute one of the few generally accepted empirical examples for sympatric speciation making them an ideal system for studying repeated evolution of adaptations and speciation at different levels of biological organization, including the genome level. Diversification occurred repeatedly in parallel including body morphology, coloration, color perception, and trophic structures such as pharyngeal jaws and hypertrophied lips. Additionally, parallel speciation happened in the two small crater lake radiations, where ecomorphologically similar species evolved repeatedly. Genomic differentiation associated with oligogenic traits (e.g., hypertrophic lips and coloration) is shallow, remaining polymorphisms, but much higher for polygenic traits (e.g., body shape and pharyngeal jaw morphology) that distinguish new species.

Keywords *Amphilophus citrinellus* · Speciation · Parallel evolution · Genetic polymorphism · Sympatric speciation · Natural experiment

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J. Torres-Dowdall · A. Meyer (✉)
Zoology and Evolutionary Biology, Department of Biology, University of Konstanz, Konstanz, Germany
e-mail: julian.torres-dowdall@uni-konstanz.de; axel.meyer@uni-konstanz.de

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1 Introduction

One of the most debated topics in evolutionary biology is the role of geography in the origin of biodiversity. There is no doubt about the importance of geography for speciation, given its direct impact on gene flow and selection (Nosil 2012). However, disagreements continue about the necessity of physical barriers (e.g., geographic isolation) that impede gene flow for the evolution of new species and about how common speciation in the absence of such barriers is (i.e., speciation with gene flow; Mayr 1963; White 1978; Coyne and Orr 2004). As with many debates in evolutionary biology, the issue of geography was already foreshadowed in Darwin's writings. His views appeared to be ambiguous about the topic, but it is evident that he thought that it is feasible that speciation can occur under different biogeographic scenarios. However, emphasis on the role of natural selection during speciation and Darwin's "principle of divergence" facilitated the acceptance of the idea that speciation most commonly occurs independently of the geographic setting and is due to disruptive selection during competition for resources (Mayr 1963; Coyne and Orr 2004).

That speciation without geographic barriers, or in other words speciation with gene flow (the term "sympatric" was first introduced by Edward B. Poulton in 1904, see Mallet 2004), is possible prevailed until the emergence of a population-genetic thinking after the rediscovery of Mendel's laws (for a detailed revision of speciation during the first 100 years after "The Origin," see Mayr 1963). With an increasing understanding of genetics, the debate about the role of geography became focused on the impact of restriction of gene flow during speciation (Futuyma and Mayer 1980). This also affected the view of the involvement of natural selection in the process of speciation (Mayr 1963; Mallet 2004). In allopatric speciation, extrinsic factors (e.g., geographical barriers) cause a reduction of gene flow between diverging gene pools with natural selection acting only later, possibly contributing to further divergence. However, during sympatric speciation, natural selection plays a fundamental role in initially splitting apart the gene pools (Mayr 1963). The relevant question then became: Can natural selection effectively reduce gene flow among individuals without geographic isolation?

One of the strongest critics of the idea of sympatric speciation was Ernst Mayr who strongly influenced the view on that topic for several decades. In his book *Animal Species and Evolution* (1963), Mayr devoted a chapter to debunking the idea that speciation could proceed without geographic isolation. He critically analyzed the topic, finding no theoretical or empirical evidence in support of sympatric speciation, and concluded that "*All these considerations help to make clear why geographic isolation is a prerequisite for successful speciation*" (1963, p. 480). As part of this criticism, Mayr also attacked the idea of ecological speciation, arguing that there was no evidence that this is "*a process distinct from geographical isolation*" (Mayr 1963). Thus, the view that natural selection played either no role or only a minor role and that speciation was a by-product of geographic separation but not due to local adaptations to particular ecological conditions did prevail in evolutionary biology for several decades. Natural selection became increasingly seen only as the key driving force on the path toward better adaptations within a population, but not as the mechanism for speciation (Meyer 2011).

As predicted by Mayr (1963, p. 451), the idea of sympatric speciation was raised again not long after he criticized it, mostly through genetic models by John Maynard Smith (Maynard Smith 1966; White 1978). In particular in the last decade or so, several models have shown that speciation with gene flow is theoretically possible, although it requires particular conditions to occur (Gavrilets 2004; Bolnick 2006; Bolnick and Fitzpatrick 2007; Gavrilets et al. 2007). This resurgence of interest in sympatric speciation was accompanied by a renewed emphasis on the role of natural selection as a driver of biological diversification, not only by making it possible for speciation to occur in sympatry, but because of its potential to accelerate the process in allopatry (Gavrilets 2004; Nosil 2012; Hendry 2016). Thus, it is now clear that sympatric speciation is not impossible as first postulated by Mayr (but see Mayr (2001) for his opinion on the examples of sympatric speciation in cichlids), but it does not appear to be particularly common. Only few empirical cases have emerged that appear to be best explained by sympatric speciation (reviewed in Coyne and Orr 2004; Bolnick and Fitzpatrick 2007; Bird et al. 2012; Meyer and Kautt 2014; Foote 2018). This paucity of convincing cases of sympatric speciation is mainly because ruling out other speciation mechanisms is extremely challenging. In particular, it requires rejecting the possibilities that (1) the observed phylogenetic pattern is the consequence of gene flow between nonreciprocal sister species occurring in sympatry and (2) speciation actually occurred in allopatry and current sympatry is due to secondary contact (Coyne and Orr 2004).

The Nicaraguan Midas cichlid species complex (*Amphilophus citrinellus* spp.) constitutes one of these few generally accepted empirical examples for sympatric speciation (Barluenga et al. 2006; see in the following). Midas cichlids very rapidly formed small radiations in an interesting geographic setting including two great lakes and several isolated crater lakes (Elmer et al. 2010a; Meyer 2011; see in the following). Thus, this species complex provides a valuable model for the study of the roles of biogeography and natural selection during the formation of adaptive radiations and speciation more generally. In the following, we discuss, with examples, how natural selection has facilitated divergence in allopatry and has repeatedly driven speciation in sympatry in this lineage. We then briefly discuss why, of all the species that inhabit the Nicaraguan lakes, only Midas cichlids radiated, whereas other fish lineages, including other cichlids, did not.

1.1 Discovery of the Midas Cichlid Species Complex

The name of the Midas cichlid species complex comes from the fact that a few individuals in the population would lose their melanophores during ontogeny and become “gold,” as if the King Midas from Greek mythology had touched them—King Midas was gifted, or cursed, with the ability to transform anything he touched

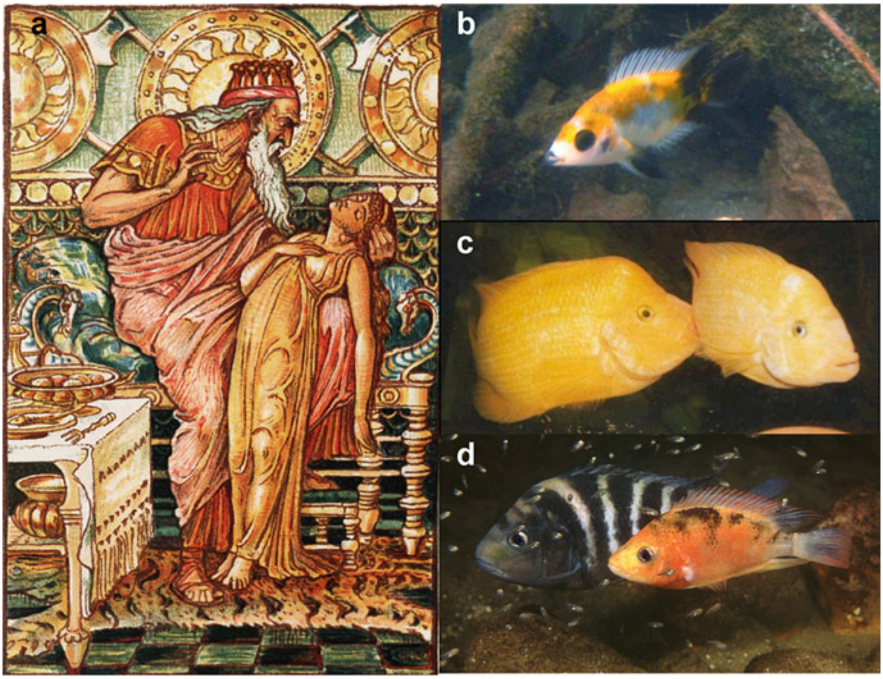

Fig. 1 (**a**) The common name of the *Amphilophus citrinellus* species complex, Midas cichlids, is in reference to the King Midas of the Greek mythology, who transformed everything he touched into gold, including his own daughter (illustration by Walter Crane, 1893). During development, genetically determined gold individuals "transform into gold" by losing their melanophores and exposing the underlying xanthophores. (**b**) This process includes melanophore death and migration and sometimes results in beautiful mosaic fish with white, orange, and black body parts. (**c**) Gold Midas cichlids most often breed assortative; but (**d**) mixed couples are also seen in nature, probably affecting the pattern of genetic divergence between morphs (Photos **b** by Andreas Härer, **c** and **d** by Ad Konings)

into gold (Fig. 1a). Louis Agassiz was the first to describe a Midas cichlid species from a specimen with hypertrophied lips, naming it *Amphilophus froebelii.* This species was presented as new to science during the meeting of the Boston Society of Natural History on October 6, 1858 (Agassiz 1859), and although the published article was written by a scribe, Agassiz is credited with the establishment of both the genus *Amphilophus* and the type species *A. froebelii*. The description given was quite vague, and no type specimen was designated. Therefore, although the genus name was maintained, the species name was considered a *nomen oblitum* because it went unused for more than half a century (Barlow and Munsey 1976; Stauffer and McKaye 2002). A few years later, in 1864, Albert Günther formally described the first two species of the Midas cichlid complex. First, he described *A. labiatus* (as *Heros labiatus*) from Lake Managua (Günther 1864a). Shortly after that, he described *A. citrinellus* (as *Heros citrinellus*) from Lake Nicaragua (Günther 1864b). Curiously, but maybe not too surprisingly, the original descriptions of both species were done based on gold individuals (Fig. 2a). Later, it was clear that these species were polymorphic in terms of coloration (Figs. 1, 2, and 3, see Sect. 5). Within a few years, many additional species were described that subsequently were synonymized either to *A. citrinellus* (*H. basilaris* Gill and Bransford 1877, *Cichlasoma granadense* Meek 1907) or *A. labiatus* (*H. erythraeus* Günther 1867; *H. lobochilus* Günther 1867; *C. dorsatum* Meek 1907). This attests to one of the most distinctive, yet vexing, characteristics of the Midas cichlid species complex: its impressive amount of phenotypic variation, both within and across species (Fig. 2b). Seth E. Meek, in his *Synopsis of the Fishes of the Great Lakes of Nicaragua* wrote: "Of all the species [of] fishes in these lakes, this one is by far the most variable. I made many repeated efforts to divide this material listed below in from two to a half-dozen or more species…" (Meek 1907, p. 122). Later, he concluded: "it is possible that more than one species should be recognized here, and no doubt such will some day be the case…" Noticeably, he nonetheless split the two species currently accepted from the great lakes of Nicaragua into six species, two of which were described there as new species (Meek 1907).

More than a hundred years passed until a new Midas cichlid species was described. George Barlow, who contributed significantly to our understanding of the ecology and behavior of Midas cichlids, together with John W. Munsey described *A. zaliosus*, the Arrow Midas cichlid, an endemic species from crater Lake Apoyo (Barlow and Munsey 1976). The description of this species brought renewed attention to the Midas cichlid lineage because it raised the possibility that *A. zaliosus* evolved in sympatry to its sister species. Five more endemic species were more recently described from the same crater lake, *A. chancho*, *A. flaveolus*, and *A. astorquii* by Stauffer et al. (2008); and *A. supercilius* and *A. globosus* by Geiger et al. (2010b). Also four species endemic to crater Lake Xiloá (*A. amarillo*, *A. xiloaensis*, and *A. sagittae* (Stauffer and McKaye 2002); and *A. viridis* (Recknagel et al. 2013)) were described during that time. These descriptions mattered not only because they led to the recognition of a second potential case of a small adaptive radiation within a crater lake, but also because *A. sagittae* has a striking morphological resemblance to *A. zaliosus* from Apoyo with a similarly elongated body shape associated with an open-water, limnetic life style. Thus, Midas cichlids not only constitute an example of multiple radiations, but the parallelism in these species also emphasizes the potentially deterministic role of natural selection in speciation and the formation of adaptive radiations (Elmer et al. 2010a, 2014).

Demographic models suggest that most Midas cichlid species arose within historical times (less than 2000 years ago) from a common ancestor inhabiting the great lakes (Kautt et al. 2016a, b, 2018, 2020; Machado-Schiaffino et al. 2017). To date, 13 species of Midas cichlids have been described; yet, more genetic clusters are being identified (Kautt et al. 2018). One critical point is that it is easier to determine species limits when they co-occur rather than when they are geographically isolated, and this problem is particularly tricky in the Midas cichlid system that is distributed in several completely isolated crater lakes and two large source lakes (Kautt et al. 2018). Thus, many times after a long collection day in Nicaragua, we found ourselves looking into a bucket full of fish, as Seth Meek

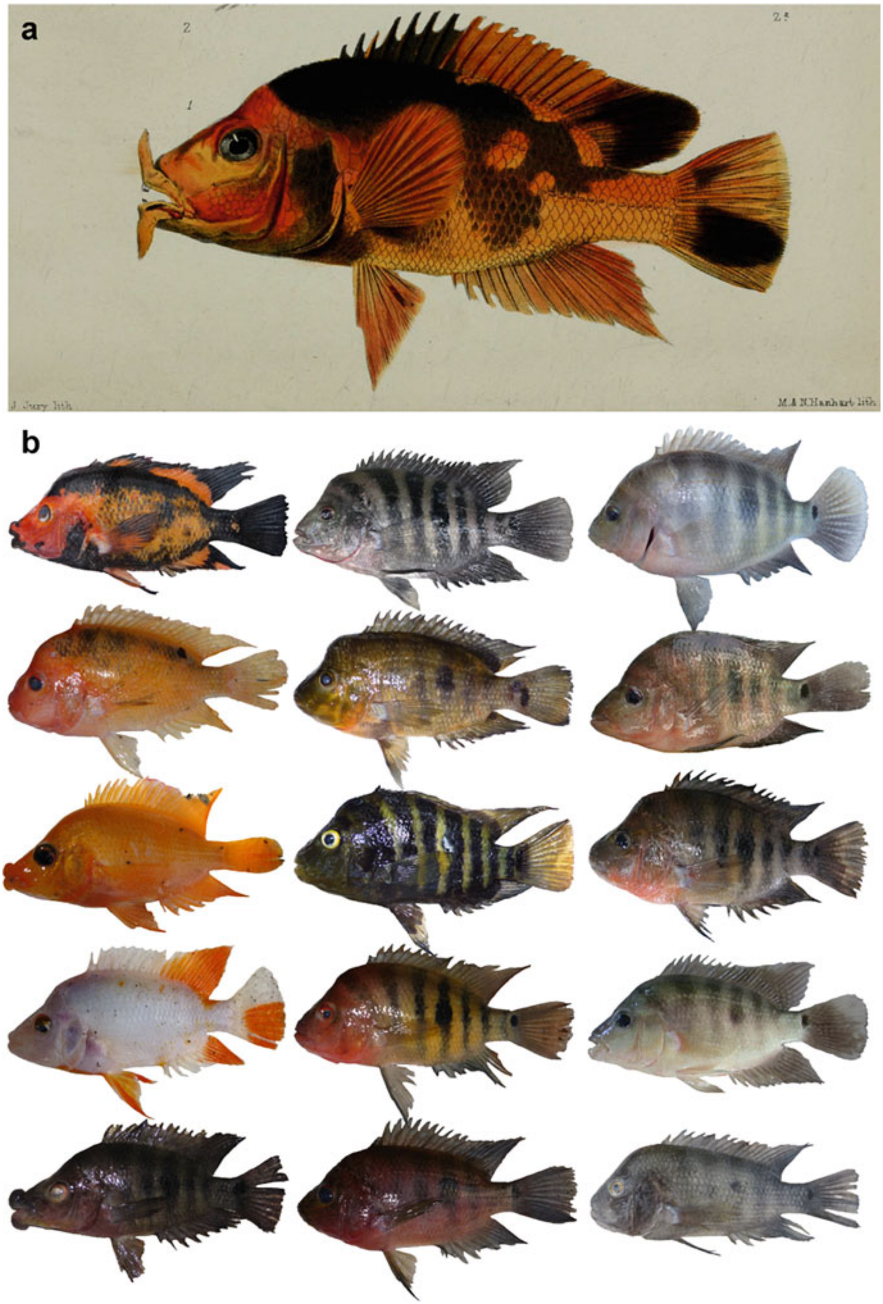

Fig. 2 (**a**) Illustration of a gold, thick-lippy fish accompanying the description of *Amphilophus labiatus* by Albert Günther in 1864. (**b**) Midas cichlids are extremely variable along different phenotypic axes as depicted by these specimens collected from two lakes, Nicaragua and Masaya, with only two species described: *Amphilophus citrinellus* and *A. labiatus*. Most prominent is the variation in the abundance and distribution of melanophores, xanthophores, and leucophores (fish in the first column) and lip size (drawing in **a** and top and lowest three fish in the first column).

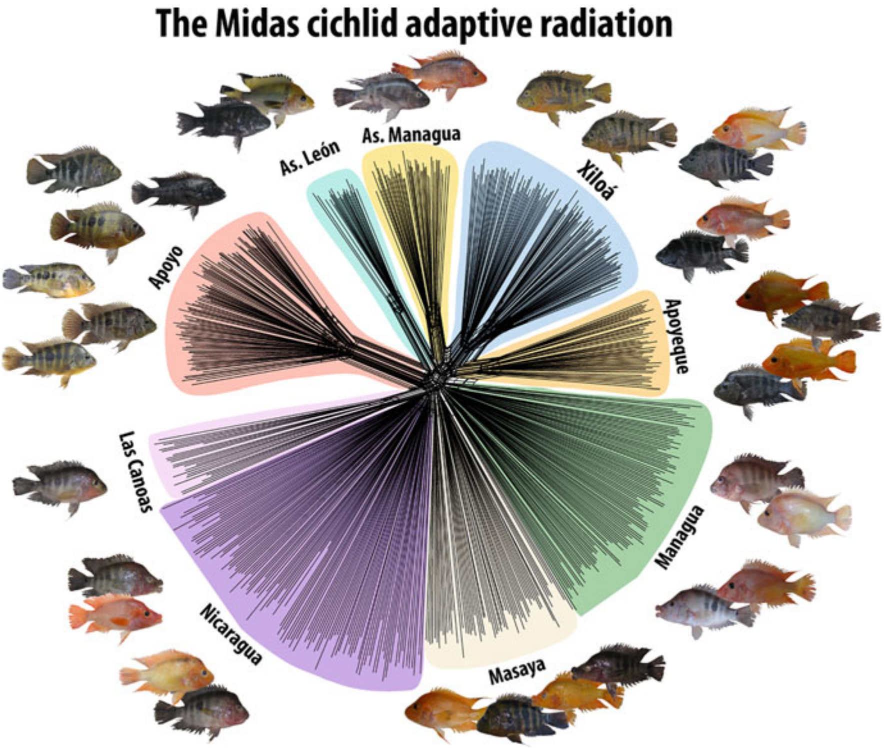

Fig. 3 Neighbor-net split graph based on genetic distance (modified from Kautt et al. 2018), and pictures of the Midas cichlids within each lake. Representatives of the different species are depicted as isolated fish, whereas polymorphisms within species are depicted as overlapping fish (pictures by Andreas Kautt)

did more than a hundred years ago, and wondering if only one species is in our bucket or many of them.

2 The Ecological Setting

The country of Nicaragua is located in the Central American Isthmus (Fig. 4), and from west to east, it can be divided into the Pacific Coastal Plain, the Nicaraguan depression, the Interior Highlands, and the Atlantic Coastal Plain (Weyl 1980; Kutterolf et al. 2007). The Nicaraguan depression is considered as a tectonic graben

Fig. 2 (continued) Moreover, impressive variation in coloration is also seen in fish showing the “normal” pattern of melanophores’ distribution (fish in the second column). A third axis of phenotypic variation is seen in body shape (third column)

Fig. 4 Geographic location and physical characteristics of the Nicaraguan great lakes and crater lakes

with a Late Miocene origin. This 45-km-wide depression contains two large lakes that formed during the late Pleistocene (Kutterolf et al. 2007). Lake Nicaragua (Cocibolca) is the largest lake in Central America and the 19th largest in the world, with an estimated surface area of 8300 km^2. Lake Managua (Xolotlan) is smaller, but still large with a surface area of 1042 km^2 (estimates for both lakes vary, see Cole 1976; Meyer 2011). Both lakes are part of the San Juan River drainage that discharges into the Caribbean. Detailed analysis of the sediments of both lakes showed that there has never been a connection to the Pacific, as previously considered, and that these have always been freshwater lakes (Swain 1966). Both lakes are relatively shallow, with an average depth of only 9 and 12 meters for Managua and Nicaragua, respectively (Cole 1976). Lake Managua is located upstream of Lake Nicaragua, with its surface 9 m higher than the latter (Incer 1976). Both lakes are connected by the Tipitapa River, which flows through the Tisma Pond, but the connection is intermittent due to variation in the water levels of the two lakes (Montenegro Guillén 1992; Meyer 2011).

The Central American Volcanic Arc, which formed during the late Cretaceous due to the subduction of the Cocos plate beneath the Caribbean plate, crosses the Nicaraguan depression and both great lakes from north to south. This resulted in a series of 12 volcanic complexes in Nicaragua, some of which are still active today (Kutterolf et al. 2007). The calderas of inactive volcanoes eventually filled up with groundwater or rainwater and became crater lakes. In Nicaragua, there are eight crater lakes known to have populations of Midas cichlids (Figs. 2 and 3; Table 1). How these crater lakes were colonized is unclear, and several hypotheses have been proposed including “fish rains” produced by hurricanes, drops by piscivorous birds, and human activity (Villa 1976; Meyer 2011). Demographic models estimate that the colonization of the crater lakes occurred quite recently, with crater Lake Apoyo being the oldest colonization (1680 generations ago; Kautt et al. 2016a) and crater Lake Apoyeque the youngest (580 generations ago, one to one and a half generations per year is estimated for Midas cichlids; Machado-Schiaffino et al. 2017). The source of Midas cichlids of all crater lakes is the great Lake Managua, except Lake Apoyo whose source is the great Lake Nicaragua (Kautt et al. 2018).

The crater lakes inhabited by Midas cichlids differ to a certain degree in their physicochemical characteristics, including size, depth, water chemistry, and load of suspended particles (Fig. 4; Barlow et al. 1976; Recknagel et al. 2014; Kautt et al. 2018). Nonetheless, these crater lakes share several characteristics that depart from those in the great lakes in similar ways. For example, all crater lakes are significantly deeper and smaller, and their littoral zone is minuscule compared to that in the great lakes (Recknagel et al. 2014; Kautt et al. 2018). Additionally, the crater lakes are characteristically oligotrophic, having low levels of nutrients for primary production, hence contrasting with the eutrophic characteristics of the great lakes (Swain 1966). Thus, the crater lakes share a series of characteristics that provide a drastically different fish habitat than those of the great lakes. For these reasons, the Midas cichlid species complex provides a replicated system to the study of adaptive evolution and speciation under different geographical settings.

Table 1 Fish diversity of the Nicaraguan lakes

a. Fish species reported from the Nicaraguan lakes

		Crater lakes							Great lakes	
Family[a]	Species[b]	Apoyo	Masaya	Asososca León	Apoyeque	Xiloa	Tiscapa	Asososca Managua	Lake Managua	Lake Nicaragua
Atherinopsidae (3)	*Atherinella sardina*	x	x			x		x	x	x
Cichlidae (18)	*Amatitlania nigrofasciata*		x			x			x	x
	Amphilophus longimanus		x			x			x	x
	Amphilophus rostratus					x			x	x
	Archocentrus centrarchus					x			x	x
	Hypsophrys nematopus		x			x			x	x
	Hypsophrys nicaraguensis					x			x	x
	Parachromis dovii		x			x			x	x
	Parachromis managuensis	x	x	x	x	x	x	x	x	x
Clupeidae (1)	*Dorosoma chavesi*		x			x			x	x
Eleotridae (1)	*Gobiomorus dormitor*	x	x			x		x	x	x
Heptapteridae (4)	*Rhamdia nicaraguensis*					x			x	x
Poeciliidae (11)	*Poecilia gillii*[c]					x			x	x
	Poecilia mexicana[d]	x	x	x	x	x			x	x
Synbranchidae (1)	*Synbranchus marmoratus*					x			x	x

b. Fish species only reported from the great lakes and the San Juan River	
Atherinopsidae (3)	*Atherinella hubbsi, A. milleri*
Bryconidae (1)	*Brycon guatemalensis*
Carcharhinidae (1)	*Carcharhinus leucas*
Centropomidae (2)	*Centropomus parallelus, C. pectinatus*
Characidae (10)	*Astyanax aeneus, A. cocibolca, A. fasciatus, Bramocharax bransfordii, Bryconamericus scleroparius, Carlana eigenmanni, Hemibrycon* sp., *Hyphessobrycon tortuguerae, Roeboides bouchellei, R. guatemalensis*
Cichlidae (18)	*Amatitlania septemfasciata, Amphilophus alfari, Cryptoheros spilurus, Herotilapia multispinosa, Oreochromis aureus, O. niloticus, Parachromis friedrichsthalii, P. loisellei, Tomocichla tuba, Vieja maculicauda*
Gerreidae (1)	*Eugerres plumieri*
Gymnotidae (3)	*Gymnotus carapo, G. cylindricus, G. maculosus*
Haemulidae (1)	*Pomadasys crocro*
Heptapteridae (4)	*Rhamdia guatemalensis, R. laticauda, R. quelen*
Lepisosteidae (1)	*Atractosteus tropicus*
Loricariidae (1)	*Hemiancistrus aspidolepis*
Megalopidae (1)	*Megalops atlanticus*
Mugilidae (1)	*Agonostomus monticola*
Poeciliidae (11)	*Alfaro culturatus, Belonesox belizanus, Brachyraphis* sp., *Phallichthys amates, P. tico, Poecilia sphenops, Poeciliopsis gracilis, Priapichthys annectens, Xenophallus umbratilis*
Pristidae (3)	*Pristis pectinata, P. perotteti, P. pristis*
Rivulidae (1)	*Cynodonichthys isthmensis*

[a] Number in parenthesis indicates the number of species per family described for the great lakes, crater lakes, and San Juan River

[b] The list of species was extracted from ERM (2015), Härer et al. (2017b), and references within

[c] The phylogenetic position of the Nicaraguan taxon related to *P. gillii* is controversial (Bagley et al. 2015; Palacios et al. 2016; Härer et al. 2017b)

[d] *Poecilia mexicana* is most likely polyphyletic, including an undescribed taxon controversial (*P. sp. ‘tipitapa’*; Bagley et al. 2015; Härer et al. 2017b)

2.1 Other Fish Species in Nicaraguan Lakes

Midas cichlids are one of the most common fish species in the great and crater lakes of Nicaragua, and they dominate most of these lakes in terms of fish biomass (Dittmann et al. 2012). Yet, they are not the only fish inhabiting the great and crater lakes. Surveys on the fish fauna of the great lakes and associated rivers have been scarce (Meek 1907; Astorqui 1971; ERM 2015; Härer et al. 2017a), but more than 50 species have been identified (Table 1). The great lakes count includes three species of elasmobranchs, the bull shark (*Carcharhinus leucas*) and two sawfish (*P. pristis* and *P. perotteti*), and the tropical gar (*Atractosteus tropicus*) among the most curious parts of their fish fauna. It is unfortunately likely that the sharks and the sawfish have been driven to extinction due to overfishing in the last decades. The most diverse family of bony fishes in the great lakes are the cichlids, with 17 species documented for the lakes, including two introduced species of tilapia (*Oreochromis niloticus* and *O. aureus*). Of these 17 cichlid species, only a subset colonized the crater lakes (Table 1, the composition varies across crater lakes) and only one cichlid species, besides Midas cichlids, is present in all the crater lakes (the top predator *Parachromis managuensis*). Curiously, this species is now very abundant in crater Lake Tiscapa, but was not found there by Meek one hundred years ago (Meek 1907), suggesting that humans might have introduced it into the lake in recent years. Studies on these species have been conducted in an effort to understand why Midas cichlids are the only lineage that radiated in the crater lakes (see Sect. 6) and not, for example, any other cichlid species or the livebearing fishes of the Family Poeciliidae, of which only two species are found in Xiloá, but seven more co-occur in the great lakes and in the San Juan River.

Much of this intra- and interspecific diversity is threatened. In 2013, the Hong Kong Nicaragua Canal Development Group (HKND) of China obtained a 50-year concession from the Nicaraguan government to build and use an interoceanic shipping canal. The construction of the canal is highly contested because of its potential social and ecological impacts (Meyer and Huete-Perez 2014; Huete-Perez et al. 2015, 2016). Currently, the project appears to be stalled, and for the last 3–4 years, there has been no official information from the Nicaraguan Government about the future of the canal. However, due to the major impacts to the environment and the imperilment of the fauna that its construction might cause, it is important to remain alert to the future decisions of the Nicaraguan government about the plans of the canal.

3 Parallel Phenotypic Divergence and Allopatric Speciation: Interlacustrine Radiation of Midas Cichlids

The allopatric origin of biodiversity is well-documented and, accordingly, not controversial. However, what role natural selection plays during allopatric speciation is still debated among evolutionary biologists. Genetic divergence between isolated populations could be the result of nonselective processes (i.e., genetic drift); however, the process of speciation can be extremely slow under these conditions (Coyne and Orr 2004; Gavrilets 2004). Natural selection is thought to accelerate this process, and thus, it is considered fundamental in radiations occurring in allopatry (also referred to as geographic radiations, see Simões et al. 2016).

In Midas cichlids, variable levels of genetic differentiation were found in pairwise comparisons of populations inhabiting different lakes, from $F_{\mathrm{st}} \approx 0.05$, when comparing fish from the two great lakes, to $F_{\mathrm{st}} \approx 0.5$, when comparing populations from different crater lakes (Bunje et al. 2007; Kautt et al. 2018, 2020). This might be due to the fact that only a low number of individuals might have colonized each of the crater lakes from the great lakes, resulting in genetic bottlenecks that might have increased genetic divergence among geographically isolated populations (Bunje et al. 2007; Kautt et al. 2018). Demographic models estimated that only a few hundred individuals colonized each of the crater lakes (Kautt et al. 2016a, b, 2018, 2020; Machado-Schiaffino et al. 2017). However, these models also support the prediction that a second colonization event followed by admixture resulted in increased standing genetic diversity in most crater lake populations (Kautt et al. 2018, 2020). Natural selection is thought to have played a strong role driving phenotypic diversification by sorting this genetic diversity. This effect is most evident in the cases of parallel evolution that can be observed in the comparisons of the two small radiations of crater Lakes Xiloá and Apoyo (see Sect. 4.1; Elmer et al. 2010a, 2014; Kautt et al. 2016a), but also in consistent phenotypic changes seen across multiple crater lakes (e.g., Torres-Dowdall et al. 2017b; Kautt et al. 2018). In the following, we present and discuss two such examples, one considering morphological adaptations to the geomorphological characteristics of crater lakes, and a second one about the physiological adaptation of the visual system to the new photic conditions experienced in those lakes.

3.1 Parallel Evolution in Body Shape After Crater Lake Colonization

One of the most dramatic phenotypic changes observed in Midas cichlids after the colonization of crater lakes is in body shape. Midas cichlids from the great lakes Managua and Nicaragua have a deep body, where the ratio of body depth to standard length is high. This morphology is thought to be adaptive to the shallow, benthic environment they occupy in these great lakes. In the crater lakes, Midas cichlids evolved an elongated body shape compared to their ancestral populations (Klingenberg et al. 2003; Recknagel et al. 2014; Kautt et al. 2018). In some of these crater lakes, there was also an increase in variation in body shape (across and within species, see Sect. 4.1), but on average, there was a parallel change in body shape in all the crater lakes, where the ratio of body depth to length was reduced compared to great lake Midas cichlids (Kautt et al. 2018).

This divergence in body shape between the ancestral form and the derived crater lake Midas cichlids has been shown to be maintained under common garden conditions (Kautt et al. 2016b), suggesting that the trait is to some degree heritable. Fish body shape can plastically respond to environmental conditions (Wimberger 1992), such as water flow (Langerhans 2008; Franssen et al. 2013) or chemical cues (Abate et al. 2010; Torres-Dowdall et al. 2012). However, a split brood experiment exposing juveniles of four species of Midas cichlids to low versus high water flow for 6 months found no effect of treatment in the ratio of body depth to length (Kautt et al. 2016b). Instead, the three species from crater lakes maintained their more elongated body compared to great lake Midas cichlids. This is further supported by studies of F2 hybrid crosses finding significant QTL associated with body elongation (Franchini et al. 2014a). Interestingly, this study found that few genomic regions of large effect contributed to most of the divergence in Midas cichlids' body elongation. The study was conducted crossing two Midas cichlid species from crater Lake Apoyo, so this might not be representative of the genetic architecture of this trait across the whole radiation. However, demographic modeling indicated that morphological change occurred quite rapidly after crater lake colonization, but it slowed down later (i.e., the amount of change exponentially decreased with time since colonization; Kautt et al. 2018). This pattern is consistent with few alleles of large phenotypic effect contributing to change in body shape (e.g., Orr 2005; Kopp and Hermisson 2007).

A similar pattern is observed across different fish species, like sticklebacks (*Gasterosteus* spp.; Schluter 1993) and whitefish (*Coregonus* spp.; Landry et al. 2007), where limnetic (elongated) and benthic (deep-bodied) morphs evolved repeatedly. This is also well-documented across cichlid lineages, for example, after the colonization of Ugandan crater lakes by haplochromine cichlids. Cichlids in 13 Ugandan crater lakes have evolved a more elongated, slender body shape than their source population from Lake Edward (Machado-Schiaffino et al. 2015). Why would crater lake cichlids evolve elongated body shapes consistently and repeatedly in distantly related species? The parallelism seen within the Midas cichlid radiation, and when comparing crater lake cichlids from Uganda and Nicaragua, strongly suggests that the evolution of body shape is driven by natural selection. The geomorphological characteristics of crater lakes might provide the ecological scenario where elongated body shapes might be advantageous. The steep banks and shores of crater lakes result in a reduced littoral zone that might render the limnetic zone ecologically more relevant for fish. In fact, the divergence in body shape between ancestral and derived Midas cichlid species is negatively correlated with the total littoral zone of the crater lake (Recknagel et al. 2014; Kautt et al. 2018). Models considering the biomechanics of swimming predict the evolution of body shape associated with habitat complexity (Webb 1994; Langerhans and Reznick 2010); and the colonization of more open-water habitats has been repeatedly shown to be related to the evolution of more elongated, streamlined body shapes (Schluter 2000; Gow et al. 2008; Landry and Bernatchez 2010). Midas cichlids with more elongated body shapes have higher swimming endurance than deep bodied fish

(Raffini et al. 2020), providing a functional link between the ecological setting of the crater lakes and the evolution of morphology.

In summary, all crater lake Midas cichlids have independently evolved elongated body shapes compared to that found in source population from the shallow great lakes, apparently as an adaptation for increasing swimming performance in the more open-water environment. This parallelism is suggesting an important role for natural selection acting on standing genetic variation originally introduced from the ancestral great lakes in driving morphological evolution in crater lake Midas cichlids toward a predictable adaptive outcome. However, other factors might also have contributed to the evolution of body shape. In particular, there is a negative correlation between amount of phenotypic change and size of the founder population (Kautt et al. 2018), suggesting that drift might be an important factor in shaping evolution (e.g., Kolbe et al. 2012). An alternative explanation for this pattern is that later admixture events in some crater lakes constrained the amount of phenotypic change. Unfortunately, it might be difficult to contrast these potential explanations with the current data and the small number of crater lakes that have been colonized by Midas cichlids.

3.2 Parallel Evolution of the Visual System

Visual sensitivity is another trait that evolved divergently and in parallel after colonization of at least two crater lakes (Apoyo and Xiloá) (Torres-Dowdall et al. 2017b). The visual sensitivity of an organism is the integration of several phenotypic characteristics of its eyes. For example, the part of the light spectrum that reaches animals' retinas is limited by their ocular media (e.g., cornea and lenses), which selectively filters out light of particular wavelengths—most often highly energetic short wavelengths that might damage the retina. Additionally, the visual pigments in the photoreceptors of the retina could have peak sensitivities at different parts of the light spectrum (Yokoyama and Yokoyama 1996; Bowmaker 2008). These peaks of sensitivity are the particular wavelength at which light absorption is at its maximum, which depends on the interaction of the two components of visual pigments (Cronin et al. 2014; Carleton et al. 2016). One component is the opsin protein, a transmembrane G-protein-coupled receptor. Vertebrates have different opsin gene paralogs coding for proteins with peak sensitivities at different parts of the spectrum (i.e., different spectral classes: short-, medium-, and long-wavelength sensitivity). Midas cichlids, like other cichlids (Carleton et al. 2016; Escobar-Camacho et al. 2017), have eight opsin paralogs; one sensitive under dim light conditions (rhodopsin) and seven sensitive under bright light and responsible for color discrimination (Fig. 5a). The second component of visual pigments is the chromophore, a light-absorbing molecule covalently bound to the opsin protein. When a photon of the proper wavelength hits a chromophore, it changes its configuration and initiates a transduction cascade by affecting the tertiary structure of the opsin protein (Fain et al. 2010). Aquatic vertebrates have two types of chromophores, one derived from

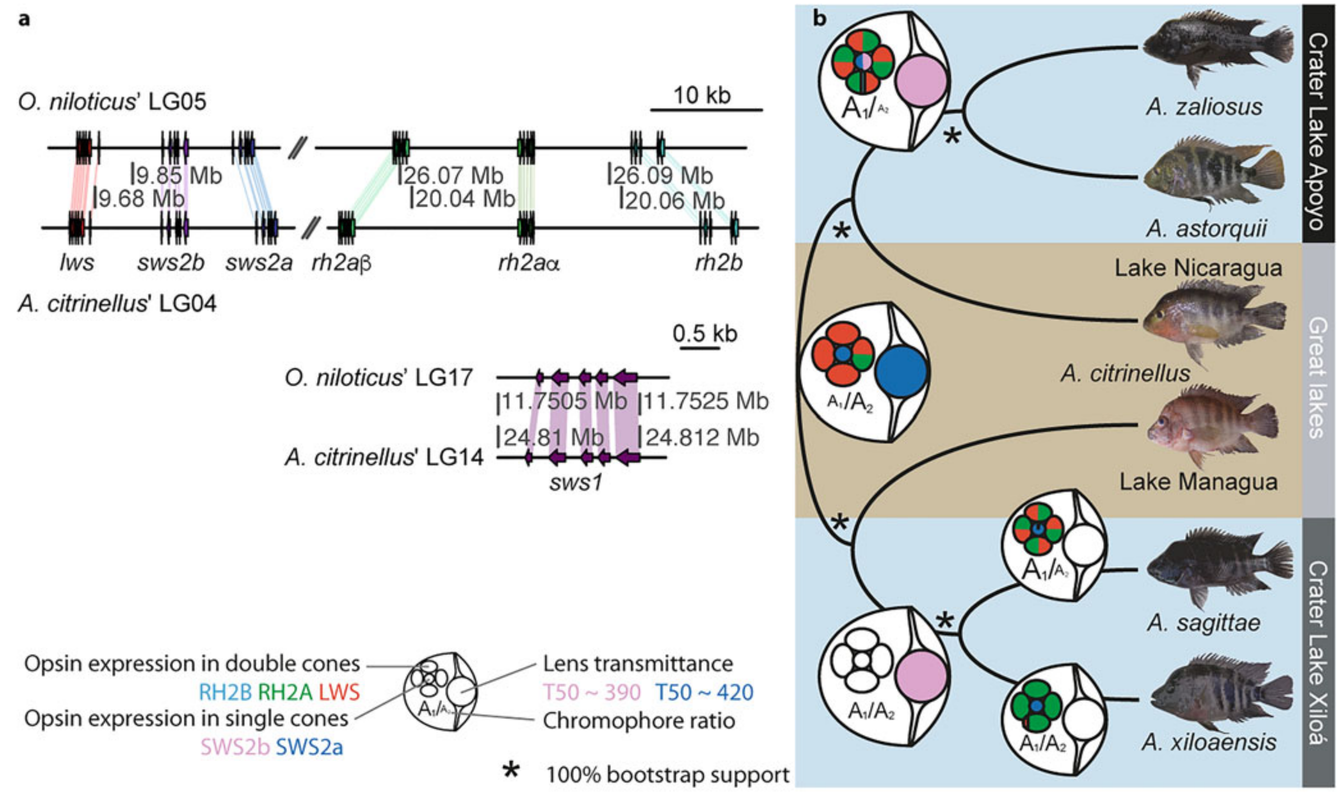

Fig. 5 (**a**) Opsin gene synteny between the African Nile Tilapia (*Oreochromis niloticus*) and the Nicaraguan Midas cichlid (*Amphilophus citrinellus*). (**b**) Schematic representation of the phenotypic changes in the visual system of Midas cichlids associated with the colonization of the clear water crater lakes from the turbid water great lakes. In fish from two crater lakes, lenses became more transmissive and expression of *rh2a* increased and that of *lws* decreased. In all crater lake species, except for *A. xiloaensis*, chromophore usage changed from mainly A2 to mainly A1, depicted in the figure as differences in font size (modified from Torres-Dowdall et al. 2017b)

vitamin A1 and a second one from vitamin A2. Switching from A1 to A2 chromophore usage shifts the sensitivity of a visual pigment toward longer wavelengths within the same spectral class (Wald 1961; Hárosi 1994). Midas cichlids have taken advantage of all these molecular mechanisms to adapt to new light conditions they encountered after the colonization of the crater lakes to shift their visual sensitivity in an integrated manner according to the prevailing light conditions (Torres-Dowdall et al. 2017b).

The great lakes Managua and Nicaragua are very shallow, and the wind keeps stirring the sediments of the bottom maintaining them suspended in the water column (Fig. 4). Hence, the great lakes are extremely murky and very little light penetrates into the water column. Contrary to this, the crater lakes are smaller, very deep, and surrounded by crater rims that protect them from the action of the wind. The result is that sediments rapidly precipitate and the water is very clear, allowing a lot of light to penetrate to greater depths. This has two consequences for the light environment in crater lakes; first, there is proportionally more light than in the great lakes at any given depth. Second, the light spectrum is broader than in the great lakes, particularly due to more available light at short wavelengths (Torres-Dowdall et al. 2017b). Given the importance of the visual system for all daily activities of these fish, strong selection pressure to adapt to these new light conditions is expected. Indeed, the visual system of crater lake Midas cichlids has evolved an increased sensitivity to light in the shorter part of the light spectrum (Torres-Dowdall et al. 2017b); and these modifications appear to have occurred through ontogenetic changes and to have been facilitated by adaptive developmental plasticity of the ancestral population (Härer et al. 2017b).

Given the broader light spectrum experienced by fish in the clear water crater lakes, it would be expected that the ocular media diverges from that found in fish from the turbid great lakes by becoming more transmissive. Indeed, crater lake Midas cichlids' crystalline lenses are clearer, allowing more light in the short-wavelength part of the spectrum to go through and to reach the retina. The increased breadth of light reaching the retina is expected to impose selection on the visual pigments in the photoreceptors of the retina favoring a shift in their sensitivities toward shorter wavelengths. This resulted in three changes in the visual pigments of crater lake Midas cichlids (Fig. 5b). First, opsins that were only expressed during early development in Midas cichlids from the great lakes, but not in adults, are retained in the adult phenotype of crater lake Midas cichlids (Härer et al. 2017b; Torres-Dowdall et al. 2017b). Midas cichlids, like other cichlid species (O'Quin et al. 2011; Carleton et al. 2016), undergo an ontogenetic shift in visual sensitivity due to differential patterns of opsin expression across ages. Larvae express a set of opsins that constitutes visual pigments sensitive at shorter wavelengths, including UV light. As development progresses, this set of expressed opsins changes, and this process ends with adults expressing opsins that constitute visual pigments with sensitivities at longer wavelengths (Härer et al. 2017b). However, crater lake Midas cichlids appear to have a paedomorphic visual system compared to fish from the ancestral great lakes. Adult Midas cichlids in the crater lakes express a set of opsin genes that resembles the phenotype seen in juveniles (~6-month-old fish) from the great lakes and have overall short-wavelength shifted sensitivities (Härer et al. 2017b). Second, the pattern of expression of those opsins that are commonly expressed in adult fish from the great lakes was also modified. Crater lake Midas cichlids upregulated mid- and short-wavelength-sensitive opsin genes and downregulated long-wavelength sensitive ones, resulting in retinas with proportionally more photoreceptors sensitive at shorter wavelengths (Torres-Dowdall et al. 2017b). Finally, Midas cichlids from the crater lakes were also found to have short-wavelength shifted sensitivities compared to fish from the great lakes due to changes in chromophore usage (Torres-Dowdall et al. 2017b). Midas cichlids from the great lakes use predominantly A2 derived, but in the crater lakes most fish change chromophore usage to mainly A1 derived, effectively shifting visual pigment sensitivity toward shorter wavelengths. Thus, all these mechanisms contributed to tuning visual sensitivity toward shorter wavelengths, which are considered adaptive to the light environment of the crater lakes (Torres-Dowdall et al. 2017b). These changes are likely to be heritable to some extent, as the differences seen in nature between the fish from the crater lakes and their source population from the great lakes were maintained when fish were reared under common garden conditions in the laboratory. Interestingly, six other cichlid species that also colonized crater lakes have a short-wavelength shifted visual sensitivity compared to the ancestral populations from the great lakes, but the underlying molecular mechanisms are not exactly the same as those seen in Midas cichlids (Härer et al. 2018). These differences were mainly due to differences in the pattern of opsin expression in the crater lakes. While all species shifted sensitivities toward short wavelengths, only *Amatitlania siquia* retained a juvenile pattern of opsin expression in adults after colonizing the crater lakes, as Midas cichlids from crater Lake Apoyo did. Unlike Midas cichlids, four species changed the expression of green sensitive opsins. Nonetheless, in all cases, it resulted in a short-wavelength shifted visual sensitivity (Härer et al. 2018).

One question that remains is, how are the observed differences during ontogeny produced? The ontogenetic shift seen in visual sensitivities when comparing the derived Midas cichlid species from the crater lakes to their source populations in the great lakes may indicate differences in the thyroid metabolism of the retina of these fish. Thyroid hormone (TH) has been shown to play an important role in the developmental progression from short- to long-wavelength shifted visual sensitivities (Ng et al. 2001; Cheng et al. 2009; Novales Flamarique 2013). Comparisons of circulating levels of TH during development, indirectly measured using deiodinases (genes that are involved in TH metabolism) as proxies, between *A. citrinellus* from Lake Nicaragua and *A. astorquii* from crater Lake Apoyo have shown striking differences with *A. citrinellus* having higher levels of TH (Härer et al. 2017b). Moreover, this effect was validated by rearing Midas cichlids in water supplemented with TH, finding that the progression in opsin gene expression got accelerated (Härer et al. 2017b), as it occurs in other vertebrates (Roberts et al. 2006; Cheng et al. 2009). Disruption of the TH metabolism, by rearing Midas cichlids in complete darkness, also resulted in elevated levels of TH and acceleration of developmental progression from short- to long-wavelength shifted sensitivities (Karagic et al. 2018). Ongoing experiments are aiming to determine if the retina regulates TH metabolism independently of the rest of the body, which will decouple the effect of TH on eye development from overall development.

4 Sympatric Speciation: Midas Cichlids' Intralacustrine Radiations

The likelihood of the evolution of reproductive isolation without barriers to gene flow (i.e., sympatric speciation) and how commonly it occurs in nature remains one of the most debated topics in evolutionary biology (Mayr 1963; Coyne and Orr 2004; Bolnick and Fitzpatrick 2007; Bird et al. 2012; Meyer and Kautt 2014). The idea of species evolving in sympatry through adaptation to different ecological niches is already present in Darwin's "On the Origin of Species" (1859), and it was for some time considered to being the most common mode of speciation (Mayr 1963; Coyne and Orr 2004). The idea that natural selection could have played a role in the process of speciation without geographic isolation was criticized by the proponents of the Modern Synthesis, especially by Ernst Mayr (reviewed in Bird et al. 2012). Following the publication of Mayr's influential book *Animal species and evolution* (Mayr 1963), most biologists considered allopatric speciation the most common mode of cladogenesis, and sympatric speciation was disregarded as unlikely or as an impossible process. However, the interest in sympatric speciation revitalized during the last 30 years, as theory showing that it is possible was produced and more credible empirical examples accumulated (Coyne and Orr 2004; Bolnick and Fitzpatrick 2007; Bird et al. 2012; Meyer and Kautt 2014).

However, verifying putative cases of sympatric speciation remains challenging because the process of speciation is traditionally thought to occur over long time scales. Thus, inferences about the probability of this event occurring in sympatry have to be drawn from indirect evidence, and most often alternative explanations cannot be completely discarded (Meyer and Kautt 2014). With the goal of guiding research, Coyne and Orr (2004) proposed four criteria that need to be satisfied for validating sympatric speciation as the most likely mode of speciation: (a) the considered species have a sympatric distribution; (b) there should be genetically based reproductive isolation; (c) there is a phylogenetic sister relationship between the species; and (d) there was no historic phase of geographic isolation. Very few cases satisfied these four criteria, and none of them does so without criticism (Bolnick and Fitzpatrick 2007; Meyer and Kautt 2014). One of the few accepted cases are the small adaptive radiations of Midas cichlids in Nicaraguan crater lakes (Barluenga et al. 2006). In the following, we examine the available evidence supporting this claim for the radiations in crater Lakes Apoyo and Xiloá (associated with body shape changes); then, we discuss the case of fish with thin and hypertrophied lips from two crater lakes and the great lakes; and finally, we argue for a role of pharyngeal jaws in this process.

4.1 Rapid and Parallel Intralacustrine Speciation Along the Benthic-Limnetic Axis

Midas cichlids are perhaps most well-known for sympatric speciation and parallel evolution of benthic and limnetic species within crater Lakes Apoyo and Xiloá (Barluenga et al. 2006; Elmer et al. 2010a, 2014; Kautt et al. 2012, 2016a). The limnetic species from crater Lake Apoyo, *A. zaliosus*, was the first species to be described from the crater lakes within the Midas cichlids species complex (Barlow and Munsey 1976). Since then, there have been many attempts to reconstruct the evolutionary history of this species and, in particular, to find out if it evolved in the absence of geographic barriers to gene flow. A case for sympatric speciation was first presented by Wilson et al. (2000) and later by Barluenga and Meyer (2004) and Barluenga et al. (2006). These studies used mitochondrial, microsatellite, and *AFLP* markers and concluded that crater Lake Apoyo Midas cichlids constitute a monophyletic clade; and therefore, *A. zaliosus* diverged in sympatry from *A.* cf. *citrinellus* from the same crater lake. At the time the other species from the lake had not been formally described yet. This interpretation was rapidly challenged, arguing that the results were also compatible with the alternative explanation of divergence in allopatry followed by a second colonization event of the lake by a second species (Schliewen et al. 2006). Subsequent work using different molecular markers have found support for the monophyly of Apoyo Midas cichlids (Geiger et al. 2010a; Kautt et al. 2012, 2016a, 2018, 2020; Elmer et al. 2014). The species from Lake Xiloá have received less attention, partly because the barrier isolating it from Lake Managua is small as the crater rim has eroded and recent oscillations in the water level of both lakes might have connected them. Thus, it has been assumed that several of these events must have occurred in the past contributing to the diversity of Midas cichlid of Xiloá. However, it was also concluded that the species within this lake constitute a monophyletic group (Kautt et al. 2012, 2016a, 2018, 2020; Elmer et al. 2014). Recently, Kautt et al. (2016a) pointed out that validating the fourth criteria proposed by Coyne and Orr (2004; no historic phase of geographic isolation) is more challenging than demonstrating monophyly, as secondary contact and introgressive hybridization might result in similar patterns (e.g., Martin et al. 2015). Using demographic models based on a comprehensive genome-wide dataset, they concluded that speciation within crater Lakes Apoyo and Xiloá occurred in sympatry and found only little evidence that secondary contact of partially divergent genetic pools was involved in the process (Kautt et al. 2016a). Thus, taking all evidence into account and considering the different methodologies used, there is strong support for the evolution of multiple Midas cichlid species in the absence of barriers to gene flow within the crater Lakes Apoyo and Xiloá, providing a very valuable, replicated system to study speciation with gene flow.

Three additional factors make the intralacustrine radiation in crater Lakes Apoyo and Xiloá truly remarkable. One is that the evolution of a limnetic species occurred in parallel in Apoyo and Xiloá (Elmer et al. 2010a, 2014). The level of parallelism is notable, with multiple traits varying in the same direction, including pharyngeal jaw, body shape, and trophic niche (inferred from stable isotopes; Elmer et al. 2014). The most impressive parallelism is in body shape, where the angles of morphological divergence of *A. zaliosus* and *A. sagittae* from their respective source populations are almost identical (Kautt et al. 2018). The second factor is the speed at which these radiations occurred. Demographic models using genome-wide data suggest that the crater Lakes Apoyo and Xiloá were colonized less than 2000 generations ago and that the split among species occurred less than 900 generations ago (Kautt et al. 2016a). Finally, even though most of the attention has been paid to the divergence between benthic and limnetic species, at least four and three species that could be characterized as benthic have evolved within Apoyo and Xiloá, respectively (Stauffer and McKaye 2002; Stauffer et al. 2008; Geiger et al. 2010b; Kautt et al. 2016a). All these species appear to have originated within a very short period of time (on the order of a few hundred generations), thus, being better represented by a polytomy than dichotomous branching of species (Kautt et al. 2016a). Very little is known about the axes of variation within the benthic species in each of the lakes. However, comparative analyses of trophic niches (considering stable isotope signatures and gut microbiomes) are starting to clarify this issue (Franchini et al. 2014a; Härer et al. 2020). Thus, the extremely young Midas cichlid radiations present the opportunity to ask what are the conditions that promote and facilitate sympatric speciation.

Gavrilets et al. (2007) pointed out that speciation in crater lakes is theoretically possible if four conditions are met: (i) the strength of selection for local adaptation is intermediate; (ii) the traits controlling local adaptation are determined by few loci of major effect; (iii) carrying capacity of the crater lakes is intermediate; and (iv) the loci controlling for nonrandom mating have a strong effect. Unfortunately, measuring the strength of selection in nature has been challenging in the Midas cichlid lineage, so there is no direct support for the first condition. There have been a series of studies that allowed us to determine the plausibility of the other conditions. QTL analyses of a hybrid cross between the limnetic species (*A. zaliosus*), and one of the benthic species (*A. astorquii*) from Lake Apoyo found a few genomic regions associated with body shape (Franchini et al. 2014b, 2016a). Nonetheless, a large percentage of the body shape variation in the F2s remained unexplained with 12%–20% of the variation being explained by all the significant QTLs. Moreover, machine learning-based analyses on re-sequenced genomes of all species from crater Lakes Apoyo and Xiloá indicate the presence of numerous selection sweeps across the genome, suggesting a polygenic basis for trait divergence (Kautt et al. 2020). Thus, there is not much support for *condition ii*. Demographic models estimate much smaller population sizes for crater lake populations than those estimated for the great lakes, suggesting lower carrying capacity (Kautt et al. 2016a, b). Moreover, these models suggest that the process of disrupting selection did not start immediately after colonization, but that population size increased first, probably reaching carrying capacity for fish resembling the ancestral morph, and then Midas cichlids diversified within crater lakes (Kautt et al. 2016a, b, 2018). Thus, there is at least some support for condition *iii*. Finally, there is conflicting evidence for *condition iv*. Support for strong assortative mating comes from field surveys of Midas cichlid breeding couples (Stauffer et al. 2008; Elmer et al. 2009) and mate choice experiments conducted under laboratory conditions (Kautt et al. 2020), where in both cases, fish mate strongly assortatively based on species identity. However, no assortative mating based on morphology was observed when females from one of the two crater lakes where the limnetic morph evolved were offered males of both morphs from the other lake. For example, Xiloá females of a benthic and a limnetic species were tested in community tanks with Apoyo males of a benthic and a limnetic species. Thus, the effect of the loci controlling nonrandom mating might be strong, but the mating cue is not necessarily associated with morphology.

A recent study using genomic markers identified a few wild-caught specimens from crater Lake Xiloá that appear to be hybrids between the limnetic species *A. sagittae* and its most closely related species, the benthic *A. xiloaensis* (Kautt et al. 2016a). This might suggest that reproductive isolation between the two young species is incomplete. Notably, F_{st} values between them are relatively high ($F_{\mathrm{st}} = 0.228$; $P < 1 \times 10^{-14}$; Kautt et al. 2016a), suggesting that gene flow albeit being low does occur between these species. This finding is puzzling. An exciting potential explanation is that the putative hybrids are in the process of becoming a new, independent population occupying a distinct ecological niche and speciation is ongoing. This is supported by the finding of divergent morphology and significant F_{st} between the hybrids and the parental species (hybrids, *A. sagittae*: $F_{\mathrm{st}} = 0.109$; hybrids, *A. xiloaensis*: $F_{\mathrm{st}} = 0.129$; both $P < 1 \times 10^{-14}$; Kautt et al. 2016a). Further ecological and genomic work will be required to validate this hypothesis.

In any case, the conditions proposed by Gavrilets et al. (2007) are barely met or not met at all in the small radiation of crater Lakes Apoyo and Xiloá. Yet, sympatric speciation did occur in these two crater lakes. Moreover, even when all the conditions were assumed to be true, in many cases the simulations did not result in sympatric speciation, and when it occurred, the time to divergence was relatively long (e.g., around 20,000 years). These results are not very compatible with our current findings on the system, where radiation occurred two independent times (out of six crater lakes) and relatively rapid (around 2000 generations) (Kautt et al. 2016a). Interestingly, a different model predicts a scenario that is highly similar to what is observed in the Midas cichlids from the crater lakes (Bolnick 2006). In particular, this model predicts the evolution of multiple species almost simultaneously and in a very short time span, resulting in hard polytomies. These predictions are strikingly similar to the results of demographic models in Midas cichlids (Kautt et al. 2016a). However, the model has a series of assumptions that were criticized on the base of their biological realism (e.g., Gavrilets 2004, 2005). One such assumption is that the trait of ecological relevance also plays a role in mate choice (e.g., magic trait). This could hold true for hypertrophied lips (e.g., Machado-Schiaffino et al. 2017; see Sect. 4.2), but it does not appear to be the case for body shape (see earlier). Another criticized assumption is that the ecological trait distribution is smaller than the resource distribution. This is possibly the case in the Midas cichlids, as the crater lakes differ significantly from the great lakes that served as source populations. New resources, not previously encountered in the great lakes, could have been available for fish after the colonization of the crater lakes. Still another assumption, not yet studied in the Midas cichlid complex, is that females can sample at low cost a large number of males before mating. Violating this assumption still can result in sympatric speciation, unless the cost is really high (Bolnick 2006). Midas cichlids are currently very dense in the crater lakes they inhabit (Dittmann et al. 2012), so females could potentially be very choosy without paying a very high cost. However, current densities not necessary reflect those at the period when reproductive isolation evolved (Kautt et al. 2018). Thus, further exploring if the conditions of the model are satisfied in the Midas cichlid system is of major importance.

Incipient speciation along the limnetic–benthic axis might also be occurring in a third crater lake, Asososca Managua (Kusche et al. 2014; Kautt et al. 2016b). The Midas cichlid species in this crater lake (*A. tolteca*) satisfies some of the conditions necessary, although not sufficient, for sympatric speciation to occur (Nosil 2012). This species is highly variable in terms of ecomorphological traits, with some individuals having a limnetic-like and others a benthic-like body shape (Kusche et al. 2014; Kautt et al. 2016b). Importantly, this variation was associated with habitat use—limnetic-shaped fish were more common in the middle of the lake—and with trophic level—limnetic-shaped fish have a higher trophic level (Kautt et al. 2016b). Phenotypic plasticity does not seem to be the cause of this variation, as a split brood experiment rearing fish under different levels of water flow had no effect on body elongation (Kautt et al. 2016b). However, intermediate phenotypes are common in the lake, rendering a continuous, rather than a bimodal trait distribution. Moreover, the ecomorphological divergence was not associated with genetic divergence. This lack of genetic structuring was found in different studies using different molecular markers, all of them not finding any evidence for more than one genetic cluster in crater Lake Asososca Managua (Barluenga and Meyer 2010; Kusche et al. 2014; Kautt et al. 2016b, 2020). Hence, it seems possible that the processes of disruptive selection and assortative mating have been at work in *A. tolteca*, but that genetic differentiation has not built up at neutral markers across the genome yet. This is possible; neutral genetic differentiation may not be expected in the earliest stages of divergence (Elmer et al. 2010a; Colborne et al. 2016). Alternatively, the strengths of assortative mating and disruptive selection are not strong enough, and therefore, the population is stalled in its divergence (e.g., Matessi et al. 2001; Bolnick 2006). In any case, the Midas cichlid species complex presents three replicated cases of divergence along a benthic–limnetic axis, which are at different evolutionary stages due to the different history of the three crater lakes.

4.2 Midas Cichlids with Hypertrophied Lips

Hypertrophied lips have repeatedly evolved in the cichlid lineage, providing a striking case of convergent evolution (Kocher et al. 1993; Oliver and Arnegard 2010; Colombo et al. 2013; Manousaki et al. 2013; Burress 2014; Henning and Meyer 2014; Henning et al. 2017; Machado-Schiaffino et al. 2017). Species with hypertrophied lips (also referred as thick-lipped species) can be found in the three African great lakes, among South American riverine cichlids of the genera *Crenicichla* and *Gymnogeophagus*, and in the Midas cichlid species complex. Only one species with hypertrophied lips has been formally described within the Midas cichlid complex, *Amphilophus labiatus*, which is found in the two great lakes, Managua and Nicaragua. But Midas cichlids with thick lips are also present in two crater lakes, Apoyeque and Masaya, and a few specimens were observed in crater Lake Xiloá (personal observation). Unlike *A. citrinellus*, *A. labiatus* is not found in the rivers connected to the lake nor in any other drainage where Midas cichlids are found. Thus, the current hypothesis is that lips evolved within the great lakes, although it is not clear if the trait is associated with population structure or if it evolved in the absence of extrinsic barriers to gene flow. There is evidence that in the great lakes, the genome of the two lineages became divergent enough to be called different species quite recently (Kautt et al. 2020). Whole-genome comparisons between *A. citrinellus* and *A. labiatus* suggest that there were high levels of gene flow between the two lineages until around ten thousand years ago (assuming 1.5 years generation time and mutation rates previously published for cichlids). Thus, these two species appear to have evolved in sympatry within the great lakes. There is compelling evidence that ecological divergence might have played a role, which combined with assortative mating, raises the interesting possibility that hypertrophied lips worked as a magic trait, affecting both, ecological performance and mate choice (Machado-Schiaffino et al. 2017).

Hypertrophied- and thin-lipped fish differ in their trophic niches (Elmer et al. 2010b; Colombo et al. 2013; Manousaki et al. 2013; Machado-Schiaffino et al. 2017). Hypertrophied lips are thought to help fish suck mollusks and arthropods from crevices among rocks, which is supported by the finding that fish with thick lips are more effective than thin-lipped fish in removing food items from structures resembling crevices (Baumgarten et al. 2015; Machado-Schiaffino et al. 2017). Moreover, *A. labiatus* fish that are forced to feed from crevice-like structures show adaptive plasticity, developing larger lips than individuals that feed from soft surfaces (Machado-Schiaffino et al. 2014). However, this trades off with the ability to capture evasive prey from the water column, a task in which thin-lipped fish are significantly more efficient (Fig. 6a; Machado-Schiaffino et al. 2017). Furthermore, gut content analyses (Elmer et al. 2010b; Colombo et al. 2013) show that the diet of thick-lipped Midas cichlids consists mainly of arthropods and hard-shelled invertebrates, whereas remains of fish and other evasive prey are the main items found in the guts of thin-lipped Midas cichlids from the same lake. This ecological divergence is also evidenced in stable isotope analyses finding that thick-lipped fish have a lower trophic level than thin-lipped Midas cichlids (Manousaki et al. 2013). The ecological divergence has been tested under natural conditions, where thick- and thin-lipped fish were kept in field enclosures associated with rocky or sandy habitats. As expected, thick-lipped Midas cichlids outperformed thin-lipped fish in the rocky environment, although no difference was found in the sandy habitat (Machado-Schiaffino et al. 2017). All these studies have provided strong evidence that there is ecological divergence between Midas cichlids with and without hypertrophied

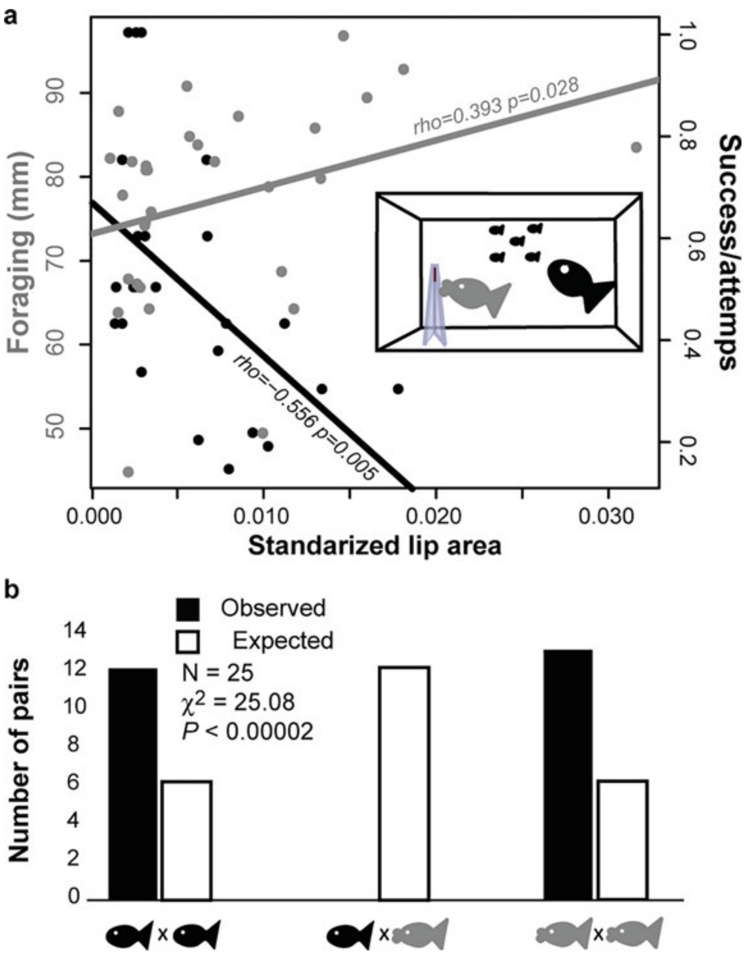

Fig. 6 (**a**) Thick- and thin-lipped Midas cichlids trade off in their ability in removing food items attached to crevices (e.g., invertebrate larvae, depicted as gray) and their success catching evasive prey (e.g., smaller fish, depicted in black). (**b**) Thick- and thin-lipped fish mate assortative, with no disassortative couples seen in laboratory crosses (modified from Machado-Schiaffino et al. 2017)

lips. Also, fish with intermediate phenotypes were shown to perform worse than the two extreme ones; strongly suggesting that hybrids would have lower fitness than either parental species, potentially resulting in extrinsic postzygotic isolation. Hence, natural selection is expected to have favored individuals that mate assortatively, facilitating the evolution of reproductive isolation.

There is strong evidence for premating reproductive barriers associated with lip morphology. A field survey in crater Lake Apoyeque found strong departure from random mating between thick- and thin-lipped Midas cichlids (Fig. 6b; Machado-Schiaffino et al. 2017). The number of disassortative couples found was significantly lower than the number expected given the relative abundance of both morphs. When this experiment was repeated under laboratory conditions and using Midas cichlids from the great lakes, not a single disassortative couple was formed (Machado-Schiaffino et al. 2017). Thus, it is clear that mating is not random; however, it also suggests a cost for choosiness given that disassortative couples were seen in the field but not in the lab, although this could be due to the lake of origin of the species used in each experiment. It is also likely that intrinsic postzygotic isolation is evolving among these species, as a large number of malformed specimens were recovered from forced crosses between them (A.M. *unpublished data*).

The presence of hypertrophied lips gives the impression of similarity among *A.* cf. *labiatus* fish from different lakes. In fact, overall head shape shows parallel changes when comparing thick- and thin-lipped fish from the different lakes (Manousaki et al. 2013; A.M. *unpublished data*). However, overall body morphology is more similar within lakes than within morphs. This means that in general there is one axis of morphological divergence that is better explained by lake of origin, and a second axis that is better explained by lip morph. Thus, it remains unclear if hypertrophied lips evolved only once or multiple times in the Midas cichlid species complex. The most parsimonious would be to assume that it evolved once and then it spread into the two great lakes and crater lakes Apoyeque and Masaya, and several lines of data support this. Analyses of *AFLP* data found no differentiation between *A. labiatus* and *A. citrinellus* in Lake Nicaragua, suggesting that there are only islands of differentiation or simply that these two described species represent a single genetic pool (Kautt et al. 2012). RADseq data and data from re-sequenced genomes show that thick- and thin-lipped Midas cichlids genetically cluster by lake rather than by morph, but both datasets identify the two species as independent genetic clusters within the two great lakes (i.e., F_{st} values are lower between morphs within lakes than across lakes within morphs; Machado-Schiaffino et al. 2017; Kautt et al. 2020). Nonetheless, genome-wide differentiation between morphs is the highest in the older great lakes but the lowest in the youngest crater Lake Apoyeque (Machado-Schiaffino et al. 2017; Kautt et al. 2020). This pattern of genomic differentiation across lakes agrees with a single origin of hypertrophied lips if gene flow is assumed to have occurred between the thick- and thin-lipped species of Midas cichlids, and this trait has a simple genetic architecture.

As mate choice experiments showed (Machado-Schiaffino et al. 2017), thick- and thin-lipped fish mate mostly assortatively. However, a very low number of disassortative couples are still observed in nature (at least in crater Lake Apoyeque) allowing for gene flow between species. Moreover, an increased cost of being choosy during mating could be expected when population densities are low, as might have occurred immediately after the colonization of the crater lakes (Machado-Schiaffino et al. 2017). These conditions would promote higher levels of introgression, which are expected to result in patterns of genetic differentiation similar to the ones observed (e.g., more divergence among lakes than between morphs and lower divergence in crater lakes).

Studies focusing on the genetic architecture of the trait also point to a single origin of hypertrophied lips. Crosses between thick- and thin-lipped species of Midas cichlids strongly suggest that the hypertrophied lip phenotype is controlled mainly by one locus of major effect (although other loci of lower effect might be involved), different from what was found in African cichlid thick-lipped species (Henning et al. 2017). New analyses based on whole-genome resequencing on a large number of wild-caught specimens provide additional support to this conclusion (Kautt et al. 2020). In the otherwise flat landscape of genomic differentiation between Midas cichlids with different lip morphology within each of the lakes they inhabit, there are a few islands of high genomic differentiation, with one shared peak across all lakes. This peak coincides with a region of genomic association with lip morphology identified by a genome-wide association analysis. The fish with hypertrophied lips from the different lakes share a putatively causal haplotype in this region of differentiation that shows signatures of a selective sweep (Kautt et al. 2020).

Current work is focused on reducing the genomic interval associated with hypertrophied lips, and most likely, the functional locus responsible for this phenotype will be found soon. Two inward rectifier potassium channel genes are located in the proximity of the region of genomic differentiation between morphs, and these might play a role in tissue swelling in fish with hypertrophied lips (Kautt et al. 2020), but further studies are required to determine if they play a role at all and what is their specific function. Identifying the causal locus will allow us to determine if the exact same mutation is responsible for hypertrophied lips in Midas cichlids across all the lakes; or if different mutations or even different loci are the underlying molecular cause (Elmer and Meyer 2011). Finding that all thick-lipped Midas cichlids share the same mutation would provide support to the hypothesis of a single speciation event, most likely in sympatry within one of the great lakes, followed by (1) colonization of other lakes by *A.* cf. *labiatus*, most likely at the same time as *A.* cf. *citrinellus*, and (2) some introgression occurring with *A.* cf. *citrinellus*. If this were the case, then the most plausible scenario is that few individuals of each species colonized the crater lakes after they became habitable. There, due to low population density and increased cost of finding mates, assortative mating broke down and gene flow increased between these species homogenizing their genomes. Divergent selection favored the maintenance of both morphotypes evidenced in the signatures of selection seen in the small region of genomic differentiation between morphs (Kautt et al. 2020). Whether the crater lake populations are currently diverging again or stalled in their current state as a stable polymorphism is a very interesting question that certainly would be a topic of future research in the system (Machado-Schiaffino et al. 2017). Nonetheless, it is notable that even though most of the conditions proposed by Gavrilets et al. (2007; see detail earlier) as favorable for sympatric speciation to occur are met in this system, particularly the oligogenic basis of the trait and the strong assortative mating, genome-wide differentiation associated with lip morphology is very low, contrary to what is seen in the small adaptive radiations of crater Lakes Apoyo and Xiloá where divergent traits are highly polygenic (Kautt et al. 2020).

4.3 The Pharyngeal Jaws and Their Role in Midas Cichlid Sympatric Speciation

Pharyngeal jaws have long been suggested to play a pivotal role in the spectacular evolutionary success of cichlids (Liem 1973). This is because this second set of jaws allowed the decoupling of prey capturing and processing during feeding. In cichlid fish, the oral jaw is highly specialized for prey capturing potentially due to the effectiveness of the pharyngeal jaw in prey processing (Liem 1973; Hulsey et al. 2006). This functional modularity allows cichlids to exploit different niches and potentially adapt to new niches more rapidly than other fish can. The high diversity in the structure and mechanics of the pharyngeal jaws reflects this. For example, Central American cichlids show several transitions between robust pharyngeal jaws having few, large teeth (i.e., molariform) and more slender pharyngeal jaws having many small pointy teeth (i.e., papilliform) (Fig. 7; Hulsey 2006). The Midas cichlid adaptive radiation is not an exception with regard to the importance of the pharyngeal jaws. Many of the main axes of divergence seen across Midas cichlid species are associated with divergence in the pharyngeal jaws (Meyer 1990a, b; Barluenga et al. 2006; Manousaki et al. 2013; Elmer et al. 2014).

There is a clear relationship between diet and the lower pharyngeal jaw (LPJ) morphology. Both major types of LPJ, molariform and papilliform, are commonly found in Midas cichlid species. Molariform LPJs are more efficient in crushing hard-shelled prey, such as snails (Hulsey 2006). However, this advantage trades off with the ability to process soft prey for which papilliform LPJs are most efficient (Meyer 1989). For example, in crater Lake Xiloá, more than 90% of Midas cichlids with molariform LPJ are found to have eaten snails; whereas fewer than 20% of fish with papilliform LPJ were found to have snails in their stomach (Meyer 1990a). Moreover, the proportion of Midas cichlids with molariform LPJ is strongly associated with the abundance of snails in a lake. In crater Lake Masaya, snails are uncommon or absent and almost all Midas cichlids have papilliform LPJs, whereas in crater Lake Xiloá, where snails are abundant, up to 50% of the fish have a molariform LPJs (Fig. 7; Meyer 1990a). Although some of the variation in this trait is heritable, LPJ morphology is highly plastic in response to food hardness (Muschick et al. 2011).

The LPJ appears to have played a very important role in the process of sympatric divergence of Midas cichlids, both between thin- and thick-lipped fish as well as between benthic and limnetic fish. In the lakes where they coexist, thin- and thick-lipped fish differ significantly in LPJ morphology (Elmer et al. 2010b; Manousaki et al. 2013). It would be expected that thick-lipped fish commonly forage in rocky habitats and consume a large proportion of hard-shelled invertebrates (e.g., snails and arthropods; see Sect. 4.2). However, the opposite pattern is found in most lakes. The strongest differences are seen in fish from Lake Nicaragua, where *A. labiatus* (thick-lipped) have more papilliform LPJ than *A. citrinellus* (thin-lipped) (Manousaki et al. 2013). In other lakes, the data are inconclusive. In crater Lake Apoyeque, Elmer et al. (2010b) found thick-lipped fish to have more papilliform LPJs than thin-lipped fish, but the opposite pattern was found by Manousaki et al.

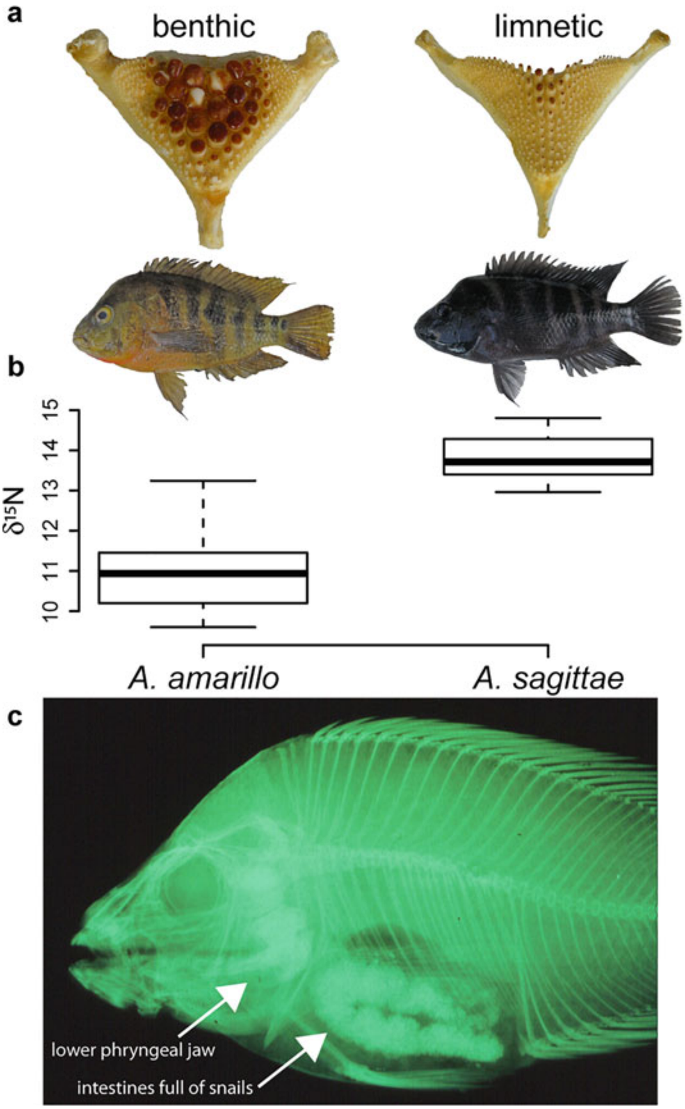

Fig. 7 (**a**) Benthic (*A. amarillo*) and limnetic (*A. sagittae*) species from crater Lake Xiloá differ significantly in the morphology of their lower pharyngeal jaw (LPJ), with the former having molariform LPJ and the later a papilliform LPJ. (**b**) This is associated with differences in their diet as indicated by significant differences in the ratios of stable isotopes of nitrogen. (**c**) The lower trophic level seen in the benthic species is associated with a higher consumption of snails. X-ray photo of an *A. amarillo* specimen with its intestines full of fragmented pieces of snail shells

(2013). In crater Lake Masaya, no fish was found to have a clear molariform LPJ, but thick-lipped fish tend to have more robust LPJs than thin-lipped ones (Manousaki et al. 2013). Thus, difference in LPJ morphology has apparently contributed to divergence between thick- and thin-lipped Midas cichlids, but not necessarily in a parallel manner across lakes (Manousaki et al. 2013).

LPJ morphology has evolved in parallel along the benthic–limnetic axis in crater Lakes Apoyo and Xiloá. The limnetic species of these two lakes (*A. zaliosus* and *A. sagittae* from Apoyo and Xiloá, respectively) have more gracile LPJs carrying many pointy teeth than the coexisting benthic species (Fig. 7; Barluenga et al. 2006; Elmer et al. 2014). The papilliform LPJs are expected to increase handling efficiency of live prey (Hulsey et al. 2005), in agreement with the higher proportion of evasive prey found in the limnetic species diet (Elmer et al. 2014). Analyses of a hybrid cross between the limnetic and a benthic species from crater Lake Apoyo revealed that the major *QTLs* for LPJ shape and for body shape co-localize. Thus, the integrated genetic architecture of these two traits might have played a fundamental role promoting rapid adaptive divergence in sympatry (Fruciano et al. 2016a).

Besides the work by Fruciano et al. (2016a), little has been done to determine the genetic architecture of LPJ morphology. The main reason for this is that the LPJ is a complex structure, and several different components have functional importance and need to be considered (e.g., pharyngeal jaw shape and weight, tooth size and number, and suture structure; Meyer 1990b). Even though Fruciano et al. (2016a) found a *QTL* for LPJ shape, no *QTL* was found for LPJ size. Other traits were not analyzed for this particular cross. Analyses of a hybrid cross between *A. labiatus* and *A. citrinellus* suggest that there are five small-effect *QTLs* for tooth size, but no significant ones for tooth number (Kautt et al. 2020). Analyses of hybrid crosses in African cichlids, on the other hand, did find some *QTLs* for tooth number, both in the pharyngeal and oral jaws (Hulsey et al. 2017). Although these two jaws are functionally and mechanically independent (Hulsey et al. 2006), they might not be genetically independent. The number of teeth in the pharyngeal and oral jaws are correlated; and the major *QTL* for these two traits are co-localized (Hulsey et al. 2017). It is still unclear if the same pattern is seen in Midas cichlid fish, but currently there is work being conducted in this area and soon these questions will be clarified. Thus, the Midas system could provide an ideal group of species to link genotype to phenotype in the pharyngeal jaws of cichlids.

5 The Intriguing Case of Color Polymorphism: Stable Polymorphism or In Vivo Speciation?

One of the most intriguing and interesting phenotypic variations in the Midas cichlid species complex is its polymorphism in coloration, with melanic and amelanic, “gold” morphs. The gold morph can be found in almost all Midas cichlid populations, except for the species from crater lakes Tiscapa and Apoyo, where only a few gold specimens have been spotted, and two of the four species of Lake Xiloá (*A. amarillo* and *A. viridis*). When present, the gold morph constitutes a small proportion of the population, commonly between 5% and 10% of the fish, and this value is roughly similar across all lakes and has been stable for at least the last 50 years (Barlow 1976; Torres-Dowdall et al. 2014; Kautt et al. 2020). Gold fish are born with melanophores, but at some point during development, these are lost due to apoptosis. The rest of the fish do not undergo such a significant change in coloration during ontogeny, and therefore have been commonly referred to as “normal,” in reference to its much greater frequency in nature, but “dark” or “melanic” are also commonly used. On average, fish that bear melanophores (i.e., dark pigment) are perceived as darker. However, since melanophores present motility in response to many factors, these fish can also be quite pale-gray. Whether pale grey can be consistently considered darker than orange is unclear, although it is possible when considered in terms of contrast with the environment. Of all the terms used to refer to this morph, melanic fish is technically more sound, as the difference with the gold morph is that they retain their melanophores. The gold morph of Midas cichlids has evoked the attention of researchers for a long time, and extensive work has been done to understand its evolution and ecology and its potential role in the adaptive radiation of this lineage; yet, the factors that influence the frequency of this polymorphism and its relationship to speciation are still unclear.

There is strong evidence that the gold phenotype is genetically determined. Crosses of gold and melanic fish have consistently resulted in a 3:1 gold to melanic ratio, strongly suggesting that the phenotype has a Mendelian genetic architecture, and it is controlled by a single locus with the gold allele being dominant to the melanic one (Barlow 1983; Henning et al. 2010, 2013). However, the causal locus has been evasive even though several attempts have been made to identify it. Ongoing work suggests that the same genomic region differentiates gold and melanic fish in all the populations where both morphs coexist. This region is quite small, comprising only 230 kilobases (Kautt et al. 2020). There is some evidence that this region might be a recombination hotspot, opening the possibility that different mutations within that region could underlie the gold phenotype. However, in all crosses conducted with pairs from different lakes, the same pattern of inheritance was found (e.g., 3:1 gold to melanic ratio), suggesting that it might have a common genetic basis across all populations. The gold locus is soon to be identified, which will allow us to test for the role of natural and sexual selection in the evolution and maintenance of phenotypic diversity in nature.

Irrespectively of which is the causal locus for the gold phenotype, its effects are not evident in the early life of Midas cichlid fish. In fact, during the first few months of life, genetically determined gold and melanic fish are indistinguishable from each other. Changes in coloration rarely start before fish carrying the gold allele reach 60 mm of length. The process involves the death of most of the melanophores and the aggregation of some of them in particular regions of the body, in particular the fins and around the mouth area (Fig. 1b; Dickman et al. 1988). This pattern is strikingly similar to cases of vitiligo in humans. Concurrently with this process, xanthophores (yellow pigments) become dominant in the skin giving fish their characteristic orange coloration. Sometimes xanthophores only proliferate in a few parts of the body and leucophores (white pigments) become also abundant resulting in fish showing beautiful mosaic patterns (Fig. 1b). It is yet unclear what triggers the onset of transformation, but the timing is variable among individuals. It has been even seen, on some rare occasions, that gold fish only transform after reaching sexual maturity. Some of this variation appears to be due to a dosage effect, where heterozygotes transform later than homozygous gold fish do (A.M. *unpublished data*). This delayed transformation of heterozygotes could play a role in the maintenance of this polymorphism across populations.

Several studies have shown that this polymorphism is not selectively neutral. Gold fish differ from melanic conspecifics in their diet, competitive ability, and risk of predation. There is compelling evidence suggesting that gold individuals have a competitive advantage over dark individuals (Barlow and Ballin 1976; Barlow and Wallach 1976; McKaye and Barlow 1976; Barlow 1983; Lehtonen 2014). Laboratory experiments demonstrated that when limiting foraging territories are available, juvenile gold Midas cichlids outcompete normal, melanic fish. Yet, this is not because juvenile gold fish are more aggressive, but because they get challenged less frequently by the more abundant melanic morph (Barlow and Ballin 1976). This is also apparent in natural populations, where gold fish were less likely to be attacked by another Midas cichlid than melanic fish (McKaye and Barlow 1976; Lehtonen 2014), but also intimidate normal fish that are up to 1.2 times their own size (Barlow 1983). There is evidence that between morph competition may have resulted in differences in their diet and associated trophic structures; yet, the evidence is inconclusive. Early studies suggested that pharyngeal jaws associated with consumption of evasive prey (e.g., papilliform) were more commonly found in gold individuals than melanic ones (Meyer 1990a). However, a more recent and larger study showed that gold individuals commonly have more robust pharyngeal jaws (e.g., molariform) than melanic fish in most lakes (except for fish in lakes Managua, Masaya, and Apoyeque; Kusche et al. 2015). This difference was also reflected in the trophic level estimated based on stable isotopes analysis, although variation across lakes was evident suggesting that there is no consistent pattern (Kusche et al. 2015). Curiously, there is evidence that gold fish fail to attain territories in shallow water, where breeding is most likely to be successful due to higher access to food (McKaye and Barlow 1976; McKaye 1980; but see Elmer et al. 2009). This was explained not by competitive ability, but as a mechanism to avoid predation by piscivorous birds (McKaye 1980; Barlow 1983).

When originally postulated, the competition–predation trade-off hypothesis suggested that visually oriented piscivorous birds were the main predators of Midas cichlids and that they would preferentially attack individuals of the conspicuous gold morph in shallow waters (McKaye 1980). This hypothesis could explain both, why gold Midas cichlids are more rare than individuals of the dark morph (Barlow 1983) and why gold individuals tend to breed deeper than melanic individuals, as by doing so they can escape predation by birds (McKaye and Barlow 1976). Different studies agree that color is not selectively neutral with regard to predation risk (Annett 1989; Kusche and Meyer 2014; Torres-Dowdall et al. 2014, 2017a); yet, it is not clear which of the morph is under higher risk of predation, or whether a more complex regime involving frequency dependency or interaction with environmental parameters (e.g., photic conditions) is at play. Field studies have shown that piscivorous fish (e.g., *Parachromis managuensis* and *Gobiomorus dormitor*) are the main predators of Midas cichlids, but birds and crocodiles also prey upon them (Torres-Dowdall et al. 2014, 2017a). These studies also suggest that gold fish do not suffer higher predation risk than melanic fish do and that predation pressure does not decrease with depth. Thus, predation does not fulfill the expectations of the competition-predation trade-off hypothesis proposed to explain the maintenance of the polymorphism (e.g., McKaye 1980; Barlow 1983). Yet, the most common predator of Midas cichlids, *P. managuensis*, does indeed have a red shifted visual sensitivity (Härer et al. 2018) and, at least under laboratory conditions, it does attack gold fish more readily than melanic fish (Kusche and Meyer 2014). Thus, there is a disagreement between the tendency of Midas cichlids' main predator to attack gold fish and the pattern of predation observed in nature. A potential explanation for this is that predatory fish form search images of Midas cichlids, which will decrease the predation risk for gold fish given that they represent less than 10% of the population (Barlow 1983). Support for this hypothesis comes from the finding that small gold individuals, which are extremely rare in nature, have lower probability of a predator attack than melanic fish of the same size, but this difference disappears in large fish where the gold morph is more common (Torres-Dowdall et al. 2017a). There are still many open questions with regard to the role of predation in the maintenance of the Midas cichlid color polymorphism that demand answers. Some of these will surely be answered soon, once we identify the locus responsible for this phenotype allowing us to determine natural selection in nature.

An interesting aspect of the color polymorphism in Midas cichlids is that mating appears to be assortative (Fig. 1c, d; Barlow 1976; McKaye and Barlow 1976; McKaye 1980; Elmer et al. 2009). For example, in crater Lake Xiloá, pairs where both individuals are gold are more common (4% and 8% for *A. sagittae* and *A. xiloaensis*, respectively) than predicted given the small proportion of the population represented by gold fish (0.5% and 4%, respectively; Elmer et al. 2009). This result appears to be consistent in nature and in the lab, and across different species. Thus, given that mating is not random with regard to coloration and that color morphs are ecologically different in many regards (see earlier), this polymorphism is a prime candidate for divergence and speciation. Studies aimed to test for genetic differentiation between color morphs gave conflicting results. Microsatellite analyses concluded that there was some degree of differentiation between gold and normal fish from the great Lake Nicaragua (Wilson et al. 2000; Barluenga and Meyer 2004) and in crater Lake Xiloá between color morphs of *A. xiloaensis* (Elmer et al. 2009). However, recent analyses on a broader sampling scale (e.g., higher sample size per population and more populations) and with a much higher resolution (hundreds of markers obtained from restriction site associated DNA sequencing) did not find strong differentiation between morphs. Whole-genome resequencing data showed that there is an association between color and a very narrow region of the genome (Kautt et al. 2020). Thus, given our current knowledge, this trait is best understood as a polymorphism and probably not as a stage in incipient speciation. The fact that gold and melanic morphs are not selectively neutral and there is assortative mating suggests that there is potential for the evolution of reproductive isolation. Yet, there is still a large number of disassortative couples that increase gene flow between the two morphs, therefore decreasing overall differentiation. For example, in Xiloá, disassortative couples represent over 5% and 23% of the total couples of *A. sagittae* and *A. xiloaensis*, respectively (Elmer et al. 2009). A better understanding of selection in nature and the cost of assortative mating would be valuable to determine if this polymorphism is stable or if we are observing an onset of divergence.

6 Why Midas Cichlids?

The examples discussed earlier provide a general overview of the large degree of phenotypic diversity seen among Midas cichlid species complex in Nicaragua. This diversity is evident at different scales, from within population variation (i.e., polymorphisms), to morphological, physiological coupled with varying levels of genetic divergence within and among lakes. One of the most interesting open questions of the biodiversity of the Nicaraguan crater lake system is why Midas cichlids diversified and other lineages of cichlids, or any other species of fish for that matter, did not. This includes both, inter- and intralacustrine phenotypic differentiation, as other cichlid species do not differ particularly notably in ecomorphological traits among populations as Midas cichlids do (Fruciano et al. 2016b). There seems to be no easy answer to this question at this point, but some recently conducted studies can help to reject some hypotheses. One possible explanation is that Midas cichlids colonized the crater lakes prior to the other species. This priority advantage might have allowed them to occupy all empty niches, limiting the probability that other linages also diversify (e.g., priority effects; Fukami 2015). However, Midas cichlids do not appear to have colonized the crater lakes before other species of cichlids did (Elmer et al. 2013; Franchini et al. 2017; Xiong et al. 2020). This seems to rule out a priority effect as an explanation. A second alternative is that the source populations of Midas cichlids might harbor higher levels of genetic diversity than other cichlids species providing a more “fertile” substrate for selection to act upon after the colonization of crater lakes. Recent analyses based on genome re-sequencing of around 500 individuals suggest that indeed most of the genetic diversity in the crater lakes was introduced with the original colonizations from the great lakes (Kautt et al. 2020). However, comparative demographic analysis between Midas cichlids and *Archocentrus centrarchus* from lakes where they co-occur does not support this hypothesis of greater levels of ancestral diversity (Franchini et al. 2017; Xiong et al. 2020). In fact, *A. centrarchus* from the great lakes harbor higher levels of genetic diversity than the coexisting Midas cichlids.

There are several potential explanations for the difference in diversification and speciation rates between Midas cichlids and other cichlid lineages that need to be explored. Firstly, Midas cichlids, in particular in the great lakes, are generalists consuming a high diversity of food items (e.g., Elmer et al. 2010b; Colombo et al. 2013; Manousaki et al. 2013). Other cichlid species appear to be more specialized in their diets. For example, *P. managuensis* feed mainly on other fish, whereas *C. rostratus* feed on detritus (personal observation). Thus, Midas cichlids might be able to take advantage of new resources more easily and for disruptive selection to act upon this variation. Secondly, it is possible that mate choice is stronger or its cost lower in Midas cichlids than in other species (e.g., Bolnick 2006; Gavrilets et al. 2007). This is plausible as Midas cichlids have very large population sizes in most lakes (personal observations; Dittmann et al. 2012), which might allow choosy females to sample a large number of males at low cost. Thirdly, there could be peculiarities associated with the Midas cichlids' genome structure and transcription, such as novel microRNAs (Franchini et al. 2016; Xiong et al. 2018), that might facilitate rapid divergence in Midas cichlids (Brawand et al. 2014). This is something that we are currently exploring, but current evidence does not favor this hypothesis (Xiong et al. 2020). Finally, different levels of phenotypic plasticity across different Nicaraguan cichlid lineages might contribute to differences in their diversification rates. The role of phenotypic plasticity in adaptive evolution and speciation is highly contested. A classical view is that plasticity shields the genotype from selection (e.g., Meyer 1987; Schlichting 2004). But it has been also proposed that phenotypic plasticity might, instead, facilitate and even promote adaptive evolution and diversification, especially in the context of flexible stems (West-Eberhard 2003; Ghalambor et al. 2007; Schwander and Leimar 2011; Schneider and Meyer 2017). There are few, but interesting, cases providing evidence that phenotypic plasticity indeed might have contributed or accelerated adaptive evolution and diversification in nature (reviewed in Levis and Pfennig 2016). Midas cichlids show pronounced developmental plasticity in several traits (e.g., lower pharyngeal jaw (Muschick et al. 2011), lip size (Machado-Schiaffino et al. 2014), color vision (Härer et al. 2017b), and onset of color change (A.M. *unpublished data*)). But, also a lack of plasticity was found in body shape (Kautt et al. 2016b), and more experiments are needed to compare the reaction norms among ancestral and derived populations of Midas cichlids. Knowledge on phenotypic plasticity is, so far, limited in other Nicaraguan cichlids (but see Meyer 1987; Abate et al. 2010), especially with regard to comparisons between ancestral and derived populations. Variation in the ecology of Midas cichlids (e.g., generalists) and other cichlid species in Nicaraguan lakes (e.g., most are specialists) might favor different levels of phenotypic plasticity. Formal frameworks to test the role of plasticity in adaptation and diversification have been recently proposed (Levis and Pfennig 2016; Schneider and Meyer 2017). Following these guidelines might be fruitful in improving our understanding of why some cichlid lineages radiate while others do not. The Midas cichlid fishes of Nicaragua also provide one of the most interesting systems to address this important question in evolutionary biology. Although decades of research on various aspects of the biology of these fishes by several researchers already yielded many insights into fundamental problems in evolutionary biology, they still conceal numerous mysteries that are worth uncovering.

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The Consequences of Anthropogenic Stressors on Cichlid Fish Communities: Revisiting Lakes Victoria, Kyoga, and Nabugabo

Vianny Natugonza, Laban Musinguzi, Mary A. Kishe, Jacco C. van Rijssel, Ole Seehausen, and Richard Ogutu-Ohwayo

Abstract Lakes Victoria, Kyoga, and Nabugabo ("the Lake Victoria region") are remarkable for hosting one of the largest assemblages of cichlid fishes among the African inland lakes. Here, we review the role and severity of anthropogenic and environmental stressors on the cichlid communities in the Lake Victoria region to understand the mechanisms leading to the persistence and resurgence of some of the cichlid fishes. Our review suggests that (1) the native *Oreochromis* species populations primarily collapsed due to overfishing and that the introduced species and habitat change suppressed their ability to recover; (2) without primary triggers associated with change in the environment and habitat conditions, particularly

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V. Natugonza (✉)
Maritime Institute, Busitema University, Namasagali, Uganda
e-mail: viannynatugonza@firi.go.ug

L. Musinguzi
National Fisheries Resources Research Institute, Jinja, Uganda
e-mail: labanmusinguzi@firi.go.ug

M. A. Kishe
Tanzania Fisheries Research Institute, Dar es Salaam, Tanzania
e-mail: mariakishe@tafiri.go.tz

J. C. van Rijssel
Wageningen Marine Research, IJmuiden, The Netherlands

Naturalis Biodiversity Center, Leiden, The Netherlands
e-mail: jacco.vanrijssel@wur.nl

O. Seehausen
Center of Ecology, Evolution and Biogeochemistry, Swiss Federal Institute of Aquatic Science and Technology (Eawag), Kastanienbaum, Switzerland

Aquatic Ecology and Evolution, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland
e-mail: Ole.Seehausen@eawag.ch

R. Ogutu-Ohwayo
African Lakes Network (AFLANET), Jinja, Uganda
e-mail: ogutuohwayo@yahoo.com

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eutrophication and associated anoxia and reduced water transparency, Nile perch (*Lates niloticus*) predation alone may not have caused the massive loss of species diversity; and (3) the resurgence of haplochromine cichlids is due to a combination of general improvement in the environment and reduction in *L. niloticus* abundance, with additionally possibly some rapid ecological adaptations. We conclude that environmental stressors will likely continue to shape the ecosystems in which the remaining endemic cichlid fish diversity continue to evolve, clearly involving genetic exchange between species. If water clarity can be improved again, it is possible to maintain a diverse assemblage of endemic species.

Keywords Cichlid diversity · Ecological opportunity · Eutrophication · Resilience · Multiple stressors

1 Introduction: Cichlid Diversity and Adaptive Radiation

The family Cichlidae is the most species-rich, non-Ostariophysian freshwater fish family with 250 valid genera and 1723 valid species; when all the known species are included, cichlids constitute more than 2000 species (Fricke et al. 2020). Cichlid fishes have largely radiated into many species involving a combination of ecological opportunity, reproductive isolation (through sexual selection), and hybridization (Kocher 2004; Wagner et al. 2012; Brawand et al. 2014; Seehausen 2015; Meier et al. 2017), and geographical isolation, especially for the Amazon, the Congo, and Madagascar (Seehausen, 2015) . These fishes have evolved and adapted to specific habitat types (e.g. vegetated inshore areas, macrophyte fringes, rocky shores, sandy/muddy bottom, or open waters), trophic levels, and feeding types. This ecological specialization of cichlids has contributed to high levels of endemism, with most species restricted to specific aquatic systems (Fryer and Iles 1972).

The African Great Lakes (AGLs), in particular, are remarkable for hosting the largest numbers of endemic cichlids: Lake Tanganyika has ca. 250 endemic cichlid species (Coulter 1991); Lake Victoria has ca. 550–700 cichlid species, most endemic to the lake or specific sections of the lake (Witte et al. 2007a); and Lake Malawi has up to 600 endemic cichlid species (Genner et al. 2003). The rates at which the cichlids have radiated and speciated in these lakes vary, with the cichlids of Lake Victoria representing the fastest large vertebrate adaptive radiation (McGee et al. 2020).

On the other hand, the high degree of ecological specialization of endemic African Great Lake cichlids means that only species that are able to adapt quickly are likely to survive under the rapidly changing environmental conditions, largely emanating from increased human activities. During the last half of the twentieth century, the AGLs endured multiple anthropogenic and environmental stressors related to predation and competition from introduced exotic species, habitat degradation (resulting from eutrophication and pollution), over exploitation, invasive plants, and climate variability and change. These stressors were manifested through rapid changes in the limnological conditions of lakes and fish communities (Hecky et al. 2010; Ogutu-Ohwayo et al. 2016), with cichlids being the most affected (Lowe-McConnell 2009). The effects of these stressors on cichlid diversity and abundance have been widely discussed in the scientific literature (see Lowe-McConnell 2003). However, there is still considerable debate among scientists as to which of these stressors were most responsible for the changes in cichlid communities (e.g. van Zwieten et al. 2016; Marshall 2018).

In this chapter, we review the chronology of events leading to the changes in the diversity and abundance of cichlid communities in three different water bodies within the Lake Victoria region (lakes Victoria, Kyoga system, and Nabugabo). The aim is to update the existing literature on the role and severity of each stressor on cichlid diversity and abundance in the Lake Victoria region, and to explore the mechanisms leading to the persistence and resurgence of some of the cichlid fishes. This information will guide discussions on future management and conservation of these fisheries, given that most of the stressors are intractable and may continue to intensify.

2 The Lake Victoria Region: Past Environment and Fish Fauna

The Lake Victoria region comprises lakes Victoria and Kyoga and the associated satellite lakes (notably Lake Nabugabo) and rivers within their respective catchments (Fig. 1). Lakes Victoria and Kyoga are connected by the Victoria Nile, while Victoria and Nabugabo are separated by an extensive wetland and a sand bar. The three lakes differ in size, habitat types, and general environmental conditions; however, they are quite similar in their native fish fauna (Greenwood 1966; Witte et al. 2009).

Lake Victoria is the largest tropical lake in the world, with an area of 68,800 km^2. However, it is relatively shallow (with an average depth of 40 m and maximum depth 80 m) compared to other AGLs, e.g. Lakes Malawi (704 m) and Tanganyika (1470 m) (Lowe-McConnell 2003). In addition, Lake Victoria (estimated to be 15,000 years old) is the youngest compared to the other major AGLs, e.g. Malawi (1–two million years) and Tanganyika (9–12 million years) (Fryer and Iles 1972; Cohen et al. 1993; Johnson et al. 1996). The lake bottom has numerous habitats types, characterized by muddy, sandy, or rocky substrates. The lake shoreline has numerous bays, with patchy swamp vegetation, much of which has been converted for agriculture and settlement by the rapidly growing human population.

During the first half of the twentieth century, the lake was well-mixed, with adequate oxygen to the bottom for most of the year (Talling 1966). The phytoplankton community was dominated by large diatoms, especially *Aulocoseira* and *Stephanodiscus* spp. (Mugidde 1993), while large calanoid and cyclopoid copepods and *Chironomus* spp. (notably *Chironomus animalus*) dominated zooplankton and

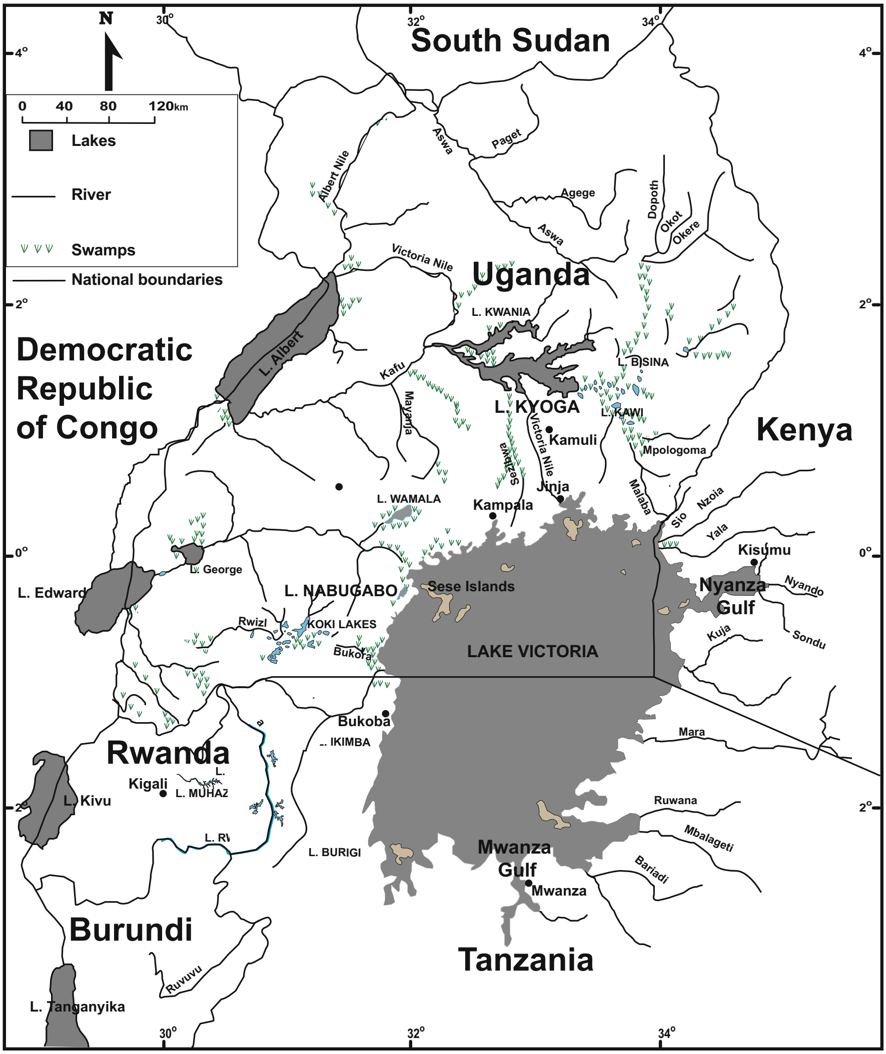


Fig. 1 Location of Lakes Victoria, Kyoga, and Nabugabo, and the associated rivers and minor lakes

macroinvertebrates, respectively (Worthington 1932a). Fish stock assessments showed that haplochromine cichlids made up more than 80% of the demersal ichthyomass and were well distributed over the entire water column (Kudhongania and Cordone 1974).

The Lake Kyoga system (which is referred to as "Lake Kyoga" in this chapter) is primarily a flooded river valley downstream of Lake Victoria to which it is connected by the upper Victoria Nile. It consists of a system of interconnected lakes, with the main lake having two arms, Kyoga and Kwania, and over 30 smaller lakes that are separated from the main lake by swamps (van den Bossche and Bernacsek 1990; Ogutu-Ohwayo et al. 2013). The area of open water is about 2600 km^2, and all the Kyoga lakes have a mean depth of 2–4 m, except the channel marking the course of the Nile River (7–9 m). At the time the first scientific survey of the lake was conducted in 1928, most of Lake Kyoga area was covered by aquatic macrophytes, with a limited portion of open, clear waters (Worthington 1929). The exceptionally heavy El Niño rains of 1961 raised the water level and submerged the open water macrophytes and marginal swamps, expanding the open water portions of the lake (Ogutu-Ohwayo 1995).

Lake Nabugabo is a small shallow open lake lying within an extensive swamp, which fills a former bay on the western shore of Lake Victoria. It is approximately 24 km^2, with a mean depth of 4.5 m. It was once a bay of Lake Victoria, but was separated from the main lake by a sand bar about 5000 years ago (Greenwood 1965; Stager et al. 2005). The first detailed survey of Lake Nabugabo in 1962 showed that the lake was well-mixed and saturated with oxygen, although its conductivity was four times lower than that of Lake Victoria (Cambridge Nabugabo Biological Survey 1962).

2.1 Fish Fauna

The Lake Victoria region was originally dominated by two endemic oreochromine cichlids, *Oreochromis esculentus* (Graham, 1928) and *O. variabilis* (Boulenger, 1906), and hundreds of haplochromine cichlids the majority of which were endemic (Graham 1929, Worthington 1929, 1932b; Greenwood 1966). The two *Oreochromis* species were restricted to shallow inshore waters (<20 m deep), but were still segregated in terms of habitat type; *O. esculentus* was associated with more open waters, while *O. variabilis* was associated with vegetated inshore areas (Greenwood 1966). The same distribution pattern was observed in Lakes Kyoga and Nabugabo, except that the segregation was not obvious due to overlapping habitats (Worthington 1929; Ogutu-Ohwayo, 1995).

Haplochromine cichlids were the most abundant in all the three lakes except that species diversity varied substantially across individual lakes; in Lake Victoria haplochromines comprised over 80% of the bottom dwelling fish biomass (Kudhongania and Cordone 1974). Until 1980, Lake Victoria alone had an estimated 500+ haplochromine species (99% of them endemic) in 12 distinct trophic groups (including phytoplanktivores, detritivores, epilithic and epiphytic algal grazers, plant eaters, oral mollusc shellers, pharyngeal mollusc crushers, zooplanktivores, insectivores, piscivores, parasite eaters, paedophages, and scale eaters) (Witte et al. 1992a, b; Kaufman 1992; Fig. 2). Lake Kyoga had comparatively low diversity, with an estimated 100+ haplochromines species, the majority of which were undescribed (Turner et al. 2001; Ogutu-Ohwayo et al. 2013). Lake Nabugabo had at least eight haplochromines species, five of them endemic to the lake (Ogutu-Ohwayo 1993; Chapman et al. 2003).

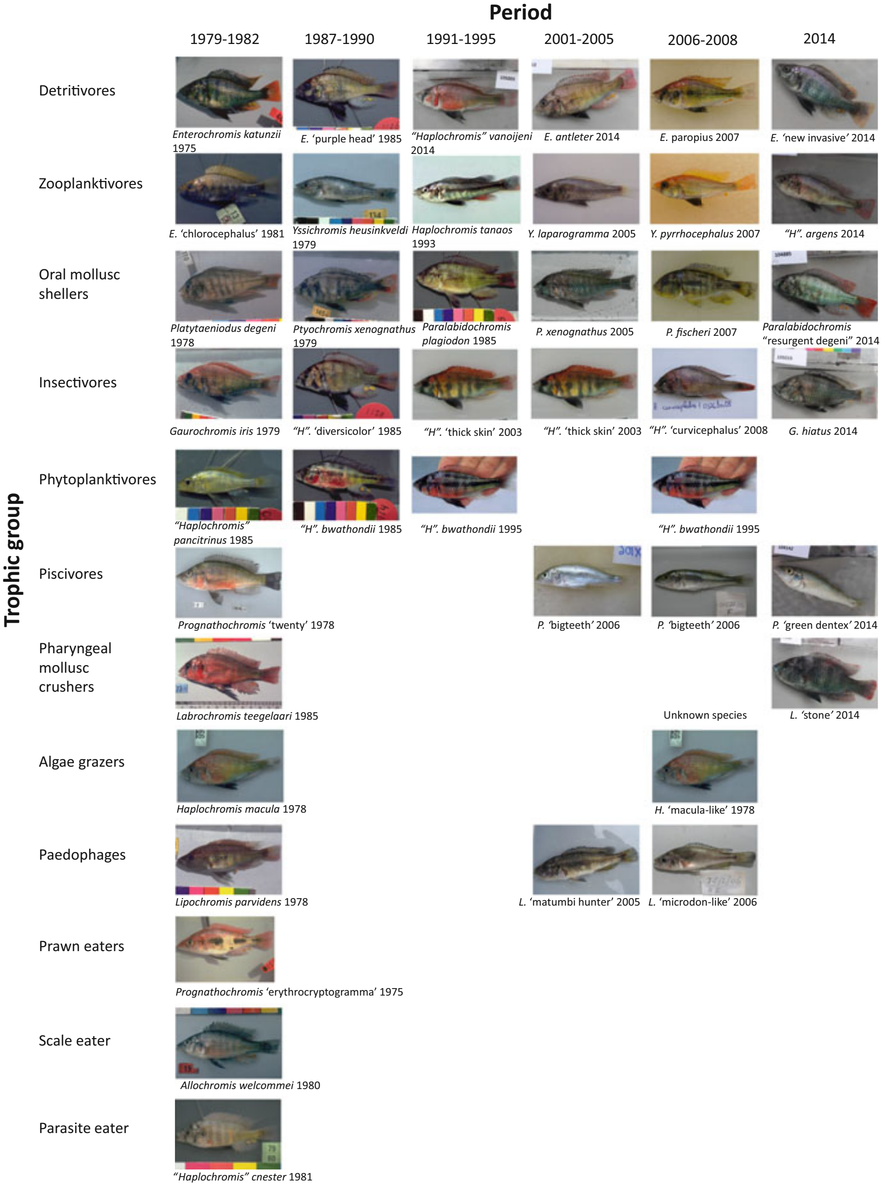


Fig. 2 Species photos that represent a trophic group for each time period on the research transect (station E-J) in the Mwanza Gulf. Representative species were selected in such a way that, when possible, each time period shows a different species per trophic group. Photos were selected, when possible, based on being representative for the species, the location (Mwanza Gulf), and the time period. When photos for a specific time period were not available or representative, a photo from a different time period was chosen. The year when the photo was taken is indicated in the photo subscript. We are unsure whether the photo of *H.* 'lividus-like' represents *H. lividus* as described by Greenwood correctly. Photos made by HEST, O. Seehausen, M. A. Kishe, F.N. Moser, and J. C. van Rijssel

2.2 *Exposure and Sensitivity to Multiple Anthropogenic and Environmental Stressors*

The Lake Victoria region is one of the most densely populated areas not only in Africa but globally, with a population density of more than 500 persons/km^2 (Kolding et al. 2014). The effects of high human population on aquatic living resources are well-known: increased demand on aquatic living resources, leading to (1) overexploitation of indigenous fisheries, (2) introduction of non-indigenous species to cope with declining catches, and (3) alteration of habitat quality through land use change in the catchment basin. Most urban areas are also located in close proximity to these water bodies, where increased loss of vegetation cover and riparian wetlands has exposed the lakes to both municipal and industrial waste pollution (Seto et al. 2012).

Cichlids, especially haplochromines, depend on light for foraging and for communication, including the visual signals used for mate choice; for example, males have diverse breeding colours which are used in female mate choice and male competition over territories (Selz et al. 2014). Changes in habitat conditions, especially when accompanied with reduction in water clarity, can affect reproductive isolation and ecological differentiation, with negative effects on overall cichlid diversity (Seehausen et al. 1997, 2008).

3 Relationship Between Multiple Stressors and Cichlid Diversity and Abundance in the Lake Victoria Region

The chronology of events in the course of the 20th and 21st centuries, leading to the changes in abundance and diversity of cichlids in the Lake Victoria region is summarized in Table 1. The main stressors can, therefore, be summarized in five major categories: (1) overfishing, (2) non-native fish species, (3) habitat degradation (eutrophication), (4) invasive weeds, and (5) climate variability and change.

3.1 *Overfishing*

Intensive fishing was the first major threat that contributed to the decline and complete disappearance of native *Oreochromis* species in the Lake Victoria region (Graham 1929; Worthington 1929). Some researchers have suggested fishing also contributed to the decline of large piscivorous haplochromine cichlids in Lake Victoria, paving the way for establishment of *L. niloticus* (Goudswaard et al. 2008; van Zwieten et al. 2016), although this hypothesis has been questioned (see Marshall, 2018). Unlike other stressors that intensified after the 1970s, the effects of intensive fishing on oreochromine cichlid species became manifest in

Table 1 Summary of the chronology and trends in different stressors and their influence on cichlids

Period	Events
Before 1908	Traditional fishing methods in the form of basket traps, hooks, and papyrus seines dominant on Lake Victoria
1908	Arrival of the railway in Kisumu, opening new markets for Lake Victoria fish, followed by introduction of more efficient flax gillnets and increasing fishing pressure
1910–1950	Fisheries of the native *Oreochromis* species in both Lakes Victoria and Kyoga decrease substantially, and generally collapse (Ogutu-Ohwayo 1990; Fig. 3), consistent with increasing fishing effort and efficiency
Early 1950s	Further improvements in technological efficiency with introduction of synthetic gillnets and outboard engines, followed by the complete collapse of the native oreochromine cichlid fishery in both Lakes Victoria and Kyoga
Mid 1950s and early 1960s	Non-native fishes introduced into Victoria (1954/1955 for cichlids and 1962–1963 for *Lates niloticus*), Kyoga (1954/1955 for both cichlids and *L. niloticus*), and Nabugabo (1960 for cichlids and 1963 for *L. niloticus*). Note that for *L. niloticus* in Lakes Victoria and Nabugabo, the stated years refer to the official years of introduction, but unreported introductions most likely happened much earlier starting in the mid-1950s (Pringle 2005). Also, for Lake Nabugabo, the year of introduction of cichlids is not certain; the only available information shows that non-native cichlids were already in the lake by 1960 (Bwanika et al. 2006)
1961–1964	Heavy rains increase lake levels, submerge aquatic macrophytes and expand open waters over Lake Kyoga and in shallow inshore areas of Lake Victoria
Mid 1960s	Introduced *Lates niloticus* is fully established in Lake Kyoga and landed catches increase rapidly
1968 onwards	Introduced *O. niloticus* is fully established in lakes Victoria and Kyoga (long after the native oreochromine fisheries had collapsed in commercial catches) and landed catches increase rapidly
1973	A trawl fishery is introduced in Lake Victoria to exploit the abundant haplochromines, but is accompanied by a decline in some haplochromine stocks
1970–1990	Eutrophication, reduced water transparency, and anoxia (attributable to both climate variability, habitat degradation, and nutrient pollution) intensify in Lake Victoria
1980–1986	Collapse of haplochromine stocks in Lake Victoria (i.e., catch rates from bottom trawls decreased from 390 kg/hr in 1981 to zero by 1986) (van Zwieten et al. 2016).
1980–1990	Establishment of introduced *L. niloticus* in Lake Victoria, with catches increasing from almost nothing in 1980 to over 300,000 tons by 1990 (Fig. 5).
1985 onwards	Stocks of *O. niloticus* and *L. niloticus* in Lake Kyoga decrease coinciding with increase in fishing effort (see Fig. 4)
1989	Infestation of Lakes Kyoga and Victoria by the water hyacinth, covering most of the inshore waters. The weed is brought under control by 1999 following the heavy storms that possibly destroyed the plants by dislodging their mats and enhanced their natural mortality and biological control by a herbivorous weevil (*Neochetina* sp.) introduced from the native range of water hyacinth in South America

(continued)

Table 1 (continued)

Period	Events
1991 onwards	Reduction in stocks of *L. niloticus* in Lake Victoria, consistent with increasing fishing effort; biomass oscillates around one million tons; resurgence of haplochromines is reported in lakes Victoria, Kyoga, and Nabugabo
2000	The water levels in lakes Victoria and Kyoga drop temporarily
2006 onwards	Cage fish farming introduced on Lake Victoria (staring in the northern shores of the lake, Uganda)
2012 onwards	Kyoga lakes invaded by the Kariba weed, *Salvinia molesta*

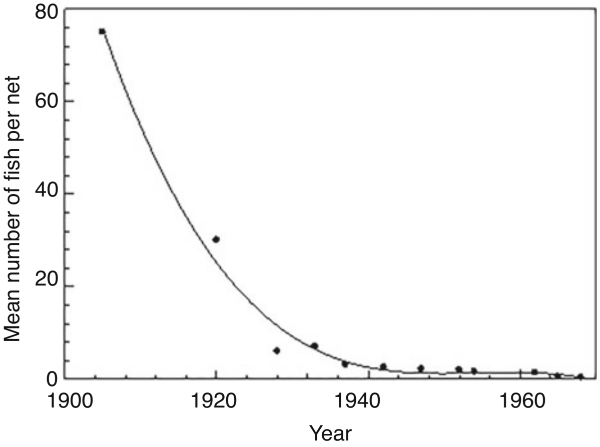


Fig. 3 Annual catch rates (number of fish per net) of *Oreochromis esculentus* in the Nyanza Gulf between 1905 and 1968. No information is available on the size of the nets, in terms of length, but the mesh size of these nets ranged between 3 and 4 inches. Data from Ogutu-Ohwayo (1990)

the early years of the twentieth century, following improvements in fishing technology and transport communication to the urban markets (Table 1). Prior to 1910, the native *Oreochromis* species were exploited using simple traditional fishing gears, consisting of basket traps, hooks, and papyrus seines, to meet the small local market demand (Graham 1929; Jackson 1971). These fishing methods were less efficient and had little impact on the stocks (Ogutu-Ohwayo 1990). The arrival of the railway in Kisumu, Kenya, in 1908, which improved access to urban markets, concomitant with the introduction of more efficient flax gillnets, substantially increased the fishing effort. *O. esculentus* was the largest and the most abundant and commercially important among the native oreochromines; its stocks decreased rapidly, with the catch rates declining from about 78 fish per net in 1910 to fewer than 2 fish per net by the 1950s (Fig. 3). Continuous improvement in fishing technology, e.g. the shift from flax to synthetic gillnets in the 1950s and a shift to smaller mesh size nets (3.5-4 inches) that harvested immature fish, further depressed the native fisheries (Jackson 1971; Ogutu-Ohwayo 1990).

In Lake Kyoga, native *Oreochromis* species also contributed more than 90% of commercial catches during the 1940s and early 1950s, but the stocks declined rapidly during the 1960s and collapsed in the subsequent decade (Ogutu-Ohwayo 1990; Ogutu-Ohwayo et al. 2013). Catch rates, for instance, decreased from about 30 fish per net per night in the 1940s to about 7 fish per net per night in the 1960s, after which the fishery collapsed and never recovered. As observed in Lake Victoria, the decline in the stocks of native oreochromines in Lake Kyoga coincided with the introduction of synthetic gillnets in 1951 and 1952, which were more efficient than the indigenous fishing gears that consisted of locally made papyrus traps (Table 1).

Why did the native oreochromine cichlids disappear very quickly? The events outlined in Table 1 show that the native *Oreochromis* species collapsed well before the introduced species became established and that overfishing was primarily responsible, while competition for resources and/or hybridization with the introduced species, particularly *O. niloticus* (Linnaeus, 1758), only suppressed their ability to recover. Yet, the present-day fishing effort in these lakes is higher by orders of magnitude compared to the effort in the 1950s and 1960s (Fig. 4c; Fig. 5d), and fishing technology has improved by several folds, but the introduced *Oreochromis* species (*O. niloticus*, *O. leucostictus* Trewavas 1933) and *Coptodon* species (*Coptodon zillii* (Gervais, 1848), *C. rendalli* Boulenger, 1897) have not collapsed. It is likely that the native fisheries were inherently less productive and less adaptable, with no capacity to sustain a commercial fishery of any nature. The native oreochromine cichlids had a narrow habitat range and were restricted to shallow inshore waters, although in the shallow lakes such as Kyoga and Nabugabo, they were found over the entire lake. First, this narrow habitat range means that the fishes had limited capacity to compete with the versatilie introduced cichlids once they became established. Secondly, these shallow areas, where the native oreochromine cichlids were concentrated, are easily accessed by fishermen, even with the most primitive parachute or dugout canoes, making the fish more susceptible to overexploitation. The introduced cichlids (both *Oreochromis* and *Coptodon* spp.) also have a narrow habitat range (the fishes are restricted to areas <20 m deep, NaFIRRI unpublished trawl survey data 2003–2017). These areas are also easily accessed by fishermen; however, the species, particularly *O. niloticus*, have adaptable life history parameters (growth rates, size at maturity, and fecundity) that enable the species to withstand high fishing pressure and changes in the environment (Bwanika et al. 2004; Njiru et al. 2007; Natugonza et al. 2015).

Limited resilience to exploitation has also been observed among haplochromine cichlids. Once the stocks of the larger native oreochromine cichlids were depleted, especially in Lake Victoria, fishing shifted to the smaller haplochromine cichlids, which were harvested using small mesh seines and trawl nets. Data from the Tanzanian waters show that the overall catch rates of haplochromines rapidly declined from 1753 kg h^{-1} in 1976 to 680 kg h^{-1} in 1982 (Goudswaard and Ligtvoet 1988). During this period, non-human predation was minimal because the native predator populations (especially the catfishes) were already collapsed due to overfishing (Goudswaard and Witte 1997), while the introduced Nile perch, *Lates niloticus* (Linnaeus, 1758), was not yet abundant; eutrophication, especially in the offshore waters, only became pronounced beginning in the mid-1980s (Hecky et al. 2010). It seems possible, therefore, that haplochromines were already exhibiting signs of distress from fishing even before the impacts of *L. niloticus* and eutrophication became apparent. Limited resilience of haplochromine cichlids to fishing has also been observed in other cichlid-dominated lakes such as Lake Malawi (Turner 1977a, b).

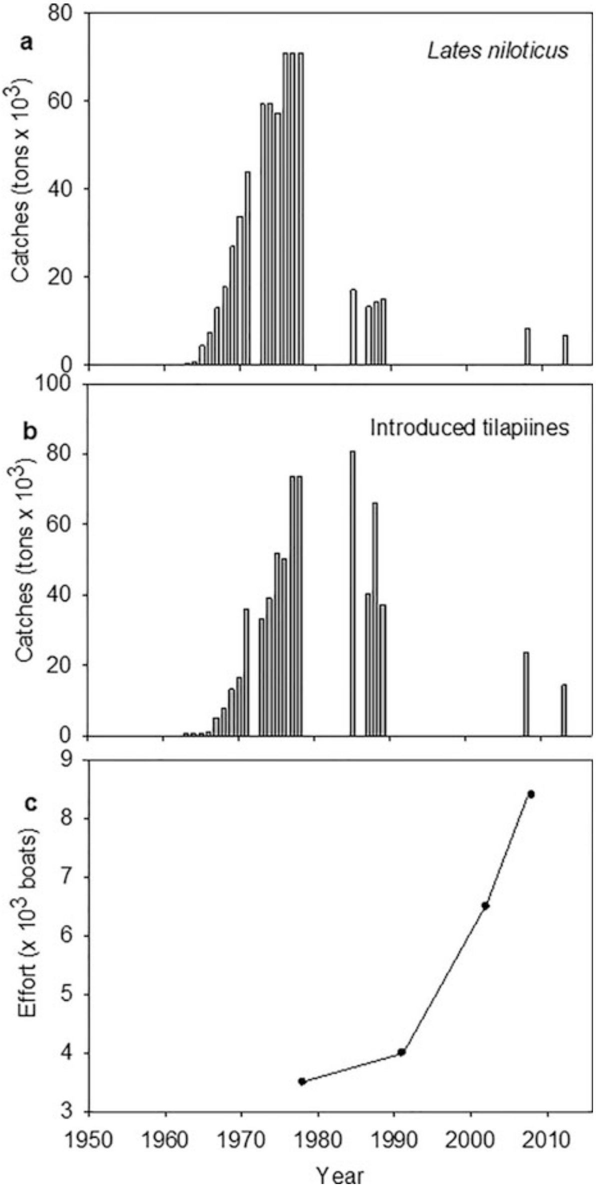
3.2 Non-native Fish Species

Although non-native species introductions can have positive outcomes, e.g. trophic subsidy, competitive release, or predatory release, in many instances, when they become invasive, they exert negative ecological and evolutionary impacts ranging from behavioural shifts of native species in the presence of invaders to complete restructuring of food webs (Rodriguez 2006; Schlaepfer et al. 2010). The events in the Lake Victoria region represent classical examples of both positive impacts (e.g. increased fishery production and transformed livelihoods of fishers and riparian communities) and negative impacts (e.g. biodiversity loss) of the introduced fish species (Witte et al. 1992a, b; Ogutu-Ohwayo 1990, 1993).

The large piscivorous *L. niloticus* and four other species, *O. niloticus*, *O. leucostictus*, *C. zillii*, and *C. rendalli*, were introduced into the Lake Victoria region in the 1950s and 1960s (Ogutu-Ohwayo and Hecky 1991; Pringle 2005). Introduction of *L. niloticus* was primarily intended to feed on haplochromine cichlids, which were abundant in this lake, and convert them into a suitable commercially important table and recreational fish. The introductions in Lakes Kyoga and Nabugabo were possibly experimental, though conducted late, following the recommendation by Worthington (1932b). Worthington (1932b) suggested that the introduction of *L. niloticus* into Lake Victoria would be considered if experimental introduction in Lake Nabugabo could be effected and there was evidence of a natural balance between *L. niloticus* and other fishes in the lake. In contrast, both *Oreochromis* and *Coptodon* species were introduced to compensate for the diminishing catches of the native oreochromine cichlids (*O. esculentus* and *O. variabilis*). However, only *O. niloticus* contributed substantially to the commercial fisheries (Ogutu-Ohwayo 1990).

There were time variations in the establishment of introduced species in different lakes, although the pattern of establishment was generally consistent. In Lake Kyoga, both *L. niloticus* and *O. niloticus* took approximately 10 years before they contributed substantially to the fisheries. Landings increased eightfold between 1960 and 1980, but later declined and stabilized at low numbers, especially beginning in the mid-1980s (Fig. 4). The reduction in landings coincided with the increase in fishing effort as manifested by the twofold increase in the number of fishing boats (Fig. 4). In Lake Victoria, however, the establishment of introduced species took a longer period (approximately 25 years), but after establishment, the fishery dynamics were similar to those of Lake Kyoga. Landings of *L. niloticus* also rapidly increased

Fig. 4 Annual catches of (**a**) *L. niloticus* and (**b**) introduced cichlids, mainly *O. niloticus,* and (**c**) fishing effort on Lake Kyoga (Data from Ogutu-Ohwayo et al. 2013)



from almost nothing to 330,000 tons between 1980 and 1990, but declined afterwards and stabilized at lower levels following the rapid rise in fishing effort (Fig. 5). Although the introduced *Oreochromis* and *Coptodon* species started appearing in the catches at the same time in both Lake Victoria and Lake Kyoga (i.e. in the mid-1960s), the contribution to the commercial fisheries in Lake Victoria was only realized in the late 1990s (Fig. 5). The parallel success of *O. niloticus* alongside the piscivorous *L. niloticus* may be related to their origin: both species are native to the

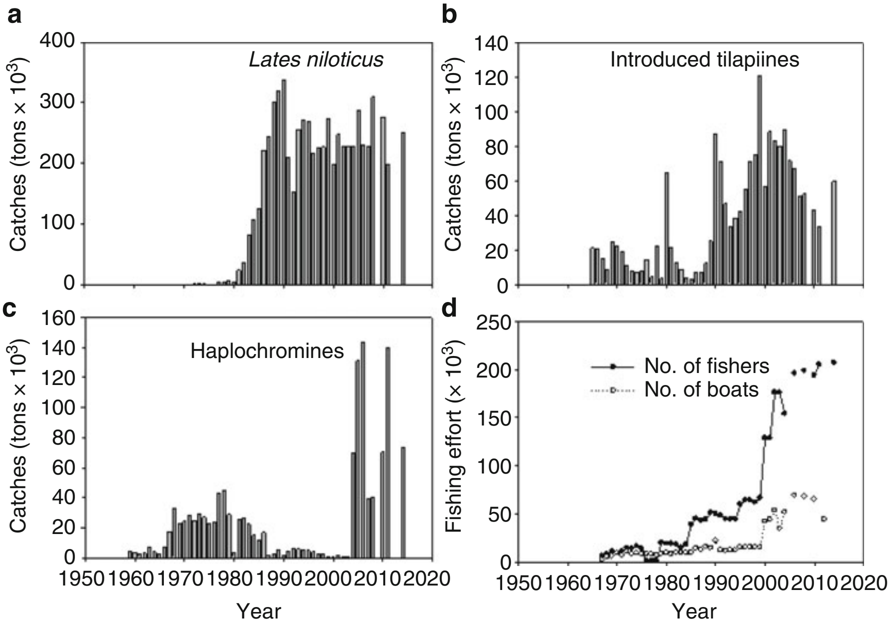


Fig. 5 Annual catches of (**a**) *L. niloticus*, (**b**) introduced cichlids, and (**c**) haplochromines, and (**d**) fishing effort (given as the number of boats and fishermen) on Lake Victoria. Data from Kolding et al. (2014) supplemented by LVFO (2016)

Nile below the Murchison Falls, Lake Albert, Lake Turkana, the Chad basin, and rivers of West Africa (Lowe-McConnell 1987). Therefore, *O. niloticus* may have already evolved behavioural responses to overcome predation by *L. niloticus*.

3.2.1 Impact on Native Oreochromine Cichlids

The introduced cichlids may not have directly contributed to the collapse of native oreochromine cichlids, but rather exacerbated the effects of intensive fishing and habitat modification through direct competition and/or hybridization. The cichlids that were introduced in the Lake Victoria region have overlapping ecological requirements as the native oreochromines. In lakes Victoria and Kyoga, the native *O. esculentus* and *O. variabilis* were ecollogically segregated, where the smaller *O. variabilis* were common in areas covered by aquatic vegetation closer to the shore, while *O. esculentus* were found in more open waters. The introduced *O. leucostictus* and *C. zillii* occupied the same vegetated inshore habitat as *O. variabilis*, which may have created competition for space. *Oreochromis niloticus*, on the other hand, occupied more open waters, directly competing with *O. esculentus*.

The disappearance of native oreochromine cichlids has also been observed in other lakes where *O. niloticus* has been introduced; *O. spirulus* (Günther, 1894) and

O. macrochir (Boulenger, 1912), for instance, have disappeared from lakes Naivasha (Kenya) and Itasy (Madagascar), respectively, following the introduction of *O. niloticus* (Siddiqui 1977; Welcomme 1984).

3.2.2 Impact on Haplochromine Cichlids

The role of *L. niloticus* in the massive loss of haplochromine cichlid diversity has been widely discussed (van Zwieten et al. 2016; Marshall 2018). Generally, the increase in *L. niloticus* biomass in all the lakes where the species was introduced was accompanied by a rapid decline in haplochromines as manifested in both the landings (Fig. 5) and standing stock biomass (Fig. 6). Whereas landings may be

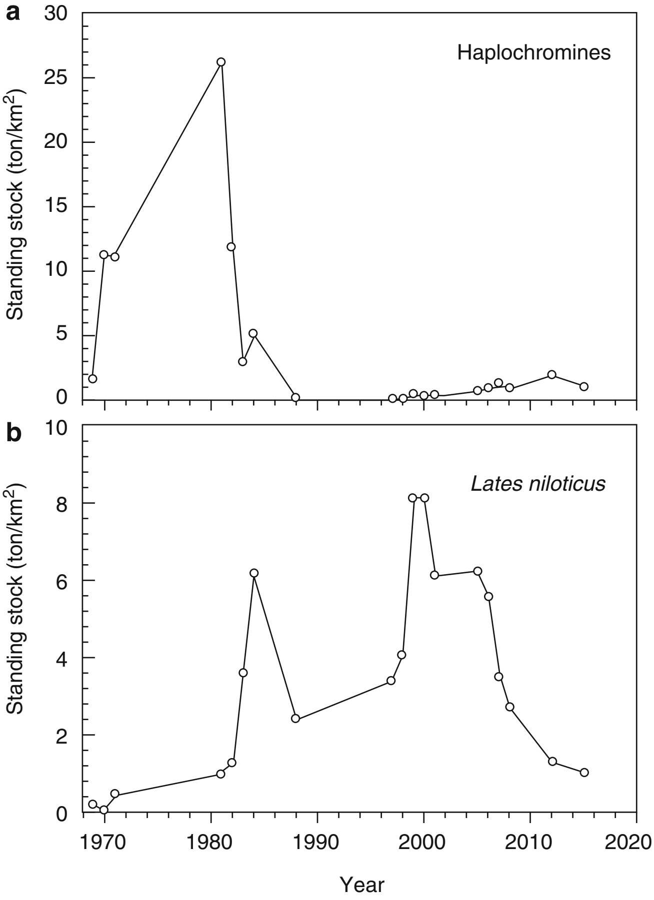


Fig. 6 Biomass of (**a**) haplochromine cichlids and (**b**) *L. niloticus* in Lake Victoria based on bottom trawl surveys in for the period 1969–2015 (NaFIRRI unpublished data)

influenced by other factors, particularly changes in fishing behaviour and catchability of the target species, the concomitant reduction in standing stock biomass shows that abundance of haplochromines was greatly diminished. An estimated 40% of the 500+ haplochromine species disappeared from Lake Victoria alone, which has been attributed to several factors: (1) predation by *L. niloticus* (Witte et al. 1992a, b; Marshall 2018) and (2) a combination of stressors, including fishing, eutrophication, and predation by *L. niloticus* (Witte et al. 2007a, b), and competition (McGee et al. 2015).

Different haplochromine trophic groups declined at different rates. The large piscivorous haplochromines disappeared first in both lakes Victoria and Nabugabo, possibly due to competition with *L. niloticus* for the same food resources (McGee et al. 2015) and/or the reduced ability to avoid *L. niloticus* predation due to increased blooms and reduction in visibility (Witte et al. 2007b; also see Sect. 3.3). The smaller species of the detritivore and zooplanktivore trophic guilds declined slowly, especially the latter group (Witte et al. 2007b). During the 1990s, however, some haplochromines started recovering. Data on the past and the present trends in biomass and spatial distribution of haplochromines suggest there were multiple causes for both the decline and resurgence. In the northern part of Lake Victoria, for instance, haplochromines declined drastically between 1982 and 1986, coinciding with the upsurge in *L. niloticus* biomass, and started recovering during the late 1990s following a reduction in the predator biomass (Fig. 6). However, the timing of haplochromine decline and resurgence is also consistent with the period of severe eutrophication and anoxia (Hecky et al. 1994) and the general improvement in water quality (higher oxygen levels, higher visibility, and weaker stratification; Sitoki et al. 2010; Marshall et al. 2013; van Rijssel et al. 2016), respectively. It is difficult to attribute the changes in haplochromines to a single cause, but the trends in Lakes Nabugabo and Kyoga, which are clearly associated with *L. niloticus* dynamics (Chapman et al. 2003; Ogutu-Ohwayo et al. 2013), suggest that predation played a major role in the northern portion of the lake.

Data from the southern part of Lake Victoria also show the timing of haplochromine declines to be consistent with the *L. niloticus* upsurge; however, the resurgence is inconsistent with the *L. niloticus* dynamics. In the Mwanza Gulf, haplochromines started recovering between 1990 and 1992 at the peak biomass of *L. niloticus* (Seehausen et al. 1997; Witte et al. 2007a, b). In addition, despite the low diversity, the current biomass of haplochromines, especially in the zooplanktivore and detritivore guilds, is comparable to the pre-collapse levels, and they occupy demersal open waters (Witte et al. 2007b; Kishe-Machumu et al. 2015), where *L. niloticus* densities are highest (Taabu-Munyaho et al. 2014). Therefore, predation by *L. niloticus* may have exacerbated effects of the trawl fishery (Witte et al. 2007b) and environmental change (Kudhongania and Chitamwebwa 1995; van Zwieten et al. 2016), while the improvement in limnological conditions (Sitoki et al. 2010; Marshall et al. 2013) and adaptation to the changed environment (van der Meer et al. 2012; van Rijssel and Witte 2013; van Rijssel et al. 2015, 2017) may have facilitated the recovery. In summary, it seems there are multiple causes for both the decline and resurgence of the haplochromines in different parts of the lake, but it remains difficult to pinpoint which of these contributed most to either the decline or resurgence.

3.3 Habitat Degradation

Lake Victoria changed abruptly from an oligotrophic–mesotrophic system to a eutrophic one during the early 1980s, a period when the introduced *L. niloticus* was beginning to expand. The emergence of these stressors at the same time has made the separation of primary and secondary drivers of changes in cichlid assemblages, especially haplochromines, a challenging task. Nutrient loading in Lake Victoria has been ongoing since the 1920s, primarily from land use changes in the catchment (Hecky 1993; Hecky et al. 1994). However, the impacts of eutrophication became manifest especially after 1980 with the onset of blue-green algal blooms, anoxia, reduced water transparency, and even fish kills (Hecky 1993; Mugidde 1993; Sitoki et al. 2010; Hecky et al. 2010; van Rijssel et al. 2016). The concentration of total phosphorus (TP) in the lake doubled; dissolved silicon decreased by one order of magnitude; the concentration of chlorophyll-*a* increased fivefold; water transparency diminished; and deep water anoxia intensified. The algal communities shifted from the dominance of diatoms to blue-green algae; the larger diatom genera, e.g. *Aulocoseira*, were replaced by the smaller thinly silicified genera, especially *Nitzschia*, which were adapted to low silicon concentrations (Hecky et al. 2010). The zooplankton community changed from dominance of the large-bodied herbivorous calanoid copepods and cladocerans to the small-bodied predatory cyclopoid copepods (Mwebaza-Ndawula 1994; Wanink et al. 2002). Midge larvae, particularly *Chironomus* and *Chaoborus* spp. and the detritivorous shrimp, *Caridina nilotica*, which were tolerant to anoxia, increased (Sekiranda et al. 2004; Goudswaard et al. 2006); *C. nilotica* subsequently became an important prey item in the diet of *L. niloticus* (Budeba and Cowx 2007).

These changes affected cichlid fish communities differently. The disappearance of large diatoms, *Aulocoseira*, which were the main food for *O. esculentus*, affected remnant stocks of this species. On the other hand, the increase in abundance of blue-green algae improved food availability for *O. niloticus*, which had the capacity to digest the algae (Moriarty and Moriarty 1973). This may also explain why *O. niloticus*, besides out-competing *O. esculentus*, was also able to dominate introduced *Oreochromis* and *Coptodon* species.

The blooms created by dense mats of blue-green algae decreased light penetration, but also decomposition enhanced turbidity and decreased overall water transparency. Light is important in foraging, mate recognition, and predator avoidance among cichlids, especially haplochromines (Seehausen et al. 1997, 2003). Poor vision can affect feeding specialization, and predatory species are expected to suffer most due to increased competition amongst each other and with *L. niloticus*. It is, therefore, not surprising that the large piscivorous haplochromines disappeared first in both lakes Victoria and Nabugabo, possibly because of increased competition with the introduced *L. niloticus* for prey and also the reduced ability to evade predation (Witte et al. 1992a, b; Ogutu-Ohwayo 1993; McGee et al. 2015).

The rate at which haplochromines declined between 1980 and 1985 was rapid, reflecting more of an abrupt recruitment failure, although predation by *L. niloticus* could have contributed to the decline. Detritivorous haplochromines were originally the most abundant among the 11 major trophic groups and formed approximately 60% of the total haplochromine biomass in the sublittoral and demersal waters of the Mwanza Gulf (Witte et al. 1992a, 2007b). Ogutu-Ohwayo and Hecky (1991) suggested that the development of the deep water anoxia changed habitat conditions for these detritivores and exposed them to extreme predation by *L. niloticus*. The development of deep water anoxia is not doubted (Hecky et al. 1994); however, the conditions may not have favoured *L. niloticus*, considering that the species is quite sensitive to hypoxia (Schofield and Chapman 2000). Although Wanink et al. (2001) found some *L. niloticus* in deep waters with dissolved oxygen (DO) concentration less than 2 mgL^{-1}, including areas where DO was almost zero, their numbers were comparatively lower. Under such stressful anoxic conditions, *L. niloticus* may not have had either ecological or numerical advantage to decimate detritivorous haplochromines. Instead, eutrophication and reduced water transparency could have severely interfered with haplochromine reproduction and feeding (Seehausen et al. 1997, 2003; Seehausen and van Alphen 1998; van Zwieten et al. 2016; van Rijssel et al. 2016) and caused steep decline in their populations and loss of species diversity.

The effect of habitat degradation can also be seen in the decline of native oreochromine cichlids in both lakes Victoria and Kyoga, although the effect was secondary (exacerbating the effects of overfishing). The increase in lake levels, following the El Niño rains of 1961/1962, and the subsequent submersion of open water macrophytes and marginal wetlands of Lake Kyoga as well as the inshore wetlands of Lake Victoria (Ogutu-Ohwayo et al. 2013) greatly modified the inshore habitat, which benefited the introduced species but led to the collapse of the less adaptive native oreochromine cichlids. The preferred habitat for the inshore vegetation-dwelling *O. variabilis*, for instance, was lost, and the species was later displaced from by the introduced *O. leucostictus*, which occupied the same habitat. For the open water native *O. esculentus*, which were more abundant and preferred by fishermen, the submersion of macrophytes presented two fundamental risks: (1) the fish was exposed to more fishing pressure as more open water fishing grounds were opened; and (2) the rise in lake levels also opened up more areas for *O. niloticus* spawning, allowing its proliferation.

In Lake Kyoga, at the time Worthington conducted the first survey in Lake Kyoga in 1928, most of the small fishes were found in aquatic macrophyte beds, which provided refugia from the large native predators, e.g. catfishes and lungfish (Worthington 1929). The submersion of macrophyte cover by the El Niño opened up the lake and exposed these small fishes, notably haplochromines, to increased predation pressure. Additionally, although there has not been any systematic collection of environmental data from Lake Kyoga on the nutrient status over time, the concentration of total phosphorus was three times higher soon after the El Niño rains in early 1960s compared to 1990/2000 (Evans 1962; Ogutu-Ohwayo et al. 2013). It is, therefore, likely that the submersion and decay of aquatic vegetation was also accompanied by increase in nutrients and productivity in Lake Kyoga, as well as reduced water clarity.

There is no doubt that *L. niloticus* predation contributed to the decline of haplochromines in the Lake Victoria region. However, the events leading to the disappearance and resurgence of haplochromines suggest that in the absence of primary environmental triggers, which either affected recruitment directly or compromised the ability of haplochromines to evade predators, *L. niloticus* alone may not have caused such a mass destruction of haplochromine cichlids and especially not the massive loss of species diversity. The spontaneous decline and gradual recovery of haplochromines following deterioration and general improvement in water quality, respectively, may not be a mere coincidence. Zooplanktivorous haplochromines started recovering before the detritivores, despite higher abundance of the latter before the decline in the mid-1980s (Witte et al. 2007b), and are abundant in offshore coastal demersal waters where *L. niloticus* densities are highest (Taabu-Munyaho et al. 2014). In addition, some surviving detritivores that were previously restricted to the littoral zones (0–6 m depth) have also extended their habitat and are now also present in the sublittoral zones (6–20 m depth; Seehausen et al. 1997; Kishe-Machumu et al. 2015) where *L. niloticus* is also common.

3.4 Invasive Plants

There are two aquatic weeds, water hyacinth (*Eichhornia crassipes*) and Kariba weed (*Salvinia molesta*), both native to South America, which have had substantial ecological impact in the Lake Victoria region although information on Kariba weed is scanty. Whereas the water hyacinth may have been in the Nile basin and Lake Victoria catchment since the 1950s, it was first sighted in Lake Kyoga in 1988 and in Lake Victoria in 1989 (Twongo 1991). By the mid-1990s, the weed covered 60% of the shoreline (ca. 570 ha) of the length of Lake Kyoga (Twongo 1996) and approximately 18,000 ha of the inshore areas of Lake Victoria (Albright et al. 2004). In both lakes, the weed formed extensive mats, with the zones below extensive water hyacinth mats anoxic, which changed the composition of the biota. For instance, the invertebrate communities under the water hyacinth mats were dominated by low oxygen-tolerant types such as chironomids (Wanda et al. 2001), while the fish community was dominated a few hypoxia-tolerant species, e.g. marbled lungfish *Protopterus aethiopicus* Heckel, 1851. However, the dense water hyacinth mats may have also provided refugia for the littoral, vegetation-dwelling, haplochromines, especially *Astatotilapia* species against *L. niloticus* predation (Ogutu-Ohwayo et al. 2013).

The water hyacinth was brought under control in the late 1990s by introduction of a weevil (*Neochetina* sp.) (Wilson et al. 2007), although the heavy storms of 1997

Fig. 7 A photo of dense weeds taken near Kisumu, Nyanza Gulf in October 2018

could have also enhanced their mortality by physically dislodging their mats (Williams et al. 2007). The weed is still abundant and forms dense mats (Fig. 7) in bays adjacent to the major towns and cities, and continued nutrient enrichment through discharge of municipal and industrial wastes could lead to its full-scale resurgence.

3.5 Climate Variability and Change

Climate variability and change contribute to changes in hydrology, stratification and circulation dynamics, and composition of aquatic organisms, especially to those that have the capacity to adapt fast to the changed conditions (Barange and Perry 2009; Ogutu-Ohwayo et al. 2016). Generally, climate-induced changes in fish species diversity and abundance have been most prevalent in relatively shallow systems, e.g. lakes Chad (FAO 2012), Ngami and Liambezi (Moyle et al. 2009), Rukwa (Mbungu 2015), Chilwa (Njaya et al. 2011), and Wamala (Natugonza et al. 2015), although changes have also been reported in relatively larger lakes such as Victoria (Birkett et al. 1999; Hecky et al. 2010; van Zwieten et al. 2016; van Rijssel et al. 2016) and Tanganyika (Verburg et al. 2003; Cohen et al. 2016). Warming of Lake Victoria generally begun in the early twentieth century, but the impacts on the fisheries became manifest beginning in the 1980s through eutrophication (and associated anoxia) and dramatic shifts in fish communities (Hecky et al. 2010).

The effects of warming on the physical properties of African Great Lakes have been widely discussed (O'Reilly et al. 2003; Verburg et al. 2003; MacIntyre 2012). The periodic decreases in vertical mixing observed during conditions of higher rainfall, reduced winds, and higher relative humidity can substantially affect the productivity of the lake. Vertical mixing is an important driver of the lakes' physico-chemical processes, including nutrient circulation, phytoplankton abundance, water transparency, and dissolved oxygen (DO) levels. An increase in physical stability and shallower mixing depths due to warming may intensify anoxia, and this has been observed in Lake Victoria (Hecky et al. 1994). The predicted increase in climate variability and warming (IPCC 2014) will likely affect these processes further, and fisheries will likely be dominated by species that can persist and adapt fast to the changed conditions. Data consistent with this come from work on some of the resurgent haplochromine cichlids in Lake Victoria that have undergone ecological changes of habitat choice (Seehausen et al. 1997; Kishe-Machumu et al. 2015) and diet (Katunzi et al. 2003; Kishe-Machumu et al. 2008, 2017; van Rijssel et al. 2015, 2017) and also structural modifications that may be adaptations to the changing environment and prey (van der Meer et al. 2012; van Rijssel and Witte 2013; van Rijssel et al. 2015, 2016).

4 Persistence of Cichlid Fishes Under Multiple Stressors

The ability to adapt quickly to the changed habitat conditions and to the pressures from exploitation, predation, competition, and warming climate is central to the persistence of fish under multiple stressors (Petitjean et al. 2019). The disappearance of the native *Oreochromis* and many haplochromine species from lakes Victoria, Kyoga, and Nabugabo as the stressors intensified suggest limited resilience of the species or of the species-rich communities to cope with the changed conditions. On the other hand, some of the cichlids that have persisted, and whose stocks have increased, have undergone life history modifications which may be adaptations to the new environments. The ability to adapt quickly to changing conditions may determine the future diversity and abundance of cichlid fishes more generally, not only in the Lake Victoria region but also in other lakes.

Among the oreochromine and tilapiine cichlids, only *O. niloticus* has increased and become abundant in lakes Victoria, Kyoga, and Nabugabo (Ogutu-Ohwayo 1990). The success of *O. niloticus* is associated with its life history attributes, including early maturation, a broad diet, and a wide habitat range (Fryer and Iles 1972; Martin et al. 2010). The species grows and matures faster, can mature at a wide range of body sizes, has a wider food spectrum and is less habitat restricted than any of the other *Oreochromis* or *Coptodon* species in the system, and can alter its fecundity and size of eggas in response to stressful conditions, including exploitation, habitat change, and predation (Njiru et al. 2007; Bwanika et al. 2004;

Natugonza et al. 2015). Further, *O. niloticus* is one of the few oreochromine cichlids with the capacity to digest blue-green algae (Moriarty and Moriarty 1973), which have become dominant in most lakes following eutrophication. It is likely that these life history attributes have contributed to the success of *O. niloticus*, becoming now one of the most important commercial fish species in capture fisheries in the African Great Lakes region despite heavy exploitation and environmental changes (Ogutu-Ohwayo et al. 2016).

Some haplochromine species persisted and increased in numbers, especially after the 2000s, despite the diminished diversity (Chapman et al. 2003; Seehausen et al. 1997; Ogutu-Ohwayo et al. 2013; Kishe-Machumu et al. 2015). A few species previously considered lost from the main lake have been recorded in marginal habitats in the periphery of the main lake and in the small satellite water bodies in the Lake Victoria basin (Mwanja et al. 2001; Katunzi and Kishe-Machumu 2004; Katunzi et al. 2003, 2010; Seehausen et al. 2015). Rocky shore habitats within the main lake also still support a great diversity and concentration of haplochromines (Seehausen 1996; Seehausen et al. 1997). Recent surveys of deep water sections of Lake Victoria also suggest the reappearance of deep water species, e.g. *Gaurochromis* spp. and *Labrochromis* spp., and even large piscivores of the genera *Harpagochromis* and Prognathochromis (O. Seehausen pers. comm.).

The recovery of haplochromine biomass after its nearly complete collapse, especially in the southern part of the lake, is remarkable, but its species diversity is only a fraction of what it was before the collapse. Prior to 1980, detritivorous haplochromines formed about 60% of total haplochromine biomass in Mwanza Gulf of Lake Victoria, while zooplanktivorous haplochromines constituted about 30% (Witte et al. 1992b). However, zooplanktivorous haplochromines recovered first, starting in 1991 (Seehausen et al. 1997). By 2006, this trophic group constituted 70% of the biomass in open waters despite low species diversity, although detritivores overtook them in abundance afterwards (Fig. 8).

Despite the increased abundance in the Mwanza Gulf over the past two decades, the species diversity has not recovered to its former state. Witte et al. (1992a) reported 72 different species belonging to 12 trophic groups on the research transect in the Mwanza Gulf during the period 1979–1982 based on trawl catches. This number dropped to only 12 species belonging to 5 trophic groups during the period 1987–1990, but has since been slowly increasing (i.e. 17 species in 5 trophic groups for the period 1991–1995 (Seehausen et al. 1997), 19 species in 5 trophic groups for the period 2001–2005, 27 species in 9 trophic groups for the period 2006–2008, and 26 species in 6 trophic groups during 2014 (Fig. 9); also, see Fig. 2 for the trophic groups) despite the diversity remaining below 50% of the pre-1980 period. However, it should be noted that the sampling effort in 2014 was for only six sampling days over a 2-month period (September–October) and was less intense compared to the one reported in Kishe-Machumu et al. (2015) for the period 2006–2008, which might have underestimated the species diversity for 2014.

The resurging haplochromine cichlids exhibit both morphological and ecological modifications, reflecting possible adaptation to the changing environment (Seehausen et al. 1997; Witte et al. 2008; van der Meer et al. 2012; van Rijssel

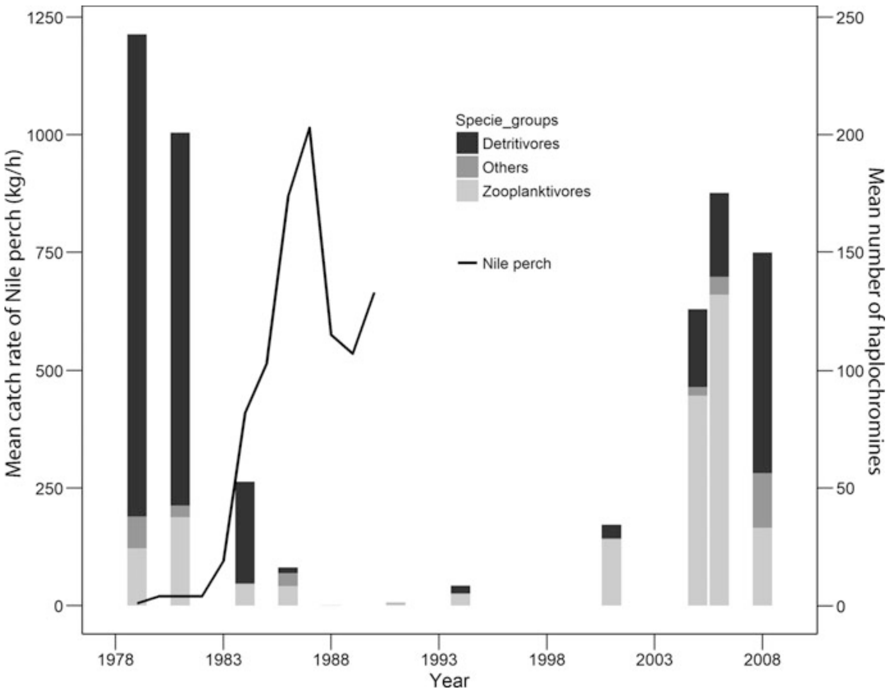


Fig. 8 Catch rates of *Lates niloticus* and haplochromine cichlids (in different trophic groups) in the Mwanza Gulf from 1979 to 2008. Haplochromine catch rates are based on 10 minutes of fishing using a small bottom trawler (Data for haplochromines from Witte et al. 2007a, for the period 1979–2005, and Kishe-Machumu et al. 2015, for the period 2006 and 2008, and that of *L. niloticus* from Goudswaard et al. 2006)

and Witte 2013; van Rijssel et al. 2015, 2016, 2017; Kishe-Machumu et al. 2017). The zooplanktivores constitute majorly three species; *Haplochromis* (*Yssichromis) laparogramma* Greenwood and Gee 1969, *"Haplochromis" tanaos* van Oijen and Witte 1996, and *Haplochromis* (*Yssichromis) pyrrhocephalus* Witte and Witte-Maas, 1987 (Kishe-Machumu et al. 2015). These species have also extended their distribution from deeper (8–14 m) (Witte et al. 1992a, b) to shallow waters or vice versa (for "*H*". *tanaos* from shallow sand bottom to deep mud bottoms, Seehausen et al. 1997) in response to the changed environment and also developed a new feeding strategy by shifting their diet from zooplankton to insects and other larger preys (Katunzi et al. 2003; Kishe-Machumu et al. 2015, 2017; van Rijssel et al. 2017). These dietary shifts are consistent with several anatomical changes in *Y. pyrrhocephalus*: the cheek depth has increased by 9% (Witte et al. 2008); the premaxilla in the upper jaw and the muscle responsible for pharyngeal biting has changed, providing greater biting force (e.g. 6% larger dentigerous arm of the premaxilla and a 64% larger musculus levator posterior depth) (van Rijssel et al. 2015; Witte et al. 2008). The ratio of the length of the intestine to standard length has also decreased (i.e., by 29–35% for the detritivorous *H.* 'paropius-like', and 35-44%

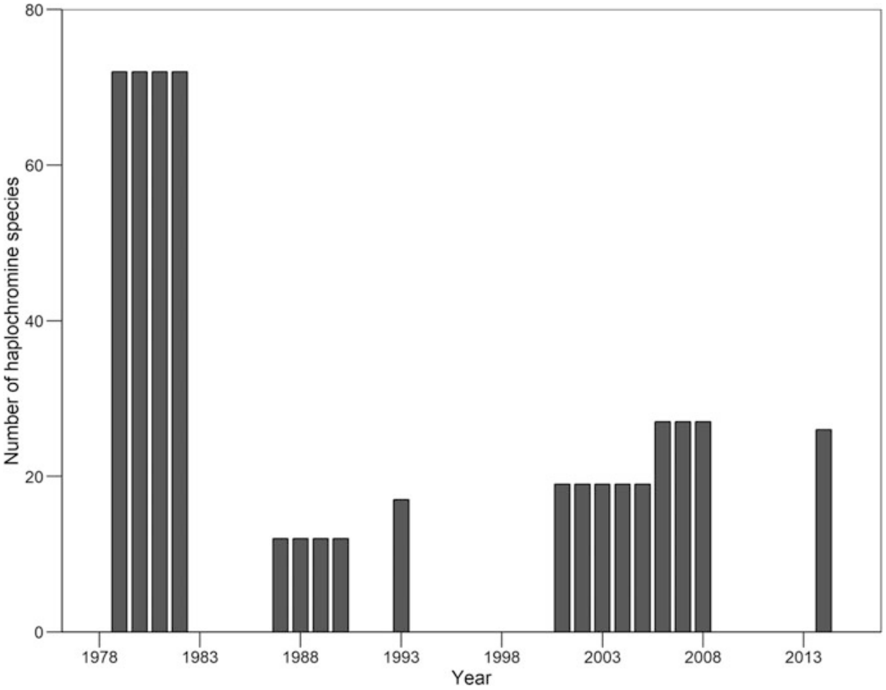


Fig. 9 Haplochromine species richness (numbers observed on the same research transect) in the Mwanza Gulf from 1979 to 2014. Species numbers are based on collection periods of 1-4 years and are depicted as species number per year. (Sources of data: Witte et al. (1992a), Seehausen et al. (1997), Witte et al. (2007a), and Kishe-Machumu et al. (2015))

for the "pooled detritivores", including *Haplochromis (Enterochromis) antleter*, *Haplochromis (E.) cinctus*, *Haplochromis (E.) coprologus*, *Haplochromis (E.) katunzii*, *Haplochromis (E.)* 'purple head), associated with the change in diet (Kishe-Machumu et al. 2008). The head surface–caudal peduncle area ratio has also decreased by 4% in *Y. pyrrhocephalus*, possibly as an adaptive response to *L. niloticus* predation (van Rijssel and Witte 2013). The gill surface area in *Y. pyrrhocephalus* has increased by 50–64% (van Rijssel et al. 2016; Witte et al. 2008) over the period, which may be a response to the reduced dissolved oxygen levels (Wanink et al. 2001). It is not clear whether the observed behavioural and morphological changes in the resurging zooplanktivorous haplochromine species are heritable and hence a product of evolution or merely phenotypic plasticity. Given that several of these species hybridized with other species in the recent decades, it is also possible that rapid evolution was facilitated by such exchange of genetic material between species (Marques et al. 2019). During the 2000s, environmental variables, including wind speed, oxygen levels, water transparency, and water temperature increased again, and the gill surface area of this species correspondingly decreased (van Rijssel et al. 2016). This observation suggests that these fishes have rapid adaptive responses to environmental changes, which may have contributed to the fast recovery of *Y. pyrrhocephalus*. The genetic or developmental basis of putatively adaptive responses of recovering cichlid species is a larger and important area of future investigation (see van Rijssel et al. 2021).

Data collected from Lake Nabugabo show that haplochromines that reappeared in the open part of this lake are those that had persisted in marginal macrophytes from where they spread into open waters following the decline in *L. niloticus* stocks (Schofield and Chapman 2000; Chapman et al. 2003). These wetlands provided structural refugia, but only favoured a few haplochromines with the capacity to survive low oxygen conditions (especially in the non-endemic genera *Astatoreochromis*, *Pseudocrenilabrus*, and *Astatotilapia*). Unfortunately, most of these wetland habitats, which, apart from being structural refugia, play a critical role in purifying water and trapping organic wastes, are increasingly being degraded, exposing the lake to land-based siltation which in turn interferes with feeding and mate choice. Similarly, haplochromine resurgence in Kyoga began following the decrease of *L. niloticus* stocks after 1990 and an increase in vegetation cover associated with water hyacinth infestation. Nonetheless, the species diversity has also remained low, and the taxa that reappeared are dominated by the insectivorous *Astatotilapia* spp., which are adapted to inhabiting marginal macrophyte beds (Ogutu-Ohwayo 1995; Ogutu-Ohwayo et al. 2013).

5 Conclusions

In this chapter, we have reviewed the past changes in the diversity and abundance of cichlid fish in three different water bodies within the Lake Victoria region to further understand the role and severity of multiple stressors on the cichlid fish communities and to explore the mechanisms leading to the persistence and/or resurgence of some of the cichlid species. We conclude that (1) native oreochromines were primarily collapsed by overfishing and that the introduced oreochromines and *Coptodon* ("tilapias") and habitat change suppressed their ability to recover once fishing shifted to the introduced species; (2) without primary environmental triggers, particularly eutrophication and reduced water transparency, which either interfered with haplochromine reproduction and feeding or compromised their ability to evade predators, *L. niloticus* predation alone may not have caused the massive collapse of haplochromine biomass and especially not the massive loss of species diversity; (3) haplochromine resurgence is linked to a combination of general improvement in the environment, eco-morphological changes that may include adaptations, and the reduction in *L. niloticus* abundance; and (4) environmental stressors are difficult to predict, but will likely continue to intensify and to shape the ecosystems in which cichlid fishes evolve, clearly involving genetic exchange between species. Cichlid fishes, therefore, may increasingly become dominated by species by capacity to adjust and adapt fast to the changing environmental conditions. If water clarity can be improved again, however, it is possible to maintain a diverse assemblage of endemic species. Research should, therefore, aim to provide information for management of highly species-diverse fisheries for resilience as multiple stressors continue to intensify.

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Rapid Evolutionary Responses in Cichlids: Genetics of Adaptation, Morphology and Taxonomic Implications

Jacco C. van Rijssel, Rob C. M. de Jong, Mary A. Kishe, and Frans Witte

Abstract The haplochromine cichlids of Lake Victoria exhibit the fastest adaptive radiation of vertebrates known. Species identification of these lacustrine cichlids has been subject of debate for many years. Over the past 35 years, environmental perturbations have resulted in phenotypic change and possibly in hybridization, making species delimitation even more problematic. In this chapter, we document the effects of a changed environment on the ecomorphology of the zooplanktivore *Haplochromis (Yssichromis) pyrrhocephalus* over a 20-year period. We found that this species has extended its habitat to shallower waters and adjusted its diet to larger and more robust prey. Adaptive morphological responses to predation, to larger and tougher prey and to a hypoxic environment were found. Whether these morphological changes are the result of hybridization, phenotypic plasticity or evolutionary adaptation remains unclear. The morphological responses are sometimes so large that they transcend morphological species boundaries and even one of the limits of the genus *Yssichromis*. The extent of the morphological responses makes clear that nuptial colouration is indispensable for species distinction and the assessment of species richness. We review advanced molecular techniques that might make it

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J. C. van Rijssel (✉)
Wageningen Marine Research, IJmuiden, The Netherlands

Naturalis Biodiversity Center, Leiden, The Netherlands
e-mail: jacco.vanrijssel@wur.nl

R. C. M. de Jong
Institute of Biology Leiden, Leiden University, Leiden, The Netherlands

Department of Hematology, Leiden University Medical Center (LUMC), Leiden, The Netherlands

M. A. Kishe
Tanzania Fisheries Research Institute (TAFIRI), Dar es Salaam, Tanzania
e-mail: mariakishe@tafiri.go.tz

F. Witte *(deceased)*
F. Witte wrote this chapter while at Institute of Biology Leiden, Leiden University, Leiden, The Netherlands

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possible to distinguish species genetically. These techniques may also reveal how adaptive responses might have played a role in the remarkable resurgence of these rapidly adapting cichlids.

Keywords Morphological change · Lake Victoria · Environmental stressor · Haplochromine cichlid · Species boundary · Genomic clustering

1 Introduction

Lake Victoria, the largest tropical lake in the world, is thought to have originated 100,000–400,000 years ago (Johnson et al. 1996; Verheyen et al. 2003). There is even geological evidence that the lake dried up completely about 15,000 years ago (Johnson et al. 1996; Stager and Johnson 2008). However, some authors have suggested that during this time, aquatic refugia may have persisted implying an older age and origin of the Lake Victoria cichlids (Fryer 2001; Verheyen et al. 2003; Fryer 2004). This latter view is supported by mitochondrial and nuclear genetic data (Nagl et al. 2000; Verheyen et al. 2003; Elmer et al. 2009). However, a recent study by Meier et al. (2017a) found evidence that supported that the "Lake Victoria Region Superflock" originated between 100,000 and 200,000 years ago and was facilitated by hybridization between divergent lineages. Despite different views on their origin, there is consensus that Lake Victoria cichlids show the fastest large-scale vertebrate species radiation in the world (Nagl et al. 2000; Seehausen 2006). That is, if we consider the Lake Victoria species flock to consist of about 500 different species. Several authors have suggested that (parts of) the Lake Victoria species flock should be considered as morphs or forms of the same species rather than as separate species (Sage and Selander 1975; Meyer 1987; Klein et al. 2007; Samonte et al. 2007).

These different views on taxonomical status are derived from differences in species definition, a problem already acknowledged by Darwin (1859). Still today taxonomists are struggling on how to define species (Mayden 1999; Mallet 2007; Pauers 2010). For Lake Victoria haplochromine cichlids, it has been suggested that the genotypic cluster species concept, defined by Mallet (1995), should be used (Witte et al. 1997; Seehausen 1998). Seehausen (1998) suggested that when groups of haplochromines, with few or no intermediates, are distinguishable in at least two features that are genetically distinct, they can be referred to as different species. These features can be male nuptial colouration, stripe pattern, body shape, jaw and tooth shape, scale morphology and squamation pattern. This seems to be a solid species concept that is still being applied by taxonomists, also in cases of allopatric variation (de Zeeuw et al. 2013). Now we possess the molecular tools to unravel the genetic basis of these features, which can provide insights into the genetic basis of adaptation and ecological speciation.

2 Molecular Tools

Genetic and genomic analyses of adaptation can be studied in two ways: variation within populations or divergence between populations. The methods used for these analyses are rapidly advancing. Here we summarize six methods (very much along the lines of Hendry 2016) used with (non-comprehensive lists of) examples from the cichlid world.

1. *Quantitative genetics* comprises subdividing phenotypic variance into different components of which additive genetic variance is generally considered the most relevant to evolution because it shows the resemblance between parents and offspring. For investigations within populations, additive genetic variance is generally estimated through parent-offspring trait correlations, relationships between siblings or pedigree-based analyses in natural or artificial populations. For investigations between populations, the starting point is often to raise individuals from different populations in a "common garden" experiment to remove plastic effects. These experiments are sometimes continued through multiple generations to also remove maternal effects. The next step is to perform "line-cross" analyses based on the comparison of pure crosses, F1 and F2 hybrids and backcrosses to parental forms. In cichlids, quantitative genetics has been applied for several phenotypic traits related to colouration; melanophores (black/brown) of scales and fins (Ding et al. 2014; O'Quin et al. 2012), xanthophores (yellow) of the fins (O'Quin et al. 2012), nuptial colouration (Magalhaes and Seehausen 2010; Barson et al. 2007; Kusche et al. 2015), female mating preference (Haesler and Seehausen 2005), female mate choice (Ding et al. 2014) and morphology-related traits; growth (Rajkov et al. 2018), general morphology (Koch et al. 2012; Theis et al. 2014), body shape (Nichols et al. 2015; Husemann et al. 2017), craniofacial traits (Albertson et al. 2003a; Magalhaes et al. 2009) and gonad size (Winkelmann et al. 2014). Quantitative genetics is perfectly suited for developing a general picture of whether and which traits are heritable, but they are not informative with regard to which genes are involved in trait development or expression.
2. *Linkage mapping* involves the detection of quantitative trait loci (QTL): regions of the genome that contribute to differences in phenotypic traits. The standard methodology is to generate F1 hybrids and to cross those F1 hybrids to generate an F2 population. The phenotypic traits are measured and genotyped at genetic markers, usually single nucleotide polymorphisms (SNPs), which are evenly distributed across the genome. Next is testing whether particular alleles at the marker loci and the phenotypic trait values correlate using statistical analyses. It is imperative to use an F2 or beyond population because recombination between the parental genomes will have reduced associations between the SNPs and QTL to which they are not linked. This analysis will result in a linkage map showing the positions of the marker loci on different linkage groups (usually chromosomes). This will also give information on the markers that are associated with loci influencing phenotypic trait values. The strength of these influences can be

inferred from calculating which percentage of variation of the trait is explained by a certain locus. This method has been applied in cichlids to find regions in the genome that relate to colour such as nuptial colouration (Streelman et al. 2003a; Parnell and Streelman 2013), melanophores and xanthophores of the fin (O'Quin et al. 2013), melanocytes and xanthophores of the fin and flanks (Albertson et al. 2014), opsins (Carleton et al. 2010; Nandamuri et al. 2018), lateral stripes (Henning et al. 2014) and morphological traits such as body shape (Franchini et al. 2014), scale shape (Albertson et al. 2018), craniofacial shape variation and traits (Concannon and Albertson 2015; Parsons et al. 2016), jaw and neurocranial shape (Cooper et al. 2011), opercular four-bar linkage apparatus (Hu and Albertson 2014), jaw laterality (Stewart and Albertson 2010), pharyngeal jaw (Fruciano et al. 2016), mandible (Albertson et al. 2005; Parsons et al. 2012), oral jaw apparatus (Albertson et al. 2003b), tooth shape (Streelman and Albertson 2006), tooth and taste bud density and tooth number (Bloomquist et al. 2015; Hulsey et al. 2017) and lips (Henning et al. 2017).

3. *Association mapping* can localize QTL in a similar way to linkage mapping. The difference is that association mapping proceeds by screening a large number of individuals from natural populations and relates between individual variation in alleles at marker loci and phenotypic trait values. Recombination in natural populations should allow persistent statistical associations between phenotypic traits and marker loci that are close together on a chromosome only. When the location of the marker on the linkage map is known, it can be used to infer locations of QTL. Association mapping has been used in cichlids to infer QTL of nuptial colouration (Streelman et al. 2003a; Roberts et al. 2009), opsins (Schulte et al. 2014) and the mandible (Roberts et al. 2011).
4. *Genome scans* involve genotyping large numbers of genetic markers, also usually SNPs nowadays, in multiple individuals from multiple populations and then searching for markers that show the smallest or largest differences between those groups. These markers are expected to be located in or nearby QTL that are under similar (stabilizing) or different (divergent/disruptive) selection between these populations. The objective is often to infer the action of selection; however, genetic markers can also differ among populations due to drift. This is why the action of selection is usually invoked only for "outlier loci" or for loci that show the strongest correlations with environmental variables. The best way to infer these outliers is still being discussed (Cruickshank and Hahn 2014). Genome scans are increasingly being used by cichlid scientists as the costs of whole genomes have dropped rapidly in the last decade and several cichlid genomes have been completely sequenced (Brawand et al. 2014; Malinsky et al. 2015, 2018; Mcgee et al. 2015; Meier et al. 2017a). Genome scans have been used to identify markers linked to nuptial colouration (Mattersdorfer et al. 2012) and mouth asymmetry (Raffini et al. 2017), melanocytes and xanthophores of the fin and flanks (Albertson et al. 2014), colour, opsin genes, guts, dentition, jaws and brains (Loh et al. 2008, 2013) and craniofacial shape variation (Parsons et al. 2015).

5. *Gene expression*: Phenotypic differences between populations might be due to divergence at protein-coding loci but also in regulatory sequences that influence gene expression. Genes influencing divergence can therefore be inferred by looking at variation in gene expression between populations in a certain environment or between environments for a certain population. There are several methods for measuring gene expression, including quantitative PCR and next-generation sequencing methods like RNA-seq. These methods usually examine which genes are upregulated or downregulated in one environment or population in relation to another environment or population. Whether the variation in expression is found in specific genes or in upstream regulatory genes, these genes are likely to play a role in phenotypic differences between populations and environments. These gene expression differences between natural populations can, of course, reflect either sequence differences between those populations or plastic responses to local environments. There have been many gene expression studies performed that revealed genes related to nuptial colouration (Terai et al. 2003; Henning et al. 2010, 2013; Gunter et al. 2011), opsins (Carleton and Kocher 2001; Carleton et al. 2005, 2010; Parry et al. 2005; Spady et al. 2006; Seehausen et al. 2008; Hofmann et al. 2009, 2010; O'Quin et al. 2010; Escobar-Camacho et al. 2017), egg spots (Salzburger et al. 2007; Santos et al. 2014), the brain (Sylvester et al. 2010, 2013; Lee et al. 2017; Derycke et al. 2018), cellular, metabolic and biological regulation processes (Fan et al. 2012), chemical detoxification (Kavembe et al. 2015), biosynthesis, metabolic processes and development (Elmer et al. 2010), fin shape (Ahi et al. 2017), head morphogenesis (Kijimoto et al. 2005; Singh et al. 2017; El Taher et al. 2019), craniofacial morphology (Powder et al. 2015), the opercular four-bar linkage apparatus (Hu and Albertson 2014), gills (Willis et al. 2018), the brain, pharyngeal arches and teeth (Renz et al. 2011), pharyngeal arch elements (Cho et al. 2015), the pharyngeal jaw (Gunter et al. 2013, 2017; Schneider et al. 2014), oral jaws (Kobayashi et al. 2006), the mandible (Albertson et al. 2005; Roberts et al. 2011), the lips (Colombo et al. 2013; Manousaki et al. 2013), pharyngeal and oral teeth (Fraser et al. 2009), tooth and taste bud density and bone morphogenetic proteins (Bloomquist et al. 2015, 2017), (Streelman and Albertson 2006) and tooth shape and regeneration (Fraser et al. 2013).
6. *Candidate genes* are genes of which the function is known in model organisms, and these genes can be targeted in non-model organisms. The specific role of that gene can then be confirmed through several methods, including gene knockout studies or transgenics. Several genes that might play an important role in the evolution and diversification of cichlids have been discovered or targeted including genes related to nuptial colouration (Terai et al. 2003; Henning et al. 2010; Gunter et al. 2011), eggs spots (Salzburger et al. 2007; Santos et al. 2014), opsins (Terai et al. 2002; Parry et al. 2005; Spady et al. 2006; Seehausen et al. 2008; Meier et al. 2017a), epithelial morphogenesis (Fan et al. 2011), fins, facial skeleton and brain (Brawand et al. 2014), jaw apparatus and anal fin (Renz et al. 2011; Diepeveen et al. 2013) and morphological features like fin shape (Navon et al. 2017), brain (Sylvester et al. 2010, 2013), craniofacial form and

development (Albertson et al. 2005; Parsons et al. 2014; Powder et al. 2015), opercular four-bar linkage apparatus (Hu and Albertson 2014), lower pharyngeal jaw (Gunter et al. 2017), mandible (Albertson et al. 2005; Roberts et al. 2011) and tooth shape and regeneration (Fraser et al. 2013).

Combinations of the above-mentioned approaches seem to be the most efficient and promising in detecting genes or genomic regions that are of interest to the diversification of cichlids (Streelman et al. 2003b; Albertson et al. 2005, 2014; Seehausen et al. 2008; Roberts et al. 2011; Brawand et al. 2014; Hu and Albertson 2014; Parsons et al. 2015). Naturally, most of these studies focussed on traits (Fig. 1) that are thought to play a role in the diversification of cichlids and are, hitherto, also used to distinguish species.

When we are trying to distinguish species and deal with species limits, we also have to consider how extreme the intraspecific variation can be. Interspecific variation can be geographical, between different localities or allochronic, through time. As far as variation through time is concerned, morphological responses to human-induced perturbations have been described in several fish species (Hendry et al. 2008; Allendorf and Hard 2009; Aguirre and Bell 2012) including Lake Victoria cichlids (van Rijssel and Witte 2013). In the past 40 years, Lake Victoria suffered severe anthropogenic environmental changes (Witte et al. 2013a). Among these was the upsurge of the introduced Nile perch during the 1980s (Pringle 2005; Goudswaard et al. 2008). At the same time, human-induced eutrophication resulted in decreased oxygen levels and an increase of water turbidity (Hecky et al. 1994; Seehausen et al. 1997a; Verschuren et al. 2002; Hecky et al. 2010). Concurrently, the abundance of macro-invertebrates such as insects, molluscs, shrimps and a small pelagic cyprinid increased (Kaufman 1992; Wanink 1999; Goudswaard et al. 2006). Predation by Nile perch is thought to be one of the main reasons as to why 40% of the cichlid species have disappeared (Witte et al. 1992, 2007). Hybridization caused by eutrophication is also likely to have contributed to the decline of species number as well (Seehausen et al. 1997a; Witte et al. 2013b). More recently, McGee et al. (2015) found evidence supporting the theory that interspecific competition with Nile perch is largely responsible for the extinction of piscivorous haplochromines.

During the 1990s, some haplochromine species recovered (Seehausen et al. 1997b; Witte et al. 2000). These species have adapted their ecological niche (Witte et al. 1995; Seehausen et al. 1997b; Katunzi et al. 2003; Kishe-Machumu et al. 2008, 2015, 2017; van Rijssel et al. 2017) and morphology (Witte et al. 2008; van der Meer et al. 2012; van Rijssel and Witte 2013; van Rijssel et al. 2015, 2016) to the changed environmental circumstances. Some of the observed morphological differences (e.g. gill surface) were of the same magnitude, and larger, as those formerly existing between closely related cichlid species (Witte et al. 2008; van Rijssel et al. 2016). These large morphological changes imply that characters, which are used for species distinction, are not stable in a changing environment. This raises the question whether it is possible to continue to use them as distinguishing taxonomic characters in these rapidly evolving and plastic species in environments undergoing fast-paced anthropogenic changes.

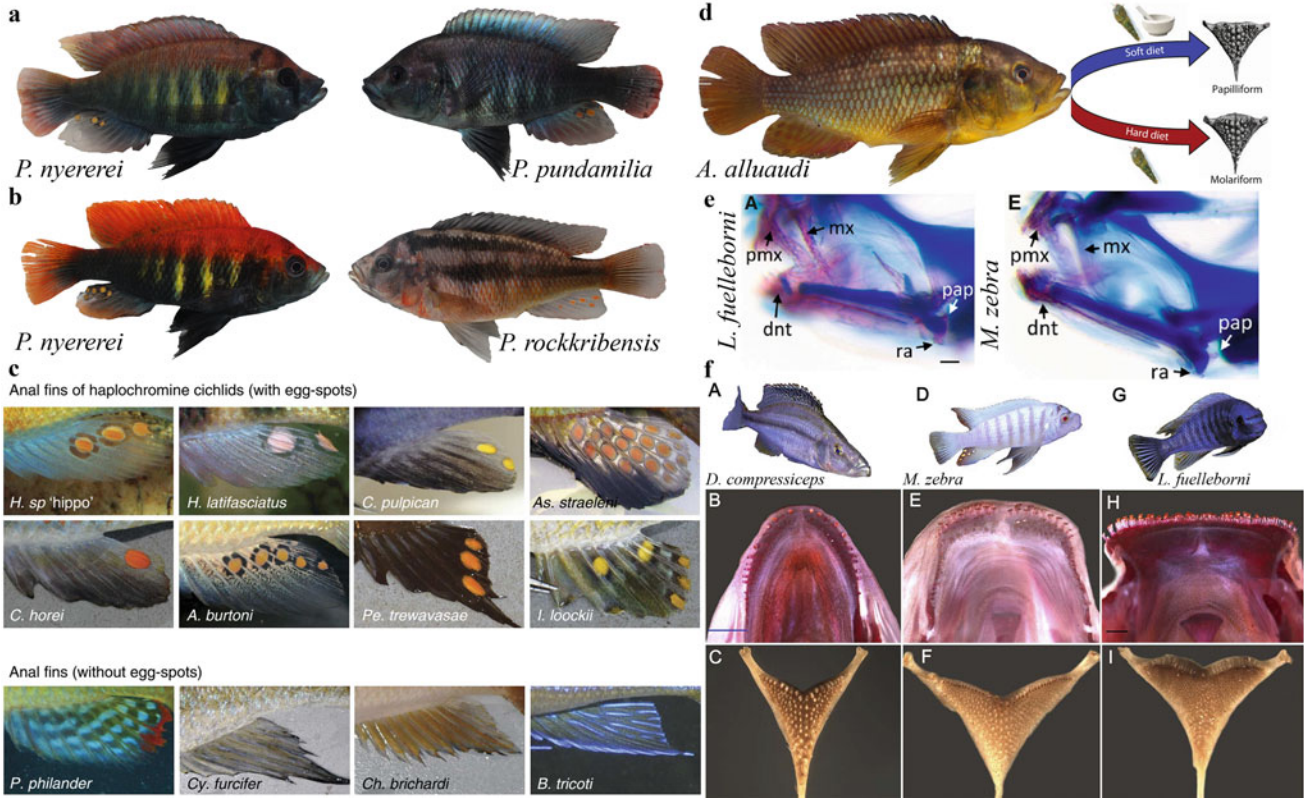

Fig. 1 Examples of traits for which genes and/or genomic regions have been discovered that are also likely to play a role in ecological speciation. (**a**) Nuptial colouration of *Pundamilia nyererei* (red) and *P. pundamilia* (blue) from Python Island, Mwanza Gulf Lake Victoria (Magalhaes and Seehausen 2010). (**b**) Horizontal stripes in *Paralabidochromis rockkribensis* (*H. sauvagei*) vs none in *P. nyererei* from Lake Victoria (Henning et al. 2014). (**c**) Male anal fin patterns

3 Case Study: *Haplochromis (Yssichromis) pyrrhocephalus*

In this chapter, we focus on ecological changes (horizontal distribution and diet) of *Haplochromis (Yssichromis) pyrrhocephalus* Witte and Witte-Maas 1987 during two periods: 1977–1982 (pristine period) and 1990–2001 (perturbed period). This species was selected as it is one of the zooplanktivorous species that resurged very successfully after the severe environmental changes in Lake Victoria (the species is now more abundant than before the environmental changes). In addition, we address the morphological responses in body shape, eyes, gills and jaws in relation to predation, turbidity, hypoxia and prey uptake during the two periods for this species as they were hypothesized to have contributed to the successful resurgence of the species (Witte et al. 2008). Implications for cichlid adaptive potential, species distinction and estimates of species numbers will be discussed.

3.1 Ecology: Horizontal Distribution and Diet

Adult and juvenile fish were caught during daytime with a bottom trawler on the research transect in the northern part of the Mwanza Gulf (Fig. 2). Fish were caught at mud bottom stations E–K varying in depth from 4 to 14 m (see Witte (1981) for more catch details). In the years 1979–1980, 12 monthly catches were conducted with a small trawler (20–25 hp outboard engine). In the period 1990–1991 (November and June), three catches were conducted with the small trawler, and in 1993 (October–December), six catches were made with a large trawler (250 hp). In the period 2006–2008, a similar trawler was used to sample fish from mud stations E–J during daytime.

Fig. 1 (continued) in East African cichlids. Haplochromine egg spots (upper panel) vary in size, shape, number and colouration. Non-haplochromines and basal haplochromine *Pseudocrenilabrus philander* (lower panel) do not show this trait (Santos et al. 2014). (**d**) The pharyngeal jaw of *A. alluaudi* becomes gracile and papilliform in response to a soft diet and becomes robust and molariform in response to a hard diet (modified after Young 2013, e.g. Gunter et al. 2013). (**e**) Ptch1 expression in Malawi cichlid craniofacial development with craniofacial outcomes of larvae at 13 dpf. *Labeotropheus fuelleborni* (A) larvae exhibit accelerated bone (pink) development compared with *Metriaclima zebra* (E), cartilage stains blue, dnt, dentary; mx, maxilla; pap, posterior articulation process; pmx, premaxilla (Roberts et al. 2011). (**f**) The lower oral and pharyngeal jaws and teeth of three Lake Malawi cichlids: A-C, *Dimidiochromis compressiceps*; D-F, *M. zebra*; G-I, *L. fuelleborni* (Fraser et al. 2009). Photos of **a**, **b** and **d** by Florian Moser

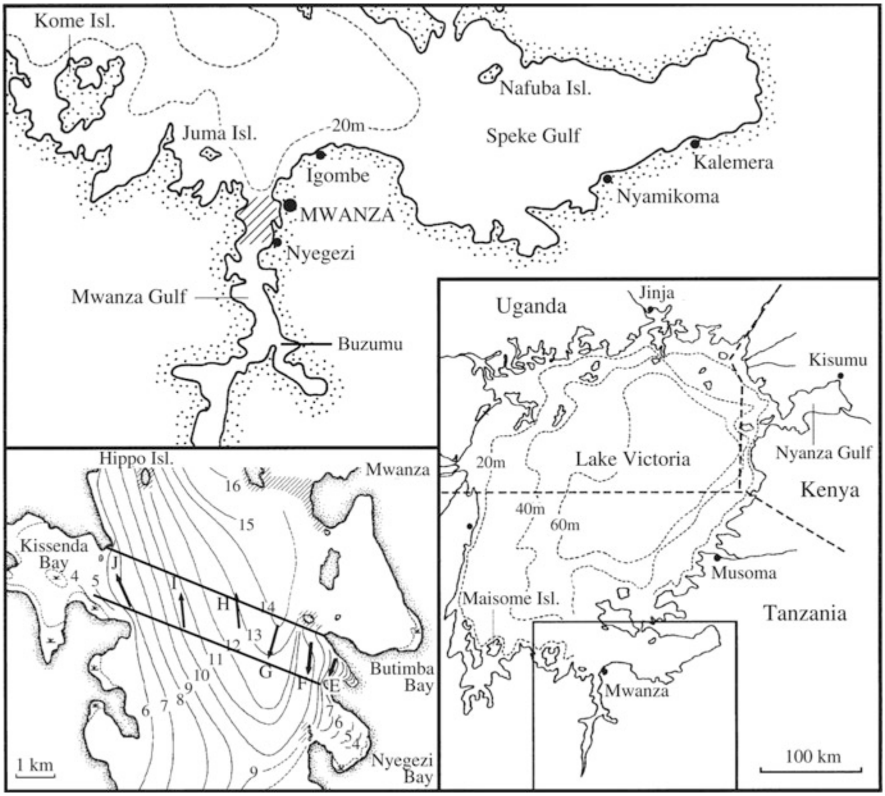

Fig. 2 Map of Lake Victoria and the Mwanza Gulf. The research area is indicated as the hatched part of the upper map. The research transect is indicated with black lines from the east to the west shore in the northern part of the Mwanza Gulf

3.1.1 Horizontal Distribution

The horizontal distribution on the transect was calculated by the number of individuals caught per 10 min trawl at a station divided by the total number caught at the transect (stations E–K, Fig. 2). Differences in horizontal distribution between stations were analysed with a Kruskal–Wallis test. When significant, pairwise comparisons between stations were made using Dunn's post hoc test (Graphpad Prism 4.0).

In the 1979–1980 period, *H. pyrrhocephalus* mainly occurred at sublittoral mud bottom stations with a depth range of 7–14 m (stations F–J). The horizontal distribution was significantly different between stations ($P < 0.001$). The species was predominantly found at station G at a depth of 13–14 m (70%). At this station, *H. pyrrhocephalus* occurred significantly more than at stations E, F and J ($P < 0.05$, Fig. 3). After its resurgence in the 1990s, the species had extended its habitat to littoral waters in the range of 4–14 m (stations E–K, Fig. 3). This habitat extension

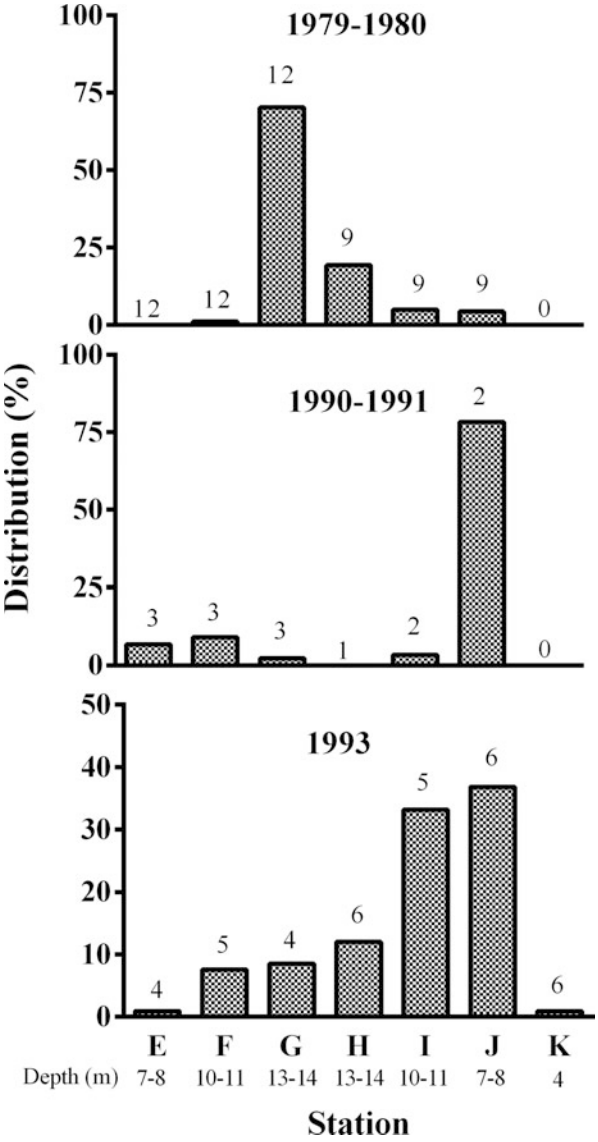

Fig. 3 Horizontal distribution of *H. pyrrhocephalus* at station E-K in 1979–1980, 1990–1991 and 1993. Numbers above the bars represent the number of catches per period. Percentages are based on total catch numbers of bottom trawls per 10 min

remained till 2008 (Kishe-Machumu et al. 2015) and is still present (J. C. van Rijssel, personal observations). In the period 1990–1991, *H. pyrrhocephalus* individuals were mostly caught (78%) at the shallow station J (7–8 m), though the distribution between stations was not significantly different. In 1993, the species occurred again more frequently at the deeper stations F–I compared to 1990–1991 (Fig. 3). In 2006–2008, the species was mainly found over station F but was regularly found at the other stations as well (Kishe-Machumu et al. 2015) as was the case in 2011 and 2014 (J. C. van Rijssel, personal observations). Although the overall horizontal distribution of *H. pyrrhocephalus* between stations was significantly different in 1993 ($P < 0.05$), no significant differences in pairwise comparisons in *H. pyrrhocephalus* numbers between stations were found. The habitat extension of *H. pyrrhocephalus* might be the result of the virtual disappearance of other competing species. For example, the zooplanktivore/insectivore *H. piceatus* used to be the dominant species at the shallow station E. In contrast to the 1970s, this station is now also inhabited by *H. pyrrhocephalus*, while *H. piceatus* seems to have been almost completely vanished from the transect since 1990 (Goldschmidt et al. 1990; Witte et al. 1992; Kishe-Machumu et al. 2015).

3.1.2 Diet

The diet of *H. pyrrhocephalus* from the period 1977–1982 was compared with the diet of *H. pyrrhocephalus* from 1999. All specimens were caught with bottom trawls during 1977–1982 and in 1999 in the northern part of the Mwanza Gulf (Katunzi et al. 2003). Diet was determined by estimating the volume percentages of prey in the stomach and intestine contents following Katunzi et al. (2003). Volume percentages per food type were estimated and corrected for the percentage of fullness. Stomachs and intestines filled for less than 25% were excluded (Kishe-Machumu 2012). Differences in diet were analysed with Mann-Whitney U tests. In the years 1977–1982, the diet of *H. pyrrhocephalus* mainly consisted of zooplankton (copepods, Table 1). In the years 1999–2001, the diet shifted towards a diet including larger and more benthic prey, as was found for detritivorous haplochromines (Kishe-Machumu et al. 2008). There was a significant increase in the volume percentages of detritus, ostracods, chironomids and molluscs ($P < 0.05$), while that of zooplankton significantly decreased ($P = 0.001$, Table 1). Several, not mutually exclusive, explanations may account for these findings: (1) an increased abundance of larger

Table 1 Mean volume percentages (± standard deviations) of stomach and gut contents of *H. pyrrhocephalus* through time (modified from Kishe-Machumu 2012)

	$n = 32$	$n = 13$	*P*-value
	1977–1982	1999–2001	
Detritus	4.2 ± 17.8	12.6 ± 16.8	**0.008**
Phytoplankton	3.6 ± 9.4	4.8 ± 11.6	0.630
Zooplankton[a]	63.9 ± 30.8	29.9 ± 27.3	**0.001**
Ostracods	0	0.8 ± 1.7	**0.005**
Chironomids	2.1± 5.9	16.5 ± 29	**0.013**
Chaoborus	15.6± 20.7	12.3 ± 25.9	0.888
Insects	6.8 ± 9.8	8.5 ± 17.8	0.817
Molluscs	0	11.4 ± 21	**0.001**
Shrimps	0	1.5 ± 5.3	0.117
Fish	0.4 ± 1.4	0.6 ± 1.2	0.088
Others	3.5 ± 9.4	1.1± 2.3	0.059

[a] *H. pyrrhocephalus* mainly fed on copepods

Significant *P*-values are indicated in bold prey types (van Rijssel et al. 2015), (2) competitive release by a decline in haplochromine species diversity and number and (3) the decreased water transparency in combination with the lower resolution in the smaller cichlid eyes (Kishe-Machumu et al. 2008; van der Meer et al. 2012).

3.2 Morphology

Standard length was measured for *H. pyrrhocephalus* caught in 1978, 1985, 1991 and 1993. Specimens collected in 1978, 1985 and 1991 were caught with bottom trawls at the northern part of the Mwanza Gulf. In 1993, specimens were caught close to Buzumu Island (station 1 in Goudswaard et al. 2011; Fig. 2) in the shallow southern part of the Mwanza Gulf. For each year, a length frequency distribution was made for comparison. For morphological character comparison, fishes were collected in the pristine period (1977–1981), which is considered as the period before the environmental changes, and in the years 1999–2001, which fall in the perturbed period: a period during the severe environmental changes (van Rijssel and Witte 2013). All morphological characters were measured from photographs (with a reference measure) using ImageJ. Body shape was analysed using a Canonical Variate Analysis (CVA) in MorphoJ 1.02 g (van Rijssel and Witte 2013). Differences in morphological characteristics between periods were tested with a general linear model (GLM), using standard length (SL) or body volume (BV) as covariate unless stated otherwise (SPSS 20). *P*-values were adjusted with a sequential Bonferroni correction.

3.2.1 External Measurements

Body shape of the fish was measured using geometric morphometry and determined by placing 21 landmarks using TPSDig2 (van Rijssel and Witte 2013). Head area and caudal peduncle area were calculated using landmarks whereby the head was considered a triangle and the tail a rectangle shape following van Rijssel and Witte (2013). The body volume was measured using volumetric displacement, while the head volume was measured and calculated using a three-dimensional truss (Witte et al. 2008). Cheek depth, eye length and eye depth were measured sensu Barel et al. (1977). The size range of *H. pyrrhocephalus* decreased from 5.5–8.0 cm in 1978 to 4.5–7.0 cm in 1985. It diminished even further in 1991 to <2.0–7.0 cm. The latter catch, which contained mainly juveniles (Fig. 4), was actually the first successful attempt to catch zooplanktivores on the transect after their disappearance in 1988 (Witte et al. 1992; Witte et al. 2007). In 1993, it seemed that the size range of the specimens was comparable to that of the early 1980s, but these fishes were caught at a different site, near Buzumu Island in the shallow (1–2 m) southern part of the Mwanza Gulf where Nile perch were rarely caught (Goudswaard et al. 2011). The decrease in size of *H. pyrrhocephalus*, as well as size at first maturity and maximum

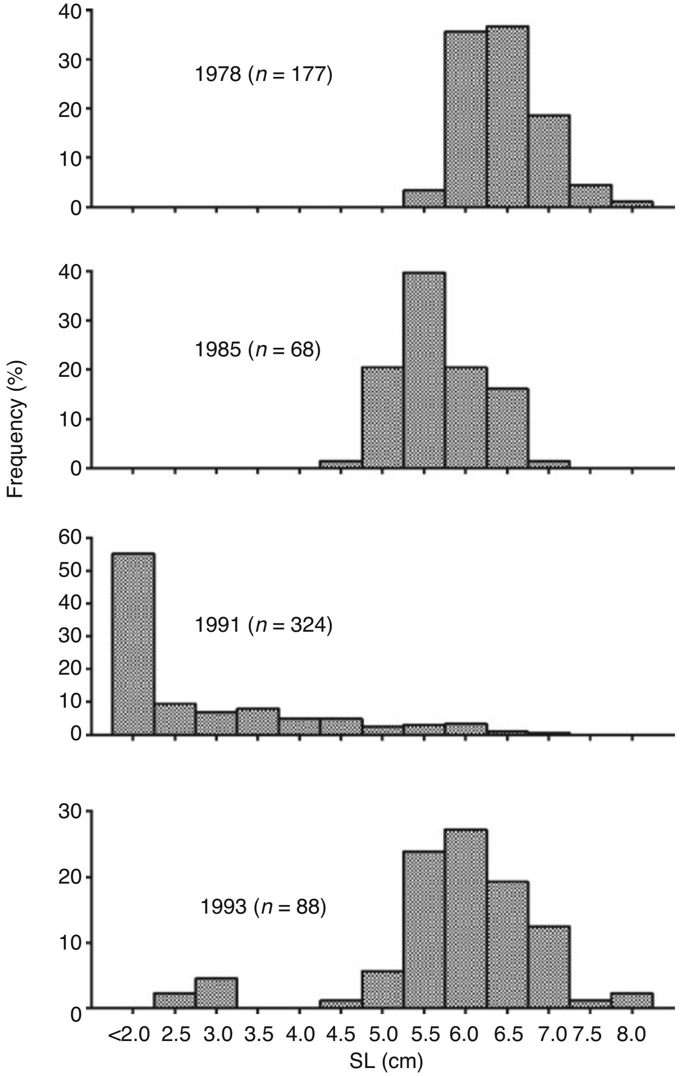

Fig. 4 Length frequency distribution of *H. pyrrhocephalus* caught at the transect (6–14 m) during the years 1978, 1985, 1991. Note that fish from 1993 were caught at Buzumu; in the southern part of the Mwanza Gulf (modified from Witte et al. 1995)

size, has been attributed to two main causes (Witte et al. 1995): (1) intensive trawling in the 1970s and early 1980s with relatively small mesh sizes selectively catching the larger individuals and (2) predation by Nile perch that might have had a preference for larger individuals (Witte et al. 1992).

In addition to a major shift in size ranges, van Rijssel and Witte (2013) found pronounced body shape changes occurring during the 1990s. They found that the head surface/caudal peduncle area ratio decreased, mainly by a decrease in head size, and attributed these changes to predation pressure by Nile perch. Similar changes have been observed in other fish species: a smaller anterior region and a larger caudal region have been documented in 16 species at high predation localities or treatments (Langerhans 2010). Predation has been found to induce these changes in several species like mosquitofishes (Langerhans et al. 2004; Langerhans 2009), threespine sticklebacks (Hendry et al. 2011) and guppies (Hendry et al. 2006). For these species, it has been shown that the changes led to enhanced burst swimming speed which contributes to predator escape performance.

Witte et al. (2008) found that the head volume in *H. pyrrhocephalus* decreased by 15.7% in the perturbed period ($P = 0.001$, Table 2). Chapman et al. (2008) hypothesized that the smaller head of *H. pyrrhocephalus* might be due to predation. Van Rijssel and Witte (2013) attributed the smaller head to tail ratio in this and other haplochromine species to predation as well. Despite this decrease in head volume, both van Rijssel and Witte (2013) and Witte et al. (2008) found an increase in cheek depth in *H. pyrrhocephalus* individuals from the perturbed period ($P < 0.001$, 4.8–8.6%, respectively, Table 2). The increase in cheek depth is presumably an adaptive response to facilitate the processing of larger prey items. The larger cheek depth increases the buccal cavity and also contributes to increased biting force (Barel 1983), which might be necessary for the uptake of larger and more robust prey items. However, conclusions about increased biting force can only be drawn when the muscle force of the musculi adductor mandibulae and the tooth-inclination are compared, which still remains to be done for *H. pyrrhocephalus*. Other morphological characters that show adaptive responses to larger and tougher prey are the premaxillary dentition, the pharyngeal crushing muscles and the gill rakers (see below).

3.2.2 Gill Rakers and Gill Surface

The first gill arch on the left side was dissected, and the number of rakers was counted under a dissection microscope sensu Barel et al. (1977). The ceratobranchial was separated from the epibranchial and photographed. Gill raker length (from tip to base) and spacing (from the middle of one raker to the middle of the next raker at the base) were measured from the second to the eighth gill raker below the apex (cartilaginous plug) on the oral side of the arch.

Witte et al. (2008) dissected all four gill arches on the right hand side of the fish. The number and length of the filaments were measured, and scanning electron microscopy (SEM) was used to count and measure the surface of the secondary lamellae from the lateral hemibranch of the first and third gill arch. The gill surface area was calculated by multiplying gill filament number by filament length, multiplied by the density and surface area of the secondary lamellae.

Both the number and the size of the gill rakers decreased in individuals caught in the perturbed period. The number decreased by 7.1% ($P = 0.03$, one-tailed Mann–Whitney U-test), while the length decreased by 24.3% (Table 2, Fig. 5, $P = 0.003$).

Table 2 Results of the general linear model (GLM) analyses of morphological characters in populations of *H. pyrrhocephalus* from the pristine and perturbed period with standard length (SL)/body volume (BV) as covariate

				Covariate SL/BV			
Morphological character	Period	N	Mean	Difference (%)	*P* period	*P* SL/BV	Source
HV (mm)	Pristine	7	919.8				
	Perturbed	7	775.7	**-15.7%**	<**0.001**	<**0.001**	Witte et al. (2008)
Cheek depth (mm)	Pristine	19/ 13	3.3/ 3.31				
	Perturbed	22/ 19	3.6/ 3.46	**8.6%/ 4.8%**	<**0.001**	<**0.001**	Witte et al. (2008), van Rijssel and Witte (2013)
Edentulous part premaxilla (%)[a]	Pristine	7	25				
	Perturbed	7	11	**14%**	**0.004**	–	This study
Cross-section m. lev. ext 4 (mm^2)	Pristine	7	0.68				
	Perturbed	7	1.25	**84.9%**	<**0.001**	0.013	This study
Cross-section m. lev. post (mm^2)	Pristine	7	0.31				
	Perturbed	7	0.67	**116.3%**	<**0.001**	0.104	This study
Gill raker length (mm)	Pristine	7	0.67				
	Perturbed	7	0.50	**−24.3%**	**0.003**	0.045	This study
Gill raker number[a]	Pristine	7	15.4				
	Perturbed	7	14.3	**−7.1%**	**0.03**	–	This study
Gill raker spacing (mm)	Pristine	7	0.62				
	Perturbed	7	0.54	**−12.7%**	**0.004**	0.093	This study
Gill surface (mm^2)[b]	Pristine	8	309.8				
	Perturbed	8	509.4	**64.4%**	<**0.001**	NS	Witte et al. 2008
LPJ length (mm)	Pristine	6	6.70				
	Perturbed	6	6.15	**−8.2%**	**0.001**	<**0.001**	This study
LPJ width (mm)	Pristine	7	5.87				
	Perturbed	7	5.48	**−6.7%**	**0.006**	**0.003**	This study
Keel depth (mm)[a]	Pristine	6	1.12				

(continued)

Table 2 (continued)

Morphological character	Period	N	Mean	Covariate SL/BV Difference (%)	*P* period	*P* SL/BV	Source
	Perturbed	6	1.05	−7.0%	0.058	–	This study
Eye length (mm)	Pristine	19/ 13	7.5/ 6.5				
	Perturbed	22/ 19	6.5/ 5.95	**−13.9%/ −8.5%**	**<0.001**	**<0.001**	Witte et al. (2008), van Rijssel and Witte (2013)

Significant differences after sequential Bonferroni corrections are shown in bold

[a] Differences in the edentulous part of the premaxilla, gill raker number and keel depth were tested with a one-tailed *t*-test and a one-tailed and a two-tailed Mann-Whitney U-test, respectively

[b] Covariate of the GLM used for gill surface was BV

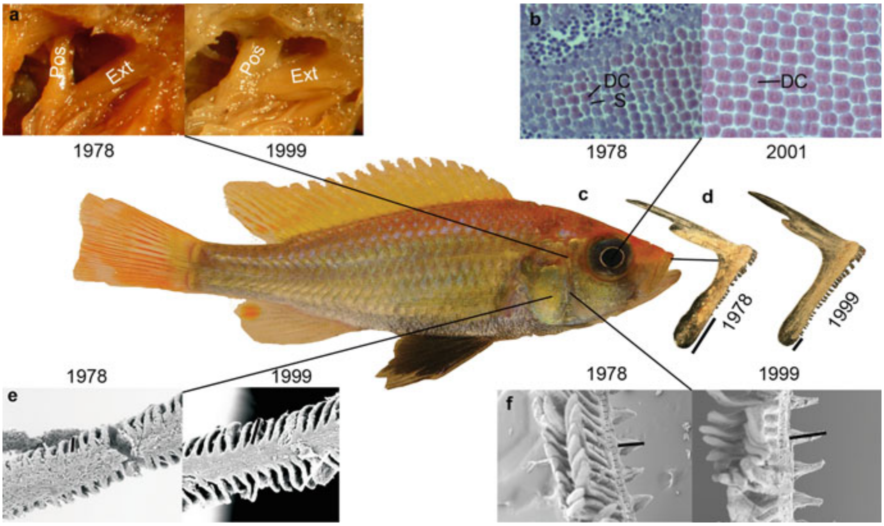

Fig. 5 Photographs of morphological characters of *H. pyrrhocephalus* in the periods 1978–1981 and 1999–2001. (**a**) The pharyngeal crushing muscles in situ; Ext, musculus levator externus 4; Pos, musculus levator posterior. Larger crushing muscles were found in 1999. (**b**) Double cone (DC) row patterns in the retina with presence of some single cones (SC) in 1978 and a lower density of double cones in 2001. (**c**) Specimen of male *H. pyrrhocephalus* caught in 2006. (**d**) Premaxilla, black bars indicate the edentulous part of the dentigerous arm; note that the right premaxilla is depicted instead of the left used in this study. An almost completely covered dentigerous arm was found in 1999. (**e**) SEM photographs of the lateral side of a gill filament with secondary lamellae; the length of the latter is indicated with black bars. Longer secondary lamellae were found in 1999. (**f**) SEM photographs of the lateral side of the gill arch with gill rakers; the length of the latter is indicated with black bars. Longer gill rakers and smaller gill raker spacing were found in 1999. Photos by Rob de Jong, Henny van der Meer, Mary Kishe, Ellen Hoogwater, Monique Welten

Gill rakers are considered to be important for particle retention during feeding in fishes. They can serve (1) as barriers that direct particle-laden water to the sticky oral roof, (2) as dead-end filters that sieve particles or (3) as sticky filters that retain particles (Sanderson et al. 2001). Although the exact mechanism of filter feeding in *H. pyrrhocephalus* is unknown, a higher number of longer gill rakers is generally seen in planktivorous fishes such as sticklebacks and coregonid fish (Schluter and Mcphail 1992; Kahilainen et al. 2011) and is related to retention efficiency (Sanderson et al. 2001). For coregonid fish, it has been suggested that a lower number of smaller, widely spaced gill rakers might be sufficient to retain larger benthic organisms while allowing mud to flow through the gill raker slits (Kahilainen et al. 2011), while a dense gill raker apparatus might clog the mud swallowed during the uptake of benthic prey (Amundsen et al. 2004; Kahilainen et al. 2011). This theory concurs with the lower number of smaller gill rakers found in *H. pyrrhocephalus* from the perturbed period as their diet consisted mainly of benthic organisms. However, the distance between the gill rakers decreased with 12.7% ($P = 0.004$) in *H. pyrrhocephalus* from the perturbed period. Although this is not in agreement with the above-mentioned theory, the actual function of gill raker spacing has been questioned in the past (Langeland and Nost 1995) and gill rakers may not serve as mechanical sieves as previously thought (Wootton 1990). Just like in the Nile tilapia, *Oreochromis niloticus* Linnaeus 1758, it might be that the gill rakers of *H. pyrrhocephalus* use mucus entrapment for aerosol filtration (Sanderson et al. 1996) or function as a cross-filter like in the Singidia tilapia, *Oreochromis esculentus* Graham 1928 (Sanderson et al. 2001). Laboratory feeding experiments on *H. pyrrhocephalus* have to be conducted to draw conclusions on particle retention for this species.

Witte et al. (2008) found in *H. pyrrhocephalus* from the perturbed period an increase in gill surface of 64.4% ($P < 0.001$; Table 2). This increase was mainly caused by an increase in filament length (12.7%, $P < 0.01$) and secondary lamellae surface (35.8%, $P < 0.001$, Fig. 5). Witte et al. (2008) suggested that the increased gill surface is an adaptive response to the decreased dissolved oxygen levels in Lake Victoria (Hecky et al. 1994, 2010; Wanink et al. 2001; Verschuren et al. 2002; van Rijssel et al. 2016). An increase of gill surface under hypoxic conditions is not uncommon in fish. Many fish species including several cyprinids (crucian carp, goldfish) and cichlids show an increased gill surface in response to hypoxia (Chapman et al. 2000; Sollid et al. 2003, 2005; Rutjes et al. 2009).

3.2.3 Premaxilla and Pharyngeal Jaws

The left premaxilla was dissected and then photographed using a digital camera mounted on a dissection microscope. From these images, the length of the dentigerous arm and the length of the toothless part of the dentigerous arm (measured from the last tooth or empty socket to the caudal tip) were obtained. From these measurements, we calculated which percentage of the dentigerous arm is toothless. In the period 1977–1981, the posterior toothless part of the dentigerous arm of the premaxilla of *H. pyrrhocephalus* was on average 25% of the total length. This decreased to 11% in the period 1999–2001 (one-tailed t-test, $P = 0.004$; Table 2, Fig. 5). In other words, the tooth bearing part of the premaxilla increased, covering the dentigerous arm of the premaxilla almost completely. Greenwood (1980) considered the large (1/4–1/3 part) edentulous part of the premaxillary dentigerous arm a diagnostic character for the genus *Yssichromis*. The genus *Yssichromis* (used as a subgenus in publications of the Haplochromis Ecological Survey Team, HEST) is the only genus whose species predominantly fed on zooplankton, while the other genera, with smaller toothless areas, fed on other prey items (F. Witte, pers. obs.). This indicates that the extension of the dentigerous area might be a response to a decrease in zooplanktivory and an increased importance of insects and other large prey.

The musculus levator posterior (m. lev. post.) and musculus levator externus 4 (m. lev. ext. 4) of the pharyngeal jaws were dissected and dried at 80 °C for 3 days, until constant weight was reached (Smits et al. 1997). The muscle volume was calculated by multiplying the dry weight by 7.08 which gives the fresh weight (Galis 1992) and then divided by 1.06: the average density of muscle (Alexander 1959). The lengths of the muscle fibres were measured in the median of their lateral side from the origin of the skull to the point where they pass epibranchial 4 (Witte et al. 2008). Finally, the cross-sectional area of the muscles was calculated by dividing the muscle volume by the average length of the muscle fibres (Galis 1992). The depth of the pharyngeal crushing muscles, the m. lev. post., had a significant increase of 64.4% in specimens from the perturbed period (Witte et al. 2008). By measuring the cross-section of both muscles (instead of length and depth only), we found an increase of 85% and 116%, respectively, in specimens from the perturbed period ($P < 0.001$, Table 2, Fig. 5). In 1996, Smits et al. compared the m. lev. post and m. lev. ext. 4 in a snail-eating and an insect-eating morph of *Astatoreochromis alluaudi* Pellegrin 1904. They suggested that the hypertrophy of these muscles is an adaptation to crushing. Similarly, we consider the larger crushing muscles of *H. pyrrhocephalus* to be an adaptive response to the larger and more robust prey in the diet.

The lower pharyngeal jaws were dissected and then photographed. From these images, LPJ length and width (Hoogerhoud 1984) and keel depth (Hoogerhoud 1986) were measured. Unexpectedly, the lower pharyngeal jaw length and width decreased with 8.2% ($P = 0.001$) and 6.7% ($P = 0.006$, Table 2), respectively, in the perturbed period. To a large extent, the decrease in head size can explain this: with head length as covariate, there was no significant effect of period on both characteristics. The keel depth also showed a decrease of 7% (although not significant, Mann–Whitney U-test, $P = 0.058$, Table 2). The keel is the insertion area of an important pharyngeal crushing muscle, the m. transversus ventralis (Smits et al. 1997). The keel depth and the other two aforementioned characteristics were expected to increase since a hypertrophied pharyngeal jaw has been found in response to more robust prey in several studies (Hoogerhoud 1986; Huysseune et al. 1994; Smits et al. 1996, 1997; Muschick et al. 2011). Although we expected an increase of the lower pharyngeal jaw, it might be that *H. pyrrhocephalus* was capable of processing the larger prey with a smaller jaw. On the other hand, the cichlid head is densely packed with structures, and a size increase of morphological characters will definitely have an effect on other structures (Barel 1993), especially when the head volume decreases as it did in *H. pyrrhocephalus*. It is likely that a combination of the decrease in head volume and the increase of the gills and pharyngeal crushing muscles has resulted in morphological constraints and that there is a morphological trade-off between these structures and the pharyngeal jaw.

3.2.4 Eyes

Van der Meer et al. (2012) isolated the eyes by dissection and made tangential sections of 5μm. These sections were photographed, and angular density and size of the double cones and the size of the single cones were measured. An unexpected finding was the decrease in eye size found in *H. pyrrhocephalus* from the perturbed period (Witte et al. 2008; van der Meer et al. 2012; van Rijssel and Witte 2013). Van der Meer et al. (2012) found that the lens radius decreased by 17.1% ($P < 0.001$), while van Rijssel and Witte (2013) and Witte et al. (2008) found a decrease in eye length of 8.5%–13.9%, respectively (Table 2). Van Rijssel and Witte (2013) also found a decrease in eye depth of 7.8 % ($P < 0.001$). With regard to the increased turbidity, we expected an increase of eye size. However, a decrease in eye size does not necessarily imply a reduction in photopic sensitivity as the photon-catching ability depends on cone size (van der Meer and Anker 1984).

For specimens of *H. pyrrhocephalus* from the perturbed period, it was found that the already scarce blue light-sensitive single cones virtually disappeared, while the density of the double cones decreased (Fig. 5). The double cone size, on the other hand, remained the same, and thus the photopic sensitivity remained unchanged. The already large cone size of *H. pyrrhocephalus*, compared to other cichlid species (van der Meer and Bowmaker 1995), may serve as a "pre-adaptation" to the increased turbidity of the lake (van der Meer et al. 2012). The decrease in double cone density is in agreement with the diet shift towards larger prey. As the actual causes of the diet shift remain unknown (see Sect. 3.1.2), it is hard to determine what has caused the photopic changes. There are two possible scenarios for the joint occurrence of the photopic and diet changes. It might be that the diet change (which may be a result of increased prey abundance and competitive release) has allowed the photopic changes to occur. On the other hand, it might be that the smaller eyes and other retinal changes have forced the diet shift towards larger prey. The origin of these changes also depends on other morphological changes like the head volume and cheek depth, for instance, which are interrelated as is shown by Barel et al. (1989). Plasticity experiments with different prey sizes at varying light intensities might provide insight which scenario was followed by *H. pyrrhocephalus*.

3.3 Mechanism Behind Morphological Changes

We show that *H. pyrrhocephalus* was able to adjust ecologically as well as morphologically to the drastically changed environment. The ecological and morphological adaptive responses are both likely to have contributed to the resurgence of this species (Witte et al. 2008; van der Meer et al. 2012; van Rijssel and Witte 2013; van Rijssel et al. 2015, 2016, 2017; Kishe-Machumu et al. 2017). This hypothesis is supported by the fact that haplochromine species that are thought to be extinct or at best are extremely rare have shown to change their body shape in a different direction compared to the resurgent species (van Rijssel and Witte 2013). This may have made them more vulnerable to predation by Nile perch (van Rijssel and Witte 2013). In addition, gill surface of two of these species, *H. piceatus* and *H. heusinkveldi*, did not increase or even decreased at the time that oxygen levels began to drop in the Mwanza Gulf, while the resurgent species including *H. pyrrhocephalus* showed an increase of gill surface (van Rijssel et al. 2016; J.C. van Rijssel, unpublished data). *Haplochromis pyrrhocephalus* is not the only recovered species showing ecological and morphological changes. Many species have extended their habitat (Seehausen et al. 1997b; Kishe-Machumu et al. 2015); and the ten species from different trophic groups that we have investigated so far have a more diverse diet than in the old ecosystem (Katunzi et al. 2003; Kishe-Machumu et al. 2008, 2017; Van Oijen and Witte 1996; van Rijssel et al. 2015, 2017). Morphological changes in response to the altered environment of Lake Victoria, such as head size, cheek depth, eye size and retinal composition, gill surface, gill raker size and number, premaxilla shape and dentition have been found for other haplochromine species as well (van der Meer et al. 2012; van Rijssel and Witte 2013; van Rijssel et al. 2015, 2016). The occurrence of morphological changes in multiple species, often in the same direction, makes these changes more likely to be adaptive. Several not mutually exclusive mechanisms may account for the observed morphological changes: directional selection, phenotypic plasticity and hybridization.

Phenotypic plasticity has been observed in several parts of the body in cichlids (Stauffer and Gray 2004), e.g. in body shape (Abate et al. 2010, Crispo and Chapman 2010a), head volume (Rutjes et al. 2009), gills (Chapman et al. 2000; Rutjes et al. 2009), pharyngeal jaw apparatus (Hoogerhoud 1986; Huysseune et al. 1994; Huysseune 1995; Smits et al. 1996, 1997; Muschick et al. 2011), premaxilla (Witte 1984; Meyer 1987; Wimberger 1991; Bouton et al. 2002) and eyes (van der Meer 1993). There is high similarity in the above-mentioned plastic responses and the morphological responses found under natural conditions in this study. However, the changes observed under natural conditions seem to be bound more by morphological and ecological constraints and selection pressures than those experienced by fishes in the lab. For example, *H. pyrrhocephalus* raised under hypoxia in the lab show an increased gill surface and an increased head volume (Rutjes et al. 2009). In contrast, *H. pyrrhocephalus* that live under hypoxic conditions in the lake show an increased gill surface and a decreased head volume probably due to predation pressure favouring smaller heads (Chapman et al. 2008; Witte et al. 2008; van Rijssel and Witte 2013).

Directional selection can generate rapid evolutionary responses in these fishes as they mature and reproduce within 1 year. Especially when morphological traits are controlled by only a few genes, the response to selection on these traits can be fast (Albertson et al. 2003a). When directional selection on morphological characters occurs that fast, it can result in morphological adaptations that surpass morphological species boundaries fairly quickly. If these morphological characters are used for assortative mate choice, rapid ecological speciation is likely to occur from reproductive isolation (Schluter 2001; Rundle and Nosil 2005). When phenotypic plasticity is involved in the morphological changes, then these should be reversible and might have less impact on speciation compared to genetically based changes. However, phenotypic plasticity is thought to play an important role in adaptive radiation (Pfennig et al. 2010). Plasticity might facilitate adaptive radiation by fast evolutionary responses to changed selection pressures through genetic assimilation or accommodation (Pfennig et al. 2010; Schneider and Meyer 2017). In this case, phenotypic plasticity can, in combination with some form of selection, play an important role in the speciation of the Lake Victoria cichlids as well. It has been shown that some cichlid species are more plastic than others (Meyer 1987; Stauffer and Gray 2004; Crispo and Chapman 2010b). So it might be that species that show higher (selection on) plasticity adapt better to a changing environment compared to species that do not, which is likely to have a bearing on the adaptive radiation of the cichlids. This is one of the reasons why more future studies should focus on disentanglement of the mechanism behind adaptive responses under natural conditions, whether it is genetically based, due to phenotypic plasticity or a combination of both. Research focused on quantitative traits and epigenetics combined with advanced molecular techniques have a high probability in revealing the responsible mechanisms of cichlid microevolution (see below).

4 Implications for Distinguishing Lake Victoria Species and Assessing Species Richness

The observed morphological changes after environmental perturbation in some cases are so large that they surpass morphological species boundaries. In the premaxilla, we found that a diagnostic character for the genus *Yssichromis* (Greenwood 1980), a large edentulous part of the dentigerous arm, almost completely disappeared; the edentulous part changed from 25% in specimens of the pristine period to 11% in the specimens from the perturbed period. Based on these observations, the relative size of the edentulous part of the dentigerous arm is not a suitable diagnostic feature. The large morphological changes observed over 20 years might raise the question how species and genus boundaries can be defined in haplochromines. As yet there is no consensus among cichlid taxonomists with regard to the species definition (Turner

1999; Turner et al. 2001; Genner et al. 2004; Pauers 2010). For the haplochromine cichlids of Lake Victoria, the genotypic cluster species concept as defined by Mallet (1995) is favoured by Witte et al. (1997) and Seehausen (1998) and was also applied by the most recent description of Lake Victoria haplochromines (de Zeeuw et al. 2013). As has been shown, the Lake Victoria haplochromines are morphologically very plastic and the changes observed in the last decades exceed formerly defined species boundaries (Hoogerhoud 1986; Witte et al. 1997, this study). If we compare the size of the morphological gaps of the allochronic populations of *H. pyrrhocephalus* with those of sympatric zooplanktivorous species in the pristine lake, we can see that some of the former are larger, and we might conclude that a new species has evolved in two decades. However, it has to be taken into account that all differences in *H. pyrrhocephalus* are found in one character complex (Seehausen 1998). Differences in the other character complexes, male nuptial colouration, stripe pattern, scale morphology and squamation have not been found in *H. pyrrhocephalus*. Therefore we conclude that, despite the large morphological changes, we are still dealing with the same species, *H. pyrrhocephalus*.

Nuptial colouration is especially important for species identification as it often mediates premating reproductive isolation (Seehausen and van Alphen 1998; Seehausen and Schluter 2004), whereas ecomorphological features were supposed to be less likely to do so (Kornfield et al. 1982). However, studies from Lake Mweru revealed that, next to nuptial colouration, ecomorphological characters seem to be important for assortative mate choice (Stelkens and Seehausen 2009). In addition, work on Cameroon crater lake cichlids suggests that several dietary and morphological features can play a significant role in assortative mating as well (Martin 2013). Certain morphological characters appear to be very sensitive to a changing environment, and phenotypic plasticity is likely to play a role in the observed morphological changes (van Rijssel et al. 2016). Plasticity can lead to an underestimation of species richness. Sympatric species of the same trophic group may converge in morphology. Consequently they might be regarded as different colour morphs, which will result in an underestimation of species numbers. The number of species is needed to determine how speciose water systems are which allows for comparisons of species richness between African lakes and can aid in unravelling the factors responsible for the adaptive radiation of species (Turner et al. 2001; Wagner et al. 2012). In addition, determining the species richness will provide more information for sustainable exploitation and conservation of the lake's remaining ichthyofauna (Balirwa et al. 2003).

The number of cichlid species in Lake Victoria before the upsurge of the Nile perch has been debated (Turner et al. 2001; Genner et al. 2004), and different estimates have been made (Witte et al. 2007). The estimates of Lake Victoria cichlids ranged from 150–170+ in 1974 (Greenwood 1974) to 300+ in 1992 (Witte et al. 1992) to 500+ by Seehausen (1999) and Witte et al. (2007). Seehausen (1996) estimated that an additional 200 species might occur as only a relatively small part of the lake has been covered during species survey expeditions, which would make a total of 700+ species. Some studies suggested that the Lake Victoria species flock does not consist of species but of a group of organisms delineated by morphology

(Sage and Selander 1975; Klein et al. 2007; Samonte et al. 2007). These authors mainly based their conclusions on a presumed lack of genetic differentiation between cichlid species. Nonetheless, molecular studies have demonstrated that haplochromine species of Lake Victoria can be genetically distinguished (Seehausen et al. 2008; Magalhaes et al. 2009; Mzighani et al. 2010). With the use of single nucleotide polymorphisms (SNPs), Keller et al. (2013) even succeeded in finding genetic distinction between phenotypically defined sister species. This same technique has been applied to the detritivorous sympatric sister species (e.g. *H. cinctus*, *H. antleter*, *H.* 'paropius-like', *H. coprologus*), occurring on the research transect in the Mwanza Gulf. The results showed that there was a clear genetic differentiation between the eight sampled species that concurred with the predefined identification based on nuptial colouration and morphology (van Rijssel, Moser, Mwaiko, Seehausen in prep.). The improved molecular techniques and the sequenced cichlid genome provide promising opportunities to reveal the actual number of cichlid species in the pristine and present lake. However, past and current environmental changes in the lake have increased interspecific gene flow (Seehausen et al. 1997a, b, 2008; de Zeeuw et al. 2010) which further complicates the assessment of current species numbers in Lake Victoria, even with the latest molecular techniques. In fact, we recently found that the oral shelling molluscivore *Platytaeniodus degeni* currently shares a relatively large amount of alleles with the species that they are morphologically very close to: the detritivore *H. antleter*, which could be a result of either introgressive hybridization or incomplete lineage sorting (van Rijssel, Moser, Mwaiko, Seehausen in prep.). We hypothesize that, when the ecosystem of Lake Victoria stabilizes or improves in terms of factors influencing cichlid hybridization (e.g. reduced water transparency due to eutrophication), the extent of hybridization will decrease, assuming that gene flow between populations diminishes. Nuptial colouration could play an important role in this process as when hybrids display assortative mating preference for their own colouration, a new species might evolve as a result of reproductive isolation. So far, assortative mating preference in hybrid cichlids seems to be absent (Haesler and Seehausen 2005; van der Sluijs et al. 2008). However, a more recent study on behavioural isolation did show that female hybrids do show preference for hybrid males based on colour and morphology (Selz et al. 2014).

5 Future Directions

To distinguish species and to determine species numbers from the period before the Nile perch boom, we think taxonomists should apply a combination of ecological, morphological and genetic approaches. Unfortunately, nuptial colouration vanishes when fish are stored in formalin and ethanol. Another maybe even larger problem lies in the genetics, as good-quality DNA is hard to obtain from formalin-preserved specimens. As long as we lack genetic (and behavioural) data to distinguish species, the genotypic species concept as applied by Witte et al. (1997) and Seehausen (1998) remains in our view the best possible way to distinguish species. Nonetheless, recent work on formalin-preserved cichlid specimens revealed that it is sometimes possible to obtain microsatellites from several species including *H. pyrrhocephalus* (J. C. van. Rijssel, P. A. Bakker, R. Vis, H. A. Zittersteijn, unpublished data). Continued efforts in this field might uncover mechanisms behind the adaptive responses and also which role these responses played in the remarkable resurgence of the haplochromine cichlids (see below).

The current molecular techniques (e.g. the use of SNPs and whole genome sequencing) allow us to genetically distinguish very closely related haplochromine (sister) species (Keller et al. 2013; Wagner et al. 2013; Ford et al. 2015; Kavembe et al. 2015). In all of these studies, species that were identified by nuptial colouration and morphology were also separated genetically. This shows the strength of these techniques, and these will be key to determine/acknowledge how species rich African lakes and rivers actually are. A recent attempt to actually test whether morphologically identified species are also separated genetically was done on the "mbuna" cichlids of Lake Malawi by Pinho et al. (2019). They used dinucleotide microsatellites and different genetic clustering methods and found that, depending on the clustering method, the population genetic and taxonomic status of Lake Malawi mbuna is one in which morphologically identified species are well-demarcated genetic entities. This is concurrent with previous findings for morphologically identified Lake Victoria haplochromine species which could be genetically distinguished as well using SNPs. Interestingly, the genetic clustering methods used by Pinho et al. (2019) revealed some misidentifications based on morphology, an incident that we experienced as well during the genetic clustering of Lake Victoria detritivores (van Rijssel, Moser, Mwaiko, Seehausen in prep.). Although Pinho et al. (2019) found a relatively low misidentification rate of ~7.5% (based on one clustering method and only including groups with $N > 5$), the use of higher resolution genomic analyses (like SNPs) might have yielded an even better match between the morphologically identified fish and the genetic clusters. As the authors mention themselves, the misidentification rate could also be partly due to the fact that morphological identification was done based on photographs that mainly give information on nuptial colouration and body shape, while meristics like gill raker counts might have aided to distinguish species as seems to be the case for some Tanganyikan cichlids (van Steenberge et al. 2018). To determine how many African cichlid species there really are (or were in the case of Lake Victoria), we suggest that at first nuptial colouration and morphology (body shape and/or meristics, depending on the age of the lake/species flock; see van Steenberge et al. 2018) should be used. These "morphospecies" should then be confirmed by high-resolution genomic clustering analyses where the resolution will again depend on the age of the lake/species flock (younger species with larger amounts of shared alleles might need higher-resolution genomic analyses to be distinguished). Even today, exact cichlid species numbers (241) are being published for Lake Tanganyikan cichlids based on described species (208) and undescribed species (55) with classification based on personal observations and opinions for the latter (Ronco et al. 2019). Genomic clustering analyses would greatly improve the uncertainty of this species number as well as a taxonomic revision of many genera of Lake Tanganyika cichlids.

In the case of Lake Victoria where some 40% of the species are thought to be extinct (Witte et al. 1992), museum specimens preserved in formalin and afterwards transferred to 70% ethanol accompanied with colour slides and descriptions of some species are all that is left for these extinct species. To determine the exact haplochromine species number of Lake Victoria, it will take (besides an extensive sampling event across the whole lake) the extraction of relatively good-quality DNA from these formalin-preserved fish. Conventional restriction site-associated DNA sequencing (RAD-seq) requires high molecular weight (Bergey et al. 2013; Tin et al. 2014), thereby making it less appropriate for degraded DNA samples. An approach that might work entails creating custom-designed RNA probes based on known restriction enzyme-associated loci generated from modern populations. This method has resulted in a 60-fold enrichment of targeted loci leading to >20,000 SNPs in historic ragweed samples (Barreiro et al. 2017), potentially enough to apply population genomics on (Meier et al. 2017b).

This approach might also be essential in unravelling whether the observed morphological changes are evolutionary adaptations that are the result of genetic changes or merely a result of phenotypic plasticity and whether hybridization has facilitated the morphological changes. It would also need a QTL map of closely related Lake Victoria cichlids and whole genomes of many Lake Victoria cichlid species as these are essential for generating RNA probes. This will provide information on the link between genotypes and phenotypes and might allow one to quantify the relative contribution of selection to the resurgence of the Lake Victoria cichlids. If this approach would be combined with pairwise comparisons on selection regimes between extinct and closely related resurgent populations using fitness surfaces (based on growth and morphology as in van Rijssel et al. 2018 and Moser et al. 2018) on the complete trophic community, one could test for differences in evolutionary responses between the extinct and resurgent populations. Ultimately, this might answer to what extent variation in the rate of response to strong selection explains extinction and survival in Lake Victoria cichlids.

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Identifying and Conserving Tilapiine Cichlid Species in the Twenty-First Century

Wanja D. Nyingi, Jean-François Agnèse, Antonia G. P. Ford, Julia J. Day, Titus C. Ndiwa, George F. Turner, and Abebe Getahun

Abstract The use of species as the unit of organismal identification has implications for policies that support conservation and management. For most fish, including tilapiine cichlids, identification in the last century supported by alpha taxonomy produced keys and descriptions of diagnostic features and designation of correct species names. The rapid increase in species discoveries in the twenty-first century has resulted in large turnover of names and descriptions. However, these updates have had little impact on conservation of tilapiine cichlids, mostly because the wide distribution of cichlid species provides the false impression of resilience to habitat disturbance. There is a need to provide clarity on intraspecific variations, in order to conserve cichlid populations threatened by species introductions and habitat loss. Here, we review some powerful tools that assess differences in morphology, trophic

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W. D. Nyingi (✉)
National Museums of Kenya, Nairobi, Kenya
e-mail: dnyingi@museums.or.ke

J.-F. Agnèse
ISEM, CNRS, IRD, EPHE, Université de Montpellier, Montpellier, France, Montpellier, France
e-mail: jean-francois.agnese@ird.fr

A. G. P. Ford
Department of Life Sciences, Whitelands College, University of Roehampton, London, UK
e-mail: Antonia.Ford@roehampton.ac.uk

J. J. Day
Department of Genetics, Evolution and Environment, University College London, London, UK
e-mail: j.day@ucl.ac.uk

T. C. Ndiwa
University of Nairobi, Nairobi, Kenya
e-mail: tndiwa@uonbi.ac.ke

G. F. Turner
Bangor University, School of Natural Sciences, Bangor, Gwynedd, North Wales, UK
e-mail: george.turner@bangor.ac.uk

A. Getahun
Department of Zoological Sciences, Addis Ababa University, Addis Ababa, Ethiopia
e-mail: abebe.getahun@aau.edu.et

M. E. Abate, D. L. G. Noakes (eds.), *The Behavior, Ecology and Evolution of Cichlid Fishes*, Fish & Fisheries Series 40, https://doi.org/10.1007/978-94-024-2080-7_9

ecology, and genomics and enable definition of units of conservation of tilapiine cichlids. We discuss advances in geometric morphometrics in morphological characterization of tilapiine cichlids. Similarly, we show how sequencing technology has influenced the definition of units of conservation, namely evolutionary significant units, which take into account gene flow between populations, and recognize demography and migrations. We also highlight next generation sequencing technology that is revolutionizing biomonitoring using environmental DNA.

Keywords Admixture · Evolutionary significant unit · Intraspecific variation · Phylogenetics · Species delimitation · Taxonomy

1 Identifying Species

The identification of species is considered the first step towards any rational biodiversity conservation (Karl and Bowen 1999). Species are the most widely recognized level of biological unit by both science and policy, and the elevation of an organism to the rank of species or demotion to a lower rank is certain to affect conservation priorities (Karl and Bowen 1999; Turner 1999).

In spite of this, the definition of species and lower taxonomic ranks such as subspecies has remained highly contentious leading to a deadlock among some taxonomists on their validity (Turner 1999; Samadi and Barberousse 2006). The role of alpha taxonomy has been to provide a means of identification of taxa through keys and descriptions of diagnostic features, including the preservation of a museum-type specimen; provision of a “correct” name for an organism from a long list of synonyms; and to state phylogenetic and other relationships between different taxa (Whitehead 1990; Turner 1999).

However, molecular studies have revealed extensive variation at the population level highlighting the shortcoming of alpha taxonomy in recognizing intraspecific diversity, which in many cichlids is very high (e.g. Wagner and McCune 2009). As a consequence, some taxonomists have proposed the abolition of the subspecies level as a unit of classification (Minelli 1993; Meyer 1987; Nelson 1999). Conservation biologists have in the last two decades introduced concepts that take into account population level variations while reflecting important evolutionary lineages (Avise 1994). These include the evolutionary significant unit (ESU) proposed by Ryder (1986), which defines a group of populations that are morphologically and genetically differentiated, ecologically distinct, and possessing unique adaptations and distinct evolutionary history (Ryder 1986; Waples 1991).

Problematically, the units of conservation have subsequently been described with several different definitions and, in common with species concepts, depend somewhat on the context in which they are used (reviewed in Fraser and Bernatchez

2001). As the continuation of gene flow between distinct populations has been increasingly recognized, further developments of the management unit (MU) concept suggested that demography and migration must be considered in defining units for conservation, specifying the threshold of genetic divergence as the level at which populations are demographically distinct, rather than the complete absence of gene flow (e.g. Palsbøll et al. 2007). More recently, the advance of sequencing technology and increased use of genomics has allowed researchers to identify ever more structured intraspecific groups, but the translation of identified structuring into conservation recommendations and standardized guidelines for utilizing genomic data remains lacking, leading to calls for a more uniform approach in the interpretation of genetic data in an evolutionary framework (Coates et al. 2018).

In this chapter, we focus on tilapia cichlid species, which comprise the most economically important species in fisheries and aquaculture, but have typically received less research attention than the cichlid adaptive radiations in the East African Great Lakes from a phylogenetic and evolutionary perspective.

Tilapia is a common name used for a diverse freshwater group of fishes from the family Cichlidae. Tilapiine cichlids are known to inhabit various ecosystems ranging from lakes, wetlands, and watercourses to estuaries and sometimes even marine habitats. These fishes are indigenous to Africa and the Middle East and, until recently, were classified into three main genera based on various factors that included parental care behaviour, morphology, and meristic and biogeographic traits. Substrate spawning tilapias were grouped into the genus *Tilapia*; the bi-parental and paternal mouth brooders under *Sarotherodon*; and maternal mouth brooders in the genus *Oreochromis* (Trewavas 1983). More recently, Dunz and Schliewen (2013) split *Tilapia* into a number of genera, based on molecular phylogenetic data. Other minor tilapia genera include *Danakilia* and *Alcolapia*, dwarf species adapted to extreme environments, and the Middle Eastern genera *Tristramella* and *Iranocichla*.

1.1 Morphological Characterization

Earlier studies of phylogenetic relationships among tilapiine cichlids were mainly based on analysis of morphological characters. Despite the high morphological diversity of cichlids, there are only a few morphological characters used in assessment of their evolutionary relationships (Stiassny 1991). Despite this limitation, tilapiine cichlids have successfully been characterized using morphological features (Seegers et al. 1999). The first comprehensive morphological studies on Nile tilapia (*Oreochromis niloticus*) were carried out by Trewavas (1983), who used meristics and traditional morphometrics to group natural populations into seven subspecies (see Sect. 3.3). This work has served as the reference for the mouthbrooding tilapiine species for many years.

Morphometric studies entail quantitative studies of biological shape variation and covariations of shape with other biotic and/or abiotic factors (Webster and Sheets 2010). Three different approaches to morphometrics had been developed over time. The first approach was popularly known as traditional morphometrics. This method involved summarizing morphology in terms of length measurements, ratios, and/or angles. The second approach is landmark-based geometric morphometrics. This method is a development from the former, and it has the ability to summarize shape in terms of landmark configurations and is inherently multidimensional. It has proved successful in delimiting cryptic species where taxonomic species could not be discriminated by traditional phenotypic characters (e.g. Mutanen and Pretorius 2007; Francuski et al. 2009a, b; Gurgel-Gonçalves et al. 2010) and where genetic barcoding could not be used to diagnose species (Chevasco et al. 2014; Schwarzfeld and Sperling 2014). The third approach is outline-based geometric morphometrics, which has the ability to summarize the shape of outlines or surfaces lacking homologous landmarks, through the use of sliding or semi-landmarks (Webster and Sheets 2010). Currently, geometric morphometrics is used widely in morphological characterization of tilapiine cichlid fishes (see Box 1 for details of methods). For instance, morphological studies by Ndiwa et al. (2016) on five natural populations of Nile tilapia from the Kenyan Rift Valley revealed the existence of morphological differences between the populations supporting the Trewavas (1983) classification, and results obtained by genetic studies on the same populations were congruent, confirming the accuracy of the method. Morphological studies on natural populations of cichlids have also been carried out by Kerschbaumer and Sturmbauer (2011) in order to elucidate pathways of cichlid evolution. Advances in technology and computational power mean that 3D image analysis is increasingly accessible, but may be best used in analyses of specific structures, as 3D imagery has not shown any greater resolution than 2D images in discriminating populations or species of cichlids using whole body images but may incur substantially greater cost (McWhinnie and Parsons 2019).

1.2 Delimiting Sympatric Populations with Diet Analyses

Diet is one of the most commonly studied ecological variables and has been used to delimit populations based on resource use. Food web ecology has been recommended to guide conservation and ecosystem management (McDonald-Madden et al. 2016). Stable isotope analysis (SIA) is a useful tool for examining diet composition based on specific isotopic signatures acquired by consumers from different food sources (DeNiro and Epstein 1978, 1981). Methods are described in more detail in Box 2 (see below).

Stable isotope analysis has been used in cichlids to characterize feeding patterns, including the discrimination of sympatric species trophic niches or trophic differentiation between sites (reviewed in Ford 2015) and to investigate impact of land uses on aquatic food webs (Britton et al. 2019). The use of stable isotope analysis in combination with stomach contents analysis has previously been useful in investigating fine-scale niche partitioning (Ford et al. 2016). For example, stomach contents can give an indication of feeding on different resources that have the same isotope ratio. A further development in dietary analysis is likely to be the use of metabarcoding of stomach contents to investigate the taxonomic composition of resource use. Such DNA analysis overcomes some of the limitations of visual inspection of stomach contents (hard to identify partially digested food items to species level) and SIA (some resource items may overlap in isotope trace so not be possible to distinguish), but requires a good reference sequence database from which to identify sequenced material in the stomach. Although not yet conducted in tilapiine fishes to our knowledge, such approaches have recently been applied to other fish groups (e.g. Jakubavičiūtė et al. 2017; Riccioni et al. 2018).

Diet and trophic diversity have been used to delimit conservation units to propose conservation measures in other freshwater fishes, such as haplochromine cichlids in lakes of the Yala Swamp as an important refuge of biodiversity from Lake Victoria (Abila et al. 2008). In other groups diet and resource use differentiation have been used to recommend conservation management areas for sea birds (Ramírez et al. 2016) and to assess foraging distribution for conservation management of sea turtles (Pearson et al. 2017) and sharks (Gracan et al. 2017; French et al. 2018).

1.3 Advances in Molecular Approaches

The increasing availability and reduced cost of massively parallel next-generation sequencing (NGS) technologies has had a substantial impact on the study of tilapiine cichlids, through both the increasing amount of population-level sequence data available and extensive and high-quality genomic resources now available (Brawand et al. 2014; Conte et al. 2017). NGS technologies have wide applicability in evolutionary and ecological research, including complex trait mapping (Day-Williams and Zeggini 2010; Nandamuri et al. 2018); adaptation (Stapley et al. 2010; Malinsky et al. 2018); and ecological genetics and adaptive radiation (Davey et al. 2010, 2011; Faber-Hammond et al. 2019), and are increasingly being used in conservation settings to define priorities for management (e.g. Funk et al. 2012; Johnson and Koepfli 2014; Grueber 2015; Supple and Shapiro 2018; Coates et al. 2018).

Evolutionarily recent cichlid adaptive radiations have proven to be difficult to phylogenetically resolve, most commonly thought to be due to incomplete lineage sorting (e.g. Wagner et al. 2013). Genome-wide sequencing approaches using NGS is allowing previously unanswered questions to be addressed. For example, restriction site-associated DNA (RAD) markers sequencing achieved phylogenetic resolution at an unprecedented level for the cichlid adaptive radiation in Lake Victoria (Wagner et al. 2013), and whole-genome resequencing demonstrated multiple cichlid radiations in Lake Malawi (Malinsky et al. 2018). Applications of NGS in tilapia have previously been focused on the commercially important Nile tilapia (Palaiokostas et al. 2013, 2015; Hong Xia et al. 2015; Conte et al. 2017; Lind et al. 2019; Tibihika et al. 2019), but an increasing number of studies are focusing on other *Oreochromis* species important to fisheries and aquaculture (e.g. Syaifudin et al. 2019).

1.4 Integrated Analysis

Integrated analysis combining several of the methods discussed in this chapter has been fundamental to evolutionary ecology study (reviewed in Ford 2015), for example, in modelling ecological traits over time, ancestral reconstruction, study of convergence, and adaptive radiation. The importance of such integrated methods was foreseen by those developing geometric morphometric methods: "it is hoped that, in future, geometric morphometrics will be combined with genetic and ecological knowledge of organisms – a new synthesis in biology" (Corti 1993). Recent cichlid evolutionary and taxonomic studies have applied such interdisciplinary approaches combining geometric morphometrics, ecological (typically diet) and genomic data to address topics including phylogeny, adaptation, and niche differentiation (Ford et al. 2016; Malinsky et al. 2018; Meier et al. 2019; Meyer et al. 2019). From a conservation perspective, the availability of increasing genomic information means that programmes must consider whether and how to preserve genetic diversity (Mable 2019). Furthermore, in conservation management, different data types can help to categorize a population as an ESU, as factors including genetic divergence, behaviour, morphology, geography, environment, life history, and socioeconomic factors such as commercial or aesthetic value may contribute to conservation value and even populations with a relatively high level of gene flow between them may inhabit different environments and exhibit varied environmental adaptations that are worth conserving (Allendorf et al. 2012).

Box 1 Geometric Morphometric Methods[1]

Morphological study of fishes for a long time largely depended on the definition of identifiable characters. The definition of discrete characteristics (e.g. meristic counts of scales and fin rays) can help to identify characters defining morphological species, but does not provide information on overall body shape differentiation. In addition to meristic counts, the use of linear

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[1] Adapted from Ford et al. (2015) with permission of the author.

Box 1 (continued)

measurements between anatomical landmarks and application of multivariate statistical methods (often considered as "traditional morphometrics") analyses the covariation of shape with other variables (Rohlf and Slice 1990). For example, the linear measurements can be compared with size or environmental variables, but this does not allow examination of overall shape. The development of geometric morphometrics is considered a paradigm shift in the field (Adams et al. 2002) and expanded upon the traditional morphometrics approach to assess geometric morphological structure using outline data or landmark points. The availability of information on the spatial covariation of landmarks was described as "a revolution in morphometrics" (Rohlf and Marcus 1993) and developed concurrently with rigorous statistical theory of shape analysis (Bookstein 1984, 1991; Kendall 1984). Critical to downstream analysis, the correlation of landmarks means that a consensus shape for the sample can be constructed, which can subsequently be used to reconstruct common ancestors between groups and to visualize the shape differences between groups (Rohlf and Marcus 1993; Klingenberg 2013).

The standard protocol employed in geometric morphometric analysis (Fig. 1) includes the following steps (Rohlf and Marcus 1993): (1) landmark data are digitized from 2D or 3D images; (2) a fitted function is used to define the relationship among landmarks (typically thin plate spline; Bookstein 1989); and (3) estimates of the fitted function are then used in downstream multivariate statistical analyses. The thin-plate spline models landmarks as if placed on a metal sheet. The sheet is then deformed to achieve the observed movements of the landmarks relative to each other. The model can thus provide visualization of contour and outline shape changes, including visualization as a warped grid. The methods are combined with relative warp analysis (Bookstein 1989), to map landmarks onto a reference configuration, which is typically derived from the mean configuration of all sampled specimens. The consensus can then be used to calculate deviations to test directionality and statistical significance (Rohlf and Marcus 1993). To ensure only variations in shape are analysed, a Procrustes superimposition (Sneath 1967; Rohlf and Slice 1990; Dryden and Mardia 1998) is used to superimpose the multiple landmark configurations (sampled from multiple individuals) and remove variation in size, position, and orientation using a least squares methodology (reviewed in Klingenberg 2010, 2013). The Procrustes superimposition minimizes the absolute differences in size between landmark figurations, but does not account for the effect of allometry: the correlation between overall size of an organism and shape. Body shape often has a strong allometric component (e.g. Sidlauskas et al. 2011). In order to avoid ontogenetic effects, studies will typically focus on adult individuals (Klingenberg 2013). Conversely, studies investigating developmental shape variation will include

(continued)

Box 1 (continued)

the widest range in individual size from various ontogenetic stages to increase the likelihood of detecting allometric effect if present.

Allometric effects may be seen in cases where the groups being compared differ in size composition, especially across different species as allometry varies with ontogeny and phylogeny (Gould 1966). A correction for the effect of allometry can be performed using a regression of shape (i.e. Procrustes coordinates) on size. The size component may be a measurement of overall size such as body length, but is more typically the centroid size of the landmark configuration (Adams et al. 2002). The resulting residuals from the regression are then used in downstream analyses (Monteiro 1999; Klingenberg 2010). Finally, the effects of shared evolutionary history may also need to be considered. For inter-species studies, phylogenetic relationship needs to be considered alongside morphometric data (Klingenberg and Marugan-Lobon 2013) as closely related species would be expected to be more similar in body shape and cannot therefore be considered independently of ancestry. Similarities in shape due to ancestry need to be excluded before variables such as environmental conditions are considered (Felsenstein 1985). Phylogenetic correction may include the use of residuals results from phylogenetic generalized least squares models, phylogenetic independent contrasts, multivariate regression, or partial least squares (reviewed in Monteiro 2013). Recent approaches also allow simultaneous correction of size and phylogeny by estimating principal components of shape data accounting for phylogenetic non-independence (phylogenetic PCA) (Revell 2009, 2011; Monteiro 2013; Polly et al. 2013). However, an important distinction is that pPCA conducts PCA taking phylogeny into account, but does not produce phylogenetically corrected PC scores.

Several statistical techniques have been employed to explore the variation of morphometric data, including PCA, discriminant function analysis (DFA), and the multi-group equivalent canonical variate analysis (CVA). There has been much discussion regarding the relative merits of these analyses for morphometric data (Klingenberg and Monteiro 2005), with some authors suggesting that only absolute values (Procrustes coordinates, Principal components) should be used (Bookstein 1991), instead of measures of relative variation (DFA and CVA). However, both DFA and CVA are frequently used by researchers comparing groups (e.g. Rüber and Adams 2001; Klingenberg et al. 2003; Francuski et al. 2009a; Arnegard et al. 2010; Odhiambo et al. 2011). Principal component analysis is a single group procedure so may fail to find differences between groups as it does not take group structure into consideration (Strauss 2010). PCA maximizes variance scores of individuals along orthogonal axes for the whole dataset, while DFA and CVA facilitate discrimination of groups by maximizing between-group variance on each axis

(continued)

Box 1 (continued)

(minimizing within-group variation). These approaches may therefore be preferable when considering differences between groups but require a priori group assignation and can result in artificial discrimination of groups when sample sizes are small (Strauss 2010). Thus, both PCA and CVA (or DFA) may be used in tandem dependent on the questions being addressed (Harvati 2003; Maderbacher et al. 2008; Spreitzer et al. 2011; Wanek and Sturmbauer 2015; Su et al. 2015).

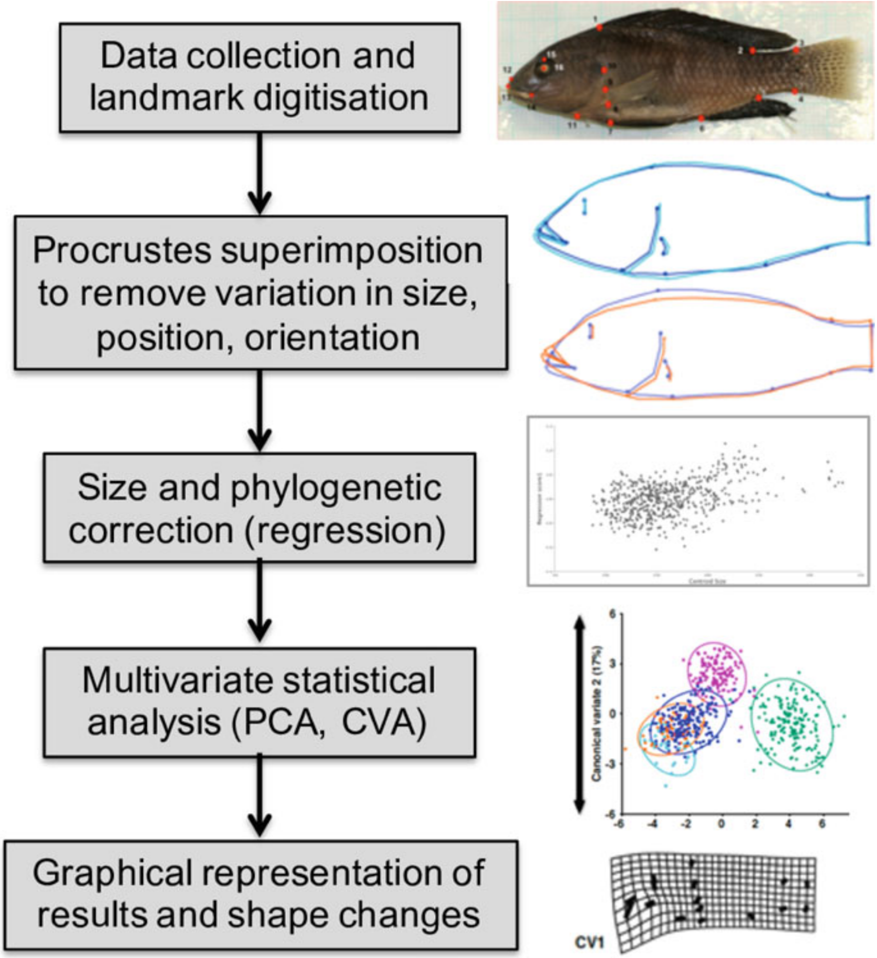

Fig. 1 Typical workflow for GMM analysis. See Box 1 for details. Figure originally published in Ford et al. (2015)

Box 2 Stable Isotope Analysis[2]

Isotopic ratios of several different elements have previously been used to investigate trophic partitioning and position within the food web. Isotopes of a specific element differ based on atomic mass (number of neutrons). Stable isotopes (nonradiogenic isotopes) do not decay, so the relative ratio of the different (heavy or light) isotope can be used to track resources through a food system (Newton 2010). Mass spectrometry is used to quantify ratios, with results standardized using an internationally recognized standard and presented using delta notation (McKinney et al. 1950) where:

$$\delta(\text{isotope}) = \text{Ratio}(\text{sample})/\text{Ratio}(\text{standard}) - 1$$

The δ value is given for the heavy isotope (Newton 2010) and given in per mille (‰) units. Carbon and nitrogen are the most commonly used stable isotopes for ecological purposes. Carbon and nitrogen both have two isotopes: C^{12} (common) and C^{13} (rare) and N^{14} (common) and N^{15} (rare) (Newton 2010). Other elements may be better suited in certain situations (e.g. Neill and Cornwell 1992), for example, sulphur exhibits a greater difference between producers in the marine environment (Connolly et al. 2004) and is capable of distinguishing between pelagic and benthic sources, while hydrogen performs well in discriminating aquatic from terrestrial (or emergent) vegetation (Middelburg 2014).

Stable isotope analysis provides complementary information to stomach contents analysis, as it represents dietary intake over a longer time period and reflect resources that have been assimilated rather than only those ingested (Vander Zanden et al. 1999; Marijnissen et al. 2008). The isotopic signature of the prey items becomes assimilated over the timescale of weeks to months in fish muscle tissue (Boecklen et al. 2011; Weidel et al. 2011), although this is likely to be dependent on body size (Vander Zanden et al. 2015). Stable isotope analysis of fish mucus is non-invasive and provides information over a shorter timescale (Church et al. 2008). The degree to which the isotopic ratios change between trophic levels is the fractionation value, D(isotope), and these changes between nitrogen and carbon isotopes are particularly useful for trophic food ecology. Nitrogen isotope ratios tend to have a large and constant fractionation value, with consumers typically exhibiting a ratio enriched by 2–4‰ relative to their food source (DeNiro and Epstein 1981; Vander Zanden et al. 1999; Post 2002; Vanderklift and Ponsard 2003; Caut et al. 2009), and so can be used to identify the trophic level of an organism. Determining the absolute trophic level position of a consumer is dependent on also analysing

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[2] Adapted from Ford et al. (2015) with permission of the author.

Box 2 (continued)

the nitrogen ratio of relevant food sources (particularly those at the base of the food chain). Carbon isotopic ratios show a much smaller fractionation value between trophic levels (DeNiro and Epstein 1978; Post 2002), and so consumer values are typically assumed to almost exactly mirror those of the sources consumed. Where a range of sources are consumed, the isotopic ratio of the consumer will reflect a mixed ratio relative to the proportions of each resource consumed (Middelburg 2014). Thus, primary consumers may exhibit intermediate carbon isotopic ratios between those of multiple resources reflecting a mixed diet, while omnivores feeding at multiple trophic levels will exhibit intermediate nitrogen levels, such that isotopic ratio values may be continuous rather than categorical based on the exact input sources to the system. The combination of these isotopic ratios is frequently visualized as a biplot, characterizing isotopic niche space (Fig. 2).

Carbon isotopic ratio values may not discriminate producers (if the values overlap at baseline), meaning that carbon values in other parts of the food chain may not be sufficient to confidently assign baseline food source. For example, terrestrial and pelagic carbon sources in aquatic systems often show extensive overlap in $\delta^{13}C$ (Pace et al. 2004), and $\delta^{13}C$ carbon values cannot reliably distinguish plants using C3, C4, or CAM photosynthetic pathways in those systems (Keeley and Sandquist 1992), because plant values are also dependent on location in the water column and water turbulence (France 1995). Baseline $\delta^{13}C$ has also been shown to vary with pH and levels of dissolved CO_2 (Smyntek et al. 2012). As a result of the variation in signatures of baseline sources, isotopic ratios are highly dependent on system inputs and vary over localized spatial scales. Hence, SIA values are not readily comparable between populations unless the baseline composition can be accounted for (Middelburg 2014).

2 Citizen Science and Mobile Technology

Further to the advances in tools outlined above, which are typically used by scientific research teams, the use of citizen science to collect data on species distribution and occurrence has grown rapidly (e.g. Kobori et al. 2016; Pocock et al. 2017). Accompanied by the growth in mobile app technology, with the deposition of GPS-tagged photographs, and online provision of species identification and field guides, has allowed the engagement of ever greater numbers of citizen scientists. The majority of citizen science applications and projects have typically focused on terrestrial species; however, technologies and projects for fish species are increasing, most targeted at fishing and angling communities (e.g. iAngler, iFish). Newer projects are now also starting to use citizen science for the collection of fish occurrence data for ecology and evolutionary research, including the FishMAP project in Southern Africa

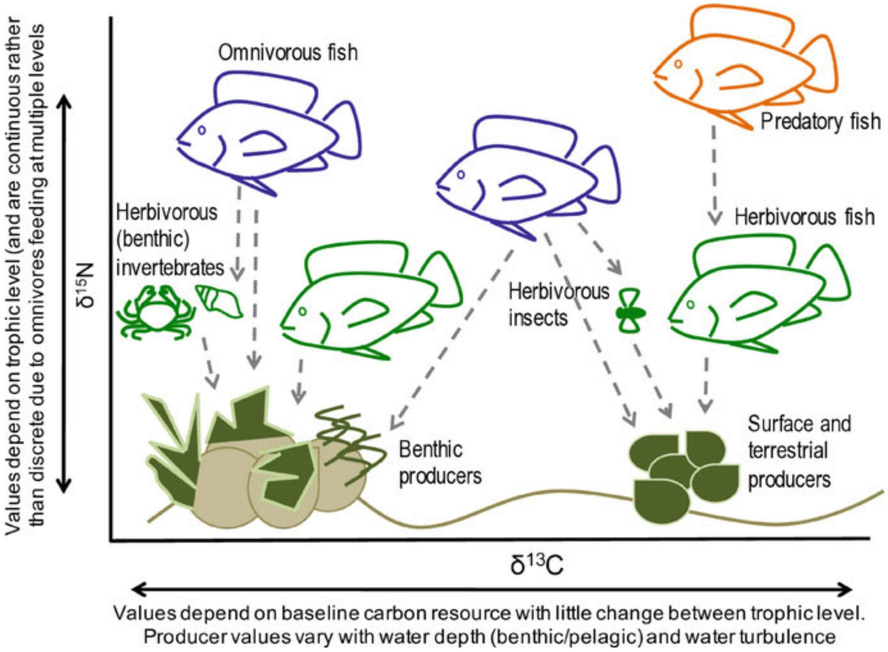

Fig. 2 Schematic stable isotope biplot of $\delta^{13}C$ and $\delta^{15}N$, demonstrating how the use of the two isotopes can distinguish consumers based on resource type and trophic level. Grey arrows indicate resource use. Colours of fish depict trophic level: green, herbivorous; blue, omnivorous; orange, predatory (secondary consumer). Figure originally published in Ford et al. (2015)

(https://www.fosaf.org.za/read-Current-138.php) and the TilapiaMap project focused on tilapia cichlid fishes in East Africa (http://tilapiamap.bangor.ac.uk/). Smartphone apps aimed at broader taxonomic groups, such as the iNaturalist and Seek apps (https://www.inaturalist.org/), are also increasingly adding data from aquatic groups although typically still have low representation of native tilapia species.

3 Defining Management Units for Tilapia

Freshwater fishes are thought to be the most threatened group of vertebrates (Reid et al. 2013; Closs et al. 2015), partly due to high levels of endemicity, narrow environmental adaptation, and habitat fragmentation. These pressures are likely to be exacerbated further by climate change, and anthropogenically driven land-use change, which have been shown to adversely affect lake cichlids (Britton et al. 2017, 2019). While cichlids exhibit extensive phenotypic plasticity, and some degree of temperature acclimation, no studies to date have reported plasticity to tolerance of water conditions, and most species are constrained to narrow levels of water temperature and salinity. In contrast to most cichlid species, tilapia exhibit the widest range of tolerances to water conditions, with several species able to tolerate high pH, salinity, or temperature (Ford et al. 2019). Most threats reported to have consequences on the conservation of natural populations of tilapia are anthropogenic activities such as agricultural irrigation, dams and associated infrastructure, overfishing, and other activities that destroy fish habitats. Because endemic populations of cichlids are often narrowly adapted to specific environments and frequently restricted to single water bodies, their diversity and genetic integrity is frequently threatened by human introductions. Such introductions often comprise tilapia species—being fast growing, tolerating a range of aquatic conditions, means many tilapia species have a high invasive potential (see Agostinho et al. 2021). Frequently, threats experienced do not operate independently, but act as multiple stressors synergistically increasing the threat that even significant plasticity cannot overcome.

3.1 Species Conservation Priorities, Threats, and Opportunities

Overfishing

The catch of tilapia continues to increase and has doubled since 2005 (FAO 2018), in contrast to other freshwater groups such as carp that have remained at steady catch levels. Overfishing has been well documented in the large African Great Lakes, and particularly in Lake Victoria (see Natugonza et al. 2021), where the evolutionary consequences of size-selected fisheries have resulted in smaller size at maturity of the introduced Nile tilapia (Ojuok et al. 2007). The recognition of overfishing in Lake Victoria has led to calls for increased cage culture of Nile tilapia to be employed in the lake in order to increase production (e.g. Aura et al. 2019). As many as 40% of tilapia species are thought to be threatened or at risk of extinction, with at least one species in Lake Malawi (*O. lidole*) thought to now be extinct in the wild due to overfishing (Hallerman and Hilsdorf 2014). Outside the East African Great Lakes, the response to overfishing and decline in tilapia stocks in many smaller lakes has been to stock natural water bodies with fish from fish farms, although there is no evidence that this enhances the recovery of fisheries. This introduction of farmed tilapia species into natural water bodies has resulted in severe threats to native tilapia species, including *O. jipe* (Bradbeer et al. 2019), *O. urolepis* (Shechonge et al. 2019), and *O. esculentus* (Hallerman and Hilsdorf 2014), which are already at low population levels due to fishing pressure.

Aquaculture and Translocations

Fish introductions outside their natural distribution ranges (mainly for aquaculture) have had substantial negative impacts on natural populations of tilapiine cichlids (Scribner et al. 2001; Canonico et al. 2005; Lind et al. 2012; Deines et al. 2016). It is estimated that the economically important Nile tilapia has been introduced in more than 120 countries (CABI 2019).

Introduced tilapias have become invasive especially in areas originally not containing any tilapiine cichlids both within and outside Africa (Bezault et al. 2011). Nile tilapia introduction into uninhabited environments can result in habitat degradation, eutrophication, and changes in water quality, as the fish preferentially feed on large algae and the increased nitrogen and phosphorous from fish waste promotes the growth of fast-growing mucilaginous algae (Figueredo and Giani 2005). Although these habitat effects may be less pronounced if the environment already hosts a tilapia species, ecological impacts can still be substantial if the introduced species occupies a different trophic niche, as has been seen in the Limpopo River in South Africa, where introduced *O. niloticus* have been differentiated from native *O. mossambicus* in phytoplankton/detritus axes (Zengeya et al. 2011). In Lake Victoria, introduction of Nile perch and Nile tilapia have been linked to disappearance of other native tilapiine species such as *O. esculentus* and *O. variabilis* (Ogutu-Ohwayo 1990; Kaufman 1992). Stomach content analysis of Lake Victoria *O. niloticus* suggests that it is largely omnivorous, eating insects, molluscs, detritus, as well as the algae that native species *O. esculentus* appears to be restricted to (Njiru et al. 2006).

Cases of hybridization have been reported as a result of introduction of non-native tilapia into areas inhabited by congeneric tilapias, which hybridize with native species (Eknath and Hulata 2009). For instance, several cases of anthropogenic hybridization have been documented including between *O. mossambicus* and *O. niloticus* (De Silva and Ranasinghe 1989), *O. mossambicus* and *O. aureus* (Hopkins et al. 1989), *O. niloticus* and *O. aureus* (Hulata 1995), *O. mortimeri* and *O. macrochir* (Gregg et al. 1998), *O. niloticus* and *O. leucostictus* with *O. urolepis* (Shechonge et al. 2018), and *O. niloticus* with *O. jipe* (Bradbeer et al. 2019). Several studies have reported cases of genetic hybridization between wild populations of Nile tilapia in Lake Baringo and Loboi Swamp with the closely related *O. leucostictus* (Nyingi et al. 2009; Ndiwa et al. 2014). It is suspected that introduction of *O. leucostictus* that led to genetic introgression in Lake Baringo intended to improve productivity in the lake which had drastically dropped. In Loboi swamp, introgression might have originated from brood stock introduced into ponds constructed within the swamp and its associated drainages.

The hybridization impact may be worse than the single introduction, due to the knock-on effects and perturbation of existing interactions. For example, in the Kafue system in Zambia, native species *O. macrochir* and *O. andersonii* do not appear to interbreed; however, in populations where *O. niloticus* has invaded, the native species interbreed with *O. niloticus* and each other, creating a hybrid swarm of mixed genetic material (Deines et al. 2014), suggesting that the presence of invasive species interrupts the existing reproductive isolation between native species.

In addition to the risks of competition and loss of genetic diversity, introductions of non-native fish from aquaculture stocks also risk the introduction of disease. At least ten sub-Saharan African countries are thought to have imported tilapia infected with tilapia lake virus (TiLV; Hounmanou et al. 2018), and the virus has been identified at subclinical (non-symptomatic) levels in Lake Victoria (Mugimba et al. 2018).

3.2 Advances in Identifying Tilapia in the Wild

The Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758), is found in almost the whole of tropical Africa from Senegal to Egypt (and Israel) up to Lake Tanganyika. It has been introduced in almost every tropical country of the world. Seven subspecies were described by Trewavas (1983): *O. n. niloticus* (Linnaeus, 1758) from the Nile and West Africa; *O. n. baringoensis* Trewavas 1983 which is endemic to Lake Baringo, Kenya; O. *n. sugutae* Trewavas 1983, endemic in Sugata River (Kenya) and its tributary the Kinyang or Kapedo; *O. n. eduardianus* (Boulenger, 1912) from Albert Nile; lakes Albert, Edward, George, and Kivu; River Ruzizi; and Lake Tanganyika; *O. n. vulcani* (Trewavas, 1933) in Lake Turkana and its affluent streams; *O. n. cancellatus* (Nichols, 1923) from the Ethiopian Rift Valley lakes and the River Awash; and *O. n. filoa* Trewavas 1983 from the Awash hot alkaline springs in Ethiopia.

However, despite numerous taxonomic investigations, the validity of a subspecific classification of the Nile tilapia remains in a relative state of uncertainty due to incongruence between genetic studies (Agnèse et al. 1997; Nyingi and Agnèse 2012) with the morphological diagnosis by Trewavas (1983). Agnèse et al. (1997) showed divergence between natural populations of West Africa, Nile, Ethiopia, and East Africa, clustering the species into three genetically distinct groups, the West African and Nile populations (including Lake Tana in Ethiopia), the East African populations (from Kenya, Uganda, and Tanzania), and finally the Ethiopian Rift Valley populations (lakes Awasa, Ziway, and Koka and the River Awash).

These genetic studies highlight a discrepancy between morphological and genetic differentiation. Traditional morphometrics (such as those applied by Trewavas 1983) are limited in their efficiency in expressing variations at the lower levels of taxa such as subspecies and population level, as they do not span all available points that describe shape and because measurements convey no information about their geometric structure (Zelditch et al. 2012).

Case Study 1: Evolutionary Significant Units

A study involving highly polymorphic and discriminative markers (mtDNA and microsatellites and geomorphometrics) on a wide range of natural populations of the Nile tilapia from Africa (687 specimens representing 22 populations for the genetic studies and 217 specimens from 16 populations for the morphometric study) provided insights into the current state of population differentiation (Nyingi and Agnèse 2012). Differences in morphology among these populations were based on shape variations in body depth, caudal peduncle depth, and the head length/depth and are consistent with environmental differences but were also found to be correlated with genetic differences.

Both genetic and geomemetrics reclassified the East African and Ethiopian populations into previously known subspecies: *O. n. vulcani* (Lake Turkana), *O. n. sugutae* (R. Sugutae), *O. n. eduardianus* (lakes Edward and Albert), *O. n. filoa* (Awash hot springs), and *O. n. cancellatus* (Ethiopian lakes and rivers except Lake Tana). However, the West African populations were found to be distinct from those of the Nile, with which they have been previously grouped into the subspecies *O. n. niloticus*, while the Nile basin was found to be closer associated with the East African populations. The population of the Lake Tana *Oreochromis niloticus cancellatus* was found by Nyingi et al. (2009) to be both morphologically and genetically differentiated from the other Nilotic populations, confirming an earlier study that had proposed a new subspecies for this population (Seyoum and Kornfield 1992a, b).

Nyingi and Agnèse (2012) used the evolutionary significant units (ESUs) concept, which they aligned to subspecies (Fig. 3) to propose conservation units. ESUs are populations that are genetically and morphologically differentiated at neutral markers, geographically isolated and that have a distinct evolutionary history. They proposed 11 ESUs as follows:

West Africa:

1. Senegal.
2. Niger.
3. Volta
4. Chad.

Nile Basin:

5. Cairo and Khartoum, lakes Albert and Edward (Uganda).
6. Lake Turkana (Kenya).
7. Lake Baringo (Kenya).
8. River Suguta (Kenya).
9. Loboi Swamp (Kenya).
10. Lake Tana (Ethiopia)

Awash Valley:

Combining *O. n. cancellatus* and *O. n. filoa.*

Case Study 2: A New and Unexpected Population in Kenya

A new and unexpected population from Loboi Swamp inhabiting warm water springs with high temperature (>36 °C) was discovered in the Lake Baringo basin of Kenya (Fig. 4), through a genetic study (Nyingi et al. 2009). This population undetected by previous expeditions and descriptions by Trewavas (1983) revealed unique molecular characteristics distinguishing it from other populations of the region (Lake Turkana, River Suguta and Lake Baringo). The new populations occur in Bogoria Hot Springs, Turtle Springs, and Chelaba Springs of the swamp and possess large number of unique microsatellite alleles and mtDNA haplotypes, indicating genetic isolation, perhaps associated with their adaptation to warm water (Fig. 5). The differences between the springs observed also indicated that the swamp provides a physical barrier leading to phenotypic plasticity (Nyingi et al. 2009; Ndiwa et al. 2014, 2016). These genetic studies further revealed hybridization of the Lake Baringo and Loboi Swamp fish with *O. leucostictus*, which was introduced in the basin for aquaculture purposes in the early 2000s (Nyingi and Agnèse 2007; Ndiwa et al. 2014).

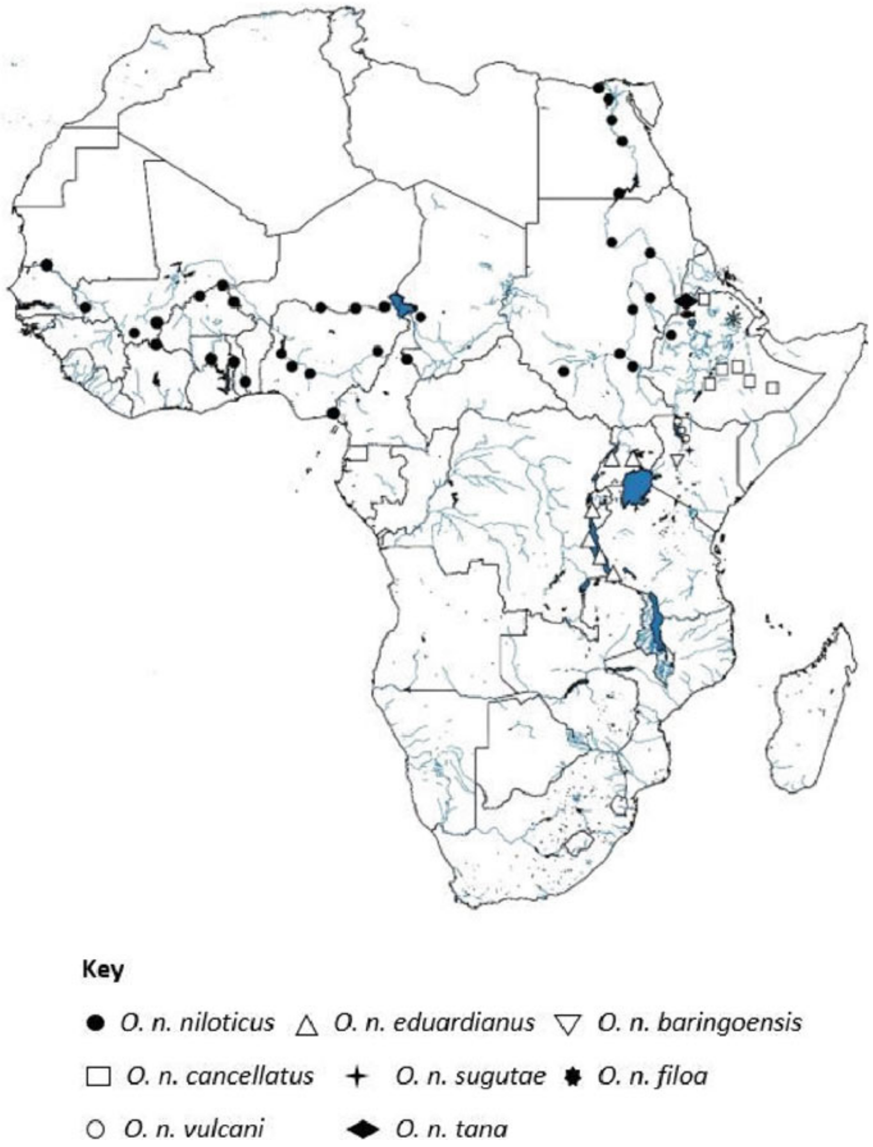

Fig. 3 Natural distribution of the subspecies of *Oreochromis niloticus* (Nyingi and Agnèse 2012)

3.3 New Methods in Biomonitoring: Environmental DNA

Measures of species diversity are central to the understanding of ecological communities and the effective monitoring of their responses to natural and anthropogenic stressors. However, the resources necessary to achieve this present a major limitation

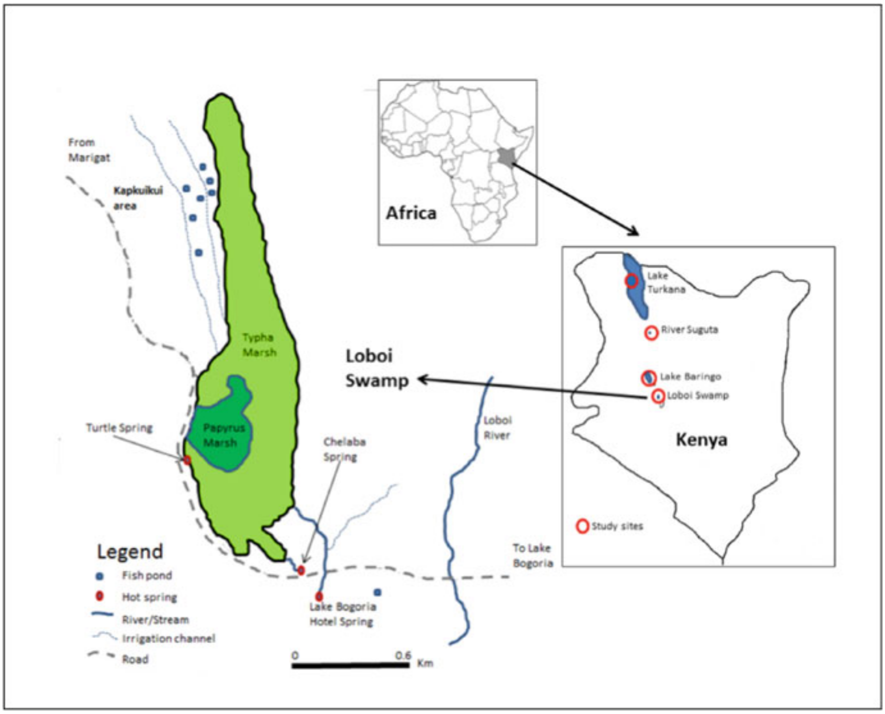

Fig. 4 Location of a recently discovered population of *Oreochromis niloticus*: map of Loboi Swamp showing the location of the three springs (Ndiwa et al. 2014)

for environmental management and research. This is particularly acute within aquatic habitats where traditional survey methods have significant associated biases as well as often being costly and destructive (Argillier et al. 2013).

Recently, environmental DNA (eDNA) approaches have emerged as a more sensitive method of surveying fish communities, as these techniques can be used to identify fish species within a habitat based on their DNA. Fishes, as with all higher organisms, continually emit DNA into the environment through decaying material, excreta, shed cells, and gametes, which leave a signature of their presence within a habitat (Thomsen et al. 2012). eDNA approaches can outperform traditional techniques in detecting the presence or absence of species, particularly those that are rare or elusive (Hanfling et al. 2016; Valentini et al. 2016) or invasive (e.g. Takahara et al. 2013). This new technology in biomonitoring has some major advantages as (1) it is less invasive compared to traditional methods, such as gill net surveys, (2) field sampling requires no taxonomic expertise, and (3) methods can be standardized allowing consistent and comparable monitoring results (Thomsen et al. 2016). In addition, it is potentially a more cost-effective method of surveying fish species and communities.

eDNA metabarcoding, using next-generation sequencing (NGS), has been effectively used for biomonitoring fish species in temperate waters, particularly lake

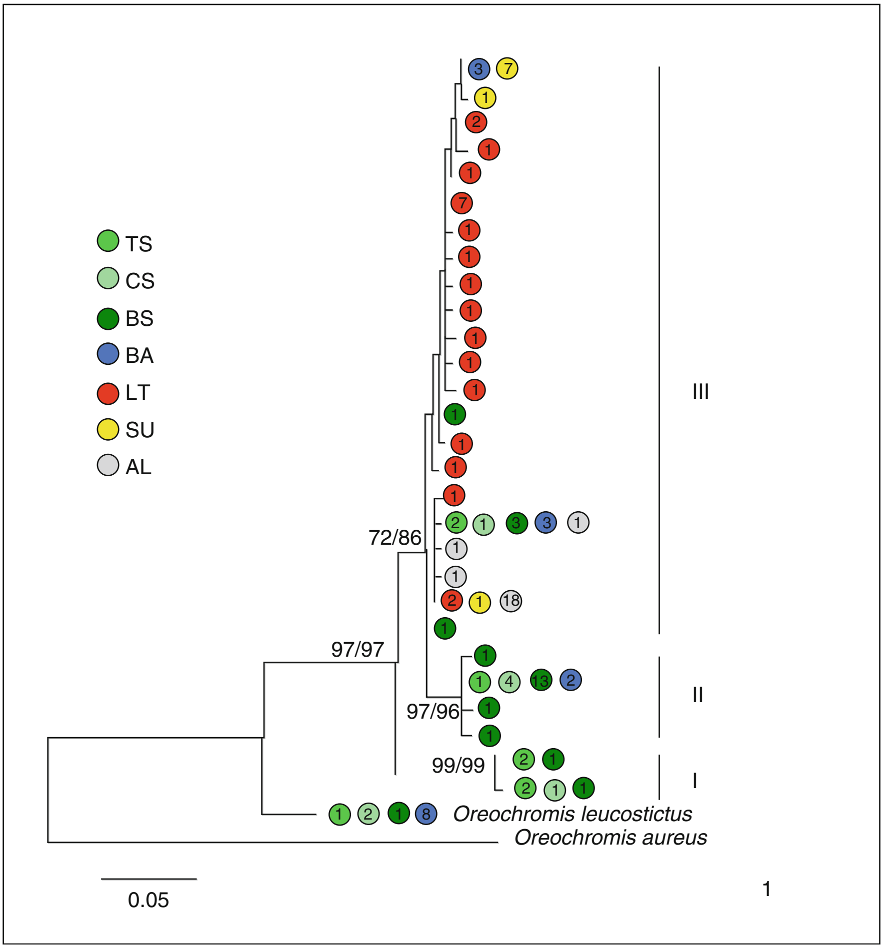

Fig. 5 The Loboi Swamp Springs contain a number of unique Nile tilapia mitochondrial haplotypes, but also haplotypes of the non-native *O. leucostictus*. Phylogenetic tree representing the genetic relationships between the 30 mtDNA haplotypes of East African populations of *Oreochromis niloticus* and *O. leucostictus*, rooted using *O. aureus*. *O. niloticus* haplotypes have been clustered in three groups (I, II, and III). Numbers above branches indicate bootstrap values (in percentage) based on 2000 replicates for ML and DM methods. The bar represents 0.05 units divergence, TS, Turtle Spring; CS, Chelaba Spring; BS, Lake Bogoria Hotel Spring; BA, Lake Baringo; LT, Lake Turkana; SU, Suguta River; and AL, Lake Albert. Values inside the circles represent number of individuals with this haplotype (Ndiwa et al. 2014)

environments (e.g. Hanfling et al. 2016). However, its application across natural environments is still in its infancy, and there has been a lack of research undertaken in the species-rich tropical ecosystems that contain much of the world's freshwater diversity (Thomsen and Willerslev 2014), in part due to logistical constraints and the limited barcode data available for tropical taxa. Despite this, the application of this new monitoring technology holds the potential to greatly enhance our ability to both monitor and understand the ecology of aquatic ecosystems, which extends to the cichlid system.

Recent research investigating fish communities from tropical waters has started to address this imbalance, demonstrating the potential of eDNA metabarcoding in surveying diverse and complex tropical ecosystems (Cilleros et al. 2019; Doble et al. 2020). The latter study by Doble et al. (2020) has been the first to our knowledge to focus on cichlid fishes, in which the authors investigated Lake Tanganyika fish communities, which include the mega-diverse cichlid adaptive radiations. This study revealed that eDNA metabarcoding using cichlid-specific primers could achieve comparable results to visual surveys, when sequencing depth and a detailed reference data base were accounted for. By demonstrating the contributions of this technology to surveying cichlid fish communities, we are confident that they will present a powerful approach for identifying rare and invasive tilapiine cichlids, not only in African waters, but where such fishes have been introduced globally, to better conserve and manage this important group.

4 Conclusions

As the last century drew to a close, the identification of cichlids saw a rapid turnover of species discoveries, aided by an equally rapid proliferation of scientific and technological innovation. In the twentieth century, species identification was largely supported by alpha taxonomy with the purpose of describing diagnostic features that support designation of species name and status. However, it became apparent that the rapid rate of species discoveries has had little or no effect on the conservation of species. In fact, species loss due to local extinctions caused by environmental degradation or invasive species over the years has further widened the margin between species identification and conservation. Alpha taxonomy, though responsible for most cichlid species names still in use, is limited by its inability to validate and describe diversity of lower taxa of biodiversity including subspecies and populations.

The advent of molecular studies, in the twenty-first century, has largely resolved the shortcomings of alpha taxonomy, revealing extensive intraspecific diversity in cichlids, and consequently justified, according to many, the need to abolish subspecies levels of classification. Species concepts that take into account variations among cichlid populations, while reflecting evolutionary lineages, are now more widely used, as units of conservation rather than a mere selection of names. An example of the evolutionary significant unit (ESU), which has been used to describe conservation units in the Nile tilapia (*Oreochromis niloticus*), has delineated what formerly represented seven subspecies in Africa, into 11 ESUs, that are morphologically and genetically differentiated. This study involved the use of highly polymorphic and discriminative DNA markers and geometric morphometrics, which enables observation of discrete variations in body shape of organisms.

The use of integrative methods or interdisciplinary approaches, that combine geometric morphometrics with genetics, and ecological knowledge has in recent years addressed diverse areas of speciation among cichlids. Another recent method is the use of stable isotope analysis (SIA) to understand trophic niches and make linkages between diet specialization and local environmental adaptation. Diet and trophic diversity studies have been used to describe conservation units of haplochromine cichlids of the Yala Swamps, which are important refugia for Lake Victoria cichlids.

The twenty-first century has also seen the advent of next-generation sequencing (NGS) technologies, which have revolutionized phylogenetic, phylogeographic, and population genetic studies by allowing multiple analyses from a single dataset. This method is not only cheaper (cheaper per base sequenced) than traditional single marker methods but also more rapid, allowing description of cichlid radiations, and resolving previously unanswered questions, bringing us closer to understanding the recent, complex adaptive radiations of Lake Victoria cichlids and the *Alcolapia* subgenus of *Oreochromis* in the Magadi/Natron soda lakes.

The advance of technology and innovation in the twenty-first century has led to faster, cheaper, and more accurate methods of species discovery, but has even more importantly created a bridge for science and policy by defining units of conservation where policy interventions and on-the-ground behaviour change actions can lead to overall societal gains. More and more, scientists are continuing to ensure participatory methods of research that ensure information sharing and feedback mechanisms that stimulate bottom-up conservation measures. The use of mobile technology for science has facilitated citizen science in recent times, with phone apps such as TilapiaMap enabling identification and mapping distribution of tilapia species in Africa.

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Introduced Cichlids in the Americas: Distribution Patterns, Invasion Ecology, and Impacts

Angelo A. Agostinho, Jean C. G. Ortega, Dayani Bailly, Weferson J. da Graça, Fernando M. Pelicice, and Horácio F. Júlio

Abstract The Cichlidae is one of the most diverse fish families in Neotropical and Afrotropical regions. It includes many species that are valued for aquaculture, the aquarium trade, and sport fishing, which has resulted in their introduction into different ecosystems worldwide. In the Americas, non-native cichlids have been recorded from southernmost Canada to northern Argentina, and North America has received the largest number of non-native cichlids followed by South and Central America. This group has a set of life history traits (e.g., parental care, multiple spawning, and piscivorous or omnivorous diets) that favors its occupation of new environments. This review provides information about non-native cichlids in the

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A. A. Agostinho (✉) · D. Bailly · H. F. Júlio
Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais da Universidade Estadual de Maringá, Maringá, Estado do Paraná, Brasil

Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura da Universidade Estadual de Maringá, Maringá, Brazil
e-mail: agostinhoaa@nupelia.uem.br; dayanibailly@gmail.com; juliojr@nupelia.uem.br

J. C. G. Ortega
Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais da Universidade Estadual de Maringá, Maringá, Estado do Paraná, Brasil
e-mail: ortegajean@gmail.com

W. J. da Graça
Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais da Universidade Estadual de Maringá, Maringá, Estado do Paraná, Brasil

Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura da Universidade Estadual de Maringá, Maringá, Brazil

Programa de Pós-Graduação em Biologia Comparada da Universidade Estadual de Maringá, Maringá, Brazil
e-mail: weferson@nupelia.uem.br

F. M. Pelicice
Programa de Pós-Graduação em Ecologia de Ecótonos da Universidade Federal do Tocantins, Palmas, Brazil
e-mail: fmpelicice@gmail.com

M. E. Abate, D. L. G. Noakes (eds.), *The Behavior, Ecology and Evolution of Cichlid Fishes*, Fish & Fisheries Series 40, https://doi.org/10.1007/978-94-024-2080-7_10

watersheds of the American continents including their distribution, predominant introduction vectors, reasons for success, and impacts on local ecosystems.

Keywords Non-native cichlids · Introduction vectors · Impacts of cichlid invasions · Trait-invasion relationships

1 Introduction

Biological invasion is the process by which species reach new regions or localities beyond their natural range, and although this process has occurred naturally throughout the history of the planet, recent invasion rates are much higher than in the past (Ricciardi 2007). Human activities have enhanced the transportation, release, and establishment of thousands of non-native animals and plants. That is troubling because biological invasions can severely disturb native biota in multiple ways, including predation, hybridization, parasitism, competition, and habitat loss, which affect community structure and important ecosystem functions (Arthington 1991; Canonico et al. 2005). Not surprisingly, coupled with habitat destruction, invasions are at the forefront of the current biodiversity crisis, particularly in aquatic ecosystems (Johnson et al. 2008).

At each introduction event, an invading species must pass through several obstacles to become established and to spread, including geography, captivity or cultivation, survival and reproduction, and dispersal (Blackburn et al. 2011). Human activities may aid species in overcoming constraints, particularly geographical barriers and captivity (Leprieur et al. 2008; Wilson et al. 2009). Many introduced species are not randomly chosen from the species pool but are selected for their economic value (Su et al. 2014), but once released, they must overcome other obstacles such as environmental limits related to survival, feeding, reproduction, and dispersal (Blackburn et al. 2011). In fact, after releasing, the traits of the species and the characteristics of the donor and invaded communities may determine whether establishment occurs (Marchetti et al. 2004a, b). In general, non-native species in an invaded community came from a more species-rich donor. Indeed, interactions between species, forged by the relationship between coevolution and niche, are an important component of biotic resistance (Fitzerald et al. 2016). However, human disturbance and propagule pressure may also play significant roles (Lockwood et al. 2005; Leprieur et al. 2008).

Fish species have been introduced on a global scale at an unprecedented rate with invasive species now occupying many drainages worldwide (Rahel 2007; Leprieur et al. 2008). In particular, the Cichlidae is a species-rich family found in the Neotropics, Asia, and the Afrotropics (Kullander 2003; McMahan et al. 2013), whose species have been extensively introduced or released into different river basins around the world. Cichlids show many characteristics that make them suitable for different human uses (e.g., ornamental fishkeeping, aquaculture, and fisheries), such as their diversity in morphology and color, physiological tolerances, ease with which they can be bred and fed, and market acceptance. Emblematic examples include the tilapias (Canonico et al. 2005; Shelton and Rothbard 2006) and species of peacock bass (Britton and Orsi 2012; Espínola et al. 2010), which have been introduced into several biomes and ecoregions beyond their natural range. Significantly, cichlids, especially tilapias, account for much of the global aquaculture yield (Casal 2006; Shelton and Rothbard 2006). However, such widespread use has neglected the risks and potential impacts of fish invasions (Vitule 2009; Vitule et al. 2009).

Here, we review the current understanding of non-native cichlids in the Americas. In particular, we analyze (1) the distribution of non-native cichlids across the American continent, (2) the predominant vectors responsible for their introductions, (3) the reasons behind the success of the Cichlidae in their spread and establishment in novel environments, and (4) the main impacts to invaded ecosystems.

2 Distribution of Non-native Cichlids in the Americas

In the Americas, several freshwater fishes have been continuously introduced into different drainages, and the Cichlidae is one of the major families (see Shafland et al. 2008; Ortega et al. 2015). To survey the non-native cichlid species that occur in the Americas, we compiled data from an extensive number of sources as we primarily searched (1) the Web of Science$^{\text{TM}}$ and the gray literature (addresses below), including data available from Fishbase (2) and Eschmeyer's Catalog of Fishes Online Database (3) supplemented by information from georeferenced fish species occurrence data from different natural history museums worldwide (sources (4) through (10)):

1. Web of Science: http://www.isiknowledge.com/
2. Fishbase: https://www.fishbase.de/
3. Eschmeyer's Catalog of Fishes Online Database: http://www.calacademy.org/scientists/projects/catalog-of-fishes
4. FishNet: http://www.fishnet2.net
5. Global Biodiversity Information Facility: http://www.gbif.org/
6. The Nonindigenous Aquatic Species website of the United States Geological Survey: http://nas.er.usgs.gov
7. The National Institute of Invasive Species Science: https://data.nal.usda.gov/dataset/national-institute-invasive-species-science-niiss-database
8. SpeciesLink: http://splink.cria.org.br
9. Lower Colorado Basin GIS Fish Data website: http://www.peter.unmack.net/gis/fish/Colorado
10. Fishes of Texas (Hendrickson and Cohen 2015): http://www.fishesoftexas.org/data

In our search, we also gathered information about the native range, the invaded countries, the types of occupied environments in non-native areas, the introduction vectors, and the impacts of the introductions.

We found that 62 non-native cichlid species occur in the Americas (Table 1). Among them, 22 species originate from Africa (as well as Eurasia for some species),

Table 1 Non-native cichlid species occurring in the Americas and information inherent to the introduction process

Species	Native range	Non-native range	Environment	Introducing vector	Impact	References
Amatitlania nigrofasciata	Central America: Pacific slope, from Sucio river, El Salvador to Suchiate River, Guatemala; Atlantic slope, from Patuca River, Honduras to Jutiapa River and Guatemala	North, Central and South America: Canada, United States, Mexico, Puerto Rico, Colombia, and Peru	C, R, S	Aquarium	Competition with natives (interference on growth and recruitment of native fish)	Ortega et al. (2007), Page and Burr (1991), Tippie et al. (1991)
Amphilophus citrinellus	Central America: Atlantic slope of Nicaragua and Costa Rica (San Juan river drainage, including lakes Nicaragua, Managua, Masaya, and Apoyo)	North and Central America: United States, Puerto Rico	C, Ri, R	Aquarium	Unknown	Courtenay and Stauffer (1990)
Amphilophus labiatus	Central America: Atlantic slope of Nicaragua, in Lakes Nicaragua and Managua	North and Central America: United States, Puerto Rico	R	Aquarium	Unknown	Devick (1991)
Amphilophus trimaculatus	North and Central America: Pacific slope rivers in El Salvador, Guatemala, and Mexico	North America: United States	L, RP	Aquarium	Unknown	Conkel (1993)
Andinoacara aff. *pulcher*	Central and South America: Trinidad and Tobago and adjacent Venezuela	North and South America: United States, Colombia, and Guyana	R	Aquarium	Unknown	U.S. Geological Survey (2019)

Astatotilapia calliptera	Africa: Lakes Malawi, Chiuta, and Chilwa; Lower Zambezi, Buzi, Pungwe, and Save River systems	North America: United States	Not-specified	Likely aquarium	Unknown	U.S. Geological Survey (2019)
Astronotus aff. *ocellatus*	South America: Amazon River basin in Peru, Colombia, and Brazil; French Guiana	North, Central, and South America: Canada, United States, Puerto Rico, and Brazil[a]	C, P, RP, R	Aquarium and fishery	Reduction of fish diversity	Galván-Guevara and De La Ossa (2011), Kline et al. (2014), Latini and Petrere (2004)
Astronotus crassipinnis	South America: Amazon River basin, in the Bolivian; Amazon and Madre de Dios river drainage in Peru; Paraná river basin, in the Paraguay drainage in Paraguay and Brazil	North and South America: United States and Brazil[a]	La, R	Aquarium Damming Stocking Fish farming	Unknown	Garcia et al. (2018)
Australoheros aff. *facetus*	South America: coastal drainages of Uruguay and Rio Grande do Sul, Brazil	South America: Chile	Not specified	Aquarium	Predation on native invertebrates	Aviles et al. (2018)
Caquetaia kraussii	South America: Atrato, Cauca, and Magdalena River basins and Lake Maracaibo basin in Colombia	North and South America: United States, Colombia, Venezuela	Not specified	Aquarium Fish farming	Unknown	Galván-Guevara and De La Ossa (2011)
Chindongo socolofi	Africa: endemic to Lake Malawi. Occurs on the Mozambique coast of the lake. Probably introduced in Otter Point and Thumbi West Island	North America: United States	Not specified	Fish farming	Unknown	U.S. Geological Survey (2019)

(continued)

Table 1 (continued)

Species	Native range	Non-native range	Environment	Introducing vector	Impact	References
Cichla kelberi	South America: Brazil in Araguaia-Tocantins basin	South America: Argentina, Brazil[a], and Paraguay	L, Ri, R	Game fish Stocking	Unknown	Kullander and Ferreira (2006), Ortega et al. (2015)
Cichla monoculus	South America: Amazon River basin and Oyapock river basin: Brazil, Colombia, French Guiana, and Peru	North and South America: United States, Brazil[a], Bolivia, Colombia[a], Ecuador, Venezuela	R	Game fish	Fish predation and spread of parasites	Chellappa et al. (2003a, b), Santos et al. (2001), Frankel et al. (2015)
Cichla ocellaris	South America: Marowijne drainage in Suriname and French Guiana to the Essequibo drainage in Guyana	North, Central, and South America: United States, Dominican Republic, Puerto Rico, Panama, Colombia, Bolivia, Brazil, Peru, and Venezuela	C, La, R	Game fish Stocking	Fish predation, reduction of fish diversity	Galván-Guevara and De La Ossa (2011), Godinho et al. (1994), Kline et al. (2014), Shafland (1999), Winemiller et al. (1997), Zaret (1980), Zaret and Paine (1973)
Cichla piquiti	South America: Brazil in Araguaia-Tocantins basin	South America: Brazil[a], Bolivia, and Paraguay	L, Ri, R	Game fish	Fish predation	Luiz et al. (2011), Resende et al. (2008), Sarmiento et al. (2014), Súarez et al. (2013)
Cichla temensis	South America: Amazon River basin in the Negro and Uatumã River drainages; Orinoco River basin in tributaries of the Orinoco River in Venezuela and Colombia	North and South America: United States, Brazil, and Guyana	C	Game fish	Unknown	Winemiller et al. (1997)

Cichlasoma aff. *bimaculatum*	South America: Orinoco River basin, in the Caroni in River Venezuela; Guianas, from the Essequibo River to the Sinnamary River; Amazon River basin, in the upper Branco River basin	North and South America: United States and Brazil[a]	L	Aquarium Fish farming	Eggs predation	U.S. Geological Survey (2019)
Coptodon rendalli	Africa: Kasai drainage (middle Congo River basin), throughout upper Congo River drainage, Lake Tanganyika, Lake Malawi, Zambesi, coastal areas from Zambesi Delta to Natal, Okavango, and Cunene	North, Central, and South America: United States, Mexico, Antiqua and Barbuda, Cuba, Dominican Republic, El Salvador, Puerto Rico, Argentina, Brazil, Colombia, Paraguay, and Peru	R	Fish farming Weed control	Increase of phytoplankton biomass and potential contribution to eutrophication	Mirande and Koerber (2015), Pelicice et al. (2014), Silva et al. (2014), Cassemiro et al. (2018)
Coptodon zillii	Africa and Eurasia: south Morocco, Sahara, Niger-Benue system, rivers Senegal, Sassandra, Bandama, Boubo, Mé, Comoé, Bia, Ogun and Oshun, Volta system, Chad-Shari system, middle Congo River basin in the Ubangi, Uele, Ituri, and Itimbiri (Democratic Republic of the Congo), lakes Albert and Turkana, Nile system, and the Jordan system	North, Central and South America: United States, Mexico, Antiqua and Barbuda, Puerto Rico, and Guyana	R	Fish farming Control of aquatic plants and mosquitoes	Habitat alteration by elimination of aquatic macrophytes	Crutchfield et al. (1992), Cassemiro et al. (2018)

(continued)

Table 1 (continued)

Species	Native range	Non-native range	Environment	Introducing vector	Impact	References
Cryptoheros spilurus	Central America: rivers flowing into Lake Isabel, Atlantic slope from Belize to Nicaragua. Belize, Guatemala, Honduras, and Nicaragua	North and Central America: United States, Mexico, Costa Rica, and Panamá	C, R	Aquarium	Unknown	Froese and Pauly (2019)
Geophagus aff. *brasiliensis*	South America: coastal drainages of Brazil and Uruguay	North America: United States	L	Aquarium Fish farming	Unknown	Courtenay and Stauffer (1990)
Geophagus aff. *proximus*	South America: Amazon River basin in Brazil and Peru	South America: Brazil[a]	R	Aquarium	Competition for food resources	Moretto et al. (2008)
Geophagus surinamensis	South America: Saramacca and Suriname Rivers in Suriname; Marowijne River in Suriname and French Guiana	North and South America: United States, Brazil[a], and Colombia	Not specified	Aquarium	Unknown	Kullander and Nijssen (1989)
Hemichromis bimaculatus	Africa: widely distributed in West Africa, where it is known from most hydrographic basins, associated with forested biotopes. Also reported from coastal basins of Cameroon, Democratic Republic of the Congo, and Nile basin	North, Central, and South America: Canada, United States, and Brazil	Not specified	Fish farming	Unknown	Froese and Pauly (2019)

Hemichromis elongatus	Africa: Cameroon to the Republic of Congo, and the entire Congo River, Okavango, and Zambesi system. Also reported from west Africa (Guinea, Sierra Leone, Liberia, Togo, Benin, Nigeria)	North America: United States	C, R	Aquarium	Unknown	Skelton (1993)
Hemichromis letourneuxi	Africa: northern and central Africa	North America: United States	Ri, S, C, Sw	Aquarium	Predation on fish, snails, and shrimps	Kline et al. (2014), Loiselle (1992), Porter-Whitaker et al. (2012)
Herichthys carpintis	North America: Atlantic Slope of Mexico	North America: United States	Not specified	Likely aquarium	Unknown	U.S. Geological Survey (2019)
Herichthys cyanoguttatus	North America: originally restricted to the lower Grande River drainage in Texas, the United States, and south to northeastern Mexico	North and Central America: United States, Mexico[a], and Puerto Rico	La, C, Ri, R	Aquarium	Competition for spawning space	Page and Burr (1991), Palacio-Núñez et al. (2010b)
Heros aff. *severus*	South America: Orinoco River basin and Amazon River basin in Brazil, Colombia, and Venezuela	North America: United States	Ri, L	Aquarium	Unknown	Galván-Guevara and De La Ossa (2011), Kullander (1986)
Heterotilapia buttikoferi	Africa: lower reaches of coastal rivers from Guinea-Bissau (Geba and Corubal rivers) to west Liberia (St. John River)	North America: United States and Brazil	C	Aquarium	Unknown	Santana et al. (2017), Sampaio et al. (2017)

(continued)

Table 1 (continued)

Species	Native range	Non-native range	Environment	Introducing vector	Impact	References
Hypsophrys nicaraguensis	Central America: Atlantic slope, from the San Juan drainage, including Lake Nicaragua, in Costa Rica and Nicaragua, to the Matina River drainage in Costa Rica	North America: United States	R, S	Unknown	Unknown	U.S. Geological Survey (2019)
Laetacara araguaiae	South America: Amazon basin	South America: Brazil	R, Ri	Aquarium	Unknown	Garcia et al. (2018)
Labeotropheus fuelleborni	Africa: Eastern Africa: Lake Malawi	North America: United States	Not-specified	Aquarium	Unknown	Courtenay and Stauffer (1990)
Mayaheros beani	North America: Pacific slope of Mexico	North America: United States and Mexico[a]	L, Ri, R	Aquarium	Unknown	Courtenay and Stauffer (1990)
Mayaheros urophthalmus	North and Central America: Atlantic drainages from Mexico to Nicaragua	North America: United States	Ri, Sw	Aquarium	Competition for spawning substrate, nest predation, and fish predation	Devick (1991), Kline et al. (2014), Loftus (1987), Porter-Whitaker et al. (2012), Trexler et al. (2000)
Maylandia zebra	Africa: Lake Malawi	North America: United States	R	Aquarium	Unknown	Froese and Pauly (2019)
Melanochromis auratus	Africa: Lake Malawi	North America: United States	La	Aquarium	Unknown	Courtenay and Stauffer (1990)
Mesoheros festae	South America: Pacific drainages from the Esmeraldas river in Ecuador to Tumbes river in Peru	South America: Colombia	Not specified	Unknown	Unknown	Galván-Guevara and De La Ossa (2011)

Neetroplus nematopus	Central America: Atlantic slope of Nicaragua and western Costa Rica	Central America: Costa Rica[a]	Ri	Unknown	Competition for territory	van Breukelen (2015), Cassemiro et al. (2018)
Oreochromis aureus	Africa and Eurasia: Jordan Valley, Lower Nile, Chad Basin, Benue, middle and upper Niger, Senegal River	North, Central, and South America: United States, Mexico, Antiqua and Barbuda, Bahamas Costa Rica, Cuba, Dominica, Dominican Republic, El Salvador, Haiti, Nicaragua, Panama, Puerto Rico, Brazil, and Peru	Ri, La, P, R	Fish farming Stocking Aquarium	Fish predation, competition for food, spawning grounds, and space	Córdova-Tapia et al. (2015), Kline et al. (2014), Lozano-Vilano and García-Ramirez (2014), McCrary et al. (2007), Scoppettone et al. (2005), Wohlfarth and Hulata (1983), Cassemiro et al. (2018)
Oreochromis macrochir	Africa: central and southern Africa	North America: United States	R	Fish farming; stocking	Competition	Devick (1972)
Oreochromis mossambicus	Africa: lower Zambezi, Lower Shiré and coastal plains from Zambezi delta to Algoa Bay. Occurs southward to the Brak River in the eastern Cape and in the Transvaal in the Limpopo system	North, Central, and South America: United States, Mexico, Antiqua and Barbuda, Bahamas, Barbados, Costa Rica, Cuba, Dominica, Dominican Republic, El Salvador, Granada, Guatemala, Haiti, Honduras, Jamaica, Nicaragua, Panama, Puerto Rico, Santa Lúcia and Trinidad and Tobago, Bolivia, Brazil, Colombia, Guyana, Peru, Suriname, and Venezuela	Ri, S, P, R, E	Fish farming Control of aquatic plants and mosquitoes	Competition for food, spawning grounds, and space, spread of parasites	Galván-Guevara and De La Ossa (2011), Kline et al. (2014), Kottelat and Whitten (1996), Lozano-Vilano and García-Ramirez (2014), McCrary et al. (2007), García-Vásquez et al. (2017), Cassemiro et al. (2018)

(continued)

Table 1 (continued)

Species	Native range	Non-native range	Environment	Introducing vector	Impact	References
Oreochromis niloticus	Africa: naturally occurring in coastal rivers of Israel Nile basin (including lake Albert, Edward, and Tana), Jebel Marra, Lake Kivu, Lake Tanganyika, Awash River, various Ethiopian lakes, Omo River system, Lake Turkana, Suguta River, and Lake Baringo. In West Africa natural distribution covers the basins of the Senegal, Gambia, Volta, Niger, Benue, and Chad, with introduced specimens reported from various coastal basins	North, Central and South America: Canada, United States, Mexico, Costa Rica, Cuba, Dominican Republic, El Salvador, Granada, Guatemala, Haiti, Honduras, Jamaica, Nicaragua, Panama, Puerto Rico, Santa Lucia, São Vicente and Granadinas, Suriname, Trinidad and Tobago, Argentina, Bolivia, Brazil, Colombia, Ecuador, Guiana, Mexico, Paraguay, Peru, and Uruguay	La, R	Fish farming	Competitive displacement, alteration of water quality, alteration of phytoplankton community structure, and spread of parasites	Figueredo and Giani (2005), Martin et al. (2010), García-Vásquez et al. (2017), Cassemiro et al. (2018)
Oreochromis urolepis	Africa: Rufigi River and its tributaries; the Kilombero and Great Ruaha Rivers, but not in the delta; the Kingani, Mbenkuru, and Wami Rivers, all in Tanzania	North and Central America: United States and Puerto Rico	Ri, C, L	Fisheries Fish farming Aquarium Control of aquatic plants and mosquitoes	Unknown	Page and Burr (1991), Cassemiro et al. (2018)

Parachromis motaguensis	Central America: Atlantic slope of Guatemala and Honduras in the Motagua River basin; Pacific slope, from the Naranjo River (Guatemala) to Choluteca River (Honduras)	North and Central America: Mexico, El Salvador, Belize, Panama, Nicaragua, and Costa Rica	L, Ri i	Game fish Fish farming Aquarium	Displacement of native species of commercial value	Amador-del Ángel et al. (2015), Amador-del Ángel and Wakida-Kusunoki (2014)
Parachromis dovii	Central America: Atlantic slope, from the Aguan River (Honduras) to the Moín River (Costa Rica); Pacific slope from the Yeguare River (Honduras) to the Bebedero River (Costa Rica)	Central America: Puerto Rico and El Salvador	R	Aquarium	Unknown	U.S. Geological Survey (2019)
Parachromis managuensis	Central America: Atlantic slope from the Ulua River (Honduras) to the Matina River (Costa Rica)	North, Central, and South America: Canada, United States, Mexico, Cuba, El Salvador, Guatemala, and Brazil	P, C, La, R	Fisheries Fish farming Aquarium	Unknown	Barros et al. (2012), Kline et al. (2014)
Pelmatolapia mariae	Africa: coastal lagoons and lower river courses from the Tabou River (Côte d'Ivoire) to the Kribi River (Cameroon)	North America: United States and Mexico	S, Sw, C, La, P	Aquarium	Competition for territory and food	Brooks and Jordan (2010), Courtenay and Deacon (1983), Kline et al. (2014), Cassemiro et al. (2018)
Pelvicachromis pulcher	Africa: west-central Africa: Niger River system	North America: United States	R	Aquarium	Unknown	Devick (1991)

(continued)

Table 1 (continued)

Species	Native range	Non-native range	Environment	Introducing vector	Impact	References
Petenia splendida	North and Central America: Atlantic slope of Grijalva river to Usumacinta River (Mexico), Usumacinta River (Guatemala), and Belize	North and Central America: United States, Mexico, and Costa Rica	P, C	Likely aquarium	Unknown	U.S. Geological Survey (2019)
Pseudotropheus johannii	Africa: Lake Malawi	North America: United States	R	Aquarium	Unknown	Courtenay and Stauffer (1990)
Pterophyllum scalare	South America: Amazon River basin, in Peru, Colombia, and Brazil, along the Ucayali, Solimões and Amazon rivers; rivers of Amapá, Rio Oyapock in French Guiana; Essequibo River in Guyana	North and South America: United States, Brazil[a]	La	Aquarium	Unknown	U.S. Geological Survey (2019)
Rocio octofasciata	North and Central America: Atlantic slope from southern Mexico (Papaloapán river) to Honduras (Ulua river)	North and Central America: United States and Costa Rica	La, Ri	Aquarium	Unknown	Page and Burr (1991)
Sarotherodon melanotheron	Africa: lagoons and estuaries from Mauritania to Cameroon	North and Central America: United States and Dominican Republic	R, L, Br	Aquarium Fish farming	Reduction of aquatic vegetation	Courtenay et al. (1974), Cassemiro et al. (2018)

Satanoperca pappaterra	South America: Amazon River basin, in the Guaporé River in Brazil and Bolivia; Paraná River basin, in the Paraguay River drainage in Brazil and northern Paraguay (to the Aquidabán River)	South America: Brazil[a]	R, L	Aquarium Fish farming	Unknown	Garcia et al. (2018)
Symphysodon aff. *aequifasciatus*	South America: eastern Amazon River, lower reaches of Amazon River and affluents east of the confluence of the Negro and Solimões rivers	South America: Guyana and Suriname	Not specified	Aquarium	Unknown	U.S. Geological Survey (2019)
Symphysodon aff. *discus*	South America: Amazon River basin in Brazil, near the mouth of the Negro River, in the lower Abacaxis River, and in the lower Trombetas River	North America: United States	Not specified	Likely fish farming	Unknown	U.S. Geological Survey (2019)
Telmatochromis bifrenatus	Africa: endemic to Lake Tanganyika	North America: United States	Not specified	Likely aquarium	Unknown	U.S. Geological Survey (2019)
Thorichthys meeki	North and Central America: Atlantic slope, in the Usumacinta River drainage, the Belize River drainage, and near Progreso, in Mexico, Guatemala, and Belize	North and Central America: United States, Mexico[a], and Puerto Rico	C, R	Aquarium Fish farming	Unknown	Courtenay and Stauffer (1990)

(continued)

Table 1 (continued)

Species	Native range	Non-native range	Environment	Introducing vector	Impact	References
Tilapia sparrmanii	Africa: Kasai drainage including the Lulua and Kwango (middle Congo River basin), upper Congo River basin including the upper Lualaba, Luvua, Lake Mweru, Luapula, Lufira, and Upemba region, upper Cuanza, Cunene, Okavango, Lake Ngami, Zambezi, Limpopo, Sabi, Lundi, northern tributaries of the Orange River, Lake Malawi, and Bangweulu	North and South America: United States and Brazil	Not specified	Likely fish farming	Unknown	U.S. Geological Survey (2019)
Trichromis salvini	North and Central America: Atlantic Slope of Belize, Guatemala, and Mexico	North and Central America: United States, Mexico[a], and Antiqua and Barbuda	C, RP	Aquarium	Unknown	Courtenay and Stauffer (1990)
Vieja melanurus	North and Central America: Atlantic Slope: Belize, Guatemala, and Mexico	North, Central, and North America: United States, Mexico[a], Puerto Rico, and Peru	R	Aquarium	Unknown	Conkel (1993)

[a] Countries encompassing the native range of the species, but with occurrence records also in non-native areas

Non-native range information was derived from literature data compilation, including the information provided by occurrence data from GBIF, FishNet, SpeciesLink, NAS-USGS, NISS, Lowe Colorado basin GIS fish data, and Fishes of Texas. Environment column corresponds to the habitats occupied by species in non-native region. In “Environment”: Br = brackish; C = channels; E = Estuaries; L = lagoons; La = lakes; P = ponds; R = reservoirs; Ri = Rivers; RP = Rock pits; S = streams; Sw = Swamps

20 from South America, 9 from Central America, and 3 from North America. Seven species are native to both North and Central America, and one is native to both Central and South America (Fig. 1; Table 1).

Non-native cichlids are found from southernmost Canada to northern Argentina. North America has received the largest number of non-native cichlids followed by South and Central America (Table 1). In our analysis, the United States was the dominant receptor country, with 51 out of 52 of the non-native species recorded in North America. Puerto Rico was the most invaded country in Central America (15 out of 23 species), and Brazil was the main receptor in South America (20 out of 31 species). Common cichlids introduced to American hydrographic basins are shown in Fig. 2.

In the Americas, non-native cichlids have successfully colonized different natural and artificial environments including rivers, lakes, lagoons, canals, estuaries, ponds, and reservoirs (Table 1), which illustrates the high physiological plasticity of the group. For example, cichlid species thrive in the harsh conditions of salt waters and thermal springs (see Scoppettone et al. 1998; Schofield et al. 2011; Lowe et al. 2012) or unstable environments such as reservoirs (see Agostinho et al. 2007; Moretto et al. 2008; Espínola et al. 2010; Ortega et al. 2015). Reservoirs, in particular, seem to be the main receptor environment of non-native cichlids in the Americas, harboring at least 33 species. African cichlids, especially tilapias, are pre-adapted to live in lentic environments, which they are typically able to successfully colonize (Cassemiro et al. 2018); a recent study revealed that Neotropical reservoirs had been invaded by 71 non-native fishes, with Cichlidae as the most rich-species family (Ortega et al. 2015). The authors found *Oreochromis niloticus* and *Coptodon rendalli* (=*Tilapia rendalli*) to be the most common species, being recorded in approximately 50% of the studied reservoirs. These results are consistent with the idea that reservoirs facilitate biological invasions (Johnson et al. 2008; Clavero and Hermoso 2011). Although these species have preference for lentic biotopes, they can be found in rivers, streams, canals, and estuaries, allowing them greater ability in dispersion process (Cassemiro et al. 2018).

The available information on the impacts of non-native cichlids on native communities and environments reveals that the damage primarily results from competition (for food, spawning areas, and space), predation, and the alteration of the characteristics of the recipient habitats. Many cichlid species are voracious predators (e.g., *Cichla* species) and competitors (e.g., *Amatitlania nigrofasciata*, *Mayaheros urophthalmus*, and *Oreochromis* spp.) that present varying degrees of threat to native fish fauna.

2.1 Distribution of Non-native Cichlids in the American River Basins

To assess the distribution of cichlid fish in continental waters, the georeferenced occurrence data of the species provided by FishNet, GBIF, NAS-USGS, NIIS, SpeciesLink, Lower Colorado, and Fishes of Texas were mapped onto the

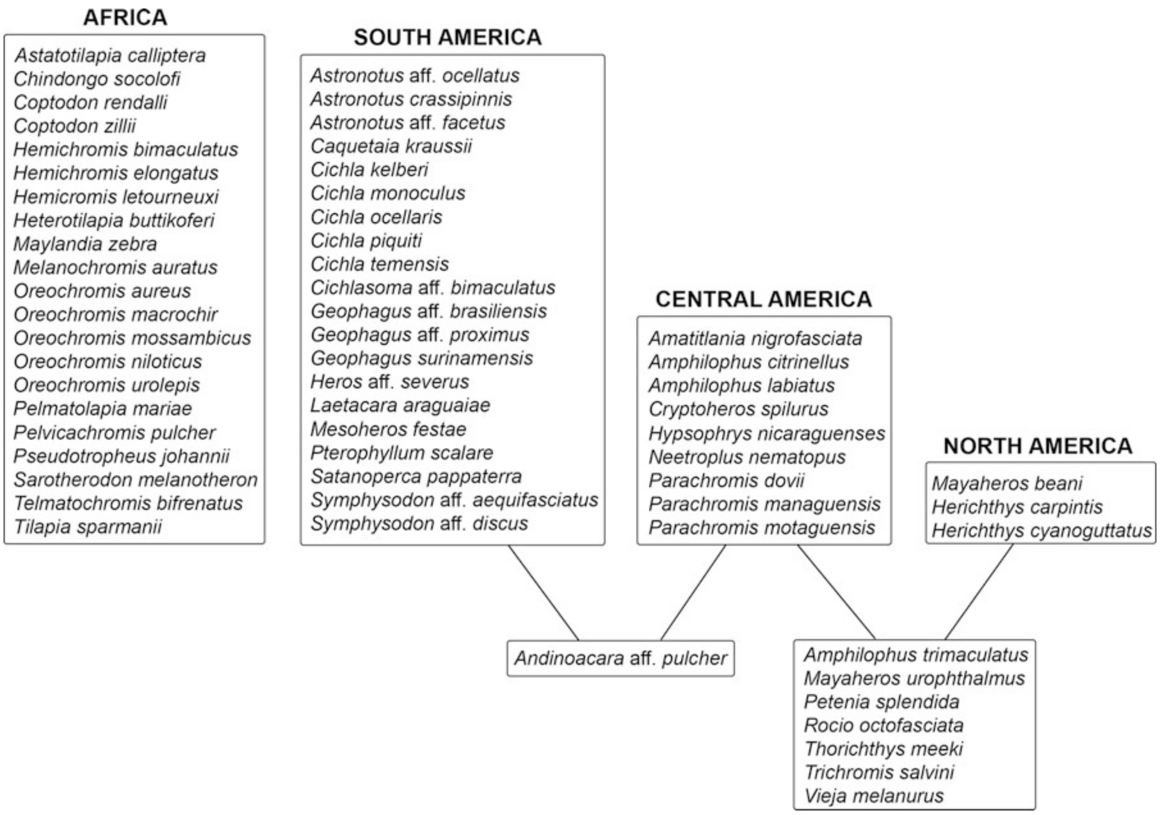

Fig. 1 Classification of non-native cichlid species in the Americas by their continent of origin (see details in Table 1)

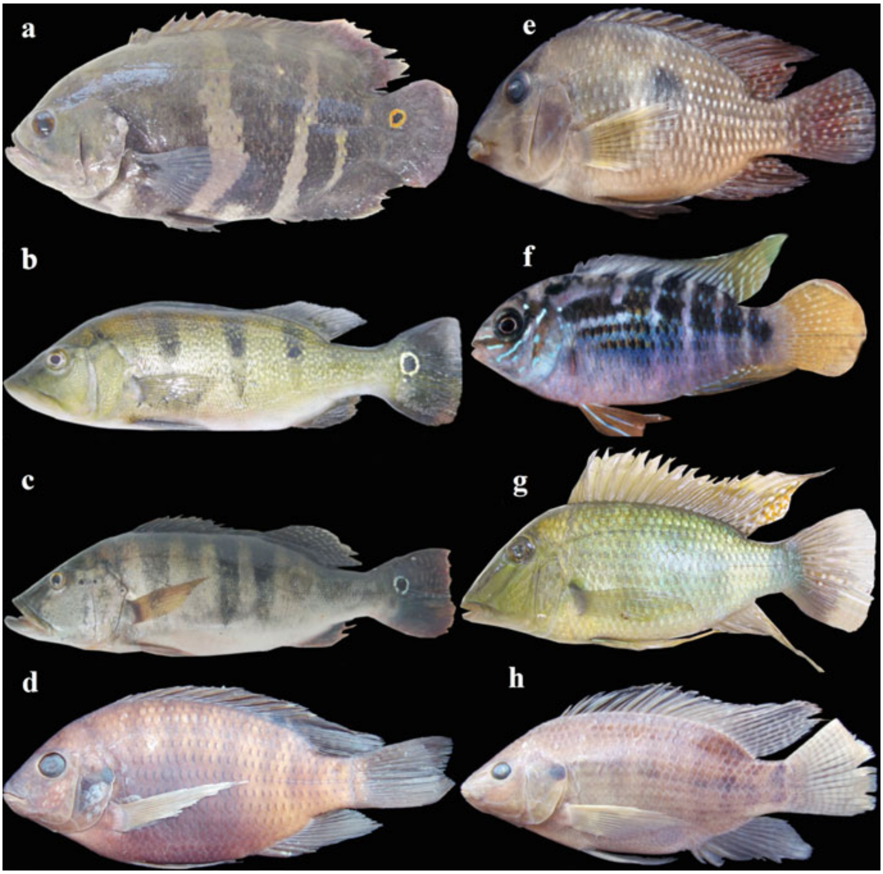

Fig. 2 Some common cichlids introduced into American river basins. (**a**) *Astronotus crassipinnis*, (**b**) *Cichla kelberi*, (**c**) *Cichla piquiti*, (**d**) *Coptodon rendalli*, (**e**) *Geophagus* aff. *brasiliensis*, (**f**) *Laetacara araguaiae*, (**g**) *Satanoperca pappaterra*, and (**h**) *Oreochromis niloticus*. Photo modified from Ota et al. (2018) used with the authorization of Dra. Carla S. Pavanelli (editor-in-chief of Neotropical Ichthyology)

geographical limits of the major American river basins (Fig. 3). For the American cichlid species, the occurrence records from the native range were removed. Thus, the mapping involved 52 cichlid species with occurrence records available in non-native areas (see Table 2). Note that this analysis only considers georeferenced occurrences (i.e., occurrences of non-native cichlid with recorded latitude and longitude) from the databases aforementioned; thus, it is expected that the data do not cover all the information on cichlid introduction existing in the literature. For instance, there were no georeferenced occurrences of non-native cichlids in Chile, while there have been introduction events reported there (see Iriarte et al. 2005). We also stress that our analysis is limited to indicate the species with occurrence already

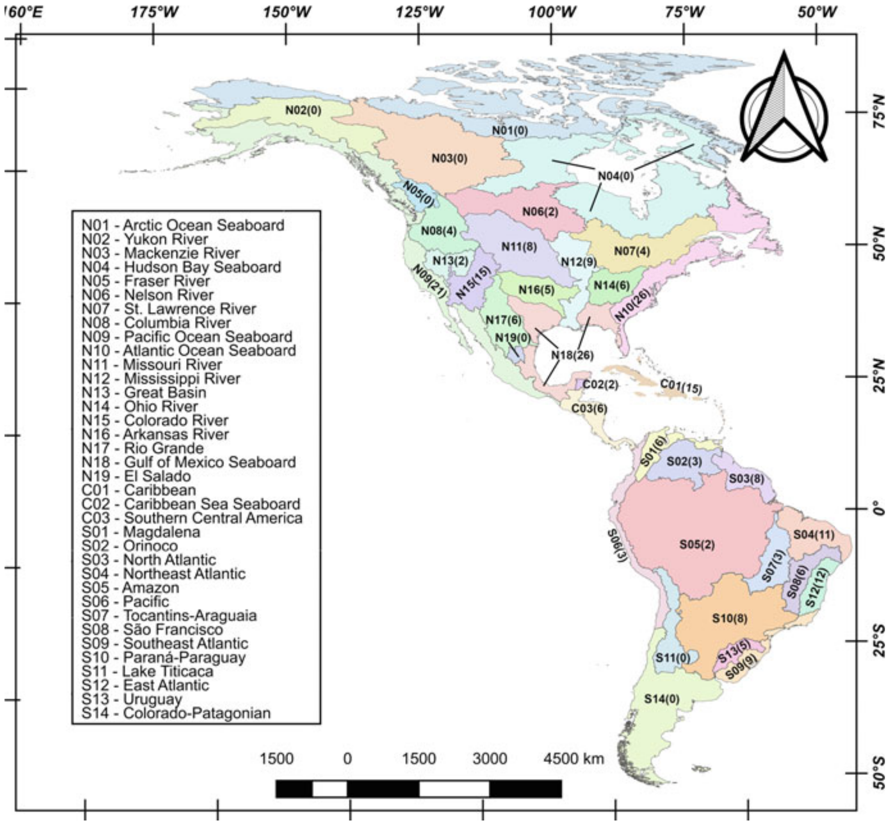

Fig. 3 Richness of non-native cichlid species in the 36 major hydrographic basins of Americas. Number in parentheses corresponds to the number of non-native cichlid species. "N" represents the basins of North America (N01 to N19); "C" represents the basins of Central America (C01 to C03), and "S" represents the basins of South America (S01 to S14). Colors represent the limits of each individual river basin

recorded in river basins, not reflecting the current status of invasion or introduction of the species.

In general, introduced cichlids have not been recorded in higher latitude river basins (N01-N05, S14, and S11), mainly occurring in coastal drainages of North America (Fig. 3). Atlantic Ocean Seaboard and Gulf of Mexico with 26 species and Pacific Ocean Seaboard with 21 species were the main basins receiving non-native cichlid fish in North American continent. The history of introductions in Florida has contributed to markedly high non-native cichlid richness of the two first river basins. Nearly 200 freshwater fish species have been introduced in the state, and at least 42 of them are currently established (Schofield and Loftus 2015), numbers that justify the recent designation of Florida as a hotspot of freshwater fish alien species (Dawson et al. 2017). The non-native ichthyofauna of Florida comprises 33 valid species of cichlid fish, of which 13 have been pointed out as permanently established

Table 2 List of non-native cichlid species recorded in the 36 major hydrographic basins of the Americas

Basins	Species
N01—Arctic Ocean Seaboard	–
N02—Yukon River	–
N03—Mackenzie River	–
N04—Hudson Bay Seaboard	–
N05—Fraser River	–
N06—Nelson River	*Amatitlania nigrofasciata*, *Hemichromis bimaculatus*
N07—St. Lawrence River	*Astronotus* aff. *ocellatus*, *Heterotilapia buttikoferi*, *Oreochromis niloticus*, *Parachromis managuensis*
N08—Columbia River	*Amatitlania nigrofasciata*, *Coptodon zillii*, *Oreochromis aureus*, *Oreochromis mossambicus*
N09—Pacific Ocean Seaboard (*including Hawaii)	*Amatitlania nigrofasciata*, *Astronotus* aff. *ocellatus*, *Cichla ocellaris*, *Coptodon rendalli*, *Coptodon zillii*, *Cryptoheros spilurus*, *Hypsophrys nicaraguensis*, *Mayaheros beani*, *Mayaheros urophthalmus*, *Oreochromis aureus*, *Oreochromis macrochir*, *Oreochromis mossambicus*, *Oreochromis niloticus*, *Oreochromis urolepis*, *Parachromis managuensis*, *Pelvicachromis pulcher*, *Petenia splendida*, *Pterophyllum scalare*, *Rocio octofasciata*, *Trichromis salvini*, *Vieja melanura*
N10—Atlantic Ocean Seaboard	*Amatitlania nigrofasciata*, *Amphilophus citrinellus*, *Astatotilapia calliptera*, *Astronotus* aff. *ocellatus*, *Cichla ocellaris*, *Cichlasoma* aff. *bimaculatum*, *Coptodon zillii*, *Geophagus surinamensis*, *Hemichromis bimaculatus*, *Hemichromis letourneuxi*, *Herichthys carpintis*, *Herichthys cyanoguttatus*, *Heros* aff. *severus*, *Heterotilapia buttikoferi*, *Mayaheros urophthalmus*, *Oreochromis aureus*, *Oreochromis mossambicus*, *Oreochromis niloticus*, *Parachromis managuensis*, *Pelmatolapia mariae*, *Pterophyllum scalare*, *Rocio octofasciata*, *Sarotherodon melanotheron*, *Telmatochromis bifrenatus*, *Thorichthys meeki*, *Trichromis salvini*
N11—Missouri River	*Amatitlania nigrofasciata*, *Astronotus* aff. *ocellatus*, *Herichthys cyanoguttatus*, *Heros* aff. *severus*, *Oreochromis aureus*, *Oreochromis mossambicus*, *Rocio octofasciata*, *Vieja melanurus*
N12—Mississippi River	*Amatitlania nigrofasciata*, *Amphilophus citrinellus*, *Astronotus* aff. *ocellatus*, *Coptodon zillii*, *Herichthys cyanoguttatus*, *Oreochromis aureus*, *Oreochromis mossambicus*, *Oreochromis niloticus*, *Parachromis managuensis*
N13—Great Basin	*Coptodon zillii*, *Parachromis managuensis*

(continued)

Table 2 (continued)

Basins	Species
N14—Ohio River	*Astronotus* aff. *ocellatus*, *Herichthys cyanoguttatus*, *Oreochromis aureus*, *Oreochromis mossambicus*, *Oreochromis niloticus*, *Pterophyllum scalare*
N15—Colorado River	*Amatitlania nigrofasciata*, *Astronotus* aff. *ocellatus*, *Cichla ocellaris*, *Coptodon zillii*, *Herichthys cyanoguttatus*, *Heros* aff. *severus*, *Maylandia zebra*, *Melanochromis auratus*, *Oreochromis aureus*, *Oreochromis mossambicus*, *Oreochromis niloticus*, *Oreochromis urolepis*, *Parachromis managuensis*, *Pelmatolapia mariae*, *Thorichthys meeki*
N16—Arkansas River	*Astronotus* aff. *ocellatus*, *Cichla ocellaris*, *Cichla temensis*, *Herichthys cyanoguttatus*, *Oreochromis aureus*
N17—Rio Grande	*Mayaheros beani*, *Oreochromis aureus*, *Oreochromis mossambicus*, *Pelmatolapia mariae*, *Pterophyllum scalare*, *Symphysodon* aff. *discus*
N18—Gulf of Mexico Seaboard	*Amatitlania nigrofasciata*, *Amphilophus citrinellus*, *Andinoacara* aff. *pulcher*, *Astronotus* aff. *ocellatus*, *Caquetaia kraussii*, *Cichla ocellaris*, *Cichla temensis*, *Cichlasoma* aff. *bimaculatum*, *Coptodon rendalli*, *Coptodon zillii*, *Cryptoheros spilurus*, *Hemichromis letourneuxi*, *Herichthys cyanoguttatus*, *Mayaheros urophthalmus*, *Melanochromis auratus*, *Oreochromis aureus*, *Oreochromis mossambicus*, *Oreochromis niloticus*, *Oreochromis urolepis*, *Parachromis managuensis*, *Pelmatolapia mariae*, *Petenia splendida*, *Rocio octofasciata*, *Sarotherodon melanotheron*, *Thorichthys meeki*, *Tilapia sparrmanii*
N19—El Salado	–
C01—Caribbean	*Amatitlania nigrofasciata*, *Amphilophus citrinellus*, *Amphilophus labiatus*, *Cichla ocellaris*, *Coptodon rendalli*, *Coptodon zillii*, *Oreochromis aureus*, *Oreochromis mossambicus*, *Oreochromis niloticus*, *Oreochromis urolepis*, *Parachromis dovii*, *Parachromis managuensis*, *Sarotherodon melanotheron*, *Thorichthys meeki*, *Vieja melanurus*
C02—Caribbean Sea Seaboard	*Cryptoheros spilurus*, *Oreochromis niloticus*
C03—Southern Central America	*Cryptoheros spilurus*, *Oreochromis mossambicus*, *Oreochromis niloticus*, *Parachromis managuensis*, *Petenia splendida*, *Rocio octofasciata*
S01—Magdalena	*Coptodon rendalli*, *Oreochromis niloticus*, *Oreochromis mossambicus*, *Cichla ocellaris*, *Andinoacara* aff. *pulcher*, *Amatitlania nigrofasciata*
S02—Orinoco	*Andinoacara* aff. *pulcher*, *Mesoheros festae*, *Oreochromis mossambicus*

S03—North Atlantic	*Astronotus* aff. *ocellatus*, *Cichla monoculus*, *Cichla temensis*, *Coptodon rendalli*, *Coptodon zillii*, *Geophagus surinamensis*, *Oreochromis mossambicus*, *Oreochromis niloticus*
S04—Northeast Atlantic	*Astronotus* aff. *ocellatus*, *Astronotus crassipinnis*, *Cichla kelberi*, *Cichla monoculus*, *Cichla ocellaris*, *Cichlasoma* aff. *bimaculatum*, *Coptodon rendalli*, *Geophagus* aff. *proximus*, *Geophagus surinamensis*, *Oreochromis niloticus*, *Pterophyllum scalare*
S05—Amazon	*Coptodon rendalli*, *Oreochromis niloticus*
S06—Pacific	*Geophagus surinamensis*, *Oreochromis mossambicus*, *Oreochromis niloticus*
S07—Tocantins-Araguaia	*Coptodon rendalli*, *Oreochromis niloticus*, *Tilapia sparrmanii*
S08—São Francisco	*Astronotus* aff. *ocellatus*, *Cichla kelberi*, *Cichla monoculus*, *Cichla piquiti*, *Coptodon rendalli*, *Oreochromis niloticus*
S09—Southeast Atlantic	*Astronotus crassipinnis*, *Cichla kelberi*, *Cichla ocellaris*, *Coptodon rendalli*, *Geophagus* aff. *proximus*, *Hemichromis bimaculatus*, *Oreochromis niloticus*, *Parachromis managuensis*, *Pterophyllum scalare*
S10—Paraná-Paraguay	*Cichla kelberi*, *Cichla monoculus*, *Cichla piquiti*, *Coptodon rendalli*, *Geophagus* aff. *proximus*, *Laetacara araguaiae*, *Oreochromis mossambicus*, *Oreochromis niloticus*
S11—Lake Titicaca	–
S12—East Atlantic	*Astronotus* aff. *ocellatus*, *Astronotus crassipinnis*, *Cichla kelberi*, *Cichla monoculus*, *Cichla ocellaris*, *Cichla piquiti*, *Cichla temensis*, *Coptodon rendalli*, *Geophagus* aff. *proximus*, *Geophagus surinamensis*, *Oreochromis niloticus*, *Parachromis managuensis*
S13—Uruguay	*Cichla kelberi*, *Cichla monoculus*, *Coptodon rendalli*, *Oreochromis niloticus*, *Satanoperca pappaterra*’
S14—Colorado-Patagonian	–

The categorization of species in the respective basins was based on 52 species with occurrence records available in non-native areas, considering the databases GBIF, FishNet, SpeciesLink, NAS-USGS, NISS, Lowe Colorado basin GIS fish data, and Fishes of Texas. “N” represents the basins of North America (N01 to N19), “C” represents the basins of Central America (C01 to C03), and “S” represents the basins of South America (S01 to S14) species (Schofield and Loftus 2015; US Geological Survey 2019). Vast anthropogenic modification, especially in south Florida, has provided hydrological alteration and interconnected networks of disturbed habitats that favors non-native fish species (Courtenay and Robins 1973; Loftus and Kushlan 1987). In addition, the Florida subtropical climate allows the success of species inhabiting similar climate from Africa, Asia, and Americas (Fuller et al. 1999; Schofield et al. 2010), including natural biotopes in national parks, natural reserves, and refuges (Kline et al. 2014).

In the western portion of North America, the impressive number of non-native cichlids in the Pacific Ocean Seaboard is mainly related to the elevated concentration of occurrence records in Hawaii and California. At least 72 fish species have been introduced into the Hawaiian Islands, of which 18 valid species belong to the family Cichlidae (Eldredge 2000; US Geological Survey 2019). In Hawaii tilapias were introduced for mosquito control, aquatic weed control, aquarium, and potential baitfish, imposing multiple detrimental risks to native species (Eldredge 2000; Englund 2002; Englund et al. 2000). In California, the rapid development history has resulted in highly disturbed aquatic environments statewide, as well as a scenario of frequent introductions (Marchetti et al. 2004b; Moyle and Marchetti 2006). Historically, more than 200 non-native fish species have been recorded in California, of which 10 are valid cichlid species (US Geological Survey 2019). Moyle and Marchetti (2006) have documented invasions by 110 fish species, with Cichlidae ranking among the families with higher number of established species.

In Central America, especially the Caribbean Islands have been the target of cichlid introductions (15 species) (Fig. 3). In the Caribbean region, invasive species have contributed to human-mediated species extinctions, and freshwater fish (with cichlids represented essentially by tilapiine species) is the group with the greatest number of introduced taxa (Kairo et al. 2003). Puerto Rico and the Dominican Republic constitute the most tilapia-rich nations of the Caribbean (Cassemiro et al. 2018). In the former, tilapias have been pointed out as abundant in reservoirs, estuaries, and coastal lagoons (Burger et al. 1992; Ferrer-Montaño et al. 2005, 2006; Neal et al. 2009). In the latter, the available literature reports the frequent use of tilapias in farming activities, not providing information about the abundance in natural environments (see Phillips et al. 1994; IDIAF 2003; El-Sayed 2006). In Aruba, Bonaire, and Curaçao, tilapia have colonized fresh, brackish, and salt waters (Hulsman et al. 2008).

The East Atlantic with 12 species and Northeast Atlantic with 11 species were the most cichlid-rich South American basins (Fig. 3). In both regions, cichlids have been introduced by direct stocking for food (tilapia - Chellappa et al. 1999, 2003a, b; Novaes et al. 2014), sport fishing (tucunaré, apaiari), or escape from aquaculture cage (tilapia), especially in reservoirs (Dias et al. 2005; Gomes et al. 2008; Cassemiro et al. 2018). Nowadays, *Cichla* and tilapias species are the main cichlids spread in rivers, weirs, and reservoirs (Silva and Araújo 1996; Gomes et al. 2008; Santos et al. 2016a, b; Sarmento-Soares and Martins-Pinheiro 2014; Franco et al. 2018; Mendonça et al. 2018), contributing around 40% of the reservoir fishery yield of the northeastern Brazil (Chellappa et al. 2003a).

In the Paraná-Paraguay river basin, eight cichlid fish (three species of the genus *Cichla*, three tilapiine species, one *Laetacara*, and one *Geophagus*) have been recorded (Fig. 3, Table 2). In the basin, *Cichla* species have thrived in rivers, lagoons, and bays of Pantanal (Matias et al. 2001; Resende et al. 2008; Ortega 2015), as well as in dammed environments of Upper Paraná river (Pelicice and Agostinho 2009; Espínola et al. 2010; Kovalenko et al. 2010a). Tilapia species as *O. niloticus* and *C. rendalli* have been traditionally found in the reservoirs of Paraná, São Paulo, and Minas Gerais (Petesse et al. 2007; Novaes and Carvalho 2012; Ortega et al. 2015; Daga et al. 2015, 2016). Nonetheless, escapes from fish farms have frequently released lots of individuals to tributaries of the Piquiri, Ivaí, and Paranapanema rivers in the Upper Paraná River basin (Orsi and Agostinho 1999; Fernandes et al. 2003; Forneck et al. 2016; Casimiro et al. 2018). The introduced Amazon cichlid, *Geophagus proximus*, has been found in different biotopes of the Upper Paraná river floodplain and also in reservoirs and rivers of the basin (Moretto et al. 2008; Zago et al. 2013; Gois et al. 2015). The list of non-native cichlid species per basin is presented in Table 2.

Among the non-native cichlids, eight species have been recorded in at least ten river basins of the Americas (Fig. 4, Table 2). *Oreochromis niloticus* followed by *Oreochromis mossambicus* were the most frequent introduced species, occurring in 21 and 16 river basins, respectively (Fig 4). In fact, such species are the most widespread tilapia species around the world (Canonico et al. 2005). Estimates have pointed out the introduction of *O. niloticus* and *O. mossambicus* in at least 85 and 90 countries with establishment in at least 49 and 72 of them, respectively (Casal 2006). In the Americas, their establishment has been reported in inland waters of several states of the United States (Peterson et al. 2004; Nico and Neilson 2019; Nico et al. 2019a). In Colombia, the government has declared *O. mossambicus* and *O. niloticus* as invasive species (Gutiérrez et al. 2010), with the latter completely established at the national scale (Gutiérrez-Bonilla and Alvarez-Leon 2011). Unlike what is observed for *O. niloticus*, in Brazilian river basins, the occurrence of *O. mossambicus* is still rare (Cassemiro et al. 2018). This species has not been explored by aquaculture activity in Brazil (Brabo et al. 2015), but if it becomes cultivated, individuals released from confinement to wild have potential to expand their range through several Brazilian basins, especially across Paraná-Paraguay river basin (Cassemiro et al. 2018).

Also, with impressive representation in the Americas, *Astronotus* aff. *ocellatus* and *Coptodon rendalli* have occurred in 13 basins, *Oreochromis aureus* and *Parachromis managuensis* have occurred in 11 basins, and *Amatitlania nigrofasciata* and *Cichla ocellaris* have occurred in 10 basins (Fig. 4). *Astronotus* aff. *ocellatus* have been more widely introduced in North American river basins (Table 2), with successful establishment in Hawaii and south Florida (Nico et al. 2019b). In the latter, the species compose a substantial proportion of the recreational fishery catch in the Everglades (Fury and Morello 1994). Conversely, South American basins have been the main target of the introductions of *Coptodon rendalli* (Table 2). In Brazil, the introduction of *C. rendalli* occurred with the principal purpose of increasing the fisheries in dammed systems (Agostinho et al. 2007),

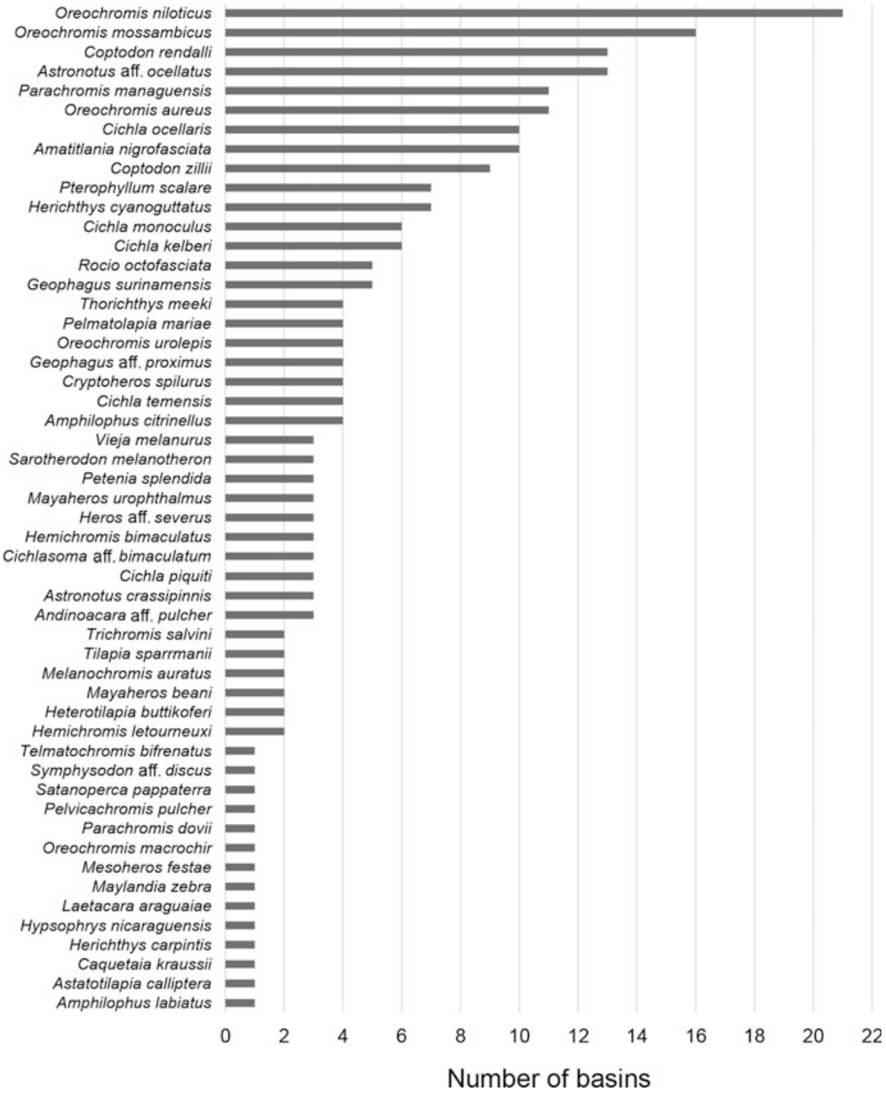

Fig. 4 Number of river basins occupied by each non-native cichlid species in the Americas

and it became a common species in reservoirs along the Paraná-Paraguay basin (Luiz et al. 2003; Baumgartner et al. 2006; Rocha et al. 2011; Ortega et al. 2015).

Oreochromis aureus individuals are essentially concentrated in North America basins and Caribbean Islands (Table 2). In Mexico the species has been found in reservoirs of the Balsas River, where it acts as an important fishery resource (Jiménez-Badillo and Nepita-Villanueva 2000); in the United States, estimates pointed out the species as established or possibly established in ten states, being considered the most widespread alien fish in Florida (Nico et al. 2019c). Already

Parachromis managuensis have been introduced in river basins of the three continents to meet the aquarium, aquaculture, and fishing demands. In the United States, the species have been historically found in different river basins from Florida, Utah, Hawaii, Nevada, and Louisiana (Minckley and Marsh 2009; Matlock 2014; Nico et al. 2019d). In Mexico, *P. managuensis* is widely distributed in the Grijalva River basin (Gómez-González et al. 2015) and in the Pedro River and Usumacinta basin (Castillo-Domínguez et al. 2011). In addition, the species was reported as established in the natural protected area of Pantanos de Centla, Tabasco region of Mexico (Mendoza et al. 2015). In Brazil the species has been introduced in the East Atlantic and São Francisco river basins (Barbosa and Soares 2009; Barros et al. 2012). Although our occurrence data have not pointed out its occurrence in the Northeast Atlantic basin, *P. managuensis* have been recently recorded in artificial ponds, rivers, stream, and reservoirs belonging to the Una, Ipojuca, Capibaribe, and Pajeú River basins of northeastern Brazil (Figueiredo et al. 2015; França et al. 2017).

Amatitlania nigrofasciata has spread predominantly through North America river basins (Table 2). The species received the status of invasive species in the Balsas River basin in the Center of Mexico due to its high abundance in the entire hydrological system (Mejía-Mojica et al. 2015). In our survey, we have registered the species in South America only in the Magdalena river basin, Colombia. However, a study has reported occurrence of the species also in the Pacific Ocean basin in the coast of Peru (Ortega et al. 2007). *Cichla ocellaris* has occurred in five North American basins, in Caribbean Islands, and in four South American basins. The species is established in south Florida, with fishable populations existing in more than 500 km of canals, in addition to numerous urban lakes in the metropolitan Miami (Shafland 1996, 1999). In the Caribbean, *C. ocellaris* has been found in reservoirs of the Puerto Rico (Bacheler et al. 2004; Bower et al. 2016), and in South America, the non-native range is mainly centered in Brazilian drainages in reservoirs (Gomiero and Braga 2004; Novaes et al. 2014; Costa et al. 2017) and in coastal shallow lakes (Menezes et al. 2012).

3 Cichlid Introduction Vectors in the Americas

Non-native cichlids have been introduced in the Americas by different vectors. The aquarium trade is the most important source of non-native species (43 species) followed by fish farming (20 species), fisheries, and stocking (Table 1). There were few or no records of bait releases, weed control, or habitat changes in the literature.

Cichlids are highly valued by the aquarium industry due to their diverse shapes, behaviors, and colors, and many are small in size (Maan and Sefc 2013; Montaña and Winemiller 2013), all of which are aspects appreciated by hobbyists. Some emblematic species that were introduced due to aquarium trade and have reported impacts (see below) are *Amatitlania nigrofasciata, Australoheros* aff. *facetus*, *Geophagus* aff. *proximus*, *Hemichromis letourneuxi*, *Herichthys cyanoguttatus*, *Mayaheros urophthalmus*, and *Pelmatolapia mariae* (Table 1). The release of aquarium fishes is an important and unmonitored invasion pathway that is responsible for one third of global aquatic introductions (Padilla and Williams 2004); this occurs because hobbyists intentionally dump unwanted organisms into the environment (Azevedo-Santos et al. 2015). In an assessment of the informal trade in social media in Brazil, Magalhaes et al. (2017) showed that one third of all species being advertised were cichlids. These authors highlight that the species being traded reach large sizes which can encourage aquarium dumping (Magalhaes et al. 2017). In the Unites States, which is among the main consumers of ornamental fishes (Padilla and Williams 2004), the aquarium trade is among the main causes of fish introductions (Fuller et al. 1999). Brazil is a major exporter (Ferraz et al. 2019) and thus the source of several species that have been introduced worldwide. There is evidence of the introduction of ornamental cichlids in several countries across the Americas, including Chile (Iriarte et al. 2005), Mexico (Miranda et al. 2012; Contreras-MacBeath et al. 2014; Mendoza et al. 2015), and Brazil (Magalhães and Jacobi 2013), and considering the high flow of non-native fishes through the ornamental trade, the propagule pressure is impressive. Magalhães and Jacobi (2013), for example, revealed that 96% of the species traded at pet stores in Minas Gerais State (Brazil) are non-native. Another study showed that three out of five non-native cichlids traded at pet stores in Mexico have high invasive potential, and they have been introduced to virtually all of the aquatic regions of that country (Mendoza et al. 2015). The lack of specific regulations and inspections facilitate the introduction and establishment of non-native fishes that originate from the aquarium trade (Vitule et al. 2014; Mendoza et al. 2015; Azevedo-Santos et al. 2015).

Cichlids are also widely used in aquaculture, particularly the tilapias of the genus *Oreochromis* and *Coptodon rendalli*, and a long history of domestication and breed selection has made these fishes suited for cultivation (Canonico et al. 2005; Casal 2006). In fact, they have particular attributes that facilitate cultivation (Pullin 1991) including (1) the quality of their meat (lack of fine intramuscular bones), (2) versatility and low cost of feeding (low trophic levels), (3) fast growth, (4) ease of reproduction, and (5) high tolerance to variation in environmental conditions. Not surprisingly, tilapias are among the ten most-cultivated species globally; in the Americas, much of the aquaculture production is from cichlids raised in ponds and cages (Shelton and Rothbard 2006). The wide use of cichlids in aquaculture has caused introductions into several ecosystems (Canonico et al. 2005), and clear examples can be found in the United States (Shelton and Rothbard 2006), Mexico (Schmitter-Soto and Caro 1997; Contreras-MacBeath et al. 2014; Ruiz-Campos et al. 2014; Amador-del Ángel and Wakida-Kusunoki 2014), and Brazil (Linde et al. 2008; Azevedo-Santos et al. 2011). Although tilapiine species account for most introductions, other cichlids have also been introduced accidentally or intentionally via aquaculture, such as *Herichthys cyanoguttatus* (Contreras-MacBeath et al. 2014), *Parachromis managuensis*, and *P. motaguensis* (Amador-del Ángel and Wakida-Kusunoki 2014).

Escapes from aquaculture facilities are difficult to avoid, and they occur for different reasons. For example, escapes are common when fish ponds are located close to water bodies subject to intense flooding (Orsi and Agostinho 1999; Cassemiro et al. 2018), and they may also occur during different stages of cultivation, such as sorting for size as well as capture and removal (Azevedo-Santos et al. 2011). In areas where aquaculture is developed, such as in Brazil, escape from fish farms typically becomes the primary source of introductions (Azevedo-Santos et al. 2011; Ortega et al. 2015), but authorities from different countries have also promoted the introduction of cichlids. In Mexico, *Oreochromis aureus*, *O. mossambicus*, *O. niloticus*, *Coptodon rendalli*, *Parachromis managuensis*, and *P. motaguensis* were introduced for aquaculture programs under governmental incentives (Amador-del Ángel and Wakida-Kusunoki 2014), and there were similar efforts in northeast Brazil, where cichlids such as *Astronotus* aff. *ocellatus*, *Cichla ocellaris*, and *O. niloticus* were widely stocked in artificial ponds and reservoirs from 1960 to 1976 (Attayde et al. 2011) to enhance the food supply for the population. In this case, governmental initiatives were responsible for the establishment success and spread of *O. niloticus* in several semi-arid river basins (Attayde et al. 2011). Governments may also facilitate introductions when appropriate regulations are lacking (e.g., Mexico; Contreras-Balderas et al. 2008), law enforcement is insufficient (e.g., in Brazil; Azevedo-Santos et al. 2015), or economic interests conflict with environmental laws (e.g., naturalization of introduced species by decree in Brazil; Pelicice et al. 2014).

Fish stocking to enhance fisheries is also an important cichlid introduction vector across the Americas as exemplified by Brazil, Mexico, and Nicaragua, where several cichlids were intentionally introduced to supply the human population with food resources (McKaye et al. 1995; Attayde et al. 2011; Miranda et al. 2012; Lozano-Vilano and García-Ramirez 2014). In Brazil, stocking programs using non-native fishes began in the Northeast in 1933 (Gurgel and Nepomuceno 1988), and the constant stocking effort resulted in self-sustaining populations of non-native species in many ponds and reservoirs, especially tilapias (Paiva et al. 1994). This strategy was then employed in other regions of the country and became the main fishery management action promoted by governmental agencies and hydropower companies during the second half of the twentieth century (Agostinho et al. 2010). However, unlike in the Northeast, most initiatives were unsuccessful or caused additional impacts on the native fish fauna and fisheries, which was a paradox because fish stocking was justified to mitigate the impacts of river regulation (Agostinho et al. 2004, 2007). In Mexico, different species of *Oreochromis* or hybrids have been introduced into lakes (Schmitter-Soto and Caro 1997), reservoirs (Ruiz-Campos et al. 2014), and even rivers inside protected areas (Miranda et al. 2012). *Oreochromis mossambicus*, *O. aureus*, and *O. niloticus*, in addition to *C. rendalli*, have been stocked in different regions to enhance fisheries (Contreras-MacBeath et al. 2014; Amador-del Ángel and Wakida-Kusunoki 2014). There are also reports of introduced cichlids in Mexico due to fish stocking in Guatemala (Contreras-Balderas et al. 2008); in this study, the authors emphasize the lack of a binational agreement aimed at regulating the stocking of these species in shared waters. In Nicaragua, authorities extensively stocked the tilapias *Oreochromis* spp. and encouraged cage aquaculture in Lake Nicaragua during the 1980s (McKaye et al. 1995).

Consequently, tilapias became established in the lake and caused major shifts in the aquatic communities and fisheries since native fish species have declined over the years (McKaye et al. 1995).

Clandestine stocking is also common across the Americas, particularly to enhance sport fisheries, and voracious predators, including *Astronotus* and *Cichla* species, have been introduced to different countries (Zaret and Paine 1973; Bacheler et al. 2004; Britton and Orsi 2012; Neal and Olivieri-Velázquez 2015). In Brazil, the introduction of peacock basses (*Cichla* spp., the tucunarés) is of great concern; several species were introduced to different non-Amazonian ecosystems (Chellappa et al. 2003a; Latini and Petrere 2004; Resende et al. 2008), and some are now widespread in artificial reservoirs (Espínola et al. 2010). This is especially troubling because *Cichla* has a strong potential to profoundly change communities and ecosystems (Zaret and Paine 1973; Latini and Petrere 2004; Pinto-Coelho et al. 2008; Pelicice and Agostinho 2009; Menezes et al. 2012). After a piscivore is established in a new environment (e.g., tucunarés), fishing could control its population size, promoting the persistence and richness of the native species (Santos et al. 2019). This is recognized in some regions of South America, where capture, consumption, and commercialization of introduced species is allowed throughout the year, including areas and during periods when native species fishing is prohibited. On the other hand, the sport fishing lobby and misinformation have persuaded lawmakers to pass laws prohibiting capture, transport, and consumption of non-native sport fishes, including voracious fishes like peacock bass (Pelicice and Agostinho 2009; Ota et al. 2019).

There are few examples of cichlid introduction for biological control. However, tilapias (particularly *Coptodon zillii* and *Oreochromis mossambicus*) were introduced to the United States for weed and mosquito control, but their efficacy has been poor (Eldredge 2000; Shelton and Rothbard 2006). A potential reason that these species were not efficient in weed control is that in the presence of alternative preys (planktonic species and benthonic invertebrates), these fish species may not select for weed species (Spataru 1978).

4 Reasons for Success

Cichlids stand out for their establishment success outside their natural range. The predominance of cichlids among non-native species (in both the number of species and individuals) has been documented by inventories conducted in different American watersheds (e.g., Contreras-MacBeath et al. 2014; Amador-del Ángel and Wakida-Kusunoki 2014; Ortega et al. 2015; Azevedo-Santos et al. 2015). Some of these species, such as tilapia and peacock bass, are characterized by their high invasive potential, becoming dominant in recipient communities (Crutchfield 1995; Starling et al. 2002; Nico et al. 2007; Espínola et al. 2010; Cassemiro et al. 2018). For example, tilapias in reservoirs are able to increase in biomass and can account for 50% to 80% of fish landings in reservoirs after the introduction (Minte-

Vera and Petrere 2000; Agostinho et al. 2007). Changes in the composition of fishing landings, with the replacement of native species with higher sale prices, creates uncertainties about the positive effect on total yield and profitability (McKaye et al. 1995; Agostinho et al. 2007; Novaes and Carvalho 2013). Furthermore, tilapiine species may dominate stream biotopes adjacent to aquaculture systems (Fernandes et al. 2003). *Cichla* introductions show similar trends to rapid proliferation since these fishes require approximately 2 years to establish populations in reservoirs and cause profound changes to fish communities (Pelicice and Agostinho 2009).

In general, introduction success depends on propagule pressure (size and number; Lockwood et al. 2005) and tolerance of the biotic and abiotic conditions in the novel environment. Once in the environment, the establishment of populations depends on the ability to grow, reproduce, recruit, and disperse, so invasive potential is ultimately associated with life history traits, including parental care, early maturation, spawning type and frequency, fecundity, egg size, generation time, aggressive behavior, and feeding flexibility (Lodge 1993; Bij de Vaate et al. 2002). Successful invaders have been associated with opportunism (r-strategists) as well as life history traits related to low longevity or short generation time, high fecundity, and small eggs with rapid development and early maturation (Füreder and Pöckl 2007). However, cichlids do not seem to fit along the r-k-strategist gradient. Instead, these fishes are equilibrium strategists (large investment in relatively few individual offspring, sensu Winemiller 1989) because they exhibit parental care, multiple spawning, territoriality, and maturation/feeding plasticity; these traits likely make them good invaders.

The survival of eggs and larvae in the novel environment is critical for the establishment of self-sustaining populations (Côté et al. 2013), and cichlids are characterized by an extensive period of parental care, extending from spawning to the fry stage (Keenleyside 1991; Noakes 1991; Wisenden 1995). Many species care for their offspring in nests constructed in the substrate (substrate brooders), while others carry eggs or larvae in their mouths (mouthbrooders) (Lowe-McConnell 2006). Regardless of the strategy, care is usually maintained until the offspring become independent (Barlow 1991; Keenleyside 1991), and this may reduce predation pressure, which is a major component of biotic resistance during the invasion process (Lockwood et al. 2007). Moreover, mouthbrooding decreases the dependency on specific nursery habitats for juvenile development (Canonico et al. 2005), allowing cichlids to thrive in environments outside their native ranges (Wisenden 1995; Marchetti et al. 2004b; Contreras-MacBeath et al. 2014).

This group also contains several species that exhibit early maturation depending on the environmental conditions. Lowe-McConnell (2006), analyzing the plasticity in size and age at first maturity, reported that populations of native *Oreochromis niloticus* in altered environments (reservoirs) can attain maturity within 3 months of hatching (c.a. 12–14 cm in length), while this age oscillates between 2 and 4 years in natural lakes (28 cm). Plasticity in early maturation constitutes a remarkable ability to track environmental changes, which is especially important for invaders facing new environments, where a given resource can be very high. In fact, the plasticity to adjusting the maturity, and therefore the offspring size, to the availability of resources gives advantages not only for colonization but also for population persistence. Multiple spawning is another relevant trait; some species are able to reproduce for prolonged periods, often over the entire year (Canonico et al. 2005; Daga and Gubiani 2012; Contreras-MacBeath et al. 2014), which provides opportunities for offspring to exploit a range of environmental windows throughout the year, increasing the chance for recruitment.

Fecundity and egg size vary among cichlids according to the parental care strategy, but there are examples of successful invasions for all reproductive strategies. Substrate brooders have higher fecundity and a smaller oocyte diameter (up to 7000 eggs and 1–1.5 mm, respectively) than mouthbrooders (up to 1000; 5 mm) (Noakes 1991), yet both (e.g., *Cichla kelberi* and *Geophagus* aff. *proximus*, respectively) have successfully invaded ecosystems in the Neotropics (Pelicice et al. 2015; Gois et al. 2015). Additionally, aggressive behavior and territoriality are remarkable in cichlids (Ribbink 1991), which enables them to efficiently repel intruders (Wisenden 1995; Medeiros et al. 2007), including large competitors (Sanches et al. 2012). This competitive ability has been considered favorable to the colonization of new environments (Canonico et al. 2005; Contreras-MacBeath et al. 2014) because it ensures access to and use of high-quality resources, such as food or space.

In addition to life history traits, factors related to propagule pressure may have determined the success of many invasions. As explained above, cichlids have attributes that make them attractive for human use, enabling their exploitation and transport outside their native ranges (Côté et al. 2013). Many cichlids, because of their colors and shapes, have high ornamental value, and several cichlids, especially the tilapias, are the main components of aquaculture systems, where escapes constitute a constant source of propagules (Britton and Orsi 2012; Azevedo-Santos et al. 2015; Ortega et al. 2015). Additionally, large predators (e.g., *Cichla* spp.) are highly desired by anglers, so multiple clandestine introductions have been carried out in several drainages (Latini and Petrere 2004; Pelicice and Agostinho 2009; Britton and Orsi 2012). Thus, the historical use of cichlids for ornamental purposes, aquaculture, and fishing created a constantly high propagule pressure across the Americas, a factor that must be evoked to explain their invasion success in some environments (Shelton and Rothbard 2006; Magalhães and Jacobi 2013).

Although there is a remarkable degree of trophic specialization among cichlids, especially in African lakes, most invasive cichlid species show dietary plasticity, including omnivory. Many species consume fish, but only a few genera (e.g., *Cichla*) show strict piscivorous diets (Lowe-McConnell 1991). The diet of *Cichla kelberi*, on the other hand, is quite flexible, depending on the time of the year and ontogenetic stage, taking, in addition to fish, insect or conspecifics (cannibalism; Mendonça et al. 2018), which represents an advantage during the novel environment occupation. We note that omnivorous and piscivorous fishes have been the most successful invaders of new environments in both Neotropical (Magalhães and Jacobi 2013; Ortega et al. 2015) and Nearctic America (Moyle and Light 1996a). The success of omnivorous fish has been attributed to their feeding plasticity being less constrained by specific limiting resources (Moyle and Light 1996b), whereas piscivores benefited from abundant resources since small fishes are common components of aquatic communities. In Neotropical impoundments, for example, non-native *Cichla* thrive on the consumption of small fishes that dominate assemblages (e.g., Fugi et al. 2008; Pelicice et al. 2015).

Finally, we highlight that several Amazonian cichlids are widespread in many non-Amazonian basins, indicating that they are stronger invaders than species from other continents (Agostinho et al. 2007; Gois et al. 2015). For example, they have successfully invaded both altered (e.g., hydroelectric reservoirs) and pristine ecosystems (e.g., floodplains and wetlands), and two non-mutually exclusive hypotheses may explain this success. First, these cichlids originate from species-rich systems, where they coevolved with different species with a myriad of ecological interactions (i.e., multiple and diffuse competition and predation), and this must favor the colonization of species-poor systems (Fitzerald et al. 2016). Second, Amazonian cichlids have invaded other Neotropical ecosystems in particular; the proximity of the donor and recipient systems and their similarities in resources, habitats, and physical and chemical conditions must increase the probability of establishment (Agostinho et al. 2015).

5 Impacts of Non-native Cichlids

Studies that evaluate the impacts of invaders on recipient ecosystems vary in their methodologies, ranging from correlative to manipulative approaches. The evidence comes from a limited number of studies (if we consider the number of introduced cichlids), but the results consistently reveal impacts at the population (e.g., Fugi et al. 2008; Sanches et al. 2012; Ruiz-Campos et al. 2012), community (e.g., Pelicice and Agostinho 2009), and ecosystem levels (e.g., Starling et al. 2002). Among the studied species, tilapias (e.g., *Coptodon zillii*, *Oreochromis aureus*, *O. mossambicus*, and *O. niloticus*) and large predators (*Astronotus* aff. *ocellatus*, *Cichla kelberi*, *C. monoculus*, and *C. ocellaris*) are prominent. Studies usually report changes in food web structure (e.g., Santos et al. 1994; Pinto-Coelho et al. 2008), species diversity (e.g., Zaret and Paine 1973; Pelicice et al. 2015), and community and population structure (e.g., Pinto-Coelho et al. 2008; Menezes et al. 2012; Gois et al. 2015), primarily due to competition for resources, predation, and changes in habitat use, which have consequently affected fisheries (e.g., McKaye et al. 1995; Attayde et al. 2011; Novaes and Carvalho 2013).

Species displacements due to spatial and trophic competition are common. In Mexico, several tilapiine species displaced native species due to overlapping spatial distributions or trophic niches. Fuselier (2001), studying five species of native *Cyprinodon* in Laguna Chichancanab, found that *O. mossambicus* displaced two native species to habitats already occupied by another species, likely disturbing the speciation process that had been operating for thousands of years. At Patzcuaro Lake, *O. aureus* showed dietary overlap with native species, likely causing the subsequent decline in their populations (Córdova-Tapia et al. 2015). In the Mexican northeast, *O. aureus* and *O. mossambicus* compete for food, spawning grounds, and space with native species. This competition for different resources threatens populations of *Chirostoma* and *Cyprinodon* species (Lozano-Vilano and García-Ramirez 2014). Although competitive displacement may affect species from different taxonomic groups, it might be stronger among other cichlids. In this context, Palacio-Núñez et al. (2010a) observed that *O. niloticus* and *Herichthys cyanoguttatus* spatially overlapped with many native species in Mexican floodplain biotopes, but the overlap with native cichlids was stronger. Examples of competitive interactions come from other countries as well. In a behavioral experiment conducted in Brazil, Sanches et al. (2012) demonstrated that *O. niloticus* was competitively superior to the native *Geophagus* aff. *brasiliensis*, even when the latter was 10% larger. In the Paraná River, Gois et al. (2015) showed that the invasion of *Geophagus proximus* coincided with the decline of *Satanoperca pappaterra*, probably because these species have similar requirements for feeding and reproduction. In the United States, the presence of *O. aureus* was linked to the decline of endangered species in streams in Nevada and Arizona (Canonico et al. 2005), and in reservoirs in North Carolina, *Coptodon zillii* proliferated following the elimination of aquatic macrophytes (Crutchfield et al. 1992) and probably caused the local extinction of some Cyprinodontiformes species. Although tilapias usually feed at low trophic levels, some species can feed on eggs, larvae, and even small fish (Canonico et al. 2005). Additionally, habitat displacement by agonistic competition may expose native fishes to predation and thus decrease survival, as demonstrated experimentally with *O. niloticus* and *Lepomis miniatus* (Martin et al. 2010).

Predation by introduced cichlids has also negatively affected resident species (e.g., Latini and Petrere 2004; Pelicice and Agostinho 2009). Some cichlids, particularly peacock basses (*Cichla* spp.), are voracious predators, and these fishes have profoundly damaged the native fish fauna of different ecosystems, including Gatún Lake in Panama (Zaret and Paine 1973), reservoirs in the Paraná River basin (Pelicice and Agostinho 2009), natural lakes in the Rio Doce basin (Godinho et al. 1994; Latini and Petrere 2004), and artificial ponds in semi-arid Brazil (Menezes et al. 2012). There are also clear examples in Brazil where the introduction of peacock basses led to strong declines in the fish diversity of lakes (Latini and Petrere 2004) and reservoirs (Pelicice and Agostinho 2009). In Rosana Reservoir, in particular, Pelicice and Agostinho (2009) revealed that small fishes collapsed within 3 years of the invasion of *Cichla kelberi*. Predation experiments are still scarce, but a recent mesocosm experiment showed high prey mortality rates in the presence of *C. kelberi* (Kovalenko et al. 2010a), even when refuges were available. Furthermore, this predator affected the behavior of the native prey in a mesocosm experiment, changing its feeding activity and habitat use (Kovalenko et al. 2010a, b).

Another impact is the spread of parasites that co-invade with the invading fish (Lymbery et al. 2014). In Mexico, there are examples of such co-invasion of parasites from cichlids (Frankel et al. 2015; García-Vásquez et al. 2017). *Gyrodactylus cichlidiarum* is a monogean parasite that was spread globally with their host *Oreochromis niloticus* and *O. mossambicus* (García-Vásquez et al. 2010). This monogean was reported infecting native *Poeciliopsis gracilis* in freshwaters from Puebla state and *Pseudoxiphohorus bimaculatus* in Lake Cuitzeo (García-Vásquez et al. 2017). Another troubling fact was that *G. cichlidiarum* was also reported infecting *Poecilia mexicana*, a poeciliid introduced elsewhere which can foster the co-invasion of this parasite (García-Vásquez et al. 2017; Remya and Amina 2018). In Gatun Lake, Frankel et al. (2015) observed that *Centrocestus formosanus*, an introduced trematode with global spread, infected four cichlid species, being one native (*Vieja maculicauda*) and three introduced: *Oreochromis niloticus*, *Astronotus* aff. *Ocellatus*, and *Cichla monoculus*. From these cichlid species, *C. monoculus* was the most susceptible to infection both in field and in experimental trials (Frankel et al. 2015). These examples highlight that introduced cichlids can help to spread parasites to native fish and to increase the spatial distribution of these parasites due to co-invasion.

Finally, non-native cichlids can also have ecosystem-level effects due to nutrient excretion or selective predation of planktonic species. Following a fish kill event in an artificial Brazilian lake, Starling et al. (2002) observed that *O. niloticus* contributed substantially to the input of phosphorus to the lake and that the removal of *O. niloticus* reduced external inputs by approximately 12%. *Oreochromis niloticus* also exhibits selective feeding on large herbivorous cladocerans that can change the abundance of algae. In field enclosures, Figueredo and Giani (2005) manipulated the presence of *O. niloticus* to assess its effects on water chemistry (by increasing nitrogen and phosphorous input due to excretion) and phytoplankton assemblage structure. They found that the presence of *O. niloticus* increased the quantity of ammonium and total phosphorus via excretion (Figueredo and Giani 2005). Furthermore, its selective feeding triggered a trophic cascade that changed the algal composition and density, contributing to eutrophication (Figueredo and Giani 2005). Another field experiment that manipulated the density of *O. niloticus* showed significant negative effects on water transparency and the composition of phyto- and zooplankton (Attayde et al. 2007).

Although several cichlid species have been introduced to enhance fishery yields, the results are controversial. For example, Caraballo (2009) reported a fivefold increase in fishing yield in a Colombian reservoir after the introduction of *O. niloticus*, but fishing effort (number of fishers) also increased by six times in the same period. In Lake Patzcuaro, Mexico, Zambrano et al. (2014) described the collapse of a promising multispecies fishery after the intense proliferation of carp (*Cyprinus carpio*) and *O. niloticus* and the increase in fishing effort. In Barra Bonita Reservoir (Brazil), Agostinho et al. (2007) showed that, after an initial increase in fish landings following the proliferation of *O. niloticus*, both the total catch and catch per unit effort declined 4 years after the first record. Related to the changes after damming, there is also a trade-off between the high productivity (higher number of individuals being fished) but with lower income of fisheries based on non-native tilapias versus the higher market value and long-term sustainability of fisheries based on native species (Agostinho et al. 2007; Hoeinghaus et al. 2009; Attayde et al. 2011). There are other examples showing that non-native cichlids are prone to change fishery systems (e.g., McKaye et al. 1995; Attayde et al. 2011), so unbiased evaluations are needed before these fishes are introduced (Deines et al. 2016).

6 Final Remarks

The present work revealed the existence of several non-native cichlids in different ecosystems across the Americas including species originating from Africa and the Americas that were translocated among drainages to support human activities (i.e., aquarium trade, aquaculture, and fisheries). Some species are now widespread (e.g., *Oreochromis niloticus*), and cichlid species will continue to support human needs. Regardless of whether the pattern of human-facilitated species introduction highlighted in this review persists, novel introductions involving new species may occur in the coming years. Environmental disturbances are constantly being reported, and they cannot be ignored by the authorities and society. We understand that studies of the impacts of non-native cichlid species in the Americas are still limited, but such detailed information is strongly needed to devise better management alternatives, such as the strict prevention of new introductions or post-invasion remediation. In this sense, the ecological impacts of non-native cichlids must be properly understood, especially beyond species of *Cichla* and *Oreochromis*, and society must be informed. These species have a long history of human use, so there is confusion about their disturbance potential and even about their invasive status (Vitule 2009). Thus, environmental education is a promising avenue to avoid introductions and to develop better approaches to manage non-native cichlids (Azevedo-Santos et al. 2015). The wide range of pathways by which new species of cichlids reach new areas makes prevention initiatives very complex. The virtual invisibility of these species in the invaded aquatic environment makes their eradication highly unlikely. Prevention and population control are alternative actions to contain the impacts. Even considering the set of acts that prohibit introduction practices, initiatives in environmental education and policing are indispensable complements. The priority focus for these initiatives should be fish farming (species farmed, local, tank, and procedures) and aquarium trade (species traded and fish discards). Population size control for established non-native species has been done by the removal of restrictions on their fishing, especially for predatory species. However, this practice runs counter to the interests of sport fishing and should be the target of environmental education and official incentives for specialized fishing, through incentive tournaments and meat consumption.

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The Evolutionary Ecology of Cichlid Vision

Suzanne M. Gray

Abstract The visual ecology of cichlids has contributed greatly to our understanding of mechanisms driving spectacular, colorful cichlid radiations. Interactions between the underwater light environment, the transmission of visual signals, and the visual sensitivity of the signal receiver are integral to the processes driving this diversity. Researchers recognized the importance of vision early in the study of African cichlids, citing the diversity of habitats in which cichlids are found and brilliant male nuptial coloration as potential forces shaping visual differentiation. Later work focused more on visual systems, adapted to the local light environment, as drivers of color pattern diversification. Most recently, researchers have focused on the evolution of visual systems under both ecological and sexual selection and the mechanisms of spectral tuning by investigating opsin gene expression and co-expression across the cichlid phylogeny. In this chapter, I describe the historical context of cichlid vision research, the diversity in cichlid visual ecology, and the current state of our understanding of cichlid visual ecology. Additionally, I discuss the possible consequences of human-induced changes to the underwater visual environment for cichlid diversity and suggest avenues for future research.

Keywords Color vision · Opsin genes · Visual signaling · Communication · Light environment

1 Visual Ecology

Why is vision so important for cichlids? A dive into Lake Malawi, pulling a gill net on Lake Victoria, or a visit to your local aquarium will likely give you a clue given the extreme variation apparent in cichlid color and patterns (Fig. 1). Early research on cichlid vision focused on brilliant male nuptial coloration used in species

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S. M. Gray (✉)
School of Environment and Natural Resources, The Ohio State University, Columbus, OH, USA
e-mail: gray.1030@osu.edu

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Fig. 1 Examples of color pattern diversity in cichlids from (**a**) Thumbi Island West, Lake Malawi, (**b**) Lake Victoria, Uganda, and (**c**) the Malawi exhibit at the Toronto Zoo, Canada. (photos by S.M.G)

recognition and mate choice decisions as a driver of visual diversity; more recently, focus has shifted to the evolution of visual systems under both ecological and sexual selection as integral drivers of adaptive cichlid evolution. Advances in our understanding of cichlid visual systems and the technology used to assess visual abilities have led to new hypotheses about the proximate mechanisms promoting the evolution of visual systems and discoveries of how spectral tuning functions via, for example, through co-expression and plasticity of opsin gene expression. It is crucial, therefore, to elucidate the complexity of visual processes in order to develop a framework for assessing the evolutionary ecology of cichlid vision. In this review, I lay out the foundations of a framework based on the basic biology of cichlid vision and the historical context in which current studies are based. Within this integrated framework, including visual systems, photic environment, and colorful signals (Fig. 2), recent research has focused on the regulation of opsin gene expression and the influence of spectral tuning of photopigments on the evolution of cichlid visual ecology. A number of excellent reviews have covered various aspects of the evolution of vertebrate vision (e.g., Bowmaker and Hunt 2006), photopigment evolution and speciation (Bowmaker 1995; Yokoyama 2000, 2002, 2008; Carleton 2014), the link between visual systems and colorful signals (e.g., Osorio and Vorobyev 2008), and more specifically spectral tuning and diversification in cichlids (Carleton 2009; Hofmann and Carleton 2009; Carleton et al. 2016). Therefore, I aim to give a broad overview of the current state of knowledge of cichlid visual ecology and highlight some of the most recent research contributing to our understanding of the evolutionary ecology of cichlid vision rather than provide an extensive review of the field. I also discuss the potential implications of human-altered visual environments and suggest directions for future research.

2 Cichlid Vision

2.1 *The Cichlid Eye*

Vertebrate vision is highly conserved, and cichlid vision follows this plan. Cichlids, following the typical teleost eye plan, have a cup-shaped eye placed laterally and

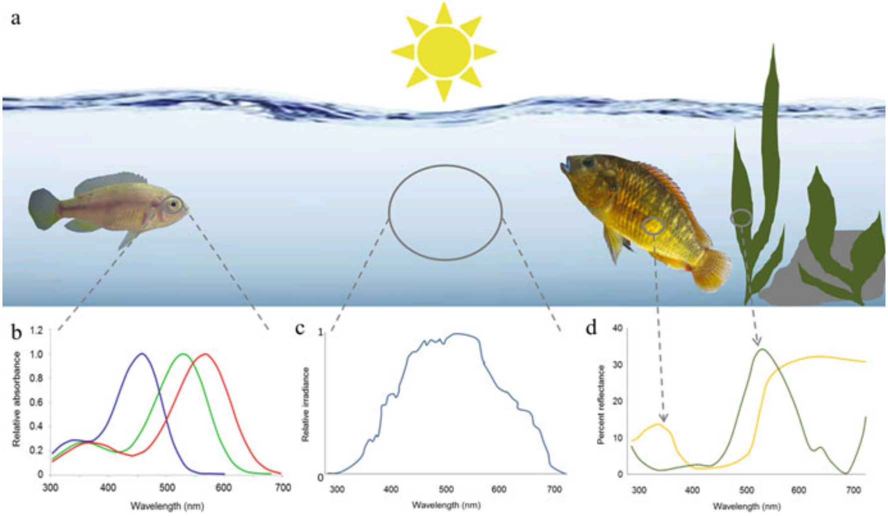

Fig. 2 Simplified diagram of important components involved in cichlid visual ecology. In this example, (**a**) a female cichlid *Pseudocrenilabrus multicolor* (Seegers) on the left is viewing a larger and more colorful male *P. multicolor* on the right (photos by S.M.G.). (**b**) Visual sensitivity represented by absorbance spectra for three cone opsins typical for Lake Victoria haplochromines; (**c**) Irradiance spectrum of the transmission medium through which the visual signal is viewed; (**d**) Reflectance spectra from a yellow color pattern (yellow curve) component of the signaler and of the background plant (green curve) against which the signaler is viewed

slightly forward on the head, a non-dilatory pupil, a spherical lens, retina, and pigment epithelium (Fig. 3a). Detailed descriptions of teleost eyes and vision can be found in various sources, including Lythgoe (1980), Fernald (1990), and Cronin et al. (2014). Here I give a brief description of cichlid visual structures to help contextualize this review. As in the typical vertebrate eye, light travels through the pupil and into the crystalline lens, which collects light, forms an image, and directs it onto the retina at the back of the eye. Two small muscles allow for slight axial adjustment of the lens position in relation to the retina to aid in focusing the image (i.e., accommodation). The gross morphology of the eye (e.g., eye size given by axial length, or the distance from the front to the back of the eye) helps to determine the visual abilities of an individual. In a simplified scenario, eyes with a longer axial length tend to have a longer focal length and thus project a larger image on the retina, providing more visual information to the brain (Howland et al. 2004). Fernald (1990) found that as Burton's mouthbrooder, *Astatotilapia burtoni*, grows, visual abilities are not compromised despite considerable enlargement of the eye over time.

The retina is composed of, from point of light entry to the back of the eye: the ganglion cell layer, inner plexiform layer, inner nuclear layer, outer nuclear layer, visual photoreceptors, and the pigment epithelium. The actual collection of photons and activation of visual processing occurs at the level of the visual photoreceptor, composed of an inner and outer segment. The inner segment contains the nucleus

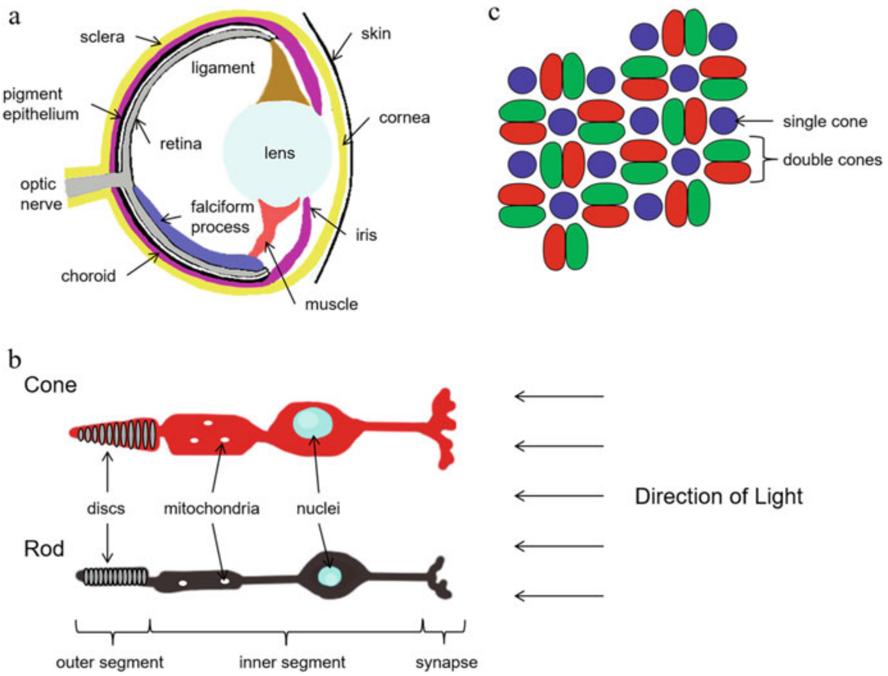

Fig. 3 Diagram of a typical (**a**) cichlid eye, (**b**) retina, and (**c**) mosaic arrangement of cone photoreceptors in the retina. In this mosaic example, three cone classes are represented by colors with a single short-wavelength sensitive SWS cone (e.g., SWS2A) surrounded by four pairs of long-wavelength sensitive LWS cones (e.g., Rh2A, LWS)

and other cellular functioning components (Fig. 3b) and sometimes oil droplets or carotenoid-derived pigments that can filter light of certain wavelengths (Bowmaker et al. 1997; Cronin et al. 2014; see Sect. 4.2 Spectral Tuning). The end of the inner segment forms a synapse that connects with other photoreceptor cells and neuronal cells, the axons of which are collected in the ganglion cell layer and leave the eye via the optic nerve.

The outer segment of the visual photoreceptor receives light travelling through the other components of the retina and is where the visual photopigments are found. Photopigments are composed of two components: an opsin protein, which is a membrane-bound G-protein coupling receptor, bound to an inactive form of a photosensitive vitamin A-based chromophore (Wald 1935). Rhodopsin and porphyropsin are the two types of visual pigments, respectively, found in marine and freshwater fishes (Toyama et al. 2008). They are distinguished by the retinal structure of the chromophores. A1 chromophores are composed of 11-*cis*-retinal whereas A2 chromophores are composed of 3,4-didehydroretinal. Most freshwater fishes, including most cichlids (Carleton et al. 2008), have predominantly A1 chromophores; however, many species exhibit a mix of A1 and A2 chromophores and the ratio of the two types can change throughout a fish's life. For example, the

A1/A2 ratio in Nile tilapia (*Oreochromis niloticus*) varies between individuals and throughout development from the larval to adult stages (Carleton et al. 2008). A shift from A1- to A2-based chromophores alters the sensitivity of the photopigment toward longer wavelengths and broadens the bandwidth of spectral absorbance.

Detection of light is facilitated by isomerization of the chromophore (e.g., 11-*cis* retinal to all-*trans* retinal) upon absorption of a single photon, changing the molecular structure of the chromophore, thus activating the opsin and triggering an enzyme cascade that makes perception of light possible. Opsin proteins are variably sensitive to different wavelengths of light and can be characterized by the wavelength of maximal or peak absorbance (λ_{max}). In most cases, one opsin class is expressed in a single photoreceptor. However, there is emerging evidence of two opsins being expressed simultaneously within a photoreceptor in some cichlids (i.e., co-expression and retinal specialization) resulting in shifts in spectral sensitivity (e.g., Dalton et al. 2014, 2016). Additionally, small changes in the opsin protein sequence can lead to changes in the λ_{max} of a photoreceptor, which I discuss in detail in Sect. 3.3.

Vertebrates have two types of photoreceptor cells, each serving different functions. Rods, as the name suggests, are typically long and cylindrical (Fig. 3b) and function as highly sensitive receptors in low or dim light conditions (i.e., scotopic vision). Cones are typically shorter and cone-shaped (Fig. 3b) and are used in bright light conditions to facilitate visual acuity and color vision (i.e., photopic vision). One of the notable differences between rods and cones is the placement of the visual photopigments. In rods, photopigments are found in disc-like layers within the cell membrane; thus maximizing sensitivity by providing more surface area for more absorption of light by photopigments. Note that a single photon activates a single opsin thus more pigments allow for better detection of low light. However, this comes at the cost of reduced speed of photon detection (Cronin et al. 2014). In cone photoreceptor cells, the photopigments are embedded directly in the plasma membrane, allowing for faster signaling at the expense of sensitivity. The size of cones, rather than the size of the eye, determines the amount of light captured (Cronin et al. 2014).

Color vision is made possible by the presence of multiple cone photoreceptor classes with opsins tuned to different wavelengths of maximal absorbance, allowing a comparison between different colors. Thus, a minimum of two photoreceptors that absorb light maximally at different wavelengths are required for color vision with the appropriate neuronal connections (see Wandell 1995). Vertebrates possess four classes of opsins spanning the visible light spectrum: short-wavelength sensitive (SWS1; UV-Violet), SWS2 (Blue), Rhodopsin-like (RH2; green), and long-wavelength sensitive (LWS; yellow-red). African cichlids have an additional three opsin genes, a result of gene duplication leading to spectrally distinct cone classes (Hofman and Carleton 2009; see Table 1).

Cones are typically arranged within the retina in a specific mosaic pattern (Fig. 3c). Fernald (1981) described the retinal cone mosaic for Burton's mouthbrooder as having a square pattern of four pairs of double cones with a central single cone, which has since been deemed the typical cichlid mosaic (Carleton and

Table 1 Visual photoreceptor classes of African cichlids[a]

Photoreceptor classes	Class names	Opsin genes	Common names	For example λ_{max} (nm) *Oreochromis niloticus*[a]	Cone type
Rod	*Scotopic or dim light vision*				
RH1	Rhodopsin	RH1	Rod		–
Cones	*Photopic or bright light and color vision*				
SWS	Short-wavelength sensitive	SWS1	UV	360	Single
		SWS2B	Violet	425	Single
		SWS2A	Blue	456	Single
RH2	Rhodopsin-like	RH2B	Blue-green	472	Double
		RH2Aβ	Green	518	Double
		RH2Aα	Green	528	Double
LWS	Long-wavelength sensitive	LWS	Yellow-red	561	Double

[a]Compiled from Spady et al. (2006)

Kocher 2001). In cichlids, the central single cone is typically small and sensitive to short wavelengths. The surrounding four pairs of double cones are sensitive to middle to longer wavelengths of light, i.e., RH2 and LWS cone classes, and cones within a pair can either be identical or one each of RH2 and LWS (Fernald 1981; van der Meer et al. 1995; Carleton and Kocher 2001). Variation in the expression of cone pigments with different λ_{max} and alterations in the protein coding sequence of opsin genes help to fine-tune the sensitivity of cone photoreceptors to match the background photic environment. Extensive research, especially over the past 40 years, has defined cichlids as a model for understanding the evolution of vertebrate visual systems and its role in adaptive radiation.

2.2 *Groundbreaking Studies of Cichlid Vision*

The extreme color variation observed among closely related cichlid species, combined with the wide variety of ecological niches they occupy, intrigued early visual scientists and prompted examination of the visual abilities of this diverse lineage of fishes (Eigenmann and Shafer 1900). With the advancement over time of techniques for quantifying variation in visual abilities, we have greatly increased our understanding not just of the visual processes involved in vision but also the underlying role of vision in adaptive divergence and speciation.

The late nineteenth and early twentieth centuries saw an upsurge in research pertaining to the morphology of the teleost retina (see Eigenmann and Shafer 1900). Morphological determination of visual acuity which is the ability of an animal to detect an object (e.g., food, predator, or mate), can be assessed by measuring gross sizes of the pupil, lens, and axial and eye diameters (Howland et al. 2004) as well as by investigating the detailed structure of the retina (Fernald 1981; van der Meer and Anker 1984; van der Meer et al. 1995). Vision depends upon the resolution of images, as determined by the density of photoreceptors, and sensitivity to different wavelengths and intensities of light as determined by the size of photoreceptors. Relatively larger eyes can accommodate either a larger number or larger sized photoreceptors; however, an increase in either variable might result in a trade-off between sensitivity and resolution (van der Meer and Anker 1984).

Early cichlid work also focused on understanding retinal morphology and the extent of color vision in cichlids. For example, Engström (1963), has reported on the lack of information for cichlids in the literature at that time, examined one specimen each of two Neotropical cichlid species, *Apistogramma ramirezii*, and the Convict cichlid (*Archocentrus nigrofasciatus*) from the aquarium trade and gave brief descriptions of the cone mosaics. In both species, the cone mosaics were square with a central single cone surrounded by four pairs of double cones (Fig. 3c). The first report on the spectral sensitivity of retinal photopigments for *Cichlasoma meeki* and *Aequidens portalegrensis* followed shortly (Schwanzara 1967). At that time, a retinal pigment extraction process combined with bleaching of the extract and using various wavelengths of light showed that the λ_{max} of the paired opsins was 500/522 nm. Fernald's work in the 1980s, using Burton's mouthbrooder as a model species (e.g., Fernald and Liebman 1980; Fernald 1984) helped to bridge the gap between reporting on retinal morphology and a better understanding of the links between visual pigment sensitivity and behavior. They reported a single, central cone in the retinal mosaic with $\lambda_{max} \sim 455$ nm and mixed double cones having $\lambda_{max} \sim 523/562$ nm in this African species. Fernald and Liebman (1980) discuss these findings in the context of the body color and patterns used in intraspecific signaling and the ambient photic environment, suggesting that the maximal absorbance of the three cone classes described likely allow for the detection of conspecifics under natural conditions.

Behavioral proxies have also been used to assess cichlid visual abilities. Visual acuity, for example, can be estimated behaviorally (Browman et al. 1990; Wanzenböck et al. 1996) by assessing the distance from an object that the fish first reacts to the object (i.e., reaction distance) using a standard reaction distance protocol (e.g., Vogel and Beauchamp 1999). Visual sensitivity, the ability to detect an object under different light intensities and colors, can also be determined using behavioral experiments. For example, the optomotor response test has been successfully used in a number of studies on fishes to test for sensitivity or detection thresholds to varying light conditions (e.g., Kröger et al. 2003; Boughman 2001; Neumeyer 2003; Maan et al. 2006). Due to an innate optokinetic response (visually induced eye movements) or optomotor response (visually induced head or body movements), fish will follow a rotating grate, with their eyes or by swimming, as long as they can distinguish the light and dark bars of the grate, but will stop swimming when a visual sensitivity threshold is reached. As the light intensity is incrementally decreased, the detection threshold is assessed as the light level one step above when the fish ceases to follow the rotating screen. The optomotor response method was used by Maan et al. (2006) to investigate detection thresholds for two sympatric and closely related Lake Victoria cichlids, *Pundamilia pundamilia* and *P. nyererei*. While the two species are morphologically and ecologically very similar, males have divergent nuptial coloration: *P. pundamilia* males are blue and *P. nyererei* males are red (Seehausen et al. 1999; Maan et al. 2004, 2006), and are respectively found in shallow and deep areas surrounding islands. Due to the relatively turbid conditions of Lake Victoria, strong light gradients can exist with shorter-wavelength (UV-Blue) light attenuating faster than longer-wavelength light (Seehausen et al. 2008). Thus, each of the two species typically occupies different photic microhabitats, with *P. pundamilia* in shallower waters dominated by short-wavelength light and *P. nyererei* in red-shifted deeper waters. The optomotor tests revealed that under decreasing intensity of blue light, female *P. pundamilia* performed better than *P. nyererei*, while the opposite pattern was found when females were tested under red light, demonstrating an association between female visual sensitivity, male color pattern, and the photic environment.

The early method of measuring the absorbance of pigments in solution to describe the sensitivity of photopigments has been supplanted by microspectrophotometry (MSP). MSP, described by Liebman (1972), is a technique that targets the opsin-containing outer segment of individual photoreceptors by focusing a narrow beam of light, typically one nanometer wide, through the outer segment. The absorbance of light through the cell is measured as a motorized monochronometer changes the wavelength of the light beam from 300 to 750 nm typically at 1 nm intervals, thus producing a spectral absorbance curve. The peak of the curve represents the wavelength of maximal absorbance, λ_{max}, for an individual photoreceptor cell. MSP results were first reported for cichlids by Levine and McNichol (1979) and Levine et al. (1979), and it is this method that Fernald and Liebman (1980) used to detect the spectral sensitivity of cones in Burton's mouthbrooder. MSP was also used to compare photopigment sensitivity across African and Neotropical species (Levine et al. 1980). MSP, coupled with access to technology for more easily measuring solar irradiance under water, has allowed researchers to develop models for understanding the perceptual abilities of cichlids under different environmental conditions (see Sect. 3.2).

Recent advances in genetic analysis of opsin gene expression have provided greater insight into the evolution of cichlid vision. Researchers can reconstitute visual pigments using quantitative reverse-transcription polymerase chain reaction (qRT-PCR) and measure maximal absorbance (similar to MSP generating λ_{max}) as well as the concentration of pigment types (e.g., Parry et al. 2005; Carleton et al. 2008; Carleton 2009). Whereas MSP is useful for determining if an animal is sensitive to particular wavelengths of light by assessing λ_{max} of individual photoreceptor cells, it does not rule out the presence of rare photopigments and does not always provide a quantitative measure of the abundance of each type of opsin pigment present. Parry et al. (2005) demonstrated a good match between MSP and qRT-PCR maximum absorbance in several Lake Malawi cichlids. Within this framework, much recent research has focused on the regulation of opsin gene expression/coexpression and the influence of spectral tuning of retinal photopigments on cichlid vision and evolution, as described below (see Sect. 4.2).

3 Visual Ecology

Sensory ecology describes the study of how animals collect, interpret, and respond to information from their environment and thus necessarily requires an understanding of sensory abilities, transmission media, signal content (Endler 1992, 1993; Cronin et al. 2014), and the variation inherent in each of these components across time, space, and level of biological organization (Dangles et al. 2009; Ord et al. 2010). The visual environment is the medium through which signals are transmitted and the background (or "visual scene") against which visual signals are viewed. Visual ecology, therefore, encompasses the integral link between the visual environment, the spectral properties of the visual signal, and the visual abilities of the signal receiver (Fig. 2). Thus, any treatment of visual ecology should incorporate these components, in addition to factors that might alter them, such as behavioral displays that can highlight certain components of a signal or environmental perturbation that might mask signals. In this section I discuss each of these components in turn.

3.1 Visual Environment: Heterogeneity and Water Clarity

The underwater visual environment is complex, more so than terrestrial environments (Lythgoe 1979; Levine et al. 1980). Cichlids are found across photic extremes, including the clear, broad-spectrum waters of Lake Malawi, the turbid waters of the white Amazon, and the tannin-stained, red-shifted waters of swamps and rivers high in dissolved organic matter. While the large-scale photic differences in bodies of water such as those found among the African rift lakes have exerted an influence on the evolution of cichlids (Hofmann et al. 2009), heterogeneity in the visual environment is also found at smaller scales within those systems. An excellent example of this are the sand and rock habitats of Lake Malawi (Fig. 4). Each of these environments provides light at different intensities and with different spectral properties (e.g., Sabbah et al. 2011) that are expected to favor different visual systems.

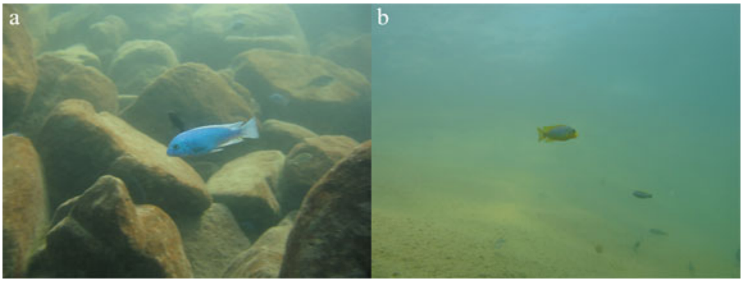

Fig. 4 Cichlid visual environments differ substantially with respect to light availability, spectral composition, and habitat complexity, as shown in adjacent (**a**) rocky and (**b**) sand habitats near Thumbi Island West, Lake Malawi (photos by S.M.G)

The photic environment influences both the ability of animals to detect objects, such as prey, predators, potential mates, and competitors, and the transmission of visual signals. Here I describe the important components of light that affect visual signals and their detection. First, light penetrating the water's surface is absorbed and scattered such that it attenuates steeply with depth and attenuation is wavelength dependent (Levine and MacNichol 1982). In clear water, the extreme ends of the spectrum (i.e., UV and red) are attenuated fastest which is why blue or mid-wavelength light dominates deep water, giving clear open water the appearance of being blue. Alternatively, water containing high concentrations of dissolved organic material or suspended particulates (i.e., turbid water) will selectively absorb and scatter short-wavelength light, shifting the underwater visual environment to longer wavelengths, giving it a yellowish or reddish appearance. Second, spatial and temporal variations in the visual environment (at many scales, from the flicker imposed by surface waves to diurnal and seasonal shifts) will influence the perception of a signal by a receiver (Lythgoe 1979). For example, light entering the water at dusk and dawn contains substantially more long-wavelength light compared to the solar zenith at noon when the sun is overhead, providing intense, broad-spectrum light. Other spatial scales of photic variation include depth, substrate, and slope of the substrate (e.g., from shore). We also expect the complexity of the habitat (e.g., rock vs. sand vs. vegetation) to influence the photic environment by creating spectrally divergent and potentially complex viewing backgrounds (e.g., Endler 1992; Shumway et al. 2007). For example, Fig. 4 shows the obvious differences in habitat complexity between adjacent rock and sand patches in Lake Malawi. Therefore, in the context of the evolution of cichlids, and cichlid vision in particular, it is essential to know something about the photic environment.

Cichlids are found across a great number and complexity of underwater visual habitats. It is thought that cichlid ancestors inhabited rivers and floodplains, thus likely experiencing medium to long-wavelength shifted and turbid photic environments resulting from high dissolved organic material and sediment flux (Bowmaker 1995). Under such visual conditions, red nuptial coloration, as displayed by Nile tilapia (considered the phylogenetic outgroup to modern cichlids; Takahashi and Sota 2016) would be particularly conspicuous if the visual system was also medium-to long-wavelength shifted. On a broad scale, many extant African cichlids are found in historically relatively clear lakes, whereas Neotropical species are often found in more turbid and or tannin-stained waters (Sioli 1984; Duncan and Fernandes 2010; Cooke et al. 2012). Across the East African Great Lakes, Lakes Malawi and Tanganyika are relatively clearer than the shallower and more turbid waters of Lake Victoria. The differences in photic environment may have influenced contemporary visual sensitivity profiles in each clade such that in the broader spectrum waters of Lake Malawi and Tanganyika there is more diversity in opsin expression and hence visual systems, including sensitivity to short-wavelength light (Carleton et al. 2000; Hofmann et al. 2009). Within the East African Great Lakes, major habitats linked with the independent evolution of two lineages include rocky outcrops and sandy bottoms (Kocher 2004). The visual environment significantly differs between these two habitats (Fig. 4): sand habitats are less complex, almost featureless zones, while rocky outcrops are relatively more complex with three-dimensional structure and associated crevices and shadows (Shumway et al. 2007; Dalton et al. 2010; Sabbah et al. 2010). Clear, broad-spectrum environments may favor UV sensitivity, especially in planktivores because the space light (i.e., down-welling, side-welling, and up-welling light) in this environment is rich in short-wavelength light (Lythgoe 1979; Hofmann et al. 2009). A fish that is sensitive to short-wavelengths can take advantage of this because of increased contrast and hence detectability of zooplankton and algae against a predominantly short-wavelength background (Utne-Palm 2002; Hofmann et al. 2009). Hofmann et al. (2009) show an association between cichlids with UV sensitivity and planktivory. Similarly, attenuation of light with depth, modified by level of turbidity or suspended particulates, has played a role in visual divergence between cichlids and speciation (Seehausen et al. 2008).

Water clarity, or the amount of suspended and dissolved solids in the water column, significantly influences the availability and color of light underwater (Lythgoe 1979; Seehausen et al. 2003). Consider your ability to detect a friend standing on the beach on a clear, sunny day versus a very foggy day—the veiling light resulting from scattering and absorption by the water droplets constituting fog obscure your friend, making them more difficult to detect and resolve. Suspended particulates differentially scatter and absorb light of different wavelengths underwater. In turbid water, high in suspended particulates, short-wavelength, higher energy photons are scattered and absorbed more than longer-wavelength photons such that with depth, the water becomes dominated by longer wavelength (yellow-red) light (Levine and MacNichol 1982). Thus, the photic environment can vary drastically across gradients of depth and water clarity, and subsequently alter the strength and shape of selection on visual sensitivity and colorful signals. Work by Seehausen et al. (2008 ibid) assessed water clarity and the spectral composition of underwater light along transects in the Mwanza Gulf of Lake Victoria, with the aim of correlating the diversity of male color morphs and distinct species with water clarity and color (see Sect. 4.1 for details of that study). As water became more turbid further into the Gulf, the intensity of light decreased and the spectral content shifted to be dominated by long-wavelength (orange) light, subsequently altering the selective pressures on cichlid vision.

Characterization of the underwater photic environment at different spatial and temporal scales is essential if we are to fully integrate our understanding of mechanisms of driving diversification in cichlid visual systems and color patterns. However, such characterizations are logistically difficult and only a few studies have attempted thorough examinations (e.g., Seehausen et al. 2008; Hofmann et al. 2009; Sabbah et al. 2011; Maan et al. 2010). The work by Seehausen et al. (2008) as described above is one such study that explored large-scale variation in photic environment directly associated with cichlid visual sensitivity and male color patterns. Another broad-scale study that provides a general assessment of the photic environment is the work by Hofmann et al. (2009) in which large differences in the photic environment between clear, deep Lake Malawi and shallow, turbid Lake Victoria are studied in the context of cichlid vision. A more detailed and localized physical characterization of the light environment was performed by Sabbah et al. (2011). They measured the spectral irradiance, background radiance and the beam attenuation coefficient (i.e., the contrast of an object against the background) along depth and slope transects in one rocky and one sandy habitat near Cape Maclear, Lake Malawi. These three variables, in addition to the spectral reflectance of an object, are required to understand how detectable that object might be in a given underwater environment (i.e., radiance contrast). Sabbah et al. (2011) detected some variations in irradiance between sand and rock habitats: longer-shifted light was found at depth in the sand compared to the rocky site. Although no difference in radiance was detected, radiance contrast calculations suggested that at depth in the sandy site objects reflecting longer wavelength light would be more detectable and shorter-wavelength signals at depth in the rocky habitat, which could have implications for detection of visual signals in those locations. One of the challenges of these types of rigorous studies is ensuring that the measurements are taken at ecologically relevant locations (e.g., where fish are present) and times (e.g., whether fish are foraging and/or mating or avoiding predators). The depths at which major differences were detected by Sabbah et al. (2011) are not necessarily where cichlids are mating, so the influence on male nuptial coloration may not be large, but maybe important for other ecological functions.

The Neotropical cichlid lineage is not as large or diverse as the African cichlids (Genner et al. 2007; López-Fernández et al. 2010, 2013); however, they are also found in diverse and complex photic environments, especially among the tributaries of the Amazon. Three broad visual environments where riverine Neotropical cichlids are found are described as clear, black, and white, each providing substantially different photic environments (Sioli 1984; Duncan and Fernandes 2010; Cooke et al. 2012). Blackwaters are typically found in organic-rich swamps or rivers and may be very clear but the tannins (dissolved organic matter) absorb short-wavelength light, thereby decreasing the intensity of light underwater and shifting the spectral composition to increasingly long-wavelength light. White water is extremely turbid with suspended sediments, which also absorb and scatter light, and depending on the size, structure, and composition of sediments, will appear muddy yellow-brown to cloudy white (Lythgoe 1979). Nicaragua's large lakes (Lakes Managua and Nicaragua) and crater lakes also harbor cichlid species complexes with parallel patterns of color diversification (Elmer et al. 2009, 2010); however, the large lakes are shallow, leading to resuspension of sediments via wind action and eutrophication, making the water very turbid, while the crater lakes are deep and clear. Characterization of the photic environment in the Neotropics has not been as rigorous as in African waters. Nor have the relationships between the photic environment, body coloration, and visual sensitivity been explored as thoroughly as in African waters to date (but see Härer et al. 2017; Hauser et al. 2017; Torres-Dowdall et al. 2017; see Torres-Dowdall and Meyer 2021).

3.2 *Visual Signals*

The visual signals of cichlids, males in particular, are what literally caught the eye of evolutionary ecologists and spurred the field to use cichlids as a model for understanding adaptive radiation. Visual signals are generated by reflection of light from an object through a medium. Signals directed toward a receiver are considered communication traits and are most effective when they provide contrast for efficient detection; whereas some patterns are meant to prevent detection by masking or camouflaging the object. Highly contrasting signals are considered conspicuous. Conspicuousness can be achieved either by contrasting with the background against which the object is viewed, or by contrasting elements within the object. For example, the dark vertical bars typical of many cichlids are viewed against a lighter background (e.g., Jordan et al. 2004), or the highly saturated and long-wavelength yellow-red egg spots of haplochromine cichlids are often circled by white rings thus increasing the contrast of the signal.

The visual signals of cichlids cover the entire visible spectrum, and often extend into the ultraviolet. Fish color patterns can be expressed in a number of ways: through pigment-containing chromatophores in fish skin or through structural components that refract and reflect light depending on the viewing angle (Grether et al. 2004; Leclercq et al. 2010). Chromatophores containing different pigments often overlay each other, and the pigment granules can be aggregated or dispersed to affect changes in color pattern. Some cichlids are known for their ability to change color rapidly (e.g., in seconds to minutes) in response to social or external cues (e.g., Muske and Fernald 1987; Nelissen 1991; Jordan et al. 2004). Jordan et al. (2004) showed that males of three Lake Malawi mbuna (rock-dwelling) cichlids, *Metriaclima zebra*, *M. benetos*, and *M. barlowi*, reflect strongly in the UV end of the spectrum, and will alter the intensity of their UV signal depending on the social context (e.g., presence of a conspecific female). Males in these species can alter their color pattern within minutes, suggesting a physiological mechanism of color change, such as expansion or contraction of pigments within the chromatophores of the skin (Grether et al. 2004). In a study investigating neuronal control of expression of the facial “eyebar” in Burton’s mouthbrooder, Muske and Fernald (1987) demonstrated that melanin pigments can be aggregated in a matter of seconds upon electrical stimulation, thus dimming the eyebar signal that is used in aggressive male–male encounters.

Longer-term, morphological, or developmental changes in color are often a result of genetic and environmental variations. For example, the acquisition and utilization of pigments such as carotenoids will alter the expression of long-wavelength yellow and red color pattern elements (Grether et al. 2004). In a recent study, among population male color differences have been reported for the haplochromine Egyptian mouthbrooder *Pseudocrenilabrus multicolor victoriae* found in a variety of habitats in the Nile River basin (McNeil et al. 2016; Fig. 2a). Males from long-wavelength shifted (but clear) swamp sites expressed more red coloration compared to males from turbid river sites that expressed more yellow coloration. Investigations into the mechanisms associated with color divergence across extreme environments (Chapman 2015) in this species are ongoing due to the complexity of the system; however, we do know that male color is at least partly controlled by dietary carotenoid uptake (McNeil et al. 2016). Vertebrates cannot synthesize carotenoids and therefore rely on acquiring it from their diet for expression of certain long-wavelength reflecting pigments (Olson and Owens 1998; Leclercq et al. 2010).

Colorful signals can additionally be enhanced by body positioning and the frequency of behavioral displays. Baerends and Baerends-van Roon (1950) outlined the first ethogram of cichlid behaviors, indicating the ways in which males will position and display their bodies toward females. As an example, in Lake Malawi I observed *Metriaclima aurora* males with intensely yellow-colored throats and abdomens (Dalton et al. 2010) swim upward from their rocky territory and directly toward a potential mate, and then immediately turn to perform a lateral display toward the female. While this behavior was observed repeatedly, formal investigation is required to determine if this upward display is perceived as more conspicuous by females and thus favored. Additionally, altering the photic environment can result in changes in the frequency of courtship displays, as first described in Threespine stickleback from the Baltic Sea. Under conditions of high eutrophication (e.g., green-shifted watercolor), male sticklebacks significantly increased the frequency of courtship displays, presumably to better attract a female when the red nuptial throat patch would be masked against the green background. The result of this more frenetic behavior did not result in higher reproductive success (Heuschele et al. 2009). We have also recently shown, using a split-brood rearing experiment with Egyptian mouthbrooder broods from one swamp (clear, red-shifted) and one river (turbid, yellow-shifted) population and a male–male competition experiment that when in turbid water males perform more aggressive behaviors toward the other males than when the pair is tested in turbid water (Gray et al. 2012). This was true for fish from both parental populations and regardless of whether they were reared under clear or turbid conditions, suggesting that *P. multicolor* can alter behavior to compensate for an altered photic environment.

The heterogeneity of photic environments occupied by cichlids, and the various ways in which signals can be expressed or altered, have contributed to the extreme diversity of color patterns observed in cichlids (e.g., Baerends and Baerends-van Roon 1950; Fryer and Iles 1972; Konings 1990; McElroy and Kornfield 1990). Yet, there are some distinct and likely convergent patterns that emerge. Among African cichlids, sister species tend to share similar morphological and behavioral traits, with the major differences linked to reproductive isolation in the form of male nuptial coloration (Seehausen 1996; Albertson et al. 1999; Danley and Kocher 2001; Allender et al. 2003; Konings 2007). For example, there is a repeated pattern of intraspecific red and blue male color morphs and red and blue sister species pairs found throughout Lake Victoria that has been shown to be related to the steepness of light and depth gradients (Seehausen et al. 1997, 2008). In the mbuna, or rock-dwelling, cichlids of Lake Malawi, parallel evolution of color patterns has also occurred (Allender et al. 2003). In the relatively clear, broad-spectrum waters of Lake Malawi, species pairs with blue or yellow males dominate more so than the red-blue pairs of Lake Victoria. Pauers et al. (2016) found independently originating stripe, bar, and solid patterns among the Lake Malawi radiation. In this case, horizontal stripes are typically associated with reducing conspicuousness to predators, whereas bars tend to be involved in communication (e.g., species or mate recognition). The Midas cichlid (*Amphilophus*) species complex of Nicaragua also shows parallel evolution of color patterns, though they exist as color polymorphisms within species (Elmer et al. 2010): “dark,” the most common morph, is greyish with various melanic patches, bars, and stripes; and the “gold” morph is yellow, orange, or white (Barlow 1983). Morphs are genetically determined in this case, with some within-morph modification of color intensity via carotenoid uptake (Henning et al. 2010).

In many cichlids, sexual dichromatism suggests that color patterns play an integral role in sexual selection (e.g., Kocher 2004) and that visual systems must be linked somehow to signals in order for the signals to be effective (Endler 1992). So, if a male expresses bright red coloration in a reproductive context, we expect that females (and conspecific male competitors) should be able to detect that signal (Gray and McKinnon 2007). The efficiency of a signal depends upon transmission of the signal through the medium, and this will change with the medium. As an example, a fish viewed in clear water will likely be much more detectable than if viewed by the same receiver from the same distance in turbid water. The same would hold true as one moves from shallow to deeper waters. This has been shown to be true for a number of cichlids (e.g., Seehausen et al. 2008) and the diversity of photic habitats has contributed to both the adaptive radiation of African cichlids and the loss of biodiversity when the photic environment is disrupted (Seehausen et al. 1997). A question of interest among evolutionary biologists is if this link between environment, signal, and visual system stem from ecological selection on visual systems with subsequent sexual selection for male color patterns that are conspicuous to females in a given photic environment (i.e., sensory drive hypothesis; discussed in detail in 4.1).

3.3 Visual Sensitivity

Detection of visual signals requires appropriate sensory structures for capturing light, thus the visual sensory system needs to respond to the spectrum of light available (Lythgoe 1979). The term visual sensitivity is used in several contexts: photoreceptor spectral sensitivity describes the spectral absorbance properties of retinal photopigments. Or, in a more holistic sense, the term is used to describe the overall spectral sensitivity of the visual system to light, including through interactions between cones and retinal neurons and further processing of a visual signal in the brain. Evidence of spectral sensitivity is much more prevalent than evidence for information processing, largely due to the ways in which each is measured. To determine photoreceptor sensitivity, either MSP of individual photoreceptor cells or reconstitution of opsin proteins is used. These techniques capture the different classes of photopigments expressed and the genetic potential (i.e., complement of opsin genes present) an individual has for spectral sensitivity. Both can also reveal the presence of rare cone photoreceptor types (e.g., Parry et al. 2005; Carleton et al. 2008), but cannot describe the mechanism of visual information processing. Determination of the spectral sensitivity of the visual system as a whole requires whole retina physiological techniques, such as electroretinograms (ERGs) or optic nerve compound action potential (CAP) recordings. ERGs measure the response to various wavelengths of light at the level of the retina (i.e., an electrode is placed near the *vitreus humor* of the eyecup near the retina) and CAPs measure the response at the level of the optic nerve. Behavioral tests, such as the optomotor response, can also provide information about visual sensitivity but at an even higher level of organization (i.e., post-processing of the visual stimulus). Thus, photoreceptor sensitivity provides information about the cone classes present and their λ_{max}, whereas ERG and CAP tests provide information about the processing of visual information, and behavioral tests are helpful for understanding post-processing responses. Ideally, a combination of tests would be used to infer perceptual abilities; however, this would be logistically difficult for the large number of species and specimens needed to characterize and compare visual system diversity across the Cichlidae.

For a growing number of African cichlids, and several Neotropical species, we know the spectral sensitivity of photoreceptors combined with their morphological arrangement found in the retina, which can infer the colors of maximal sensitivity for an individual. Fernald and Liebman (1980) provided the first documentation of retinal sensitivity for a cichlid, the Lake Tanganyikan Burton's mouthbrooder. As mentioned above, we now know that African cichlids have a suite of seven distinct cone opsin genes (SWS1 ~ UV, SWS2A ~ blue, SWS2b ~ blue, RH2B ~ blue-green, RH2Aβ ~ green, RH2Aα ~ green, and LWS ~ yellow-red) coding for distinct cone classes maximally sensitive to a particular wavelength of light, λ_{max} (Table 1). However, African cichlids typically express only three cone classes at a given time (Parry et al. 2005; Carleton et al. 2008), which also appears to be true for Neotropical cichlids (Escobar-Camacho et al. 2017). With the advancement of methodologies for measuring photoreceptor sensitivity, researchers were able to ask if there were differences in visual sensitivity between fish found in divergent ecological niches. For example, MSP was used to investigate differences in visual sensitivity between sand- and rock-dwelling Lake Malawi species, finding that species have divergent cone spectral sensitivities from each of these distinct habitats with distinct photic properties (Levine and McNichol 1979; Carleton and Kocher 2001). By combining data from MSP, opsin gene sequencing, and spectral analysis of reconstituted visual pigments, Parry et al. (2005) confirmed differences in the three cone classes expressed by several sand- vs. rock-dwelling cichlids from the Lake Malawi. For example, they found that the sand-dweller, *Tramitichromis intermedius* expressed three opsin pigments with the following λ_{max}: SWS2A = 455 nm, RH2Aα = 532 nm, LWS = 569 nm, while the rock-dweller *M. zebra*, expressed a different complement of cone opsins and associated λ_{max}: SWS1 = 368 nm, RH2B = 488 nm, RH2Aα = 533 nm. These differences in opsin expression would result in *T. intermedius* having a long-wavelength shifted spectral sensitivity compared to

Table 2 Common visual palettes of African and Neotropical cichlids

	Palette	SWS1	SWS2B	SWS2A	RH2B	RH2A[a]	LWS
African cichlids[b]							
Lake Malawi	Short	x			x	x	
	Middle		x		x	x	
	Long			x		x	x
Lake Tanganyika	Short	x			x	x	
	Middle		x		x	x	
	Long			x		x	x
Lake Victoria	Long			x		x	x
Neotropical cichlids							
Central America[c]	~long		x	x			x
Amazon Basin[d]	Long			x		x	x

[a] RH2Aα and RH2Aβ are combined here, following O'Quin et al. (2011)
[b] O'Quin et al. (2010)
[c] Fisher et al. (2015) (based on one species, *Amatitlania nigrofasciata*)
[d] Escobar-Camacho et al. (2017) (based on three species, *Pterophyllum scalare* (Angelfish), *Symphysodon discus* (Discus), *Astronotus ocellatus* (Oscar)

more short-wavelength sensitive vision in *M. zebra*. A pattern has emerged among African cichlids of specific subsets of three dominant cone classes being expressed together and further work has revealed that these subsets, or visual "palettes," can vary between species, sexes, and ontogenetically (Parry et al. 2005; Carleton 2009; Hofmann et al. 2009; O'Quin et al. 2010; Smith et al. 2011; Table 2).

Among Neotropical cichlids, the cone opsin gene complement has been characterized for only a few species to date: Trinidadian Pike cichlids (*Crenicichla frenata*) by Weadick et al. (2012); convict cichlid by Fisher et al. (2015); angelfish (*Pterophyllum scalare*), discus (*Symphysodon discus*), and the oscar (*Astrotnotus ocellatus*) by Escobar-Camacho et al. (2017). Among the Pike and Convict cichlids, these two species possess only a subset of the opsin genes found in African cichlids: SWS2A, SWS2B, RH2b, RH2a, and LWS (see Table 1 in Fisher et al. 2015). Fisher et al. (2015) determined that the Convict cichlid expresses a three-cone complement including SWS2A, SWS2B, and LWS opsins, which is a unique combination in comparison with the palettes typically expressed by African rift lake cichlids (Table 2). It also suggests long-wavelength sensitivity. A similar long-wavelength shifted palette (SWS2A, RH2a, and LWS) was discovered among the three Amazonian species examined by Escobar-Camacho et al. (2017). Interestingly, Härer et al. (2017) found evidence of shifts to more short-wavelength palettes in the Nicaraguan Midas cichlids that within the last few thousand years have colonized several clear crater lakes from the very turbid Lake Nicaragua. This limited data set suggests a reduced number of opsin genes in Neotropical cichlids (Fisher et al. 2015; Weadick et al. 2012). However, given the diversity of visual sensitivities found among cichlids as a whole, many more Neotropical species should be sampled before conclusions are drawn.

Collecting evidence for visual system sensitivity at the level of the retina or whole eye versus the photoreceptor is much more difficult and logistically limiting for large comparative studies, as it requires physiological tests of the response of photopigment cells to varying intensities and wavelengths of light in situ, using ERGs and CAPs. However, a few examples have helped us to better understand the processing of visual information in the cichlid eye. Lisney et al. (2010) used both of these methods to determine spectral sensitivity in Nile tilapia and compared their results to the MSP findings of Parry et al. (2005) and Carleton et al. (2008) for the same species. The electrophysiological studies largely matched the MSP findings (i.e., three dominant cone classes corresponding to SWS2, RH2, and LWS), although the ERG sensitivity peaks were somewhat long-wavelength shifted compared to earlier results, possibly due to differences in A1/A2 ratios in the specimens used for each study. The evidence for rare SWS cones was also stronger than from MSP studies, which found SWS cones to represent $<10\%$ of retinal photoreceptors (Parry et al. 2005). Sabbah et al. (2010) used data from whole organism ERG and opsin gene expression experiments that provided evidence of a pentachromatic visual system in cichlids (i.e., up to five cone classes interacting to determine color sensitivity). This was accomplished by modeling the results of each method for three Lake Malawi mbuna cichlids, *M. zebra*, *Melanochromis auratus,* and *Protomelas taeniolatus*. While the results of this study at first seem to suggest greater variation in visual sensitivity than previously discovered for cichlids, most earlier studies report the presence of more than three cone photoreceptors, but indicate these are typically rare, representing $<10\%$ of the total number of cone opsins expressed in the retina at a given time. The fact that those rare cones may contribute to visual sensitivity, as shown by the limited electrophysiological results (e.g., Lisney et al. 2010; Sabbah et al. 2010), is intriguing and requires further investigation. Additionally, evidence in *M. zebra* of coexpression of opsin genes within individual cones (Dalton et al. 2015, 2016), coincident with topographical variation in coexpression across the retina seems to support a more complex mechanism of visual sensitivity (Dalton et al. 2016).

Importantly, discovering the spectral sensitivity for a large number of cichlids has allowed us to specifically address questions about relationships between vision, the photic environment, and visual signals. We expect variation in sensory systems in animals found across divergent habitats, to accommodate predator avoidance, mating, and foraging (Endler 1992). Numerous studies have found that the sensitivity of vertebrate double cones, composed of mid-to-long-wavelength sensitive pigments in cichlids, tend to match the background photic environment (McFarland and Munz 1975; Loew and Lythgoe 1978; Lythgoe 1980; Loew and McFarland 1990; Cummings 2004; Dalton et al. 2014). In cichlids specifically, there is good evidence of visual sensitivity matching the photic environment and male nuptial coloration for a number of species (Carleton et al. 2006). For example, Seehausen et al. (2008) show a close correlation between visual sensitivities tuned via changes in amino acid sequences in opsin genes and male mating color in Lake Victoria cichlids; species with long-wavelength shifted sensitivity have red male nuptial coloration reflecting a longer wavelength signal. Fisher et al. (2015) also suggest that the LWS opsin found in Convict cichlids is tuned to the orange ventral patch found on females; however, further assessment of peak absorbance is still needed to confirm this (e.g., MSP, optomotor response). Additionally, UV sensitivity is important for discriminating zooplankton against light space (Utne-Palm 2002) and behavioral studies have corroborated this for some zooplanktivorous cichlids (Jordan et al. 2004; Hofmann et al. 2009).

Cichlids display the largest observed shifts in spectral sensitivity of any vertebrates, due largely to differential opsin gene expression and tuning of spectral sensitivity via changes in the amino acid sequences of opsin genes (Carleton 2009; Hofmann and Carleton 2009; Hofmann et al. 2009). Sensitivity of individual photoreceptors may be further tuned by coexpression of multiple opsin pigments within a single cell (Dalton et al. 2014, 2016). The extent of variation and lability in the visual sensitivity of cichlids has likely contributed to the adaptive radiation of cichlids.

4 Evolution of Cichlid Visual Systems

The recent and rapid radiation of cichlids in the African rift lakes is often linked directly with visual system diversity within this group (e.g., Terai et al. 2006; Seehausen et al. 2008; Brawand et al. 2014). The relative roles of natural versus sexual selection in shaping cichlid visual diversity are an area of intense research with many unanswered questions. It is likely that natural selection on visual sensitivity has played a large role in cichlid diversification, with sexual selection on male coloration leading to further speciation. Thus, recent work investigating sensory drive, or the process by which sensory systems and communication traits evolve for effective perception and appropriate responses (Endler 1992, 1993; Boughman 2002; Maan et al. 2006; Fuller et al. 2010), underscores the relevance of the light environment for effective visual communication. In this section, I review recent advances in our understanding of the contribution of sensory drive and spectral tuning to cichlid speciation.

4.1 Sensory Drive and Speciation

Sensory drive is a hypothesis for the evolution of divergent sensory traits that may contribute to speciation (e.g., Endler and Basolo 1998; Boughman 2002; Seehausen et al. 2008). Using vision as an example for this hypothesis, across different light environments (e.g., clear water vs. tannin-stained water) visual systems and signaling cues are expected to diverge to maximize efficient communication, potentially leading to premating isolation if the two become linked. In one of the most complete examples of sensory drive promoting speciation in sympatry, Seehausen et al. (2008) demonstrated links between shifts in the λ_{max} of LWS opsins, ambient light, male nuptial color, and female preference for male nuptial coloration. They used a pair of sympatric sister species, *Pundamilia pundamilia* and *P. nyererei*, that express blue and red male nuptial color patterns, respectively, and are found at multiple islands in the Lake Victoria that vary with respect to shore slope and turbidity. As described above (Sect. 2.2), in clear water longer wavelengths of light attenuate with depth faster than short-wavelengths; however, under conditions of turbidity in which the photic zone is much more shallow, light underwater becomes red-shifted with depth as the higher energy photons of short-wavelength light (UV-blue) are scattered more by suspended particulates. Therefore, the combination of turbidity and depth creates gradients of red-shifted light at depth and more blue-shifted light along shallower portions of the slope. *P. pundamilia*, having blue-gray males, is largely distributed in the more blue-shifted shallow zones and *P. nyererei*, with yellow-red males, is predominantly found along deeper portions of the rocky slope in red-shifted light (Maan et al. 2006). From extensive previous research, incorporated with new work, Seehausen et al. (2008) established a suite of evidence pointing toward sensory drive as a likely hypothesis for speciation among these closely related species.

First, water clarity and hence ambient light varied across islands and with depth, creating photic slopes that differed in steepness (Seehausen et al. 1997; Seehausen et al. 2008). Second, among Lake Victoria cichlids there is typically only a single visual palette expressed, the long-wavelength palette of cone opsins (Table 2; λ_{max} for *Pundamilia* spp.: SWS2A ~455 nm, RH2A ~ 528 nm, LWS ~ 565 nm; Carleton et al. 2005); however, there is considerable variation in the coding sequence of the LWS gene among Lake Victoria cichlids (Terai et al. 2002, Spady et al. 2005). In fact, among Lake Victoria blue-red species pairs, the species with red male nuptial coloration have LWS λ_{max} values higher than those species with blue-gray males as would be predicted by a relationship between visual sensitivity and the photic environment (van der Meer et al. 1995; Carleton et al. 2005). Third, behavioral optomotor response tests demonstrated that *P. pundamilia* had lower detection thresholds in red-shifted water and vice versa for *P. nyererei* under blue-shifted light, suggesting that each species has a visual system tuned to the ambient light environment they inhabit (Maan et al. 2006). Finally, females were shown to prefer to mate with males with the same color as conspecific males. This suite of evidence points to sensory drive as the mechanism of speciation between sister species *P. pundamilia* and *P. nyererei* such that natural selection favors tuning of the visual systems to divergent light environments and sexual selection favors male nuptial coloration that takes advantage of the predominant ambient light. Further, among the islands where *P. pundamilia* and *P. nyererei* are found, there are different degrees of distinctness between them with respect to male nuptial coloration. Seehausen et al. (2008) therefore evaluated if the steepness of the environmental gradient, mediated here by water clarity and steepness of the rocky slope, contributed to divergence in the sensory and signaling systems of these fish, with the expectation that an intermediate slope would provide enough distinction between light environments for altered visual systems to improve visual detection thresholds and enough connection between populations for low migration to produce intermediate forms that are selected against (i.e., disruptive selection) (e.g., Schluter and Nagel 1995). Thus, Seehausen et al. (2008) demonstrate a case for speciation driven by sensory drive among Lake Victoria cichlids.

In Lake Malawi, the evidence for sensory drive as a mechanism for speciation is less clear despite (1) the relative clarity of the lake, (2) the diversity in visual palettes expressed among species, and (3) repeated evolution of color patterns throughout the lake. However, a phylogenetic analysis by Pauers et al. (2016), in which they compiled visual sensitivity, color pattern, and photic environment data for 39 Lake Malawi species, found a relationship between UV color pattern elements and UV sensitivity. Of the three typical color patterns (stripe, bar, solid), they found that UV reflective patterns in barred and solid-color species were correlated with short-wavelength sensitivity (i.e., expression of SWS1). In the species with horizontal stripes, there was little to no UV reflectivity and expression of SWS2 was most common. They did not, however, find a relationship between visual sensitivity and the photic environment, similar to the findings of Hofmann et al. (2009) and Dalton et al. (2010). This suggests that the barred color pattern with UV elements and UV sensitivity co-evolved, with UV patterning potentially evolving as a means of "private" communication for mating or species identification.

With the visual sensitivity of only a few Neotropical species characterized, there has not been a comprehensive study investigating a possible role for sensory drive in the relatively ancient radiations of Neotropical cichlids in Amazonian rivers (López-Fernández et al. 2010, 2013; López-Fernández 2021) nor the more recent crater lake radiations (Barluenga et al. 2006). Hauser et al. (2017) further found that among 101 Neotropical species examined for variation in the rhodopsin gene (functioning in dim or low light environments), those species from Central America appear to have accelerated rates of evolution compared to South American species. Given the parallel evolution of color morphs within the Nicaraguan crater lakes, and the recent colonization of these clear lakes, this may be an area ripe for further study. Additionally, Weadick et al. (2012) have found molecular evidence of positive selection on the SWS2B and RH1 (rod) opsins in the Trinidadian Pike cichlid; however, studies to determine which forces might shape selection have yet to be performed.

4.2 Spectral Tuning and Adaptive Radiation

Animals that rely on vision have visual systems that are tuned to the ambient light environment and background against which objects are viewed to optimize detection (Cronin et al. 2014). This can be accomplished in a number of ways including: (1) the presence of structures such as the *tapetum lucidum* within the eyes of some fish and other vertebrates that reflects light back into the retina under low light conditions; (2) differential topographic distribution of cone photoreceptors throughout the retina to take advantage of heterogeneous light space and for different ecological tasks (Temple 2011; Dalton et al. 2016); (3) pre-photoreceptor filtering of light; and, (4) tuning the specific spectral sensitivity of photoreceptors (i.e., spectral tuning) through molecular and differential expression mechanisms

(Carleton 2009). Cichlids of the African Great Lakes have served as a model for understanding the underlying mechanisms generating visual system diversity across vertebrates.

Pre-Receptor Tuning

Several pre-receptor tuning mechanisms are found in cichlids. These can take the form differential refraction by crystalline structures or pigments in the lens or through oil droplets or carotenoid-based pigments in the inner segment of the photoreceptor cell (Cronin et al. 2014). In Lake Malawi mbuna, Dalton et al. (2010) report species-specific variation in lens transmission (i.e., T_{50}: the wavelength at which transmission of light through the lens reaches 50%). For example, solid blue *Metriaclima callainos* have $T_{50} = 360$ nm whereas *Melanochromis heterochromis*, with a horizontally striped color pattern, have $T_{50} = 400$ nm, thereby blocking most short-wavelength UV light from reaching the retina. Interestingly, *Met. callainos* expresses the SWS1 opsin while *Mel. heterochromis* expresses the longer wavelength SWS2B opsin, suggesting a link between pre-filtering media, photoreceptor sensitivity, and male nuptial coloration as described in Pauers et al. (2016). The relationship between lens transmission and opsin expression was further confirmed in a much larger sample size of 65 Lake Malawi species, with SWS1 expression corresponding with lens transmittance of UV light, SWS2B (violet) expression having a mixed result of lens transmittance between 360 and 400 nm, and those species expressing SWS2A (blue) generally displaying $T_{50} = 400$ nm (Hofmann et al. 2010a). In general, the presence of amino acids found in the lens typically filters short-wavelength light (Thorpe et al. 1993; Hofmann et al. 2010a). The patterns emerging with respect to the adaptive capacity of Lake Malawi cichlid vision is intriguing in that there appear to be strong links between UV-sensitivity coupled with lenses that transmit UV light, foraging behavior such as planktivory that is optimized by having UV sensitivity, and male nuptial coloration that uses UV reflective patterns to signal privately to conspecifics (Dalton et al. 2010; Hofmann et al. 2010a, b; Pauers et al. 2016). In this case, natural selection appears to be driving visual sensitivity, with male sexual communication taking advantage of this trait.

Spectral Tuning

Spectral tuning of visual sensitivity is the process by which sensitivity of photoreceptors is tuned to particular wavelengths (i.e., shifts in peak wavelength of maximum absorbance). There are several known mechanisms by which animals can tune spectral sensitivity to optimize vision in a given environment. The major mechanisms for tuning spectral sensitivity take place at the photopigment level, either through coding sequence changes in the opsin gene that alter the function of the protein, or via regulatory factors that alter opsin gene expression (Carleton 2009).

Research in Karen Carleton's lab (University of Maryland, College Park) has spearheaded much of the most recent advances in understanding the mechanisms underlying tuning of spectral sensitivity and correlating these processes with functional diversification, adaptive evolution, and speciation (Carleton 2009; Carleton et al. 2016). As an example, Hofmann et al. (2009) examined approximately 60 cichlid species from Lake Malawi ($n = 54$ wild-caught) and Lake Victoria

($n = 11$ lab reared) to test if changes in opsin gene coding sequences, differential opsin gene expression, and correlations between spectral sensitivity and various ecological parameters such as trophic position and ambient light environment can help explain the proximate mechanisms driving adaptive radiation in African cichlids. This work was prompted by a large suite of evidence from cichlids that directly links differences in opsin gene coding sequences with visual sensitivity tuned to match the ambient light environment (e.g., Lake Victoria: Terai et al. 2002, 2006; Carleton et al. 2005; Seehausen et al. 2008; Lakes Malawi and Tanganyika: Sugawara et al. 2005) and the fact that African cichlids have a complement of seven cone opsin genes that can be differentially expressed (e.g., Carleton and Kocher 2001; Spady et al. 2006; Carleton et al. 2008; Shand et al. 2008; Hofmann and Carleton 2009; Table 1). Hofmann et al. (2009) found that cichlids from deeper and relatively clear Lake Malawi had a higher diversity of visual profiles, or palettes, compared to a single expression profile in shallow, turbid Lake Victoria (Table 2). Lake Malawi cichlids tended to express three distinct visual palettes that span the spectrum from a short wavelength-sensitive palette, a medium (or middle) wavelength sensitive palette, and a third visual profile with expression of the longer-wavelength sensitive opsins. Lake Victoria cichlids, on the other-hand only expressed a single visual palette in the long-wavelength end of the spectrum. Additionally, they showed that Lake Malawi species with high SWS1 (UV) opsin expression were more likely to be planktivores and algae eaters and that Lake Victoria species had LWS opsins tuned to longer-wavelength as expected in the shallow and turbid waters of that lake. Importantly, their work showed that functional changes in the amino acid sequence of opsin genes operated in fine-scale tuning (shift in λ_{max} of 5–10 nm) at the extreme ends of the visual spectrum (e.g., SWS1 and LWS genes) where gene expression is bounded by available genes. Tuning by differential opsin expression, on the other hand, operates at a coarser scale among the middle wavelength opsins, creating 30–100 nm shifts in peak absorbance. Hofmann et al. (2009) comprehensive study demonstrated that both sequence variations in the opsin gene and differential cone opsin expressions are adaptive and play a role in generating the incredible diversity of visual systems within these two cichlid radiations (also see Hofmann and Carleton 2009). Evidence from multiple studies suggests natural selection has acted on cichlid opsin genes in all three African great lakes (Sugawara et al. 2002; Spady et al. 2005). Lake Tanganyika is similar to Lake Malawi in that it is relatively deep and clear with a generally broad-spectrum photic environment and contains the most diverse group of cichlids among the three African Great Lakes (e.g., Salzburger et al. 2002). O'Quin et al. (2010) discovered that Lake Tanganyikan cichlids also express the three common visual palettes found in Lake Malawi cichlids (Table 2) and suggest that the long-wavelength visual palette is likely the ancestral state, with repeated evolution of factors controlling the expression of the short- and middle-wavelength sensitive palettes.

Carleton et al. (2010) tested the mechanistic basis of spectral tuning using a rearing experiment. Two intergeneric crosses (*Dimidiochromis compressiceps* × *Copadichromis eucinostomus*, *Tramitichromis intermedius* × *Aulonocara baenschi*) between species that express different subsets of opsins were reared under controlled laboratory conditions to determine if opsin gene expression in cichlids is controlled by one or two genes. If only a few genes are involved in regulating opsin expression, thus providing some ease of lability, cichlids may be able to rapidly tune spectral sensitivity if the light environment shifts. Both cis- and trans-regulatory elements were involved in the regulation of cone opsin expression, with high correlation between some single and double cone opsin genes (Carleton and Kocher 2001), providing a possible explanation for why the three visual palettes typically observed are quite common (Hofmann et al. 2009). Furthermore, Schulte et al. (2014) have discovered a specific transcription factor (RX1) that controls SWS2A expression. They found a 413 base pair deletion in the RX1 gene of species that do not express SWS2A. Of the three SWS opsins, SWS2A has the longest λ_{max} and is found in all three of the African Great Lakes.

Ontogenetic Shifts in Sensitivity

There is also evidence in cichlids that expression of cone opsins can change throughout ontogeny and that ambient light may influence this process. For example, Nile tilapia shifts from having short-wavelength sensitive opsin palettes to long-wavelength sensitive palettes through development (Spady et al. 2006; Carleton et al. 2008). In another rearing study, Hofmann et al. (2010b) tested for plasticity in opsin expression by comparing across five Lake Malawi species reared in the laboratory under an UV-absent photic rearing environment with the known cone expression of adults from the wild. They found species-specific responses to being reared in an UV-absent environment, with expression of SWS1 downregulated (but still present) in some species, and with no response in other species, confirming a major role for genetic control of cone opsin expression (see Carleton et al. 2010) and some evidence for a plastic component. Another experiment suggests that the spectral sensitivity of adult African cichlids can change within as little as 3 days (Nandamuri et al. 2017). In this study, the authors' exposed wild-caught adults to UV deficient laboratory lighting, and lab-reared fish to high-UV lights, finding rapid shifts in SWS1 expression, suggesting that rapid, plastic responses to variation in the lighting environment are possible. Coexpression of opsin genes may also contribute to spectral tuning. Opsin coexpression can occur either by having two or more opsin proteins expressed within a single photoreceptor cell or by having multiple cones expressing different opsins (Dalton et al. 2014, 2016). The effects of coexpression on visual perception (i.e., neural processing and behavioral response to visual stimuli) remain to be tested, although advances are being made (Dalton et al. 2016).

4.2.1 Adaptive Radiation

If spectral sensitivity is adaptive, then there should be a direct link between shifts in peak absorption and behavioral detection thresholds to different photic environments. This link has been established in a number of cichlid species, including *Pundamilia* spp. from Lake Victoria as described above (Maan et al. 2006), and more recently by Smith et al. (2011) for Lake Malawi cichlids. In the latter study, Smith and coauthors tested the optomotor response of two Lake Malawi species, *Met. lombardoi* and *Mel. auratus*, that were each reared under different photic environments. They found that rearing environment influenced cone opsin expression and behavioral detection thresholds; specifically, fish that expressed relatively more LWS opsin had higher sensitivity to red (long-wavelength) light and fish that expressed relatively more RH2A and RH2B opsin were more sensitive to green (mid-wavelength) light. These tests, across multiple species from different lakes and lineages, provide a better understanding of the evolution of spectral tuning by differential opsin expression and sensory processing.

Given the diversity of available opsin genes, and evidence supporting directional selection on opsins, why do cichlids retain so many opsin genes? The answer may lie in a combination of spectral tuning across heterogeneous photic environments, and also in ontogenetic shifts in visual sensitivity. For example, Nile tilapia expresses all seven opsins throughout ontogeny, while only four opsin genes are expressed in adults. This suggests that subfunctionalization of opsin genes from the juvenile to adult state could help to maintain genetic diversity (Spady et al. 2006). The Neotropical cichlid, *Aequidens pulcher*, had reduced number of SWS photoreceptors under blue light, suggesting that excess light in one region of the spectrum can lead to reduced sensitivity in that area of the spectrum (Kröger et al. 1999; Wagner and Kröger 2005). This finding is counter to the findings from Lake Victoria cichlids that have higher long-wavelength sensitivity in red-shifted environments, thus maximizing sensitivity in the predominant range of photic environment, highlighting the variability in sensory systems among cichlids and the need for more comparative work between Neotropical and African lineages. An extreme case of reduction in visual sensitivity comes from the blind cichlid fish, *Lamprologus lethops,* of the Congo River (Schobert et al. 2013). In this species, the eyecups are present but found underneath the layers of skin and connective tissue and are much reduced in size compared to a sympatric and putative sister species, *L. tigripictilis*. While Schobert et al. (2013) were able to distinguish rod photoreceptor cells in the retina of *L. lethops*, their methodology did not provide information about cone photoreceptor cells, restricting interpretation at this time to *L. lethops* having light sensitivity and further investigation to determine if they have color and image-forming vision.

Despite the extreme variation in photic environment in South and Central American riverine habitats where cichlids are ubiquitous (e.g., “black,” “white,” and clear rivers), there has been little to no work done to examine the links between spectral sensitivity, photic environment, and behavior in the Neotropical lineage. There is great potential both in Amazonian rivers and in the crater lakes of Central America for this kind of work. In one direct comparison of African and Neotropical cichlid vision evolution, Schott et al. (2014) examined the evolution of rhodopsin (responsible for dim light, scotopic vision) among cichlid lineages, examining both ecological (riverine, lacustrine) and biogeographical (Neotropical, African) factors as drivers of RH1 diversification. A follow-up study by Torres-Dowdall et al. (2015) incorporated lacustrine Neotropical cichlids to the Schott et al. (2014) analysis, both studies finding evidence of positive divergent selection in both radiations, with stronger selection in lacustrine than riverine cichlids, and stronger selection in

African than Neotropical cichlid radiations. Additionally, Escobar-Camacho et al. (2017) suggest that their finding of a dominant long-wavelength opsin palette expressed by cichlids found in the more turbid waters of the Amazon supports the role of visual environment in selecting for spectral tuning.

We now have multiple lines of evidence that help us to better understand the proximate mechanisms driving the evolution of visual diversity among cichlid fishes: (1) tuning of spectral sensitivity by both amino acid substitutions and differential opsin gene expressions, each tuning to different parts of the visible spectrum and at different scales, and coexpression of opsins in the retina and within photoreceptor cells (Dalton et al. 2016); (2) genetic and plastic control of opsin expression; (3) only a few genes involved in regulating opsin expression; (4) at least one gene (Rx1) identified as controlling the expression of a short-wavelength sensitive opsin (SWS2A); and, (5) evidence of functionality of shifted spectral sensitivity selected by behavioral detection thresholds (Maan et al. 2006; Smith et al. 2011) as well as by sensory-driven mate choice preferences (Seehausen et al. 1997, 2008). This evidence stems largely from studies on African rift lakes studies, highlighting the need for more research on the visual ecology of other cichlid lineages.

5 Cichlid Vision and Human-Induced Environmental Change

The classic work by Seehausen et al. (1997) describes how an altered visual environment contributed to the loss of potentially hundreds of endemic Lake Victoria cichlids. Increased turbidity, either through eutrophication or increased sedimentary inputs, is cited as one of the most detrimental forms of habitat degradation leading to loss of aquatic biodiversity globally (Kemp et al. 2011; Gray 2016). It is important to note that many cichlids, especially those Neotropical species found in the extremely turbid waters of parts of the Amazon River, have likely evolved under high turbidity and/or tannin-stained conditions. However, it is the increase over natural levels induced by human activities in and around water that is concerning, especially for cichlids that have evolved and rapidly speciated in relatively clear water.

5.1 Lake Victoria Eutrophication

While the direct physiological effects of increased turbidity, such as reduced aerobic capacity due to clogged or abraded respiratory structures (e.g., Sutherland and Meyer 2007; Gray et al. 2016), can negatively impact survival of fishes, the alteration to the visual environment has greatly impacted cichlid diversity. The rapid loss of cichlid diversity in Lake Victoria is the most famous example.

Eutrophication of the southern basin of Lake Victoria starting in the ~1920s led to an approximately 50–60% decrease in water clarity in parts of the lake (Hecky 1993) and continues unchecked today with further deforestation, agriculture, and urbanization surrounding the lake. Eutrophication altered the underwater spectral composition such that less light and a narrower spectrum of light that is long-wavelength shifted dominated the visual scene. While eutrophication coincided with the introduction of the predatory Nile perch (*Lates niloticus*), and perch are likely responsible for the loss of a large number of Lake Victoria cichlids (Ogutu-Ohwayo 1990; Kaufman 1992; Witte et al. 1992; Kaufman and Ochumba 1993), their invasion does not completely explain the disappearance in a 10-year period of many of the ~200 rock-dwelling species that are rarely eaten by Nile perch. Seehausen et al. (1997) compiled a suite of evidence from mate-choice experiments in the laboratory, laboratory-rearing studies, surveys of cichlid species diversity and color differentiation across a transect of rocky islands accompanied by characterization of the underwater light environment to test the hypothesis that decreased availability of light and a shift in the underwater photic environment to longer-wavelength light due to eutrophication contributed to the loss of cichlid species. As mentioned above, sister species and morphs in Lake Victoria tend to have male nuptial color patterns at opposite ends of the visible spectrum, with pairs of species/morphs having a blue-gray male and a yellow-red male. In brief, the authors found that under broad-spectrum lighting, females prefer to mate with conspecific males; but under monochromatic light that masks male color, females mate indiscriminately. In many Lake Victoria insipient species pairs, pre-copulatory mate choice is the only form of reproductive isolation, therefore indiscriminate mating in the absence of appropriate color clues would lead to the breakdown of isolation. Indeed, Seehausen et al. (1997) found a positive correlation between the number of cichlid species and the distinctness of color morphs with water clarity and breadth of the light spectrum, suggesting that as water clarity decreases (and light becomes more monochromatic) so does the sexual selection pressure maintain differences between morphs and species pairs. The multiple lines of evidence exposed in this study demonstrate a strong relationship between human-induced disturbance of the visual environment and loss of species diversity. Since the decline in Lake Victoria Nile perch abundance in the 1990s, resurgence in haplochromine populations has been observed (see Natugonza et al. 2021). Interestingly, several studies investigating recovering cichlids have found correlations between turbidity and less colorful hybrids (e.g., Mrosso et al. 2004; Witte et al. 2013), confirming that even without being exacerbated by the Nile perch introduction, eutrophication would likely have resulted in great diversity loss.

5.2 Compensatory Responses

Organisms facing human-induced rapid environmental change are often lost, while others are able to adapt and so persist (Sih et al. 2011). Further work on Lake Victoria cichlids has demonstrated morphological adaptation of visual sensory structures since the eutrophication of the lake. Using historical (1978) and contemporary (2001) collections of two zooplanktivorous haplochromines (*Haplochromis pyrrhocephalus*, *H. tanaos*), van der Meer et al. (2012) assessed visual resolution and sensitivity based on relative lens and photoreceptor size and distribution of cones in the retina, respectively. Both species had reduced eye size in contemporary relative to historical populations likely resulting in reduced resolution, but with retinal adaptations that preserved photon capture and thus sensitivity. They also found a reduction in the density (in some cases complete loss) of single cones, suggesting a loss of sensitivity to shorter wavelengths (recalling that single cones in African cichlids are always from the SWS class of cone photoreceptors). In a darker and long-wavelength shifted environment, the benefit of short-wavelength sensitivity for detecting zooplankton against a broader spectrum background space light would be lost.

Compensatory behavior to counteract reduced visual range is also possible. For example, Gray et al. (2011) used a split-brood rearing experiment wherein fish from two divergent populations (one clear and one turbid) were reared under clear and turbid conditions, to determine if the Egyptian mouthbrooder, a widespread haplochromine cichlid of the Nile River Basin, responds to changes in water clarity. We found an increased rate of aggressive displays toward a conspecific competitor under increased turbidity, regardless of population of origin or rearing environment. In another study, we found repeated divergence in male nuptial coloration of wild-caught *P. multicolor* across habitats that vary in turbidity (McNeil et al. 2016). Together these data suggest a labile behavioral response to rapid changes in the visual environment and potential color matching associated with development under different photic environments; however, visual sensitivity and the long-term consequences of exposure to increased turbidity remain to be tested in this species. As another example, using a manipulative field experiment in southern Lake Malawi, Gray et al. (2011) showed immediate responses of the mbuna community to artificially increased turbidity. In this experiment, fish shifted behavior from territorial defense to foraging in a matter of minutes upon addition of a turbidity slurry from the surface (mimicking potential runoff, for example, during heavy rain). Again, the long-term consequences of increased turbidity in Lake Malawi and other relatively clear lakes are not certain, though the story of Lake Victoria is a likely scenario should, for example, Lake Malawi suffer more severe land-use changes and urbanization in the future.

Cichlids, and many other fishes, rely primarily on vision for those activities (e.g., mate choice and foraging) that promote reproduction and survival; however, multimodal communication is often an integral part of these processes. We may, therefore, expect that when faced with human-induced environmental change of the photic environment, reliance on visual cues may decrease while other sensory modes compensate (van der Sluijs et al. 2011). For example, sound production and audition may be used to choose mates in turbid waters when visual color cues are compromised. African cichlids from Lakes Malawi, Tanganyika, and Victoria have been shown to use sound production in several social contexts, including dominance hierarchies and courtship (e.g., Amorim et al. 2004, 2008; Smith and van Staaden 2009; Verzijden et al. 2010; Maruska et al. 2012; see Lobel et al. 2021). Smith and van Staaden (2009) studied the combined use of visual and auditory cues in several Lake Malawi mbuna, finding intra- and interspecific variations in the use of both modes simultaneously (multimodal) vs. in isolation (unimodal). Several Lake Victoria species (*P. nyererei*, *P. pundamilia*, *and Neochromis onmicaeruleus*) also have males that produce species-specific sounds during courtship and aggressive displays (Verzijden et al. 2010). In the blind Congo River cichlid, *Lamprologus lethops*, diminished and covered eyes are accompanied by significantly enlarged lateral line pores, possibly indicating a sensory adaption to low or no light conditions (Schobert et al. 2013). We are only beginning to understand the role of multimodal signaling in a reproductive context in cichlids under natural conditions, and work is therefore required to determine how this might influence the persistence of species in human-altered environments (van der Sluijs et al. 2011). Evidence from other lineages suggests that fish can compensate for altered visual regimes but with unclear consequences. As an example, in threespine stickleback from eutrophied areas of the Baltic Sea, olfactory compensation in visually compromised environments provides an alternative indicator of male quality for females choosing mates (Heuschele et al. 2009). However, choice experiments revealed that the direction of sexual selection changes when visual cues are diminished and females use olfactory cues to choose a mate, thus potentially shifting the evolutionary trajectory of the population.

Compensatory behaviors, the use of alternate sensory modes, or plastic spectral tuning may provide means for cichlids to cope with alterations to the underwater visual environment; however, the long-term consequences for diversity are not yet understood, especially with more rapid, severe, and long-lasting changes to the environment. The stability of environmental change may be an important consideration for future research. If cichlids can compensate in the short term, will they have the adaptive capacity to persist in the long term? Evidence here, for example, from the extreme diversity loss with increased algal turbidity in Lake Victoria, is not promising; however, perhaps the ability of some species to alter coexpression of cone opsin genes dependent on the light environment during development (Dalton et al. 2015) and use behavioral compensation (Gray et al. 2012) suggests that some species may have the adaptive capacity to deal with rapid alterations to the light regime and persist in colorful forms.

6 Future Research

In this review, I have only presented illustrative studies rather than fully reviewed the cichlid visual ecology literature in its entirety. Research seems to be published frequently regarding cichlid fishes, their vision, and evolution; however, as the work synthesized above demonstrates, the potential for further investigation using this system is enormous. Here, I elucidate some of the possible avenues for future research that have emerged from this review.

1. *Comparative analyses of African and Neotropical cichlids:* One of the most striking areas lacking research on the evolution of visual ecology across the Cichlidae is the geographic disparity in research between African cichlids and Neotropical cichlids. I could find only a few studies that fully examined the opsin gene complement of Neotropical cichlids. The rhodopsin studies by Schott et al. (2014), Torres-Dowdall et al. (2015, 2017), and Hauser et al. (2017), and the examination of opsin gene assemblages and expression in Amazonian species (Escobar-Camacho et al. (2017), are among the first in making broader comparative analyses exploring visual system evolution across the Cichlidae. More comparative work of this kind on the expression of cone opsins and associations with light environment and communication signals could benefit the field by generating new hypotheses about adaptive divergence under different visual backgrounds.
2. *The impact of rare cone photoreceptors:* What contribution do rare cone photoreceptor classes in the retina make to visual sensitivity? Small differences in the output from MSP and rtQPCR studies and electrophysiology studies suggest the possibility that rare cone types might play an important role in cichlid vision. However, we need to know more about these rare cones, for example, if they are transient with respect to social status, sex, or developmental stage? Or are they distributed in such a way within the retina that enhances color discrimination from a particular direction (see Dalton et al. 2016)?
3. *How fast can spectral tuning take place?* Color change in cichlid males switching dominance ranks can occur in a matter of seconds and is a physiological color change, whereas longer lasting, morphological alterations to body color that are controlled by a few (e.g., 4–7) genes in cichlids, are therefore likely less labile than opsin gene expression and can result in large (30–100 nm) shifts in peak sensitivity. It would be interesting to know how quickly shifts in spectral sensitivity via changes in cone opsin expression can occur within an individual, especially in light of rapidly changing light environments. Additionally, further understanding of the role of coexpression of opsins as a mechanism for rapid alteration to visual sensitivity is needed.
4. *What role does plasticity play in coping with altered photic environments?* Plastic responses to altered environments are known to contribute to the adaptive capacity of species. There is some evidence of plasticity in spectral tuning during development (Härer et al. 2017) and adult cichlids (Nandamuri et al. 2017), but future investigations focused on rapidly changing environments would be interesting for evolutionary studies and especially important for making species conservation projections given the changes to the underwater visual environment wrought by human activities in and around freshwater ecosystems.
5. *Multimodal communication in altered environments:* We know that some cichlids have the adaptive capacity to respond to human-induced alteration of the visual environment. Van der Sluijs et al. (2011) elucidated a number of questions that remain largely unanswered with respect to how sensory and communication systems will adapt to environmental change. They suggested a need to better understand how multiple sensory systems interact under altered conditions and if

different systems are as labile as others. One avenue for broadscale investigation would be to examine the diversity of opsin and olfactory genes (which is very large in cichlids; Nikaido et al. 2013) across environmental gradients. Simultaneous evaluation of different sensory modalities at the individual level may also be an area ripe for future research (Escobar-Camacho and Carleton 2015). Since current human-driven environmental change could shift environments out of the detection range for some senses and species, this is a critical area for further investigation (van der Sluijs et al. 2011) for species conservation.

7 Summary

Our understanding of the evolutionary ecology of cichlid vision has increased greatly over the last two decades. Roles of ecological and sexual selection in driving variation in opsin gene expression associated with different light environments and visual signals have been explored, with work on cichlids providing a model for sensory ecologists in general. However, research exploring the links between signal reception, processing, and behavioral response is still needed to fully understand the mechanistic basis for compensatory responses to altered visual environments. Given the extent to which freshwater systems are being altered by human activity, in particular increases in turbidity above natural levels from biotic and abiotic sources that alter the underwater photic environment, our improved understanding of the visual ecology of cichlids is essential for promoting the conservation of natural cichlid populations.

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The Mechanosensory Lateral Line System of Cichlid Fishes: From Anatomy to Behavior

Jacqueline F. Webb, Karen P. Maruska, Julie M. Butler, and Margot A. B. Schwalbe

Abstract The anatomy, neurophysiology, and behavioral roles of the mechanosensory lateral line system of cichlid fishes are reviewed. The lateral line system of cichlids shares fundamental anatomical features characteristic of all bony fishes and is composed of cranial lateral line canals, a trunk canal (or canals) containing canal neuromasts, and superficial neuromasts on the skin of the head, trunk, and tail. Cichlids typically have narrow cranial lateral line canals, but several genera have reduced or widened canals. A single, continuous trunk canal, which is common among bony fishes, is rare among cichlids, which typically have a disjunct trunk canal (or variations thereof) that is otherwise rare among other teleost families. Lateral line neuroanatomy and neurophysiology is well known in only a small number of cichlid species that serve as models for the study of the neuroethology of feeding and social behavior. The ability to study cichlids in the field and in the laboratory and carry out genetic and genomic analyses of complex phenotypes provides unique opportunities for novel integrative studies of the behavior and sensory ecology of these extraordinary fishes.

J. F. Webb (✉)
Department of Biological Sciences, University of Rhode Island, Kingston, RI, USA
e-mail: Jacqueline_webb@uri.edu

K. P. Maruska
Department of Biological Sciences, Louisiana State University, Baton Rouge, LA, USA
e-mail: kmaruska@lsu.edu

J. M. Butler
Department of Biological Sciences, Louisiana State University, Baton Rouge, LA, USA

Department of Biology, Stanford University, Stanford, CA, USA
e-mail: jmbutler@stanford.edu

M. A. B. Schwalbe
Department of Biological Sciences, University of Rhode Island, Kingston, RI, USA

Department of Biology, Lake Forest College, Lake Forest, IL, USA
e-mail: schwalbe@lakeforest.edu

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1 Introduction

The mechanosensory lateral line system is found in all fishes (and in larval and adult aquatic amphibians). Unlike the olfactory, visual, and auditory systems, which are defined by a bilateral pair of complex sense organs on the head (see Stiassny and Alter 2021; Schulz-Mirbach and Ladich 2021), the neuromast receptor organs of the lateral line system are distributed in stereotyped patterns within pored lateral line canals (canal neuromasts) or on the skin (superficial neuromasts) of the head, trunk, and caudal fin (reviewed in Webb 1989a). Effective lateral line stimuli are generated during social communication, by prey and predators, and they play roles in schooling, orientation (including rheotaxis), and obstacle avoidance behaviors (reviewed in Coombs and Montgomery 1999; Webb et al. 2008; Montgomery et al. 2014; Butler and Maruska 2016a).

Each neuromast receptor organ is composed of a sensory epithelium containing up to hundreds of sensory hair cells. Each hair cell has a single kinocilium (a true cilium) and multiple rows of actin-based stereocilia (stereovilli) located on its apical surface (the hair cell bundle, Fig. 1). Morphological and physiological polarization of a hair cell is defined by the relative position of the single kinocilium and the multiple rows of stereocilia. The opposing polarities of the hair cells within a neuromast (aligned 180° to one another) define a neuromast's single axis of best

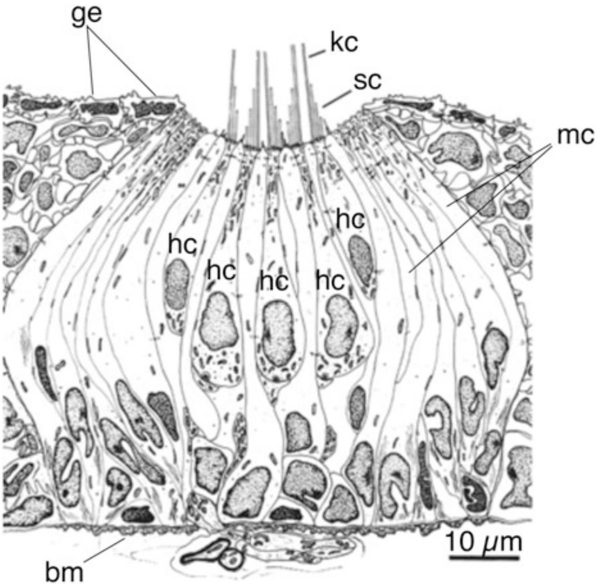

Fig. 1 A superficial neuromast in Nile tilapia (*Oreochromis* '*Sarotherodon' niloticus*) visualized with transmission electron microscopy. The neuromast sits in the epithelium (ge, general epithelial cells), above the basement membrane (bm). It is composed of hair cells (hc) each with an apical kinocilium (kc) and multiple stereocilia (stereovilli, sc), and mantle cells (mc) at the edge of the neuromasts. From Münz (1979), reprinted with permission of Springer Science Business Media

physiological sensitivity (Münz 1985; Lu et al. 1996). The mechanical linkage that exists between the hair cells and the gelatinous cupula, into which the hair bundles of all of the sensory hair cells project, enables a neuromast to respond to water flows (reviewed in Chagnaud and Coombs 2014; Van Netten and McHenry 2014). The cupula extends into the lumen of the lateral line canal (canal neuromasts) or into the water surrounding the body (superficial neuromasts; Fig. 1). Deflections of the cupula by viscous drag forces, which arise directly or indirectly from hydrodynamic (water flow) stimuli, bend the hair bundles of all of the hair cells simultaneously causing mechanically gated ion channels on the cilia to open. The magnitude and direction of the displacement of the ciliary bundles controls the amount of neurotransmitter released from the hair cells, which alters the firing rate of the primary afferent (sensory) neurons that compose the lateral line nerves and project to the lateral line centers in the hindbrain. In general, the lateral line system responds to unidirectional or low-frequency oscillatory stimuli (<1–~200 Hz) that originate from sources within only 1–2 body lengths from the receiver (Coombs and Montgomery 1999; Montgomery et al. 2014).

Here we review the anatomical structure, neurophysiology, and behavioral roles of the mechanosensory lateral line system of cichlid fishes. First, we examine the anatomical organization and structural diversity of the lateral line system, including morphology of the cranial and trunk canals, and the canal neuromasts and superficial neuromasts, among cichlid taxa (Sect. 2). We then review the neuroanatomy and neurophysiology of the lateral line system (Sect. 3), which have been studied experimentally in only a small number of cichlid species (oscar, *Astronotus ocellatus*, Nile Tilapia, *Oreochromis niloticus*, and the African cichlid, *Astatotilapia “Haplochromis” burtoni,* and the flavescent peacock cichlid, *Aulonocara stuartgranti*). We then explore the role of the lateral line system in cichlid behavior through a review of experimental work on feeding behavior (Sect. 4.1), social behavior (Sect. 4.2), and neural processing involved in some of these lateral line-mediated behaviors (Sect. 4.3). We conclude with suggestions for future study (Sect. 5).

2 Overview of the Anatomy of the Lateral Line System

The lateral line system of cichlids shares the fundamental anatomical features of the lateral line system of all bony fishes (Webb 2014a, b, 2020). It is composed of a series of cranial lateral line canals, a trunk canal (or canals) containing neuromasts, and superficial neuromasts found on the skin on the head, trunk, and tail. Canal pores link the fluid in the canals with the water surrounding the fish and are visible as perforations in the skin. The cranial lateral line canals are incorporated into an evolutionarily conserved subset of dermatocranial bones (e.g., frontal, nasal, dentary, and preoperculum; Fig. 2a–c) located within the dermis. On the trunk, the trunk canal is composed of a series of tubular canal segments that are incorporated into each of the lateral line scales, which overlap forming a continuous canal (Fig. 3;

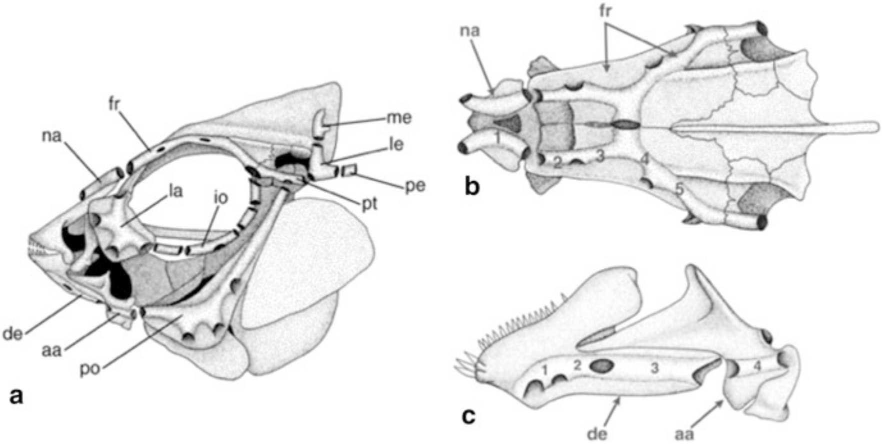

Fig. 2 Cranial canals and the trunk canal ("lateral line") in the convict cichlid, *Amatitlania nigrofasciata (= Archocentrus nigrofasciatus)*. (**a–c**) Skull indicating the pored lateral line canals that are integrated into dermatocranial bones. (**a**) Lateral view, showing supraorbital canal in the nasal (na) and frontal (fr) bones, infraorbital canals in the lacrimal (la) and series of tubular infraorbital bones (io), preopercular canal in the preoperculum (po), mandibular canal in the dentary (de) and anguloarticular (aa), otic canal in the pterotic (pt), supratemporal commissure in the lateral and medial extracapsular bones (le, me), and postotic canal in the posttemporal bone (pe). (**b**) Dorsal view showing the supraorbital canal in the nasal (na) and frontal (fr) bones. (**c**) Ventro-lateral view showing the mandibular canal in the dentary (de) and anguloarticular (aa) bones. Numbers indicate the location of canal neuromasts within the supraorbital (**b**) and mandibular (**c**) canals. (**a**) From Webb (2000) reprinted with permission of Academic Press/Elsevier, Inc. (**b**, **c**) from Tarby and Webb (2003), reprinted with permission of Wiley and Sons, Inc

Webb and Ramsay 2017). Canal neuromasts are found in predictable locations in the cranial and trunk canals, and superficial neuromasts have been found in linear series or clusters on the head (Peters 1973; Becker et al. 2016, see Sect. 2.1), or in association with the cranial and trunk canals ("accessory superficial neuromasts"; see Fig. 8).

Five cranial canal phenotypes are found among bony fishes (narrow-simple, narrow-branched, narrow with widened tubules, widened, and reduced, Webb 2014b, 2020). Narrow canals are typically uniform in diameter along their length and are well-ossified with small pores. Some fishes with narrow canals have canal pores elaborated into branched tubules that end in clusters of pores in the skin. Widened canals may vary in diameter, are not completely ossified, and have large pores overlaid by an epithelium pierced by smaller epithelial pores. They are found in only a small number of teleost families, which tend to be benthic or live at greater depths (Garman 1899; McAllister 1968), or in habitats that are light limited and/or experience lower levels of hydrodynamic noise (Coombs et al. 1988; Webb 1989b), or in waters with lower visibility or clarity (Branson and Moore 1962). These ecological correlates and the enhanced sensitivity of the large neuromasts in widened canals (Denton and Gray 1983, 1993; Van Netten and Van Maarseveen 1994),

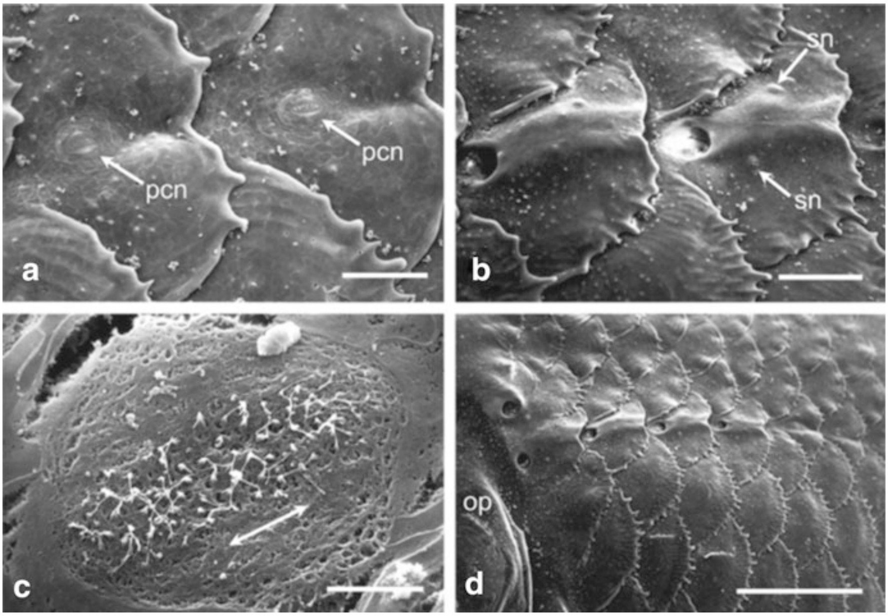

Fig. 3 Scanning electron micrographs of the developing trunk canal in the convict cichlid, *Amatitlania nigrofasciata (= Archocentrus nigrofasciatus)*. (**a**) Two lateral line scales prior to enclosure in a canal segment, showing presumptive canal neuromasts (pcn); (**b**) Two lateral line scales after the canal forms showing additional superficial neuromasts (sn); (**c**) Close-up of a presumptive canal neuromast from a; arrow indicates axis of best physiological sensitivity as determined by hair cell orientation; and (**d**) anterior end of the trunk canal (just caudal to operculum, op) showing overlapping scales

support the hypothesis that this phenotype is an adaptation for mediating behaviors in environments where high sensitivity to biologically relevant hydrodynamic stimuli (e.g., for prey detection and social communication) may provide an advantage. A reduced canal phenotype is defined by the presence of one or more incompletely formed canals or the lack of one or more canals, which leaves canal neuromast homologues on the skin (as superficial neuromasts). Fishes with reduced canals tend to live in hydrodynamically quiet habitats. Canal phenotype is diverse among cichlids, with narrow-simple, narrow-branched, widened, or reduced cranial canal phenotypes present among species (see Sect. 2.1). A recent quantitative analysis of the cranial lateral line canals among 52 phylogenetically and ecologically diverse Lake Malawi cichlid species (Edgley and Genner 2019) revealed a correlation between canal morphology and feeding habit thus suggesting an adaptive role for the lateral line system as a feature of the evolutionary radiation of these fishes.

On the trunk, there is typically one lateral line canal contained within the lateral line scales (e.g., Lippitsch 1990), but eight trunk canal phenotypes are found among bony fishes (Webb 2014b, 2020). Bony fishes more generally typically have a complete trunk canal, but a disjunct trunk canal is found in the vast majority of cichlids, and complete and reduced canals are found among only a small number of cichlid taxa (see Sect. 2.2).

Depending on their location on the head or trunk, canal, and superficial neuromasts are innervated by one of several lateral line nerves (anterior [ALLn], posterior [PLLn], and in some fish species, the middle [MLLn] lateral line nerve (Puzdrowski 1989; Northcutt and Bemis 1993; Piotrowski and Northcutt 1996; Northcutt et al. 2000). The cell bodies of the sensory (afferent) neurons that compose the lateral line nerves are found in ganglia outside of the brain that are distinct from those of the other sensory cranial nerves (e.g., Vth, VIIth, VIIIth, IXth, and Xth cranial nerves). The lateral line nerves project to the primary processing regions in the hindbrain and lateral line information is then transmitted to higher centers in the midbrain and forebrain. The peripheral and central neuroanatomy of the lateral line system has been studied in detail in only a few species of cichlids (see Sect. 3).

2.1 The Anterior (Cranial) Lateral Line System of Cichlids

Cichlids typically have a well-developed series of pored lateral line canals on the head (Fig. 2). As in other bony fishes, neuromasts are found in the epithelium in the floor of the canal, in positions that alternate with the canal pores, which are in the roof of the canal (Webb 1989b; Becker et al. 2016). Single canal pores typically occur along the length of a canal (e.g., Fig. 2), but clusters of pores may be present in the skin and are associated with individual canal pores beneath them (e.g., *Tilapia* spp. Peters 1973; pike cichlids, *Crenicichla*, Kullander 1991; *Heroina*, Kullander 1996).

Like other bony fishes, most cichlids have narrow cranial lateral line canals with relatively small pores (e.g., Fig. 2; Webb 2014b, 2020). These include most of the haplochromine cichlids of the East African Great Lakes (Greenwood 1981), *Tilapia* spp. (Peters 1973; Webb 1989b), *A. burtoni* (Butler and Maruska 2015), and New World cichlids such as the Rio Grande perch (*Cichlasoma cyanoguttatum*, Branson 1961), convict cichlid (*Amatitlania nigrofasciata* [=*Archocentrus nigrofasciatus, Cichlasoma nigrofasciatus*], Webb 1989b; Tarby and Webb 2003; Fig. 2), and the oscar (*Astronotus ocellatus*). Expanded canal pores are found in the lacrimal bone of some Lake Malawi (Webb and Kocher, unpubl. observ.) and Lake Tanganyika (Takahashi 2003) species that have narrow canals. The occurrence of expanded lacrimal pores in Lake Victoria haplochromines living at depths of >30 m (e.g., *Haplochromis pachycephalus*, *H. boops*, *H. thuragnathus*, *H. tridens*, *H. dolichorhynchus*, *H. decticostoma*; Greenwood 1967) suggests that flow stimuli can access the canal via these pores in order to stimulate canal neuromasts. Like widened canals (see below), expanded lacrimal pores would be particularly advantageous in low light environments in which nonvisual communication is likely important. Butler and Maruska (2015) have suggested that the expanded lacrimal pores in *A. burtoni* (which otherwise has narrow canals) may facilitate lateral line-mediated social communication (see Sect. 4.2).

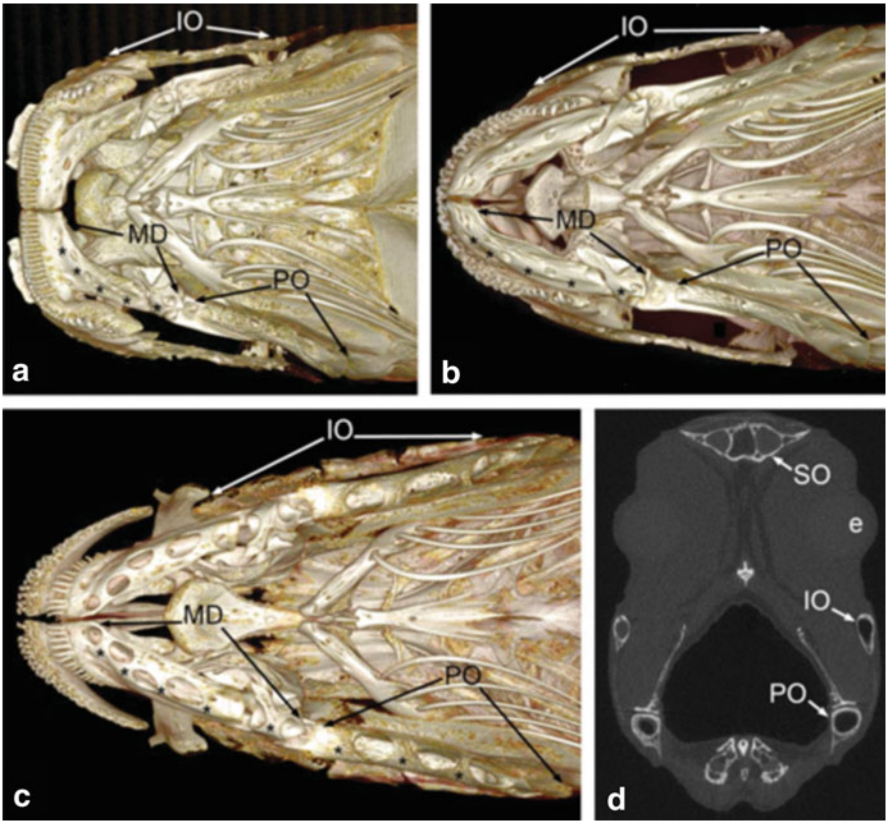

Fig. 4 3-D reconstructions (μCT) of cranial skeleton, in ventral view, showing the mandibular and preopercular lateral line canals in the mandible. (**a**) *Labeotropheus fuelleborni* (~80 mm SL, narrow canals; 18μm resolution). (**b**) *Metriaclima zebra* (~92 mm SL, narrow canals; 18μm resolution). (**c**) *Aulonocara baenschi* (86 mm SL, widened canals; 16μm resolution). The mandibular (MD), preopercular (PO), and infraorbital (IO) canals, indicated by the canal pores, are all visible. Asterisks (*) indicate the location of canal neuromasts within the MD canal, found within the dentary and anguloarticular bones of the mandible (A, B) and the canal neuromasts in the MD canal and the PO canal in the lower arm of the L-shaped preopercular bone (C). (**d**) Transverse slice (*Aulonocara baenschi*, 86 mm SL, 16μm thickness) at the level of the lens of the eye (**e**), indicating the lumen of the PO, IO, and SO canals. Webb et al. (2014a, b), reprinted with permission of John Wiley & Sons, Inc

In contrast to narrow canals, widened canals with large pores are rare among both bony fishes and among cichlids, in particular (reviewed in Webb 2014b, 2020; Figs. 4, 5, 6). In his chapter on *Haplochromis* spp. in Lake Turkana (formerly Lake Rudolf), Greenwood (1974) suggested that possession of widened ("hypertrophied," "inflated") canals in cichlids is an adaptation associated with deepwater habitats. In fact, widened canals have evolved convergently in cichlid species living in the deep waters of Lake Tanganyika (*Aulonocranus*, *Trematocara;* Fig. 7a), Lake Malawi (*Trematocranus, Alticorpus* [Pellegrin 1903; Stauffer and

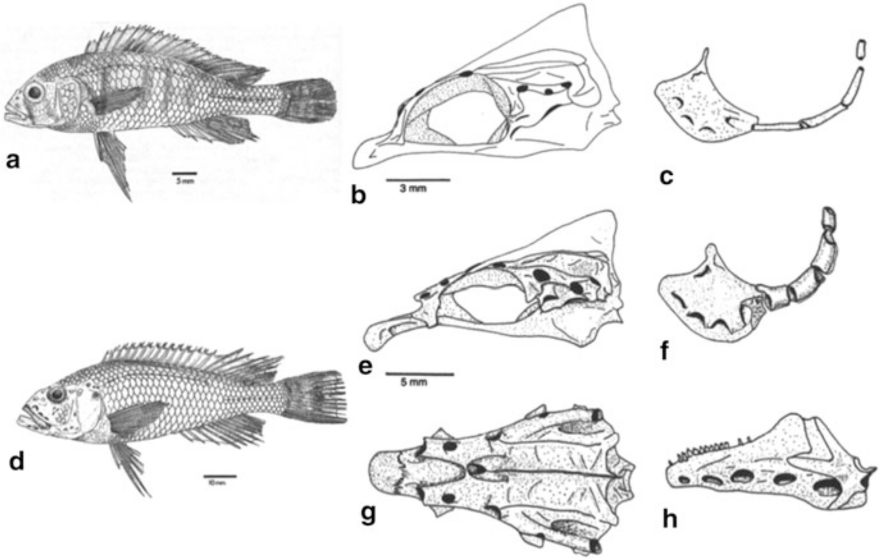

Fig. 5 Narrow and widened cranial lateral line canals in cichlids from Lake Rudolf. (**a–c**) *Haplochromis rudolfianus* (narrow canals, small pores); neurocranium (**b**) and infraorbital bones (**c**) in lateral view. (**d–h**) *Haplochromis macconneli* (widened canals, large pores); neurocranium (**e**) in lateral view, infraorbital bones (**f**) in lateral view, neurocranium (**g**) in dorsal view, and mandible (**h**) in ventro-lateral view. Note that both species have a disjunct trunk canal (**a**, **d**). From Greenwood (1974) © The Trustees of the Natural History Museum, London

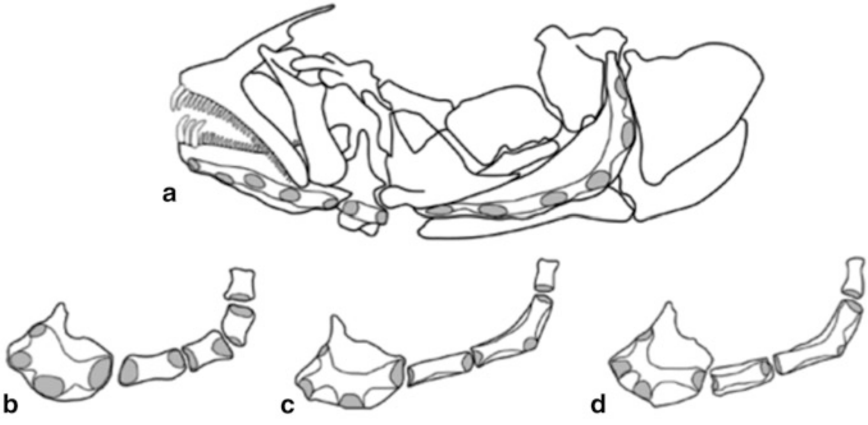

Fig. 6 Widened and narrow lateral line canals in *Teleogramma* species. (**a**, **b**) Cranial canals with large pores (gray) in *T. obamaorum* contrasted with the narrow canals with smaller pores (gray) in (**c**) *T. monogramma*, and (**d**) *T. brichardi*. Modified from Stiassny and Alter (2015)

McKaye 1988], and *Aulonocara* [Fryer 1959; Fryer and Iles 1972; Meyer et al. 1987; Konings 1990; Konings 2007]; Fig. 4c, d), and Lake Turkana (*Haplochromis macconeli*; Greenwood, 1974; Fig. 5). Greenwood (1974) reported that the widened canals in *H. macconeli* are comparable to those in *H. bullatus* (in Lake Albert) and *Aulonocara* spp. (generally at depths of <30 m depth, but some live as deep as 75 m in Lake Malawi, Grant et al. 1987), but are more pronounced than those in *Haplochromis* species living at comparable depths in Lake Victoria.

In Lake Malawi, fishes of the genus *Aulonocara* swim over sandy bottoms "scanning" for invertebrates living on or in sandy substrates (Konings 2007). This behavior was the basis for the assertion that their widened canals mediate prey detection (Fryer 1959; Fryer and Iles 1972; Konings 2007) and this has now been experimentally demonstrated in *Aulonocara stuartgranti* (see Sect. 4.1). Furthermore, some *Aulonocara* species live in caves or at depths of up to 75 m (Meyer et al. 1987; Grant et al. 1987), so their widened lateral line canals might also confer an advantage in nonvisual social communication (see Sect. 5.1). Interestingly, widened canals are not limited to cichlids living in the hydrodynamically quiet waters of the African Great Lakes. Widened "inflated" cranial lateral line canals have been noted in the riverine Malagasy cichlid, *Ptychochromoides katria*, which lives in still waters in large, deep, "boulder strewn" side pools of the Nosivolo River (Reinthal and Stiassny 1997). Widened canals are also found in cichlids in the Lower Congo River, which is characterized by dramatic rapids including high-velocity currents of >2 m/s (Jackson et al. 2009) and depths of up to 165 m. These include a blind (microphthalmic) cichlid, *Lamprologus lethops*, which is inferred to live in a deep canyon to at least 150 m (Schelly and Stiassny 2004; Schobert et al. 2012; Stiassny and Alter 2021) and *Teleogramma obamaorum*, a sexually monomorphic (thus likely nonvisual) molluscivore also thought to live in deepwater rocky habitats (Stiassny and Alter 2015; Fig. 6). Given the enhanced sensitivity of a widened canal system (Sect. 2), it is likely that these fishes live in relatively quiet microhabitats within the river, which is otherwise characterized by high levels of hydrodynamic noise.

The reduction of one or more of the cranial lateral line canals is characteristic of a relatively small number of cichlid taxa. Reduction of the infraorbital canal (and correlated loss of one or more of the infraorbital bones) is common among Lake Tanganyika species (Takahashi 2003; Takahashi and Koblmüller 2011; Fig. 7). Greenwood (1989) noted the loss or fusion of bones in the infraorbital series in lamprologine genera (including *Lamprologus*) and in *Nannochromis*. Most lamprologines have also lost the bones of the post-lacrimal infraorbital series (Fig. 7; Schelly and Stiassny 2004). In contrast, most Central and South American cichlids have a complete series of infraorbital bones, but the size and number of bones vary, likely due to bone fusions (Kullander 1989, 1990a), and others are characterized by reduction or absence of the last infraorbital bone (Cichocki 1976). The two diminutive species of *Biotoecus* (and closely-related *Taeniacara*) demonstrate the most extensively reduced cranial canal system among cichlids (Kullander 1989), which is consistent with a trend toward canal reduction in "miniature" teleost species (discussed in Webb 1989a). In *Biotoecus* spp. the lacrimal bone has three

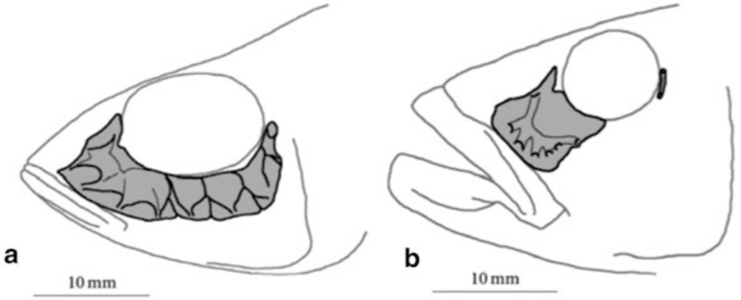

Fig. 7 Variation in infraorbital canal and bones. (**a**) Complete, but widened infraorbital series (gray) in *Trematocara unimaculatum* (Bathibatini), and (**b**) reduced infraorbital series (only infraorbital 1 [lacrimal] and infraorbital 6 are present, gray) in *Lepidiolamprologus profundicola* (Lamprologini). From Takahashi and Koblmüller (2011)

pores (instead of four, indicative of incomplete canal development) and the other infraorbital bones (and associated infraorbital canal segments) are absent. In addition, both species have an incompletely formed mandibular canal (composed of only 2–4 short canal fragments), and one also lacks the segment of the mandibular canal in the anguloarticular bone (at the posterior end of the mandible; Kullander 1989; also seen in *Mazarunia*, Kullander 1990b). Both *Biotoecus* species have completely lost or have incompletely formed cranial skeletal elements (and associated canals) at the posterior margin of the skull (e.g., extrascapulars; Kullander 1989).

Greenwood (1989) had stated that the reduction of the infraorbital canal in *Pseudocrenicichla* is a paedomorphic feature (e.g., a result of the slowing or cessation of canal development). He supported this assertion with observations of slowed canal development in *Pseudocrenicichla* compared to other taxa of comparable size that have more completely formed canals. Interestingly, in species within several genera (e.g., *Aulonocara*, *Labeotropheus*, *Metriaclima*, *Tramitichromis*) the portion of the infraorbital canal in the lacrimal bone forms early (at approximately the same time as the supraorbital and mandibular canals), but the portion of the infraorbital canal in the remainder of the infraorbital bones does not form for several weeks (Webb et al. 2014a, b; Bird and Webb 2014). This suggests that the reduction or loss of the post-lacrimal infraorbital canal is the result of paedomorphosis.

Several of the cranial lateral line canals are found in skeletal elements that play critical functional roles in feeding and respiration (e.g., preopercular canal and mandibular canal in the lower jaw). Cichlids are well known for the diversity of oral jaw morphology, which reflects their feeding habits (see Hu and Albertson 2021). For example, the blue mbuna, *Labeotropheus fuelleborni* (Fig. 4a) and the zebra mbuna, *Metriaclima zebra* (Fig. 4b) are distinguished by the morphology of their oral jaw apparatus, including differences in lower jaw length and width, which are attributed to directional selection with respect to feeding (Albertson et al. 2003; Albertson and Kocher 2006). However, Webb et al. (2014a, b) showed that, despite these differences, the diameter of the narrow mandibular and supraorbital canals and size of the canal neuromasts are not appreciably different. This study also showed that while mandible morphology in the Nkhomo-benga peacock, *Aulonocara baenschi* (Fig. 4c) appears to be similar to that in *M. zebra* and the number of mandibular canal neuromasts is the same, canal width and neuromast size diverge rather early in larval *A. baenschi* and *M. zebra,* to become the widened and narrow lateral line canals that are found in adults of these two species. Thus, the mandibular canal (and its canal neuromasts) and the lower jaw in which the canal is embedded appear to be able to evolve independently in response to what are presumed to be two sets of very different selection pressures (e.g., for sensory function and for biomechanical function, respectively). The ability of the lower jaw to evolve independently of lateral line canal morphology (*L. fuelleborni* versus *M. zebra*), and the ability of the lateral line canals (and neuromasts) to evolve independently of the bones of the lower jaw (*A. stuartgranti* versus *M. zebra*), require that the cranial lateral line canals be considered in analyses of integration and modularity in the skull of fishes, for which cichlids would be an excellent model system (Bird and Webb 2014).

In addition to the cranial canals, lines and clusters of small superficial neuromasts are found on the skin of the head (e.g., in *Tilapia* spp. Peters 1973; *Tramitichromis* sp. and *A. stuartgranti*, Becker et al. 2016; Fig. 8). For instance, in *A. stuartgranti* and *Tramitichromis*, superficial neuromasts are found in nine series, among which variation in neuromast number (single neuromasts or 2–20 neuromasts), morphology (round, diamond-shaped, grouping (in lines, clusters), and arrangement (parallel or perpendicular to the axis of the line of neuromasts) are found within an individual (Becker et al. 2016). The similarity in the placement of these series of superficial neuromasts in these two taxa, as well as in *Tilapia* (Peters 1973) suggests that the overall pattern of superficial neuromast distribution is conserved among some or all cichlids, but additional study is needed to assess this in detail.

2.2 The Posterior (Trunk) Lateral Line System of Cichlids

A single, continuous trunk canal, which is common among bony fishes, is rare among cichlids (Webb 2020). Only the New World genus *Cichla*, two African genera (*Teleogramma*, *Gobiocichla*), and some *Teleocichla* species are reported to have a complete canal (Fig. 9; discussed in Webb 1990). In contrast, most cichlids have a disjunct trunk canal, a phenotype that evolved convergently in only a few other non-cichlid percomorph families (reviewed in Webb 2014b). A disjunct trunk canal (Fig. 9) is composed of an anterior (dorsal or “upper”) portion and a straight posterior (ventral or “lower”) portion separated by a few scale rows (Webb 1989b, 1990). Haplochromines appear to all have a simple disjunct canal, but nine variants are found among cichlids (reviewed in Webb 1990; Fig. 9). These are defined by variation in the degree of overlap of the anterior and posterior portions of the canal

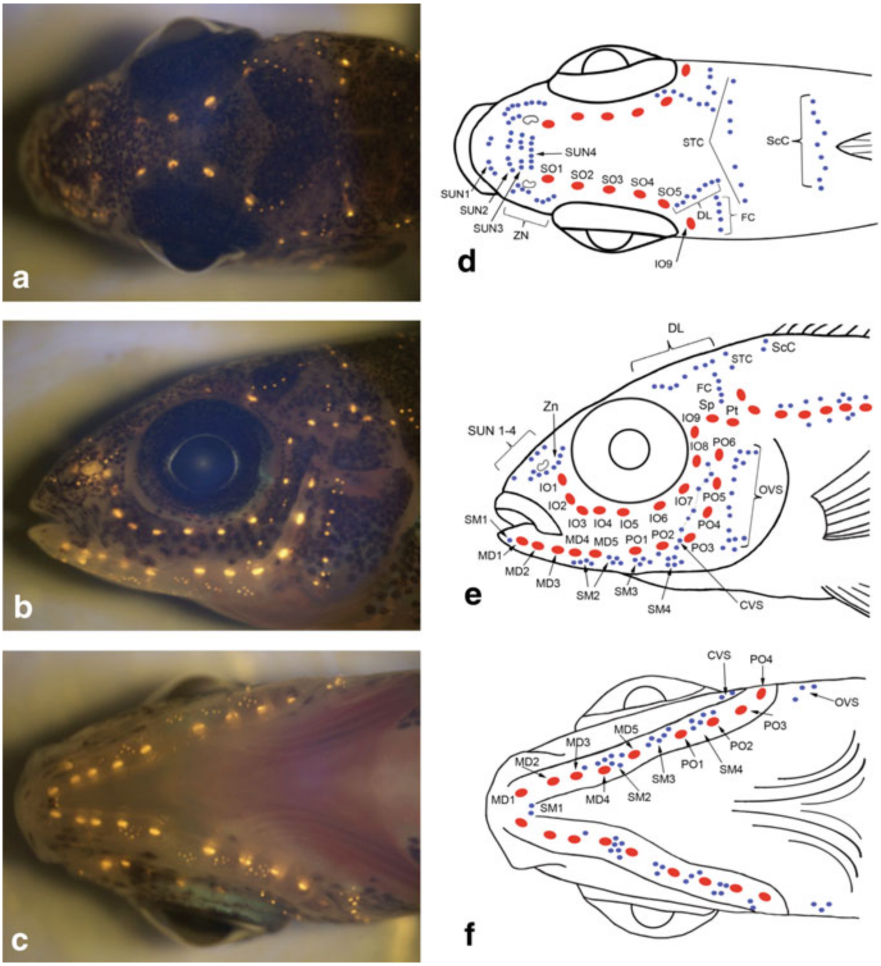

Fig. 8 Cranial neuromasts in *Aulonocara stuartgranti* in (**a**) dorsal, (**b**), lateral, and (c) ventral views of the distributions of canal and superficial neuromasts in a juvenile *A. stuartgranti* (31 mm SL) as revealed by vital fluorescent staining of mitochondria, which reveals the hair cells neuromasts (4-Di-2-ASP). Note: Canals are not visible and canal neuromasts are indeed larger than superficial neuromasts. On right, corresponding diagrammatic representations of canal (red) and superficial (blue) neuromasts based on fluorescent images of five individuals (99–154 dpf; 16–26 mm SL). Canal neuromasts (red) are numbered sequentially within a canal series (*SO* supraorbital, *IO* infraorbital, *PO* preopercular, *MD* mandibular). Superficial neuromasts (blue) are drawn larger than actual size for clarity and their names, based on location, are derived from Peters (1973). From Becker et al. (2016), reprinted with permission of John Wiley & Sons, Inc

(e.g., Fig. 9a–e). In genera with a broad caudal peduncle relative to body depth (e.g., *Hemibates*, *Bathybates*, *Plecodus*), the anterior portion of the disjunct canal continues to the caudal peduncle and the posterior portion of the canal may extend rostrally along the horizontal septum. In some genera, a third canal segment is added

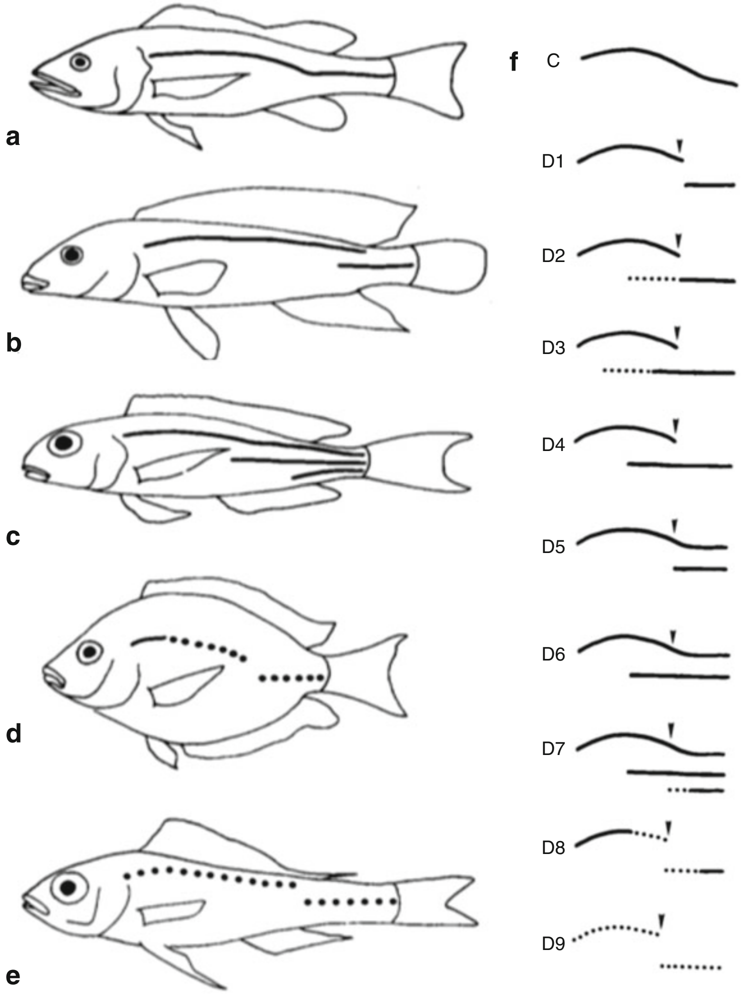

Fig. 9 Variation in morphology of trunk canals among cichlids. (**a**) *Cichla*, (**b**) *Julidochromis* (pattern *D3*), (**c**) *Xenotilapia* (*D7*), (**d**) *Etroplus* (*D8*), (**e**) *Biotoecus* (*D9*). (**f**) Trunk canal patterns—complete canal, *C* and variants on a disjunct canal, *D1–9*, found among cichlids. Lines = tubed scales, dots = pitted scales, which have been shown to house superficial neuromasts in some species. Arrowhead = point of overlap of the anterior and posterior portions of the disjunct trunk canal (or series of pitted scales) defined by the location of the posterior insertion of the dorsal fin. From Webb (1990), reprinted with permission of John Wiley & Sons, Inc

ventral to the posterior portion of the disjunct canal (*Grammatotria*, *Xenochromis*). In small or dwarf cichlids, the anterior and/or posterior portions of the trunk canal are partially or completely lost (*Etroplus*, *Trematocara*, some *Lamprologus;* Webb 1990; Fig. 9d), and are instead represented by a series of pitted scales. In *Biotoecus* (which also has reduced cranial lateral line canals; Sect. 2.1) the entire trunk canal is absent (Kullander 1989) and has been replaced by series of superficial neuromasts (presumably canal neuromast homologues) sitting in scale pits (Fig. 9e; Webb 1990).

The adaptive significance of the disjunct trunk canal in cichlids remains elusive. However, the neuromasts in the anterior and posterior portions of a simple disjunct canal are innervated by different branches of the posterior lateral line nerve (PLLn; Münz 1979) suggesting that a comparison of stimulus inputs from the two portions of the trunk canal may be behaviorally significant (see Sect. 3.1). The way in which a simple disjunct trunk canal pattern develops (Peters 1973; Webb 1990) can explain the evolution of the variants on a disjunct canal found among cichlids (Webb 1990). After neuromasts on the trunk differentiate from one or more migrating primordia (well-documented in zebrafish and a few other teleosts, e.g., Ghysen et al. 2014), lateral line scales form beneath each presumptive canal neuromast (Fig. 3). Then canal segments in each of these scales enclose the neuromasts, progressing in a rostrocaudal direction (as a complete trunk canal does in other fishes) and the canal segments that comprise the posterior portion of the canal (along the horizontal septum) develop in a caudorostral direction (*Tilapia* spp., Peters 1973; Webb 1989b, 1990). Thus, the degree of overlap of the anterior and posterior portions of the disjunct canal (Fig. 9) can be attributed to variation in the timing and extent of the development of the two portions of the canal (heterochrony, Webb 1990). Detailed comparative developmental studies (including the study of the migration of lateral line primordia in embryos and early larvae, as done in the zebrafish; discussed in Webb 2014a) are still needed to fully understand the diversity of trunk canal patterns found among cichlids is generated.

In addition to the canal neuromasts in the trunk canal, accessory superficial neuromasts are also found in the skin just dorsal to and ventral to the canal segment in each lateral line scale. These smaller superficial neuromasts have hair cells that are oriented either rostro-caudally or dorso-ventrally and often occur in “orthogonal pairs” (e.g., Webb 1989b, 1990; Fig. 10b). Thus, the neuromasts on the trunk are sensitive to water flow acceleration (canal neuromasts) as well as to flow velocity (superficial neuromasts) approaching from different directions. Some of these superficial neuromasts appear in larvae prior to canal formation, but others appear in the skin as the canal encloses around the canal neuromast (Peters 1973; Webb 1989b) and continue to increase in number.

Finally, neuromasts have been found on the caudal fin of cichlids. Tubed lateral line scales (“accessory caudal LL scales”), which presumably contain neuromasts, extend onto the caudal fin in most South American genera (e.g., Stiassny 1982; Kullander 1990a, b; Kullander and Staeck 1990). In other taxa, multiple lines of superficial neuromasts are reported to extend onto the caudal fin in the epithelium between fin rays (e.g., in *Tilapia*, Peters 1973; *A. nigrofasciata*, Webb 1989b, *A. burtoni*, Butler and Maruska 2015; *A. stuartgranti* and *Tramitichromis* sp., Fig. 10e, f).

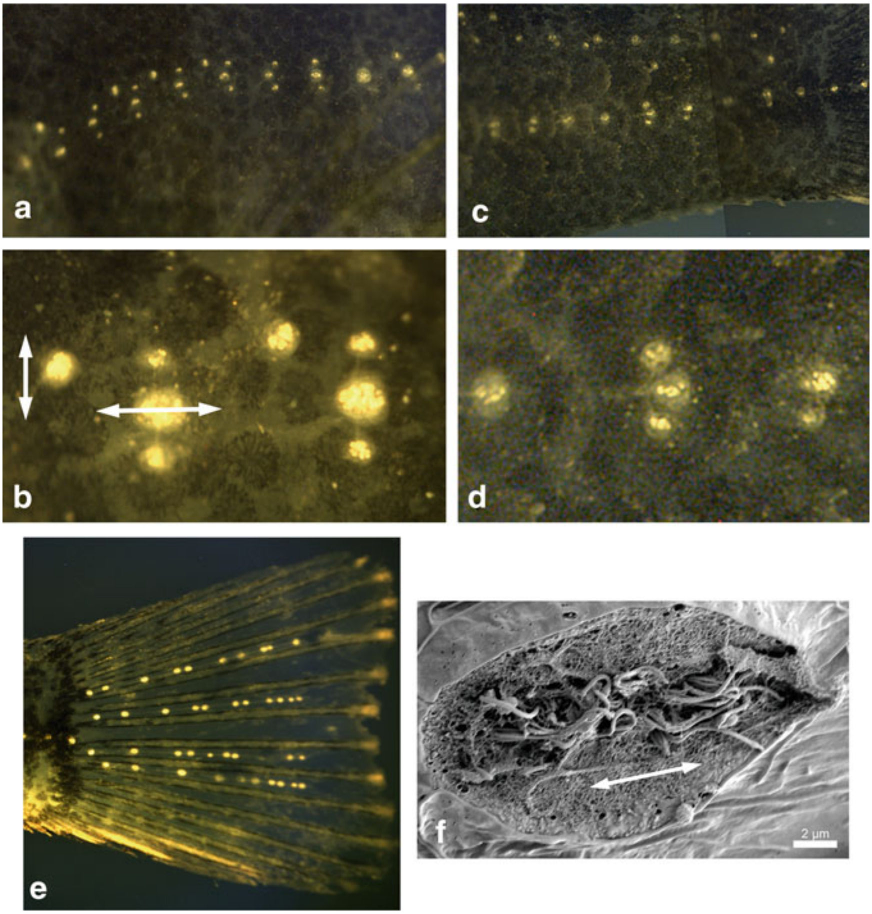

Fig. 10 Neuromasts on trunk and caudal fin of *Aulonocara stuartgranti* revealed by fluorescent staining of mitochondria in sensory hair cells (4-Di-2-ASP; e.g., see Becker et al. 2016). (**a**) Anterior portion of trunk canal with multiple neuromasts on each scale, overlying each myomere. (**b**) Enlargement of four neuromasts on each of two scales. The large central neuromast on each scale is the presumptive canal neuromasts (which will become enclosed in a canal segment), and the other neuromasts remain superficial. (**c**) Anterior (dorsal) and posterior portion of trunk canal on the caudal peduncle showing multiple neuromasts on each scale overlying each myomere (15 mm SL). (**d**) Enlargement of neuromasts on three scales in the posterior portion of the canal (as in **c**). The large central neuromast on each scale is the presumptive canal neuromast, and the other neuromasts will remain superficial. (**e**) Lines of superficial neuromasts on the caudal fin (13 mm SL). (**f**) Scanning electron micrograph of one neuromast on the caudal fin (as in **e**). Double-headed arrows (in **b**, **f**) = axis of best physiological sensitivity of hair cells

3 Neuroanatomy, Physiology, and Central Processing

Peripheral and central processing of hydrodynamic stimuli by the mechanosensory lateral line system has been explored in many species of teleosts, but few studies have specifically focused on cichlids. However, it is likely that the largely conserved features of the neuroanatomy and neurophysiology of the lateral line system among teleost fishes (see reviews by Boord and McCormick 1984; McCormick and Braford 1988; Bleckmann 2008; Bleckmann and Mogdans 2014; Chagnaud and Coombs 2014; Van Netten and McHenry 2014; Wullimann and Grothe 2014) are also found in cichlids. Using various teleost taxa, it has been shown that superficial and canal neuromasts differ with reference to many morphological, biophysical, and physiological response properties (Kroese and Schellart 1992; Van Netten and McHenry 2014; Chagnaud and Coombs 2014). While superficial and canal neuromasts clearly represent different sub-modalities of the lateral line system, their relative contributions to various lateral line-mediated behaviors has not been studied in any one fish species. A detailed discussion of physiological processing mechanisms in the peripheral lateral line system of teleosts is provided in several recent reviews (Chagnaud and Coombs 2014; Van Netten and McHenry 2014; Mogdans 2019). The results of the small number of neurophysiological studies that have focused on cichlids are highlighted below.

3.1 Peripheral Processing of Mechanosensory Information

Neuroanatomical and electrophysiological analyses of the trunk lateral line system have been reported in a seminal study of the Nile Tilapia (Fig. 11; Münz 1985). Afferent (sensory) neurons innervating the neuromasts on the trunk show spontaneous firing activity with different discharge patterns (regular, irregular, bimodal, silent; Fig. 11b), which are similar to those generated by lateral line afferents in other fishes (Coombs and Janssen 1990; Tricas and Highstein 1991; Kroese and Schellart 1992; Maruska and Tricas 2004). Afferents with irregular spontaneous activity were most common, and a positive relationship was found between spontaneous discharge frequency, sensitivity, and conduction velocity (Münz 1985). The larger diameter afferents that innervate the canal neuromasts have a higher discharge frequency and are more sensitive to hydrodynamic stimuli than smaller diameter afferents. These experiments also revealed that most canal neuromasts each form a separate functional unit, while superficial neuromasts arranged in a row on each scale are innervated by the same afferent nerve and function collectively as a unit (Fig. 11c; Münz 1985). Importantly, in *Tilapia* and other teleosts, single afferents innervate either canal neuromasts or superficial neuromasts, but not both, indicating that hydrodynamic information transmitted by these two sub-modalities arrives in the hindbrain via distinct projections. This study also revealed that canal and superficial neuromasts have different frequency sensitivities; canal neuromasts

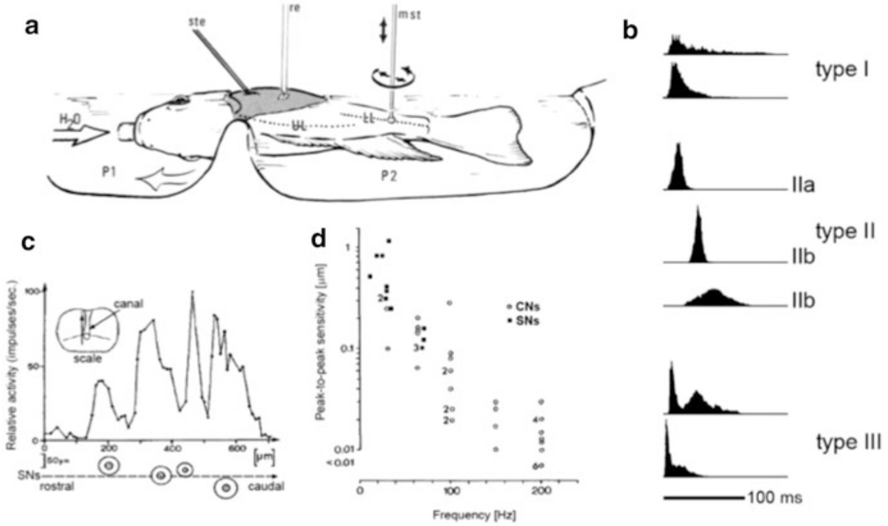

Fig. 11 Recordings from sensory afferent neurons of the lateral line system in Nile tilapia, *Oreochromis niloticus*. (**a**) Experimental setup for recording activity of afferent neurons innervating the trunk canal. The fish was restrained in a basin with two chambers (P1, P2). Arrows in the P1 chamber symbolize the stream of respiratory water. The shaded part of the trunk was above the water surface during the experiment. (**b**) Interspike-interval histograms of the spontaneous resting activity of afferents. Histograms were calculated from 500 consecutive impulses without stimulation. Typical distributions for neurons of types I (irregular), II (with subpopulations **a** and **b**; regular), and III (bimodal) are shown. (**c**) Activity of a primary afferent following stimulation of superficial neuromasts (SN) in the row parallel to the trunk canal using small water jets from a micropipette. Neuronal activity increases each time the water jet strikes a SN. SN arrangement along the scale (drawn in the lower part of the graph) was determined by staining after the experiment. The 1:1 correspondence of SN and activity peaks indicates that all neuromasts in the SN row parallel to the canal (see inset) are innervated by the same afferent neuron. Neural activity was normalized to 100 impulses/sec at maximum. (**d**) Center frequencies of afferents innervating SNs (closed squares) and canal neuromasts (CN, open circles) in relation to the absolute sensitivity of afferents at this frequency. Sensitivity is given as stimulus amplitude in peak-to-peak μm displacement required to obtain 20% modulation in response of afferents. Neurons with the same value are indicated by numbers placed beside the symbol. Abbreviations: *UL* upper trunk lateral line, *LL* lower trunk lateral line, *ste* electrode for electrical stimulation, *re* recording electrode, *mst* sphere for mechanical stimulation (arrows indicate directions of possible movement). Modified from Münz (1985), reprinted with permission by Springer-Verlag

respond best to higher frequency stimuli (~100–200 Hz) while superficial neuromasts respond best to lower frequencies (~10–70 Hz; Fig. 11d). In *Tilapia*, most afferents recorded from both canal and superficial neuromasts responded as acceleration detectors (Münz 1985), but subsequent studies in other fishes showed that canal neuromasts respond as acceleration detectors (expected frequency–response curve slopes of ~40 dB decade^{-1}) and superficial neuromasts function as velocity detectors (expected frequency–response curve slopes of ~20 dB decade^{-1}) (Kroese and Schellart 1992; Chagnaud and Coombs 2014). Finally, thresholds for afferent responses were ~0.01 µm (10 nm, peak-to-peak displacement) in *Tilapia*, which is similar to that for other teleosts and within the ranges for both behavioral responses to a vibrating sphere driven by a minishaker and hydrodynamic cues produced by live prey and other moving fish (Coombs and Janssen 1990; Coombs and Montgomery 1999; Hanke and Bleckmann 2004; Montgomery et al. 2014).

The ability to detect particle motion stimuli and discriminate between stimuli at different frequencies was examined in the oscar using behavioral and psychophysical analyses of unconditioned responses to dipole stimuli delivered by either a shaker table or a minishaker-driven vibrating sphere (Lu et al. 1996; Nauroth and Mogdans 2009; Mogdans and Nauroth 2011). In these studies, detection of particle motion stimuli could be mediated by both the lateral line system and the otolithic endorgans of the inner ear (saccule, lagena, and utricle), so the lateral line system was chemically inactivated (using gentamicin or cobalt chloride) to determine whether responses were mediated specifically by the lateral line system. However, the results indicated that the involvement of the inner ear during these discrimination tasks could not be entirely ruled out, because it is likely that both lateral line and auditory systems contribute to perception of particle motion stimuli. Nevertheless, these studies demonstrated a behavioral detection threshold of 5.9 nm peak-to-peak water displacement at the skin surface in response to a 100-Hz vibrating sphere (dipole stimulus, Mogdans and Nauroth 2011), and an even smaller, 1–2 nm displacement detection threshold using cardiac conditioned responses to stimuli generated by a shaker table. These values are within the range of detection thresholds (behavioral and neural) reported for other fishes. Mogdans and Nauroth (2011) showed that the oscar was also able to discriminate a 100-Hz stimulus from a 70-Hz (and lower) stimulus, and this frequency discrimination ability was maintained when fish were tested in turbulent water conditions (e.g., as in lacustrine vs. riverine habitats). The detection and discrimination abilities of the oscar were similar to those of the goldfish (*Carassius auratus*), which has well-developed narrow canals and a proliferation of neuromasts, in addition to a Weberian apparatus (bones connecting the swim bladder to the inner ear found in all otophysan fishes, but not in cichlids), which enhances pressure sensitivity and extends the frequency range of the inner ear (i.e., Nauroth and Mogdans 2009). There is also some evidence that the lateral line system mediates the Mauthner cell-mediated escape response in *A. burtoni* (Canfield and Rose 1996), a common behavior found across fish species (Medan and Preuss 2014). The ability of cichlids to detect nanometer-scale water displacements even in the presence of hydrodynamic noise highlights the opportunity for lateral line inputs to play a role in many behaviors that are critical for survival.

3.2 Central Processing of Mechanosensory Information

Mechanosensory input from the neuromasts is carried by the anterior (ALLn) and posterior lateral line (PLLn) nerves to the hindbrain. A middle lateral line nerve

(MLLn) innervates canal and superficial neuromasts in the post-otic region of the head in some fishes (Puzdrowski 1989; Northcutt et al. 2000), but has not been reported in cichlids. Central projection patterns of the various branches of the ALLn and PLLn are known in several teleost species (McCormick 1989; Weeg and Bass 2000; Tomchik and Lu 2005; Maruska and Tricas 2009; Wullimann and Grothe 2014), but this feature of lateral line neuroanatomy has been described in detail only in the pike cichlid (*Crenicichla lepidota*; McCormick 1983), the oscar (Meredith 1984), and the Mosambique tilapia (*Oreochromis mossambicus*; Kortje et al. 1991).

3.2.1 Hindbrain Input and Processing

In all teleosts studied to date, primary lateral line afferents terminate ipsilaterally (i.e., on the same side) in hindbrain nuclei, which are largely separate from the octaval nuclei where the eighth (VIII) nerve terminates (e.g., descending, DON; magnocellular, MgON; tangential, TON; and anterior, AON octaval nuclei). In the oscar, primary afferents of both the ALLn and the PLLn mostly project to the medial octavolateralis nucleus (MON) and caudal octavolateralis nucleus (CON), with some variation in termination patterns among different nerve branches along the rostro-caudal and dorso-ventral axes within these nuclei (Fig. 12; Meredith 1984). Primary lateral line nerve projections were also observed within the eminentia granularis of the cerebellum and in some regions of the corpus cerebellum. The rostro-caudal projection sites within these cerebellar regions were also directly related to the rostro-caudal locations of the neuromasts on the body surface (e.g., nerve branches innervating canal neuromasts on the head projected more rostrally in cerebellar regions than did nerve branches innervating neuromasts on the trunk). Terminal fields from afferent nerve branches innervating neuromasts of closely positioned canals (e.g., different canals on the head) also overlapped extensively in the hindbrain of the oscar, while those supplying distantly located canals did not (e.g., head canal versus trunk canal, which are innervated by the ALLn and PLLn, respectively) (Fig. 12). Thus, there is some evidence for at least a crude somatotopic representation of the lateral line periphery in the hindbrain of cichlids, which is also found in other teleosts (McCormick 1989; Wullimann and Grothe 2014).

In the pike cichlid, the lateral line nerves terminate in the MON, CON, dorsal portion of the magnocellular octaval nucleus (MgON), and lateral portion of the eminentia granularis (McCormick 1983). One interesting feature in the pike cichlid is the presence of a small fascicle of nerve fibers, the lateralis branchlet, which separates from the main PLLn and courses rostrally to enter the hindbrain along with the anterior portion of the eighth nerve (VIIIa; Fig. 13a). This branchlet terminates in the ventral portion of the MON and dorsal portion of the MgON, with ascending and descending tracts that also terminate in the MON, CON, as well as in the eminentia granularis. However, the functional significance of this lateralis branchlet is unknown.

The central projection sites of the lateral line and eighth (VIIIth) nerves do show some overlap in some cichlid species, suggesting that some integration of

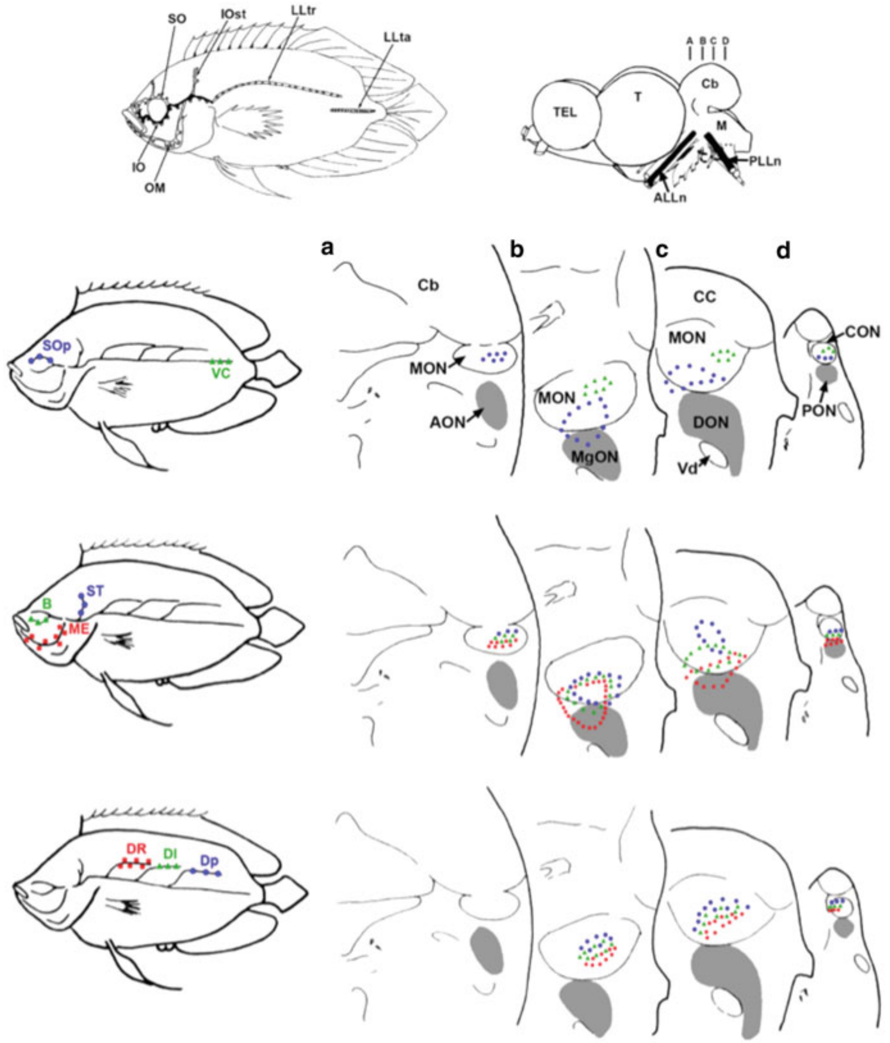

Fig. 12 Central projections of primary afferent neurons in the lateral line system of the oscar, *Astronotus ocellatus*. Lateral view of the fish is shown at left, with the lateral line nerve rami that innervate neuromasts in the vicinity superimposed on the drawing. Symbols over specific lateral line nerve branches on each drawing are used to indicate the corresponding terminal fields of those branches in the transverse sections of the hindbrain shown at right (**a–d**). Octaval nuclei that primarily receive auditory and vestibular inputs are shaded in gray (AON, DON, MgON, and PON) and lateral line nuclei are drawn in outline (MON, CON). Insets at top show a lateral view of the fish with the distribution of lateral line canals for reference (left side; surface pores are indicated with open circles), and a lateral view of the brain with the approximate locations of each transverse brain section (**a–d**) indicated (right side). Abbreviations: *ALLn* anterior lateral line nerve, *AON* anterior octaval nucleus, *B* ramus buccalis, *CC* cerebellar crest, *Cb* cerebellum, *CON* caudal octavolateralis nucleus, *DON* descending octaval nucleus, *DI* dorsal-intermediate ramus, *DP* dorsal-posterior ramus, *DR* dorsal-rostral ramus, *IO* infraorbital canal, *IOst* supratemporal subdivision of the infraorbital canal, *LLta* lateral line tail canal, *LLtr* lateral line trunk canal, *M* medulla, *ME*

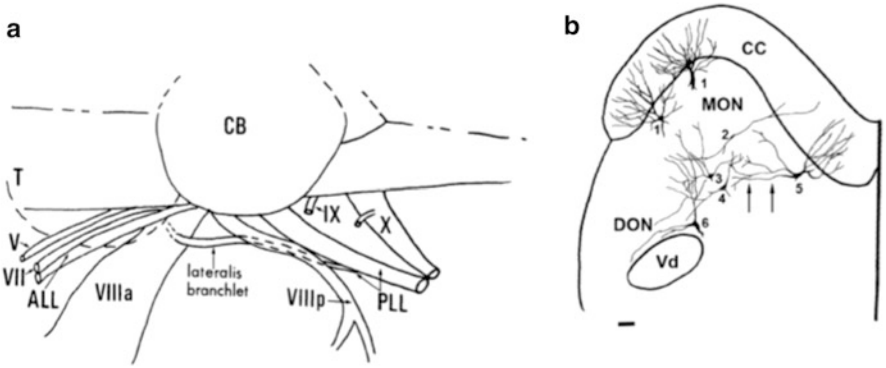

Fig. 13 Peripheral lateral line nerves in the pike cichlid (*Crenicichla lepidota*) and the octavolateralis region of the hindbrain in the oscar (*Astronotus ocellatus*). (**a**) Dorsal view of the caudal portion of the brain of the pike cichlid showing entry point of the lateral line nerves, other cranial nerves, and the location of the lateralis branchlet. Dashed line labeled "T" indicates the border of the tectum. Modified from McCormick (1983), reprinted with permission from Elsevier BV. (**b**) Diagram illustrating the neuronal morphology of cells in the octavolateralis processing region in the oscar brain, drawn as a composite from Golgi-impregnated transverse sections. Cells are labeled as follows: 1, Purkinje-like cells of the dorsal lamina with short ventral dendrites and dorsal extensions into the cerebellar crest (CC); 2, small spherical cell with dendrite penetrating the cerebellar crest; 3, Polygonal cell within the confines of the medial octavolateralis nucleus (MON); 4, Fusiform cell in the MON with some dendritic processes extending into the octaval column; 5, Purkinje-like cell with long ventral dendrites indicated with arrows; 6, Large cell of the descending nucleus of the octaval column (DON) with dorsal dendrites extending into the MON. Midline is to the right, and scale bar = 100μm. Abbreviations: *ALL* anterior lateral line nerve, *CB* cerebellum, *IX* glossopharyngeal nerve, *PLL* posterior lateral line nerve, *Vd* descending tract of trigeminal nerve V, *V* trigeminal nerve, *VII* facial nerve, *VIIIa* anterior ramus of the eighth nerve, *VIIIp* posterior ramus of the eighth nerve, *X* vagus nerve. Modified from Meredith (1984), reprinted with permission of John Wiley & Sons, Inc

octavolateralis (auditory, vestibular, and mechanosensory) information occurs in the primary processing regions in the brain. For example, in the pike cichlid, lateral line and eighth (VIII) nerve afferents both terminate in the dorsal region of MgON, while in the oscar there is overlap in the MgON, as well as in the PON, and DON. Furthermore, in the oscar, the lateral line afferent neurons terminating in the MgON are primarily from neuromasts on the head (Fig. 12). In addition, there are also neurons in the MON that extend dendrites into the more ventrally located octaval nuclei (e.g., DON), as well as octaval neurons with dorsal dendrites

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Fig. 12 (continued) ramus mandibularis externus, *MgON* magnocellular octaval nucleus, *MON* medial octavolateralis nucleus, *OM* opercular mandibular canal, *PLLn* posterior lateral line nerve, *PON* posterior octaval nucleus, *SO* superficial ophthalmic canal, *SOp* ramus superficialis ophthalmicus, *ST* ramus supratemporalis, *T* tectum, *TEL* telencephalon, *VC* ventral-caudal ramus, *Vd* descending tract of trigeminal nerve. Modified from Meredith (1984), reprinted with permission from John Wiley and Sons extending into the overlying lateral line terminal regions (e.g., MON) (Fig. 13b; Meredith 1984). While the overall significance of this overlap requires further study, it suggests there is some integration of auditory and lateral line information in the hindbrain, particularly in the MgON, which may be important for processing low-frequency stimuli at close range (Braun and Sand 2014). Interestingly, in larval Mozambique tilapia (15 days post-hatch), lateral line and eighth (VIIIth) nerve afferents already have overlapping projections in a region near the MgON as well as in the eminentia granularis (Kortje et al. 1991), which may be of functional significance for the ability of these young fishes to avoid predators, detect prey, and orient in their environment.

Physiological studies also provide evidence for functional overlap in lateral line and auditory systems. Several studies have used auditory evoked potentials (AEP = ABR, auditory brainstem response) to measure "hearing" thresholds of several cichlid species (Kenyon et al. 1998; Ripley et al. 2002; Ladich and Wysocki 2003; Smith et al. 2004; Maruska et al. 2012; see Schulz-Mirbach and Ladich 2021; Lobel et al. 2021). However, it is now known that at low stimulus frequencies ($\leq$100 Hz), both auditory and lateral line inputs likely contribute to these AEP responses (Higgs and Radford 2013, 2016). This provides additional evidence for the potential functional overlap of these two hair cell-based sensory systems.

In addition to the afferent nerve projections from neuromasts to the hindbrain, efferent cell bodies in the hindbrain project to the hair cells of the neuromasts in teleost fishes. This efferent system modulates the sensitivity of the lateral line system, particularly during self-generated movements such as swimming, and can also be influenced by stimuli from other senses (e.g., visual, somatosensory, vestibular, and mechanosensory [lateral line]; Roberts and Meredith 1989; Tricas and Highstein 1990, 1991; Koppl 2011; Chagnaud and Coombs 2014). The location of these efferent cell bodies has been determined in the Nile tilapia (Claas and Münz 1980). Efferent neurons in the octavolateralis efferent nucleus (OEN), situated along the ventral midline of the hindbrain, supplies the neuromasts, as in other teleosts (Roberts and Meredith 1989).

3.2.2 Midbrain and Forebrain Input and Processing

Lateral line information received by the primary lateral line centers in the hindbrain travels via ascending pathways to the "higher" centers of the brain for further processing and integration. These pathways have been studied with traditional tract-tracing techniques in several teleosts (reviewed in McCormick 1982, 1989; Wullimann and Grothe 2014), but not yet in cichlids. Ascending lateral line projections from the hindbrain terminate primarily in the ventrolateral portion of the torus semicircularis (TSvl) in the midbrain, with some projections to the deep layers of the midbrain tectum. Less is known about ascending projections to the diencephalic and telencephalic regions of the forebrain, but lateral line inputs to preglomerular regions (lateral preglomerular nucleus), the central posterior thalamic nucleus (CP), and the anterior tuberal nucleus (ATn) of the hypothalamus (midbrain) are found in several species (Wullimann and Grothe 2014). Electrophysiological recordings and tract-tracing studies in other teleosts also provide some evidence for processing of lateral line information in the pallial regions of the forebrain (lateral, central, and medial parts of the dorsal telencephalon; Dl, Dc, Dm; Yamamoto and Ito 2008; Bleckmann and Mogdans 2014; Wullimann and Grothe 2014). There is also evidence for integration of lateral line information with that from other senses (e.g., audition, vision, and somatosensation) in various midbrain, diencephalic, and telencephalic processing regions in some teleosts (Schellart 1983; Schellart and Kroese 1989; Braun and Sand 2014; Wullimann and Grothe 2014).

The analysis of patterns of immediate early gene expression indicative of neural activity is now being used as a novel, alternative approach to tract tracing for the identification of lateral line processing regions in the brain of cichlids. Butler and Maruska (2016b) used expression of the immediate early gene *cfos* as a proxy for neural activation (*cfos* expression is often related to neuron firing and transcription of downstream genes) to gain insights into which brain regions process socially relevant mechanosensory information in *A. burtoni*. Following forced territorial interactions, brain activation patterns were compared in dominant males with an intact lateral line system or in males in which the lateral line system was ablated. It was shown that in addition to known mechanosensory processing regions (i.e., MON, TSvl, and CP), several regions of the social decision-making network (SDMN, a collection of brain nuclei that includes the social behavior network and mesolimbic reward system hypothesized to mediate social decisions in vertebrates; O'Connell and Hofmann 2011) also received lateral line information that was important for opponent assessment during conflict resolution (see Sect. 4.2.1). This study provided evidence for processing of lateral line information in the anterior tuberal nucleus (ATn), lateral portion of the dorsal telencephalon (Dl), and the supracommissural nucleus of the ventral telencephalon (Vs), at least in the context of territorial interactions.

In summary, peripheral and central processing of lateral line information in the cichlid species examined thus far is similar to that described in other teleosts. Cichlids are sensitive to hydrodynamic stimuli with displacements in the nanometer range, and information on the source of environmental water motion stimuli is detected by superficial neuromasts and canal neuromasts whose sensory afferents project somatotopically to the octavolateralis regions of the hindbrain. As this lateral line information is relayed to higher processing centers in the midbrain and forebrain, its integration with inputs from other senses in decision centers provides the basis for lateral line-mediated behaviors such as feeding, predator avoidance, and social communication.

4 Lateral Line-Mediated Behaviors

When an animal moves underwater, it inevitably generates water flows that can be detected by the lateral line system of nearby fishes. For survival, feeding, predator avoidance, and reproductive behaviors are arguably the most important aspects of a fish's life. The lack of experimental data on the role of the lateral line system in behavior in cichlids (and in fishes more generally) is due in part to the difficulties in identifying and characterizing mechanosensory stimuli, and the inability to efficiently ablate the entire lateral line system without introducing toxicity effects or having impacts on other sensory systems. However, recent evidence provides data for the role of the lateral line system in feeding as well as in a wide range of social behaviors in several species of cichlids (see Jordan et al. 2021; Félix and Oliveira 2021).

4.1 Feeding Behavior

In many fishes, feeding behavior is mediated by not only the visual system and chemosensory systems, but by the lateral line system. The lateral line system detects hydrodynamic cues generated by the movement and respiratory currents generated by prey on the water surface, in the water column, or in association with the substrate (reviewed in Montgomery et al. 2014). In the absence of evidence to the contrary, cichlids are generally considered to be visual feeders given the importance of vision in other aspects of their behavior (Fryer and Iles 1972; see Gray 2021; Takeyama 2021). However, the lateral line system likely contributes to the detection of prey in certain cichlids, especially those species with widened cranial lateral line canals. For instance, *Tramitichromis* sp. is a diurnal visual feeder from Lake Malawi with narrow lateral line canals that feed on benthic invertebrates in sandy substrates by plunging its head in the sand and sifting out prey with their gill rakers from a mouthful of sandy sediment (Schwalbe and Webb 2014). In contrast, the peacock cichlids of Lake Malawi (*Aulonocara* spp.) have widened lateral line canals also feed on benthic invertebrates in sandy and muddy substrates, but employ a different prey detection strategy. They swim in short bursts and glide just above the sand, then direct strike at invertebrate prey submerged in the substrates that are detected with their lateral line system (Schwalbe et al. 2012).

The anatomy of the cranial lateral line system in *A. stuartgranti* (see Figs. 4, 8) suggests that this species detects flows generated by its benthic prey with the canal neuromasts in the ventrally facing mandibular, lower preopercular, and infraorbital canals, and perhaps with the clusters of very small superficial neuromasts located in the epithelium overlying the mandibular canal (see Fig. 8; Becker et al. 2016). However, as in other fishes, prey detection is likely influenced by a range of cues produced by prey (e.g., visually cues [static, motion], chemical cues [olfactory and gustatory]) in addition to hydrodynamic cues (Schwalbe and Webb 2014). In laboratory studies, *A. stuartgranti* was shown to locate prey (adult brine shrimp) at a range of light intensities and in the dark, preferring live (mobile) over dead (immobile) prey, thus suggesting the role of the lateral line system (Fig. 14a; Schwalbe et al. 2012; Schwalbe and Webb 2014, 2015). Analysis of prey detection behavior showed that when light was present *A. stuartgranti* used a combination of vision and lateral line cues to detect prey. In the dark, they used lateral line cues to

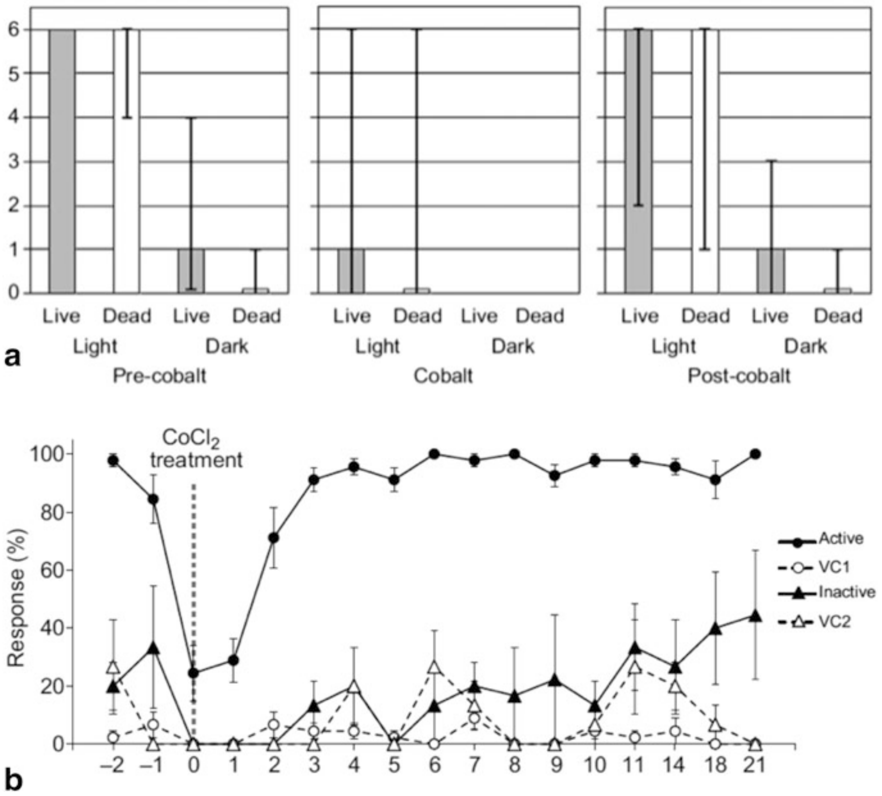

Fig. 14 Lateral line mediated feeding behavior in *Aulonocara stuartgranti*. (**a**) Number of strikes (median ± min/max) on live ($N = 6$) and dead ($N = 6$) adult brine shrimp. * = significant differences between number of strikes on live and dead prey ($P < 0.05$). (**b**) Percentage of responses by *A. stuartgranti* ($N = 5$ fish) to active and visual control 1 (VC1) holes (trials with flow; 4.8 mL min^{-1}), and inactive and visual control 2 (VC2) holes (in trials with diverted flow) before and after treatment with cobalt chloride ($CoCl_2$). Day 0 sessions were carried out within 2 hours of $CoCl_2$ treatment (vertical dotted line). Symbols represent the mean (± s.e.m.) response and bite response based on each fish's mean response to each hole type. From Schwalbe et al. (2012) and Schwalbe et al. (2016), reprinted with permission of Company of Biologists Ltd

detect live prey, but this ability was lost when their lateral line system was inactivated with cobalt chloride (Fig. 14a). The inability to detect prey in the dark when the lateral line system was inactivated suggested that chemical cues were insufficient to trigger prey strikes in the dark (Schwalbe et al. 2012). However, the absence of prey strike responses may have been due to the inactivation of the olfactory system by cobalt chloride (Butler et al. 2016). Nevertheless, the contribution of the lateral line system in prey detection by *A. stuartgranti* was further confirmed with the analysis of conditioned behavioral responses to artificial water flows in the absence of visual or chemical prey cues, and the extinction of these responses after inactivation with cobalt chloride (Fig. 14b; Schwalbe et al. 2016).

These studies provided the first experimental evidence for the sensory basis for prey detection in cichlids, the role of the lateral line system in particular, and the potential for nocturnal feeding in *Aulonocara* spp., all of which have important implications for our understanding of cichlid ecology.

4.2 Mechanosensory Signaling During Social Interactions

A potential role for mechanoreception in social interactions was suggested early on (Dijkgraaf 1933; Noble and Curtis 1939) given the interactions of blinded fishes with conspecifics, but little empirical data has been available for cichlids (or for teleosts in general) to demonstrate its importance. To date, only one study has directly tested the hypothesis that mechanosensory signaling is used for communication during social interactions in cichlids (Butler and Maruska 2015).

To understand the potential role of mechanosensory signals in communication during social interactions, it is first important to describe the behaviors producing water movements that can be detected by the lateral line system of nearby fish. Baerends and Baerends-van Roon (1950) described what they referred to as "signal movements," and of these, the majority are described, at least in part, as involving water being pushed at other fish. Work in other cichlid fishes further describes and classifies these behaviors (Fig. 15; Noble and Curtis 1939; Aronson 1949; Dijkgraaf 1963; Fernald 1977; Fernald and Hirata 1977; Munro and Pitcher 1985; Enger et al. 1989; Mackereth and Keenleyside 1993; Barlow 2000). For example, frontal displays, in which one individual pushes water at another individual with an open mouth and flared operculae (providing a visual stimulus) is performed by several cichlid species. The convict cichlid produces successive powerful body and tail movements that simultaneously produce large low-frequency (<10 Hz) velocity flows and higher frequency acceleration components of up to 100 Hz (Bleckmann et al. 1991) forming vortex streets (i.e., complex, three-dimensional hydrodynamic stimuli that can contain high-frequency components) that are detected by both superficial and canal neuromasts and are likely produced in other cichlids during typical close-range social behaviors (e.g., body quivers, frontal and lateral displays, chasing).

Lateral displays are commonly performed during territorial disputes. During a lateral display, one fish orients parallel to another, fully erects the dorsal, anal, and caudal fins, and distends its jaws to create a display suggesting a larger body size. While this is a visual signal related to size, several other species also generate mechanosensory stimuli by shaking their body during visual displays. This hydrodynamic information could provide additional information related to size or strength of the opponent based on the velocity of the generated water movements. Baerends and Baerends-van Roon (1950) noted that tail-beating accompanied many lateral displays and that the water movements created by this behavior could be seen by observers. Tail-fluttering, or the rapid elevation and depression of the tail, which also produces water movements, is seen in many cichlids during aggressive encounters

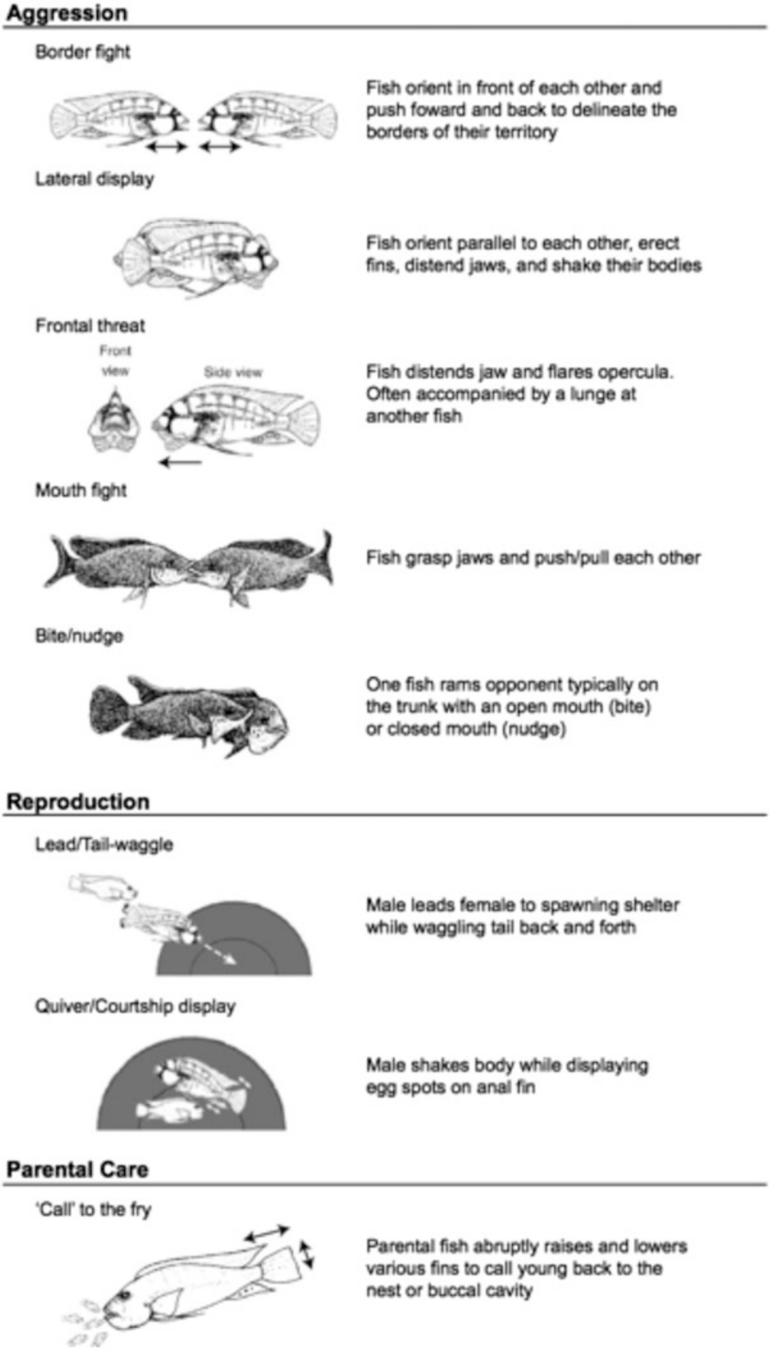

Fig. 15 Social behaviors in *Astatotilapia burtoni* and *Tilapia natalensis* (=*Oreochromis mossambicus*). During aggressive behaviors (border fights, lateral displays, frontal threats, mouthfights, bites, nudges, and butts), fish generate mechanosensory signals that can be detected

and in egg-laying behavior. Other common behaviors are biting and mouth-fighting, in which fish grasp the mouth of an opponent and push, pull, and turn their bodies. Although these behaviors produce tactile cues from direct physical contact, they also likely produce hydrodynamic signals that stimulate the opponent's lateral line system.

4.2.1 Role of Mechanoreception During Agonistic Behaviors

Studies of behavioral assessments including the use of game theory have shown that aggressive interactions in fishes are typically instigated by a lateral display and continue with the use of less-dangerous noncontact behaviors (Enquist et al. 1990; Leiser et al. 2004). As a fight escalates, fish resort to more dangerous contact behaviors, such as mouth wrestling and biting. In the convict cichlid, the number of lateral displays, frontal displays, and tail-beating all decreased during the duration of a fight, while contact behaviors (e.g., mouth fights and bites) stayed the same or increased (Leiser et al. 2004). The use of noncontact fight behaviors likely acts as a self-preservation technique because it allows fish to be more aware of their surroundings. For example, the South American goldeneye cichlid (*Nannacara anomala*) detects an approaching predator more slowly when engaged in contact behaviors compared with when they were engaged in noncontact behaviors (Jakobsson et al. 1995). Thus, the use of lateral line stimuli for mediating mutual assessment through the use of less-dangerous, noncontact behaviors could have overall implications for health, survival, and fitness.

Like males in other cichlid species, male *A. burtoni* are highly territorial and actively defend their spawning territories from other males using lateral displays (including body vibrations and tail-beating), frontal threats, border fights, lunges, chases, mouth fights, and biting (Fernald 1977). As previously mentioned, these behaviors produce mechanosensory signals that can be detected by the lateral line system of the opponent. When mechanosensory capabilities are impaired (via ablation with cobalt chloride or by severing the posterior lateral line nerves), male *A. burtoni* alter their use of noncontact versus contact social behaviors (Butler and Maruska 2015; Fig. 16a). During a typical agonistic interaction used to acquire a novel territory, males instigated a fight using a lateral display and then used predominately noncontact aggressive behaviors. However, males whose lateral line system had been ablated, predominantly used contact behaviors, indicating a shift in behavioral strategy, thus highlighting the importance of mechanoreception in the use of less dangerous noncontact fight behaviors (Fig. 16b). This strategy could

Fig. 15 (continued) by the lateral line system of their opponents and other nearby fish. Male *A. burtoni* (and many other cichlids) court gravid females by quivering their body and leading females back to the spawning territory while waggling their tails. Parents will "call" their young back to the nest or mouth by raising and lowering their tail fins. From Butler and Maruska (2016a), reproduced with permission by Company of Biologists Ltd

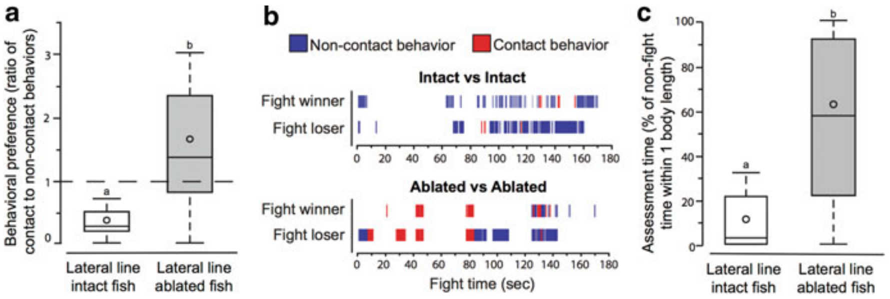

Fig. 16 Use of the mechanosensory lateral line system during aggressive interactions in *Astatotilapia burtoni*. (**a**) Males with an intact lateral line system use predominantly noncontact aggressive behaviors while males in which the lateral line system is ablated use contact fight behaviors. Ratio < 1 (below dashed line) signifies predominant use of noncontact behaviors and > 1 (above dashed line) signifies predominant use of contact fight behaviors. Different letters indicate statistical significance at $P < 0.05$. (**b**) Raster plots of noncontact (blue) and contact (red) fight behaviors during territorial interactions show a difference in the sequence of behavioral patterns. Fights between two fish with intact lateral line systems (top portion) use primarily noncontact behaviors then escalate to the use of contact fight behaviors. In contrast, fish with an ablated lateral line system used mostly contact fight behaviors from the start of the fight. (**c**) Males with an ablated lateral line system spent more time assessing opponents (= % of pre-fight time spent <1 body length away) than males with an intact lateral line system. Different letters indicate statistical significance at $P < 0.05$. Tukey's box plots used to represent behavior data: median is represented by a line and mean by an open circle, the box extends to the furthest data points within the 25th and 75th percentiles, and whiskers extend to the furthest data points not considered outliers. Absence of whiskers indicates that no data points are present outside of the 25th/75th percentile. Modified from Butler and Maruska (2015), and reprinted with permission of Company of Biologists Ltd

reflect a fish's inability to detect and avoid the approaching opponent. In addition to altering fight structure and behaviors, the lateral line system proved to be important for assessment capabilities in *A. burtoni* males (Butler and Maruska 2015). Using time spent within one body length of an opponent without performing an aggressive display as a measure of assessment, it was shown that male *A. burtoni* in which the lateral line was ablated spent more time assessing their opponents than males with an intact lateral line system (Fig. 16c). In addition, males with an ablated lateral line system were more likely to concede instead of engaging in a territorial fight. Although the role of the lateral line system in aggressive interactions has only been examined in one cichlid species, it is likely that other cichlids produce and detect mechanosensory signals as a mode of communication during similar agonistic interactions.

4.2.2 Role of Mechanoreception in Reproduction and Parental Care

The grass goby (*Zosterisessor ophiocephalus*), hime (landlocked) salmon (*Oncorhynchus nerka*), cave-dwelling molly (*Poecilia mexicana*), and Amarillo fish (*Girardinichthys multiradiatus*) are all thought to use lateral line-mediated communication in mate preference/selection, courtship, or spawning behaviors (Satou et al. 1994; Medina et al. 2013; Marchesan et al. 2000; Plath et al. 2004). Reproduction in many cichlids involves active courting of females by males involving a variety of behaviors, such as body quivers and tail-waggles (Fig. 15). These behaviors, like many aggressive behaviors, also produce hydrodynamic cues that can be detected by a female's lateral line system. Noble and Curtis (1939) observed attempts at courtship and spawning behaviors in blinded jewel cichlid, *Hemichromis bimaculatus* that led them to suggest the role of mechanoreception in these encounters. This intersexual communication was likely also dependent on chemical cues, but the role of mechanoreception cannot be discounted, and empirical testing of the role of mechanosensory signaling during courtship and spawning needs to be carried out. Furthermore, females of many cichlid species tend to prefer larger males, and when two males are visually size-matched, it is possible that hydrodynamic signals allow a female to further compare strength and vigor of males. Because of the unique and variable reproductive tactics used by cichlids, they are an interesting prospect for studying the role of lateral line-mediated spawning synchronization. For example, in some tilapia (*Tilapia macrocephala)*, males and females follow each other in a tight circle while depositing eggs and sperm into a nest (Aronson 1949), and spawning pairs of mouthbrooding species do the same during egg release, uptake, and fertilization (Salzburger et al. 2007). Thus, it is likely that hydrodynamic information helps synchronize these behaviors.

Many cichlids provide some form of parental care to their offspring, most notable is fry uptake into the buccal cavity of mouthbrooding species (see Balshine and Abate 2021). Parents generate "calls" by abrupt fin raising and lowering and occasional tail-beating (Baerends and Baerends-van Roon 1950; Fryer and Iles 1972), which generate mechanosensory stimuli. When threatened, Mozambique tilapia (*Oreochromis mossambicus*) mothers "call" to their young, who quickly return to her mouth (Fryer and Iles 1972). If the mother and fry are separated by a clear, solid barrier that blocks water flows and chemical stimuli, the fry fail to respond to the mother's signals suggesting the importance of lateral line stimuli. Fry are likely well-equipped to respond to the "calls" of the parents given that the yolk sac larvae of some mouthbrooding species (*Aulonocara, Tramitichromis*) already have neuromasts (presumptive canal neuromasts, lines, and clusters of superficial neuromasts) and the development of the cranial lateral line canals occurs before final release of transforming larvae by the mother (Bird and Webb 2014; Becker et al. 2016). Fry of the Egyptian mouthbrooding cichlid, *Pseudocrenilabrus "Hemihaplochromis" multicolor*, reportedly respond to visual cues alone (Fryer and Iles, 1972), but these results have been questioned. However, these studies suggest that only some species use hydrodynamic signaling to "call" their offspring, and this warrants further studies of the generation of mechanosensory stimuli by parents as well as lateral line-mediated responses in young in a diversity of species using modern techniques.

4.3 Neural Processing of Lateral Line-Mediated Social Behaviors

Understanding how sensory cues mediate behavioral output via the central nervous system is one of the fundamental goals of the field of neuroethology (see Félix and Oliveira 2021). As mentioned above, regions of the teleost brain implicated in social decisions also receive projections from primary lateral line processing centers, suggesting that mechanosensory signals mediate social behaviors via conserved neural networks. Areas of the social decision-making network (SDMN) that receive socially relevant mechanosensory signals were identified by comparing brain activation patterns from *A. burtoni* males (in which the lateral line system was intact or ablated using cobalt chloride and cutting of the PLLn) following a territorial interaction (Butler and Maruska 2016b; Fig. 17a). The SDMN integrates the social behavior network with the mesolimbic reward system, and is thought to evaluate the salience of a sensory cue and integrate it with internal physiology to produce a suitable behavioral response (O'Connell and Hofmann 2011). In addition to known lateral line processing regions in the brain (i.e., MON, TSvl, and CP, see Sect. 3.2 for details and abbreviations), several socially relevant brain regions also had differential activation (measured using *cfos* staining as a proxy for neural activation) between males with an intact lateral line-intact and those in which the system was ablated. Males with an intact lateral line system showed higher activation in the ATn (homologous, in part, to the mammalian ventromedial hypothalamus), Dlg (potential homologue of the hippocampus), and Vs (homologous, in part, to the medial extended amygdala), suggesting that mechanosensory signals mediate activation of these behavior regions. After identifying regions of the brain that receive mechanosensory input, multivariate analyses revealed two distinct functional networks within the SDMN during male–male territorial interactions (Fig. 17b). Functional network identification was influenced by either the presence or absence of lateral line input and co-activation of each functional network was dependent on mechanosensory input, indicating the importance of mechanosensory signals to behavioral output. In addition, a discriminant function analysis of brain activation patterns could distinguish the four groups of animals (i.e., fight winners and losers with an intact or ablated lateral line), further highlighting the importance of mechanosensory signaling in mediating activation of the social decision-making network. Behavioral preference (noncontact vs. contact behaviors) and assessment capabilities correlated with activation of mechanosensory processing brain regions (e.g., MON and TSvl) and some nodes of the social decision-making network (Fig. 18a). Although only examined in one species, this study demonstrates the role of mechanosensory signals in mediating aggressive behaviors. Future studies are needed to examine where in the brain socially relevant mechanosensory signals detected during courtship and spawning behaviors are processed, and whether they differ from regions involved in aggressive contexts.

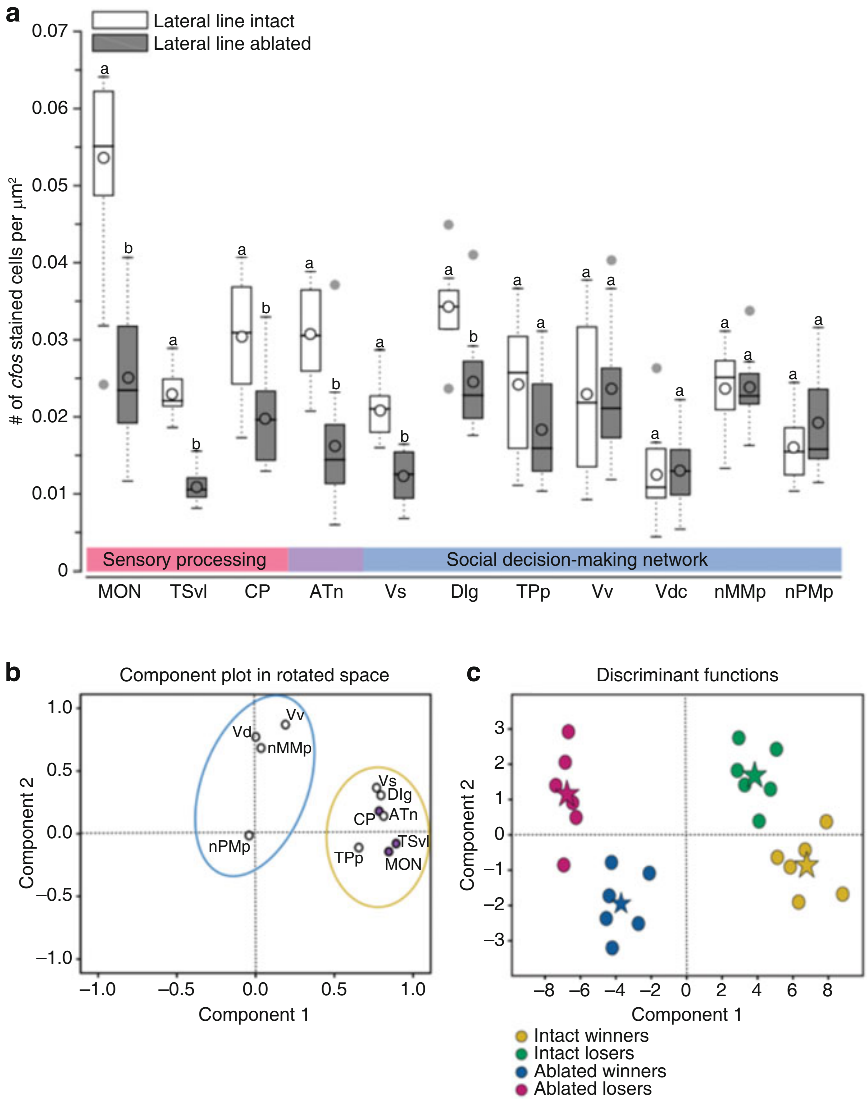

Fig. 17 Socially relevant mechanosensory information is processed in nodes of the social decision-making network (SDMN) in the brain of male *Astatotilapia burtoni*. (**a**) Following a territorial interaction, fish with an intact lateral line (white boxes) have a greater density of *cfos*-stained (immediate early gene used as a proxy for neural activation) cells than fish in which the lateral line system was ablated (gray) in lateral line processing nuclei and some nodes of the social decision-making network. See Fig. 14 for descriptions of boxplots. Outliers = closed gray circles. Pink bar = known mechanosensory processing regions, blue bar = nuclei of the social decision-making network, and purple bar = overlap of the two regions. Different letters indicate statistical significance at $P < 0.05$. (**b**) Principal component analysis is used to separate sensory (purple dots) and social (white dots) nuclei into two distinct functional networks. Yellow outlined circle encompasses the network that incorporates mechanosensory signals; the blue outlined circle encompasses the second network without lateral line input. (**c**) Discriminant function analysis distinguishes lateral line-intact fight winners (yellow) and losers (green) from lateral line-ablated fight winners (blue)

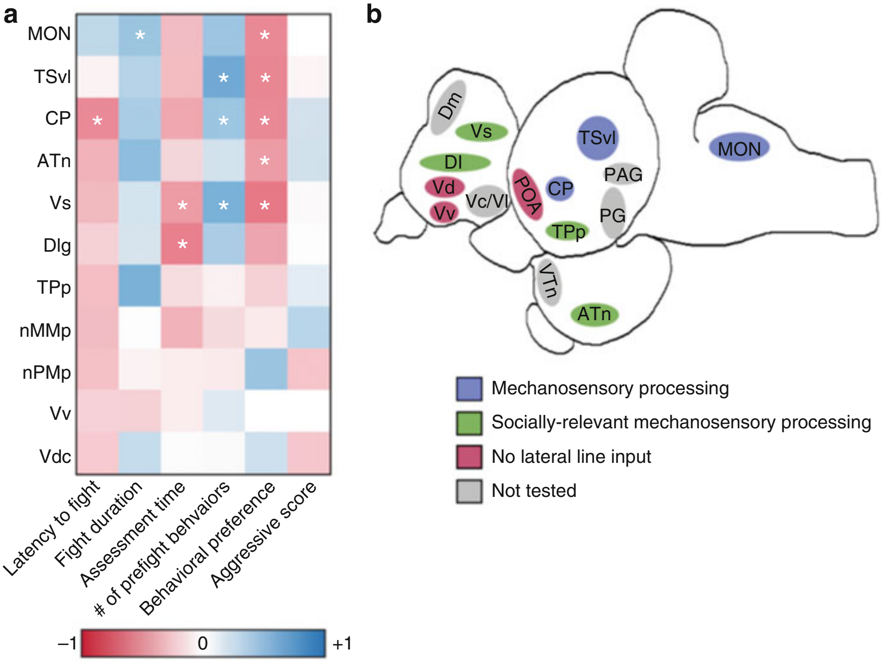

Fig. 18 Social and assessment behaviors are correlated with activation of mechanosensory and socially relevant brain nuclei in male *Astatotilapia burtoni*. (**a**) Heat map of Pearson correlation coefficients (R = color scale) for *cfos* staining in brain nuclei and fight behaviors. *statistical significance at $P < 0.05$. (**b**) Summary schematic of known locations of processing of socially relevant mechanosensory information. Blue represents mechanosensory processing regions. Green = nuclei of the social decision-making network (SDMN) that receive lateral line input and possibly use it to modify behavioral output. Pink = SDMN nuclei without evidence for mechanosensory input in this context. Gray = SDMN and sensory processing regions that have not been tested for a potential role in processing socially relevant mechanosensory signals. Locations of nuclei are only approximate. Abbreviations: *ATn* anterior tuberal nucleus, *CP* central posterior thalamic nucleus, *Dl*, lateral part of the dorsal telencephalon, *MON* medial octavolateralis nucleus, *PAG* periaqueductal gray, *PG* lateral preglomerular nucleus, *TPp* periventricular nucleus of the posterior tuberculum, *TSvl* ventrolateral portion of the torus semicircularis, *Vc/Vl* central and lateral parts of the ventral telencephalon, *Vd* dorsal part of the ventral telencephalon, *Vs* supracommissural nucleus of the ventral telencephalon, *VTn* ventral tuberal nucleus, *Vv* ventral part of the ventral telencephalon. From Butler and Maruska (2016b)

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Fig. 17 (continued) and losers (pink). Stars = the centroid for each group. Abbreviations: *ATn* anterior tuberal nucleus, *CP* central posterior thalamic nucleus, *Dlg* granular zone of the lateral part of the dorsal telencephalon, *MON* medial octavolateralis nucleus, *nMMp* magnocellular preoptic nucleus magnocellular division, *nPMp* magnocellular preoptic nucleus parvocellular division, *TPp* periventricular nucleus of the posterior tuberculum, *TSvl* ventrolateral portion of the torus semicircularis, *Vdc* caudal subdivision of the dorsal part of the ventral telencephalon, *Vs* supracommissural nucleus of the ventral telencephalon, *Vv* ventral part of the ventral telencephalon. Modified from Butler and Maruska (2016b)

5 Conclusions and Prospects for Future Research

The ability to study cichlids in the field (see Chapman 2021), rear them in the laboratory (see Parsons et al. 2021), hybridize them in order to carry out complex genetic and genomic analyses (see van Rijssel et al. 2021; Hu and Albertson 2021), study their sensory systems (see also Gray 2021; Schulz-Mirbach and Ladich 2021), and analyze their behavior (see also Lobel et al. 2021; Balshine and Abate 2021; Jordan et al. 2021; Félix and Oliveira 2021) has justified addition of cichlids to the list of "model vertebrate species" for studies of comparative and developmental morphology, sensory biology, behavior, neuroanatomy, and neurophysiology, especially that of the lateral line system.

The morphological diversity of the lateral line system in cichlids spans the range found among teleost fishes more generally (e.g., Webb 1990; Sect. 2), so cichlids can be used as a model system to explore the evolution of the lateral line system and the role of development (e.g., heterochrony, modularity, and integration) in the generation of that diversity (e.g., Webb et al. 2014a, b; Bird and Webb 2014). The occurrence of widened cranial lateral line canals in those cichlids living in deep lacustrine or riverine waters or in caves under low light conditions, and the ability to study at least some of these in the laboratory, provides an opportunity to explore adaptive evolution and the comparative neuroecology of the lateral line system. Furthermore, the well-known diversity of trophic niches and microhabitats occupied by cichlids provides a context in which to broaden our interpretation of the comparative morphology of the brain, correlative variation in brain structure and peripheral morphology of multiple sensory systems, including the lateral line system, and their relationship to the sensory and feeding ecology of cichlids (e.g., Huber et al. 1997; see Takeyama 2021).

Fishes constantly survey their environment via multiple sensory modalities, and inputs are integrated to mediate complex behaviors. The wide range of lateral line morphologies with different functional attributes (Sect. 2), and a range of well-defined feeding and social behaviors found among cichlid species (Sect. 4) make them well suited as models to analyze the complex relationship between sensory inputs and the formulation of complex behaviors, including those made under different (and changing) environmental conditions. With respect to feeding, considerations of the roles of inputs to the visual and lateral line systems (Sect. 4.1) need to be expanded to explicitly consider chemosensory modalities. Furthermore, in settings in which the light environment has been compromised resulting in alterations in visually mediated social behavior (e.g., due to eutrophication and global change), how could different species of cichlids that use different combinations of sensory modalities to detect and choose their prey respond both ecologically and evolutionarily? With respect to social behavior, if the functional overlap between the lateral line and auditory systems is important for behaviors such as predator–prey interactions and social communication (Sect. 4), then cichlids are an ideal group in which to explore the relative contributions of mechanosensory and auditory inputs generated by the same biologically relevant source using both behavioral and physiological approaches. *A. burtoni* and other cichlids use body movements during agonistic, reproductive, and parental care behaviors. Thus, future studies using this species, and others, should examine the importance of the lateral line system in detecting these hydrodynamic signals as part of the overall sensory scene, including visual, auditory, chemosensory, somatosensory, and mechanosensory inputs perceived during all aspects of social communication.

Finally, the growing availability of genomic resources for cichlids (e.g., complete genome sequences of five African cichlids are already available; Brawand et al. 2014; see Hu and Albertson 2021; Parsons et al. 2021) will facilitate exciting studies of the functional role of sensory systems, especially the lateral line system. The coupling of these genomic resources with modern neuroscience techniques, such as CRISPR/Cas9 (recently used in a cichlid; Juntti et al. 2016) and optogenetics (as used in zebrafish, *Danio rerio*, e.g., Arrenberg 2016), should be invaluable for future work on the functional roles of the lateral line system. When used to inactivate the lateral line system and eliminate mechanosensory inputs, these techniques will yield much cleaner results than those obtained using chemical, pharmacological, and physical ablation techniques. Such results should reveal the contribution of the lateral line system to the formulation of a variety of behaviors across a diverse group of cichlids.

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Sonic Cichlids

Phillip S. Lobel, James G. Garner, Ingrid M. Kaatz, and Aaron N. Rice

Abstract Bioacoustics has become a key feature of cichlid behavioral studies over the last 20 years, due in large part to new technologies and software. The hypothesis that some cichlid species produce species-specific sounds is gaining support with data from several studies. Sounds are specific to behavioral context for many species. Cichlids are advanced teleost fishes possessing a complex pharyngeal jaw. This morphological feature has been proposed as the key functional innovation responsible for the evolutionary success and explosive adaptive radiation of the group. This evolutionary success has been mostly attributed to their expanded adaptability to process a wide variety of food types due to the capability of thoroughly grinding food in the pharyngeal apparatus, an ability that most other fishes lack. The evidence regarding the role of the pharyngeal jaw complex in sound production is evaluated, and suggests that this same morphology enables cichlids to produce a complex and varied acoustic repertoire. Although, the sonic mechanism may be more complex morphologically than just the pharyngeals clacking. More studies are needed to carefully document the sounds correlated to specific behaviors of cichlids and to statistically examine the species specificity of sympatric species sounds. Future research is needed that experimentally tests the response of female fish to acoustic playback combined with visual and chemical cues in order to determine how critical sound communication is to the sympatric evolution of cichlid species.

P. S. Lobel (✉)
Dept of Biology, Boston University, Boston, MA, USA
e-mail: plobel@bu.edu

J. G. Garner
Department of Ecological Conservation, University of Massachusetts, Amherst, MA, USA

I. M. Kaatz
Stamford, CT, USA

A. N. Rice
Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Cornell University, Ithaca, NY, USA

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Keywords Cichlidae · Fish bioacoustics · Fish sounds · Fish reproduction · Fish communication · Soundscape

1 Introduction

It has been almost 60 years since the first reports on the sonic behavior of cichlids. Fryer and Iles (1972) reviewed the discoveries by Bauer (1963), Myrberg et al. (1965), and Rodman (1966) and suggested that the use of sounds by cichlids may be important as a means of species recognition and mate location. However, research on cichlid bioacoustics progressed slowly until about the year 2000 (Fig. 1, earlier reviews of cichlid sounds include Lobel 2001; Amorim et al. 2004 and Longrie et al. 2013).

Historically, research was hindered by the expense and difficulty of using hydrophones and the technology for acoustic analyses, but these former obstacles have been eliminated by modern video camcorders, personal computers, and especially new software for acoustic analysis. The first underwater study of the sonic behavior by cichlids in the wild showed that cichlids were indeed quite acoustically active in Lake Malawi and sounds differed among neighboring species (Lobel 1998). Since then, cichlid bioacoustics has become an active topic for research. Another field study, also in Lake Malawi, documented possible population variation in cichlids calls over a geographic range (Danley et al. 2012). The nature/nurture question was examined in *Oreochromis niloticus,* and suggested that the ontogeny of sound production in juveniles was innate and not learned (Longrie et al. 2008). Acoustic features that could provide signature differences were examined by Bertucci et al. (2012a, b). The Tanganyikan cichlid, *Neolamprologus pulcher*, has been proposed

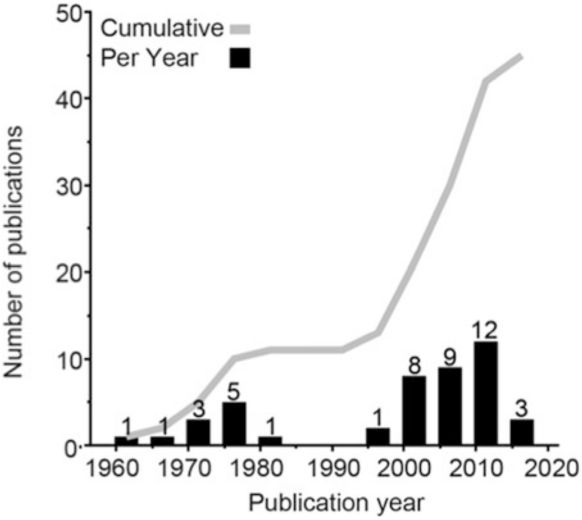

Fig. 1 Summary of scientific papers describing sound production in cichlids per year (black columns) and cumulatively (gray line). Citations for papers that describe the production of sounds or behavioral use of sounds ($N = 51$) were discovered through literature searches using the Web of Science database (with coverage from 1864-present), and the literature cited list of relevant papers (e.g., Baerends and Baerends-van Roon 1950 in the case of Raj 1916)

as a silent species based on the lack of sounds recorded under laboratory conditions (Pisanski et al. 2015), prompting a need for closer investigation of acoustic activity in other species. Laboratory experiments have shown using acoustic playback experiments that increases in noise can impact behavior by reducing behavioral activity levels that normally coincide with sound production (Slabbekoorn et al. 2012).

It has been well known for a long time that cichlids display complex behaviors during the behavior of mate selection (Baerends and Baerends-van Roon 1950; Keenleyside 1991; Barlow 2000). Cichlids are clearly multi-modal in their communication (Rosenthal and Lobel 2006; Amorim et al. 2008; Verzijden et al. 2010). Vision and coloration are key in the mate selection process for the *Pseudotropheus zebra* species complex of Lake Malawi (Couldridge and Alexander 2002). But visual cues are not necessarily the sole communication modality, nonvisual cues are implicated in experimental studies (Blais et al. 2009). Recent reviews have focused on the importance of visual cues and color patterns in the evolution of cichlid and other fishes (Rowland 1999; Seehausen et al. 1999). While visual cues are undoubtedly important, olfactory and acoustics cues also play significant roles. For example, Chien (1973) determined that the combination of visual and olfactory cues presented together increased spawning rates in the cichlid, *Pterophyllum* spp., above the rates observed when only one cue was presented; i.e., the effects of the various stimuli are additive (Rowland 1999). Visual cues are apparently not the primary cue in all species examined. Furthermore, chemical cues have received attention as being important in cichlid communication (Maruska and Fernald 2012). The exact role of acoustics in this mate selection process by cichlids is an ongoing hot topic today. During courtship, females prefer acoustic over silent males but the visual presence of the male is required (Estramil et al. 2014). Sounds and visual cues are synchronous during agonistic encounters (Bertucci et al. 2010). Blais et al. (2009) determined experimentally that visual signals alone cannot explain mate choice and that other signals must also be involved as a factor in female choice. However, they did not assess other cues such as olfaction or acoustics.

Cichlid fishes are widely studied with regard to understanding the processes of speciation (e.g., Sturmbauer 1998; Kornfield and Smith 2000; Salzburger and Meyer 2004; Kocher 2004; Salzburger 2009). The rapid and extensive species radiation (“species flocks”) seen in cichlids is unrivaled in other vertebrate groups (Liem 1973; Echelle and Kornfield 1984; Barlow 2000; Kornfield and Smith 2000; Salzburger and Meyer 2004; Turner 1999; Turner et al. 2001). One underlying mechanism for this evolutionary success is the cichlid’s complex pharyngeal jaw, a highly adaptable morphological feature (Liem 1973, 1991) coupled with the cichlid’s complex mating behavior, short generation time with numerous offspring. Cichlids provide an opportunity to observe speciation at different stages of progression, allowing investigation of the process and mechanisms of evolution (Kornfield and Smith 2000; Kocher 2004). Species divergence in closely related sympatric cichlids, especially in the Great Lakes of Africa has been hypothesized to have occurred, in part, due to assortative mating. Cichlid mate choice studies confirm that assortative mating does occur in several species in the field and in captivity

(Blais et al. 2009; Egger et al. 2008; Knight and Turner 2004; Salzburger et al. 2006). The key to understanding this process is to decipher the factors involved in cichlid mate selection. The influences of visual and chemical cues as prezygotic isolating mechanisms have been examined (Couldridge and Alexander 2002; Blais et al. 2009; Kidd et al. 2006; Maan et al. 2004; Plenderleith et al. 2005). Acoustic signals have not yet been similarly investigated.

This review will highlight the possible morphological mechanisms and biological significance for the occurrence and variability of sounds produced by cichlid species during aggression and courtship. Sounds are also associated with other behaviors, particularly feeding and swimming, which are not necessarily intentionally produced. The essential scientific question is whether certain sound patterns produced by cichlids are ethologically meaningful. For reviews of fish bioacoustics and communication including terminology (see Moulton 1960; Demski et al. 1973; Ladich 1997; Kasumyan 2009; Ladich 2015; Blaxter 1981; Fine et al. 1977; Hawkins 1986; Hawkins and Myrberg 1983; Myrberg 1980, 1981; Myrberg et al. 1978; Popper and Fay 1973, 1993; Schwarz 1985) for cichlid communication (see Nelissen 1991; Lobel 2001; Amorim et al. 2004; and Longrie et al. 2013) and for animal communication in general (see Bradbury and Vehrencamp 1998). Sound production is widespread throughout the phylogeny of fishes with evidence of sound production from 72 families (Rice et al. 2020).

2 Checklist of Sound Producing Cichlid Species

There are now a total of 39 cichlid species identified as sound producers (Table 1), and this represents an increase of an additional 19 species since Lobel (2001). One of the most conspicuous results is that all the recent studies have been on African species. Surprisingly, the last acoustic study of a Central/South American cichlid species was by Schwarz in 1980! The primary literature for cichlid acoustic biology numbers 55 publications (as of 2019). Table 1 lists the documented sound producing cichlids using the scientific name as published; and it cross-references to the most recent scientific name in current usage in FishBase (http://www.Fishbase.org), which is cross-linked to the definitive reference for current fish taxonomy, the Eschmeyer Catalog of Fishes (http://www.calacademy.org/scientists/projects/catalog-of-fishes). Cichlid species nomenclature is frequently changing and is the subject of a great deal of scientific discussion. In this review, we will try to use the most referenced names or the name cited in the original literature. Our purpose is not to update the taxonomy but only to clearly specify which species is being referenced.

The six specific questions regarding cichlid bioacoustics include:

1. Are specific sounds associated with specific behaviors?
2. What are the temporal patterns of calling activity?
3. What morphological structures produce the sounds?
4. What are the key characteristics of sound patterns that distinguish species?

Table 1 Sound producing cichlids list of synonymies

Species ($n = 39$)[a] Name in publication	Current name	Literature cited ($n = 54$)
Cichlasoma nigrofasciatum	*Amatitlania nigrofasciata* (Günther, 1867)	(1) Myrberg et al. (1965)
Cichlasoma citrinellum	*Amphilophus citrinellus* (Günther, 1864)	(1) Schwartz (1974a)
Cichlasom centrarchus	*Archocentrus centrarchus* (Gill, 1877)	(3) Schwartz (1974a, b, 1980)
Haplochromis burtoni	*Astatotilapia burtoni* (Günther, 1894)	(5) Fernald (1975), Hirata and Fernald (1975), Nelissen (1977, 1978), Maruska and Fernald (2010, 2012), Nelissen (1977, 1978)
Pseudotropheus elongatus	*Chindongo elongatus* (Fryer, 1956)	(1) Lobel (2001)
Aequidens portalegrensis	*Cichlasoma portalegrense* (Hensel, 1870)	(1) Brown and Marshall (1978)
Cynotilapia afra (Günther, 1894)		(1) Danley et al. (2012)
Pundamilia nyererei	*Haplochromis nyererei* (Witte-Maas & Witte, 1985)	(3) Verzijden et al. (2010), Slabbekoorn et al. (2012), Estramil et al. (2014)
Pundamilia pundamilia	*Haplochromis pundamilia* (Seehausen & Bouton, 1998)	(1) Verzijden et al. (2010)
Hemichromis bimaculatus (Gill, 1862)		(2) Myrberg et al. (1965), Rowland (1978)
Herotilapia multispinosa (Günther, 1867)		(2) Baylis (1974), Brown and Marshall (1978)
Labeotropheus fuelleborni (Ahl, 1926)		(1) Danley et al. (2012)
Labidochromis caeruleus (Fryer, 1956)		(1) Higgs et al. (2011)
Maylandia aurora (Burgess 1976)		(1) Danley et al. (2012)
Metriaclima callainos, Pseudotropheus callainos	*Maylandia callainos* (Stauffer & Hert, 1992)	(7) Amorim et al. (2004, 2008), Simoes et al. (2006), Smith (2007), Smith and Van Staaden (2009), Van Staaden and Smith (2011), Danley et al. (2012)
Pseudotropheus emmiltos (MCP Amorim pers. com. 2018 *M. emmiltos)*	*Maylandia emmiltos* (Stauffer, Bowers, Kellogg & McKaye, 1997)	(2) Amorim et al. (2008), Simoes et al. (2008a)
Pseudotropheus fainzilberi	*Maylandia fainzilberi* (Staeck, 1976)	(2) Amorim et al. (2008), Simoes et al. (2008a)
Metriaclima lombardoi	*Maylandia lombardoi* (Burgess, 1977)	(3) Smith (2007), Smith and Van Staaden (2009), Van Staaden and Smith (2011)

(continued)

Table 1 (continued)

Species ($n = 39$)[a] Name in publication	Current name	Literature cited ($n = 54$)
Metriaclima zebra, Pseudotropheus zebra	*Maylandia zebra* (Boulenger, 1899)	(11) Amorim et al. (2004, 2008), Simoes et al. (2006); Simoes et al. (2008a, b), Bertucci et al. (2010), Van Staaden and Smith (2011), Danley et al. (2012), Bertucci et al. (2012a, b), Bertucci et al. (2013)
Copadichromis conophorus	*Mchenga conophoros* (Stauffer, LoVullo and McKaye, 1993)	(2) Lobel (1998, 2001)
Melanochromis auratus (Boulenger, 1897)		(3) Smith (2007), Smith and Van Staaden (2009), Van Staaden and Smith (2011)
Neochromis omnicaeruleus (Seehausen and Bouton, 1998)		(1) Verzijden et al. (2010)
Neolamprologus pulcher (Trewavas and Poll, 1952)		(2) Spinks et al. (2017); Pisanski et al. (2015)
Tilapia mossambicus	*Oreochromis mossambicus* (Peters, 1852)	(9) Rodman (1966), Konstantinova et al. (1979), Amorim et al. (2003), Amorim and Almada (2005), McPherson (2012), Pujiyati et al. (2016), Lanzing (1974), Marshall (1971, 1972)
Tilapia nilotica	*Oreochromis niloticus* (Linnaeus, 1758)	(4) Bauer (1963), Longrie et al. (2008, 2009, 2013)
Tilapia nilotica × *Tilapia macrocephala*	Hybrid	(1) Bauer (1963)
Tilapia mariae	*Pelmatolapia mariae* Boulenger, 1899	(2) Kottege et al. (2015), Albrecht (1966)
Petrotilapia nigra (Marsh, 1983)	–	(1) Danley et al. (2012)
Simochromis babaulti	*Pseudosimochromis babaulti* (Pellegrin, 1927)	(1) Nelissen (1978)
Melanochromis cyaneorhabdos	*Pseudotropheus cyaneorhabdos* (Bowers & Stauffer, 1997)	(3) Smith (2007), Smith and Van Staaden (2009), Van Staaden and Smith (2011)
Melanochromis johannii	*Pseudotropheus johannii* (Eccles, 1973)	(3) Smith (2007), Smith and Van Staaden (2009), Van Staaden and Smith (2011)
Pseudotropheus "zebra gold"	Species undescribed	(3) Amorim et al. (2004, 2008), Simoes et al. (2006)
Pseudotropheus "zebra gold" x Maylandia zebra	Hybrid	(1) Simoes et al. (2008a)
Pterophyllum sp. (probably *scalare*) (Schultze, 1823)		(1) Myrberg et al. (1965)
Psuedetroplus maculatus (Bloch 1795)	*Etroplus maculatus*	(2) Raj 1916 cited in Baerends and Baerends-van Roon (1950)

(continued)

Table 1 (continued)

Species ($n = 39$)[a] Name in publication	Current name	Literature cited ($n = 54$)
Tilapia galilaea	*Sarotherodon galilaeus* (Linnaeus, 1758)	(1) Brown and Marshall (1978)
Simochromis diagramma (Günther, 1894)		(2) Nelissen (1975, 1978)
Tramitichromis intermedius (Trewavas, 1935)		(7) Lobel (1998, 2001), Rice et al. (2001), Rice and Lobel (2002, 2003); Ripley et al. (2002), Ripley and Lobel (2004)
Tropheus brichardi (Nelissen & Thys van den Audenaerde, 1975)		(1) Nelissen (1978)
Tropheus duboisi (Marlier, 1959)		(1) Nelissen (1978)
Tropheus moorii (Boulenger, 1898)		(2) Nelissen (1977, 1978)

[a] Fishbase https://www.fishbase.de/

5. Is there any relationship between body size and call characteristics?
6. How might an increase in ambient noise confound acoustic communication?

2.1 *Calling Activity and Caller Sex*

The behavioral processes of courtship and spawning are similar across cichlid species, often involving approach, leading, circling, and quivering (Baerends and Baerends-van Roon 1950; Barlow 2000; Ripley and Lobel 2004, 2005). Although the specifics of circling behavior may differ between genera (Stauffer et al. 1993), "quivering" is associated with circling and courtship in many cichlids as they swim around each other and ripple their abdominal muscles. Sound production correlates with quivering in *Tramitichromis intermedius, Copidichromis conophoros* (Lobel 1998; Ripley and Lobel 2004), *Simochromis diagramma* (Nelissen 1975), and in *Pseudotropheus* species (Amorim et al. 2004, 2008). It is likely that many cichlids that share this quiver behavior will also produce sounds. One known exception, *Oreochromis mossambicus*, does not produce sound during the specific quiver behavior but it does produce sounds during other courtship behavior (Amorim et al. 2003). Whether a fish produces sound during quivering or other behaviors, sound production appears to be regularly associated with cichlid courtship (Lobel 1998; Amorim et al. 2003, 2004, 2008). The hypothesis is that female fish could use these courtship-associated sounds as one cue to assess a potential mate's identity and quality. Actual spawning associated sounds are hypothesized to coordinate reproductive timing synchronizing gamete release.

Diel patterns of sound production in cichlids have been suggested for two cichlid species, both exhibiting a diurnal peak (Brown and Marshall 1978; Longrie et al. 2013). For *Herotilapia multispinosa*, sounds were enumerated during reproductive and agonistic behaviors during different stages of the reproductive period. Spawning is reported to be restricted to daylight hours (Brown and Marshall 1978), but no monitoring of sounds was done nocturnally. In *Oreochromis niloticus*, direct acoustic sampling of fishes over a 24-h period found peak diurnal calling activity (Longrie et al. 2013). This is an aspect of future research well worth examining in more detail. Early pre-dawn calling by males could be a stimulus for spawning. The courtship sound produced by male *Oreochromis mossambicus* was reported to facilitate oviposition in females (Marshall 1972). It is possible that some cichlids may be sonically active before daylight. Smith (2007) recorded cichlid-like sounds in the field in areas where cichlid species were present and found nocturnal peaks in the production of these sounds. On coral reefs, damselfishes (Pomacentridae) were once thought to be only acoustically active during daytime until 24-h recordings revealed pre-dawn peaks in chorus activity (Mann and Lobel 1995). It makes sense that acoustic signals would be used in low light periods, possibly as an early cue to stimulate females to initiate egg hydration prior to spawning. The technology and software for underwater acoustics have greatly advanced in recent years and allows for documenting the natural cycle of sound production for sonic fishes in the wild as well as assessing the impacts from noise pollution (Lindseth and Lobel 2018).

For species whose social behavioral context for sound production are known ($N = 39$; Table 2) as of the year 2019, 20 species produced sounds during agonistic intraspecific encounters and 30 spp. in reproductive display context (Table 2). For studies of reproductive behaviors, in all species the callers were male when sex was identified in all except *Pelmatolapia mariae* where the caller was female. Acoustic male courtship displays are known or proposed in 21 (55%) of these (Table 2). For reproduction-associated contexts monitored with a hydrophone, 30 species (79%) produce sounds in reproductive context during various aspects of nest visiting male calling in association with nest, or male courtship display to female ($n = 20$, 53%) or courtship encounters with unspecified sex ($n = 5$, 13%). Female calling in *Pelmatolapia mariae* was recorded in the vicinity of the nest area ($n = 1$, 3%). Of these, the males of four species (11%) were observed to engage in courtship with a visiting female but no sounds were observed before the recordings began which were limited to passive recording of sounds (no video) from the focal male's nest after the field observations. Both male and female cichlids have been observed to produce sounds in some species (see Table 2) although sound production by both sexes may not be universal. It should be noted that acoustic studies in fishes have largely focused on male behaviors even though in many fishes a mechanism of known sound production is present in males and females of the species (Ladich 2015). Among those cichlids where males and females have been noted to produce sounds in the context of aggression: 50% of species with specifically identified sex of caller in agonism were female and 70% were male ($N = 20$ species).

Table 2 Behavioral context of sound production in cichlids

Species[a,b] (Total = 39)	Agonism[c,d] (sex of sound producer)	Reproduction[b,d]	Literature
SOUTH AMERICAN CICHLIDS (n = 6):			
Amatitlania nigrofasciata	A (female)	–	Myrberg et al. (1965)
Amphilophus citrinellus	A (male)	–	Schwartz (1974a)
Archocentrus centrarchus	A (male & female)	–	Schwartz (1980)
Cichlasoma portalegrense	A (unknown)	–	Brown and Marshall (1978)
Herotilapia multispinosa	A (male and female)	Cd, Cf	Brown and Marshall (1978)
	A	Cd	Baylis (1974)
Pterophyllum sp. (possibly *scalare*)	A (adult pair, sex unknown)	–	Myrberg et al. (1965)
AFRICAN CICHLIDS (n = 32 species):			
Astatotilapia burtoni	A (male and female)	Cc "sexual quiver"	Nelissen (1977, 1978)
	–	Cd	Maruska et al. (2012)
Chindongo elongatus	No context	No context	Lobel (2001)
Cynotilapia afra	–	Cd hypothesized	Danley et al. (2012)
Haplochromis nyererei	A (male)	Cd	Verzijden et al. (2010)
Haplochromis pundamilia	–	Cd	Verzijden et al. (2010)
Hemichromis bimaculatus	A (male and female)	–	Myrberg et al. (1965)
	No context	No context	Lobel (2001)
Labeotropheus fuelleborni	–	Cd hypothesized	Danley et al. (2012)
Labidochromis caeruleus		Cd male "quiver" paired with female	Higgs et al. (2011)
Maylandia aurora	–	Cd hypothesized	Danley et al. (2012)
Maylandia callainos	–	Cd	Amorim et al. (2008)
	–	Cd hypothesized	Danley et al. (2012)
Maylandia emmiltos	–	Cd	Amorim et al. (2008)
Maylandia fainzilberi	–	Cd	Amorim et al. (2008)
Maylandia lombardoi	–	Cd	van Staaden and Smith (2011)
Maylandia zebra	A (male)	–	Bertucci et al. (2012a, b)
	A (male and female)	–	Simoes et al. (2008b)
	–	Cd	Amorim et al. (2008)
	–	Cd hypothesized	Danley et al. (2012)
Mchenga conophoros	A (male) irregular noisy pulses	Cd	Lobel (2001, 1998)
Melanochromis auratus	–	Cd	van Staaden and Smith (2011)

(continued)

Table 2 (continued)

Species[a,b] (Total = 39)	Agonism[c,d] (sex of sound producer)	Reproduction[b,d]	Literature
Neochromis omnicaeruleus	–	Cd	Verzijden et al. (2010)
Neolamprologus pulcher	A (male and female)	–	Spinks et al. (2017)
Oreochromis mossambicus	A (male-male, male-female groups male caller)	Cd, Cs	Amorim et al. (2003)
Oreochromis niloticus	A (male and female)		Longrie et al. (2013)
		Cd	Bauer (1963)
Tilapia nilotica x Tilapia macrocephala	–	Cd	Bauer (1963)
Pelmatolapia mariae	A (male)	–	Albrecht (1966)
		Female sound producer nest area	Kottege et al. (2015)
Petrotilapia nigra	–	Cd hypothesized	Danley et al. (2012)
Pseudosimochromis babaulti	A	Cc "sexual quiver"	Nelissen (1978)
Pseudotropheus cyaneorhabdos	–	Cd	van Staaden and Smith (2011)
Pseudotropheus johannii		Cd	van Staaden and Smith (2011)
Pseudotropheus 'zebra gold'	–	Cd	Amorim et al. (2008)
Sarotherodon galilaeus	–	Cd, Cf	Brown and Marshall (1978)
Simochromis diagramma	A (male and female)	Cc "sexual quiver"	Nelissen (1975, 1978)
Tramitichromis intermedius	–	Cd	Lobel (1998), Ripley and Lobel (2004, 2005)
Tropheus brichardi	A	Cc "sexual quiver"	Nelissen (1978)
Tropheus duboisi	A	Cc "sexual quiver"	Nelissen (1978)
Tropheus moorii	A (male and female)	Cc "sexual quiver"	Nelissen (1977, 1978)

[a] Lake Malawi *Pseudotropheus* "zebra gold" (Amorim et al. 2008)

[b] No Context: Undetermined context either agonism or courtship *Chindongo elongatus* ($n = 1$); No social contexts, agonistic-like and courtship-like displays to model *Hemichromis bimacultus* ($n = 1$); No social context, jaw clicking sounds produced in distress on land *Pseudetroplus maculatus* ($n = 1$)

[c] Agonism total ($n = 20$), female caller specified ($n = 10$), male caller specified ($n = 14$), sex could not be verified ($n = 5$)

[d] Reproductive sounds $n = 31$; Cf = female in courtship display ($n = 2$); Cd = courtship call to female by male detected with a hydrophone ($n = 20$); Cd = proposed as male display human audition no data analysis Bauer (1963) (1); Cc = male courtship call inferred from reproductive display "sexual quiver" ($n = 6$); Cs = spawning ($n = 1$); Cd hypothesized ($n = 6$) hydrophone recording of a male courting a female at his breeding cave by means of passive acoustics ($n = 6$); Female calling in the vicinity of nest paired with a male *Pelmatolapia mariae* ($n = 1$)

The pattern of sound production with reproductive behavior has not always been clear and more research is needed to define if such sounds are meaningful to the fishes. For example, in *Oreochromis niloticus* females and males produced agonistic sounds but no sounds were detected during courtship from either sex (Longrie et al. 2013). Males of *H. multispinosa* produced abundant sounds in both agonistic and reproductive contexts (Brown and Marshall 1978). In this species, males and females produced sounds throughout the egg, larval, and free-swimming young stages of offspring development during agonistic encounters with intruders. There are only five studies that statistically describe the temporal characteristics of female sounds and associated behavior in detail. These include pulsed sounds while mouthbrooding embryos for *Oreochromis niloticus* (Longrie et al. 2013); broadband frequency 2-pulsed sound in agonism for *Neolamprologus pulcher* (Spinks et al. 2017), interpulsed sounds in agonism for *Maylandia zebra* (Simoes et al. 2008b); and single-pulse sounds in the vicinity of nest with males for *Pelmatolapia mariae* (Kottege et al. 2015). Myrberg et al. (1965) described the pulse rate for *Hemichromis bimaculatus* female agonistic sounds during the parental care period.

Agonistic sounds between females were also described for *Maylandia zebra* (Simoes et al. 2008b). Female sounds were shorter in duration and consisted of fewer pulses than males (Simoes et al. 2008b). Males produce sounds during courtship-associated displays to females, and females seem to be silent in this context for video documented studies (e.g., Ripley and Lobel 2004). *M. zebra* juveniles are active sound producers during agonistic interactions, producing isolated pulses early in development (Bertucci et al. 2012a, b). There were two species (6%) where the callers also included a female although their sounds were observed anecdotally and not digitally recorded ($n = 22$ species; sex of caller specifically examined). Females of *Tramitichromis intermedius*, *Archocentrus centrarchus, Oreochromi mossambicus*, and *Astatotilapia burtoni* were observed as silent (Lanzing 1974; Ripley and Lobel 2004; Maruska et al. 2012). It is important to note that the sex of the caller is often difficult to determine exactly when recording fishes in groups and with omnidirectional hydrophones. Thus, this aspect deserves closer study.

Sounds of Juvenile Cichlids The ontogeny of sound production in cichlids has only received limited study to date. The Malawi cichlid, *M. zebra* juveniles are active sound producers during agonistic interactions, producing isolated pulses early in development (Bertucci et al. 2012a, b). Young *Oreochromis niloticus*, also produce sounds, supporting the hypothesis that sound production is not learned in cichlids (Longrie et al. 2008). The onset of vocal ability in young males of *Tramitochromis intermedius* was detected at about 7 months of age (Ripley and Lobel 2004).

3 Sound Producing Mechanism

Definitive experiments have not yet demonstrated which muscles and bones are used for sound production by cichlid fishes. The pharyngeal bones of some fishes have been implicated as the sound-producing instrument (Darwin 1874; Marshall 1962) and the same has been proposed for cichlids (Lanzing 1974; Rice et al. 2001; Rice and Lobel 2002, 2003; Marshall 1962; Nelissen 1977). Sounds produced by the pharyngeal apparatus are presumably amplified by the swimbladder (Rowland 1978; Marshall 1962). Cichlids produce a clear and distinct sound while feeding and grinding food in the pharyngeal mill, as well as during courtship and agonistic behavior (Lobel 2001; Lanzing 1974; Nelissen 1977; Rodman 1966). However, an alternative mechanism called the "buckling method" (an indirect swimbladder associated muscle mechanism) has been proposed by Longrie et al. (2009), and is discussed below. Not all sounds may be volitional, and any behavioral significance has not yet been demonstrated. For example, the agonistic "thump" described for *Herotilapia multispinosa* by Brown and Marshall (1978) coincides with a head jerking upward and downward but also coincided with well-established agonistic frontal displaying suggesting a possible volitional nature to the sounds. Sounds were also produced during jaw snapping during agonistic behaviors (Baylis 1974; Brown and Marshall 1978). Brown and Marshall (1978) described non-pulsed "thump" sounds as most likely incidental to behaviors and not communicative. Jaw snapping is proposed as a mechanism for the reproductive season of sound production in females for *Tilapia mariae* (Kottege et al. 2015). These sounds could be incidental to body movements or intentional acoustic components of displays. The specific context for these sounds was less ritualized and less tightly linked to a specific body posture or behavioral display than is typically found in other cichlids.

If cichlid pharyngeal jaws are involved in sound production, as preliminary evidence indicates, then perhaps it is possible that different pharyngeal tooth morphologies may produce different types of sounds (i.e., sounds with different individual pulse waveforms, e.g., Lobel 2001). Of course, the key experiment would be to determine if such different pulse waveforms produce different sound qualities that are directly detectable by a fish. It is possible that the simplest type of acoustic signal produced is the specific sound of individual pulses, which are then frequently repeated (Fig. 2). It may be the perceived sound of the pulse in combination with pulse rate timing that may contribute to species recognition. Prior studies in other fishes, especially the damselfishes (Pomacentridae), show that pulse number and/or repetition rate is closely correlated with the behavioral context of sounds (Hawkins 1986; Myrberg 1981, 1997; Olivier et al. 2015; Spanier 1979). Pomacentrids that produce similar sounds to cichlids have had their sound production mechanism described as including jaw element movements similar to the feeding process (Olivier et al. 2015; Parmentier and Fine 2016).

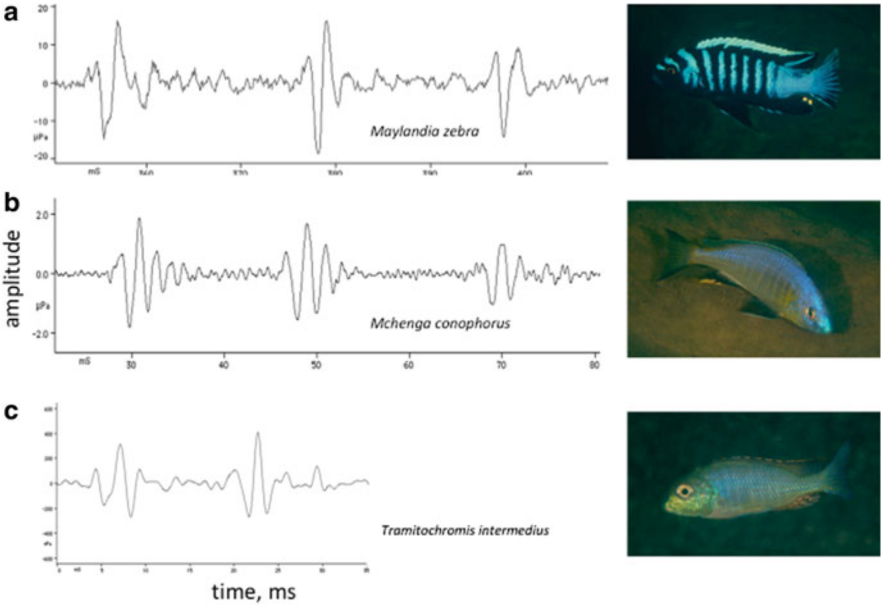

Fig. 2 Example of the waveform patterns from three cichlids in Lake Malawi. (**a**) *Maylandia zebra*, (**b**) *Mchenga conophorus*, and (**c**) *Tramitochromis intermedius.* The simplest type of acoustic signal produced is the specific sound of individual pulses, which are then frequently repeated. Field recordings made underwater of free-living fishes in their natural habitat (depth 3–8 m) at Cape McClear, Lake Malawi National Park offshore of the World Wildlife Fund Education Center and at Otter Point, August 5–27, 1990 (Lobel 1998)

Pharyngeal jaws in cichlids are well known for their advanced capability for complex muscle modulation and bone movement (Liem 1973, 1991). Four cichlid species (Tables 3 and 4) produce sounds that exhibit more complex amplitude modulation patterns and pulse repetition rates than ones produced by many other fish families with simpler and probably less manipulatable pharyngeal apparatuses. For example, the morphology of the pharyngeal jaw complex suggested a close relationship between pomacentrids (damselfishes) and cichlids within Labroidei (Wainwright et al. 2012; Lauder and Liem 1983), although this close relationship has been overturned in recent molecular phylogenies (e.g., Betancur-R et al. 2017). Cichlids differ significantly from other fishes in the muscle and bone architecture of their pharyngeal apparatus (Liem and Greenwood 1981; Kaufman and Liem 1982; Seehausen et al. 1999; Stiassny and Jensen 1987).

If this difference in pharyngeal morphology is a basis for sound production, then presumably pomacentrids may not be able to forcibly occlude or grind the pharyngeal jaws in the way that the cichlids do. The pomacentrid sound production mechanism has been described as resulting from jaw element movements similar to the feeding process (Parmentier et al. 2007; Parmentier and Fine 2016; Olivier et al. 2017). Sound production in pomacentrids has been extensively described

Table 3 Acoustic traits of cichlid species sounds associated with agonistic and reproductive behavior. Frequency range was reported if no other frequency data were available

Species ($n = 35$) (current name)	Behavioral Context	Sound pattern	Bioacoustic traits: Sound duration (ms)	Pulse #; pulse rate	Pulse duration	Intra-call interval PP = pulse period; IPI = Interpulse interval	Frequency (Hz): “PEAK” = dominant or peak; “Main, Principle, Maximum intensity, Primary” = peak; Instantaneous; “MIDDLE” = middle “FUND” = fundamental “RANGE” = minimum to maximum	Literature cited
South America ($n = 5$):								
Amatitlania nigrofasciata	A	Pulsed	ND	20 pulses/sec pulse rate (no sample size)	ND	ND	480 MIDDLE (no sample size)	Myrberg et al. (1965)
Archocentrus centrarchus	A	Pulsed	500–4000 (no sample size)	ND	ND	ND	100–700 maximum energy, 100–1300 RANGE (no samples size)	Schwartz (1974a)
Cichlasoma portalegrens	A	Single pulse “thump”	ND	ND	ND	ND	80–300 principle (no sample size); 80–600 RANGE	Brown and Marshall (1978)
Herotilapia multispinosa	A	Single pulse “thump”	93 (27–225)	Non-pulsed	ND	ND	85–1250 RANGE, 100–300 principle	Brown and Marshall (1978)
	A	Single pulse “woof”	211 (87–348)	Non-pulsed	ND	ND	85–1400 RANGE, 105–300 principle	Brown and Marshall (1978)

	A	Pulsed “volley”	359 (99–1056)	ND	37 (17–65)	82 (5–205) IPI	85–1400 RANGE, 150–450 principle	Brown and Marshall (1978)
	A, Cd and Cf	Pulsed “growl”	200 (108–1600)	ND	5 (3–10)	121 (76–316) IPI	100–600 RANGE, 150–350 principles	Brown and Marshall (1978)
Pterophyllum sp. (probably *scalare*)	A	Pulsed “broad-band high Hz pulse & low Hz pulse”	ND	6 pulses/sec pulse rate (no samples size)	ND	ND	Maximum Intensity 3300 Hz, Frequency components >10 kHz, low frequency pulse ~300 Hz (no sample size)	Myrberg et al. (1965)
Africa ($n = 30$):								
Astatotilapia burtoni	Type2 feeding & shortly after” aggression “chewing”	Pulsed	1500 (300–3500)	4 (2–8)	50 (30–90)	ND	7000 (2500 - 16,000) Main, 1250–10,000 lower & >20,000 upper frequency	Nelissen (1978)
	A & Cc Type1	Pulsed	370 (230–1410)	13 (5–37)	ND	ND	320 (120–630) Main 80–1000 RANGE	Nelissen (1978)
	Cd	Pulsed	240 ± 137 (51–695)	9 ± 4 (2–19)	10 ± 3 (5–26)	18 ± 13 (5–98) IPI	499 (129–904) PEAK; <50–1500 RANGE	Maruska et al. (2012)
Cynotilapia afra	PAM	Pulsed	446 ± 190	13 ± 6	9 ± 1.2	35 ± 6.6 PP	ND	Danley et al. (2012)
Haplochromis nyererei	A, Cd	Pulsed	In data analysis	6 ± 0.4 S.E.M.	ND	PP (in data analysis)	PEAK in figure	Verzijden et al. (2010)
Haplochromis pundamilia	Cd	Pulsed	In data analysis	7 ± 0.4 S.E.M.	ND	PP (in data analysis)	PEAK in figure	Verzijden et al. (2010)

(continued)

Table 3 (continued)

Species ($n = 35$) (current name)	Behavioral Context	Sound pattern	Bioacoustic traits: Sound duration (ms)	Pulse #; pulse rate	Pulse duration	Intra-call interval PP = pulse period; IPI = Interpulse interval	Frequency (Hz): "PEAK" = dominant or peak; "Main, Principle, Maximum intensity, Primary" = peak; Instantaneous; "MIDDLE" = middle "FUND" = fundamental "RANGE" = minimum to maximum	Literature cited
Hemichromis bimaculatus	DISPLAY TO MODEL: A "thump", A "purr" (display at model)	Pulsed "purr"; Undetermined "thumps"/burst	ND	43 ± 8 pulses/sec "purr" RATE; 11 ± 4 "thumps"/sec	ND	ND	500 maximum intensity; 500 maximum energy	Rowland (1978)
	A	Pulsed "brrr," 3–5 single pulse "thumps" 1) female "brrr" parental care 2) male "brrr" 3) male "thump"	ND	(1) 35 pulses/sec (2) 35 pulses/sec (3) 12 "thump" sounds/sec (no sample size)	ND	ND	250–350, 400–450, 500–700 ($n = 3$ individual fish) PEAK	Myrberg et al. (1965)
	DISPLAY TO MODEL: male "quiver"	Pulsed	ND	10–15 pulses/sec	ND	ND	<100 (no sample size)	Rowland (1978)

Labeotropheus fuelleborni	PAM	Pulsed	364 ± 148	12 ± 4	9 ± 1	35 ± 6 PP	ND	Danley et al. (2012)
Labidochromis caeruleus	Cd	ND	ND	ND	ND	ND	300 PEAK (no samples size)	Higgs et al. (2011)
Maylandia aurora	PAM	Pulsed	376 ± 125	12 ± 4	12 ± 2	35 ± 9 PP	ND	Danley et al. (2012)
Maylandia callainos	Cd	Pulsed	476 (349–652)	8 (6–11)	12 (10–13)	67 (50–79) PP	517 (425–620) PEAK	Amorim et al. (2004)
	Cd	Pulsed	660 ± 409	9 ± 5	ND	ND	ND	Smith (2007)
	Cd	Pulsed	ND	ND	ND	(IPI long no data)	~180–500 PEAK, ~20–1200 RANGE (multiple species pooled data, no sample size)	Smith and van Staaden (2009)
	Cd	Pulsed	618 (349–1033)	10 (6–15)	ND	73 (61–83) PP	150 (132–182) Peak1 FUND PEAK; 520 (474–567) Peak2	Amorim et al. (2008)
	PAM	Pulsed	205 ± 108	11 ± 2	5 ± 1	17 ± 4 PP	None	Danley et al. (2012)
Maylandia emmiltos	Cd	Pulsed	760 (302–987)	16 (10–22)	ND	48 (31–62) PP	134 (112–145) Peak1 FUND PEAK, 448 (418–485) Peak2	Amorim et al. (2008)
Pooled data: *Maylandia emmiltos, Maylandia fainzilberi and Pseudotropheus "zebra gold" x M. zebra*	Cd	Tonal sound; **COMPLEX** frequency modulated tonal and pulsed	514 ± 131 (282–833); 550 ± 119 (334–796)	ND	ND	ND	44 ± 20 (23–86); 34 ± 8 (22–54) PEAK	Simoes et al. (2008a)
Maylandia fainzilberi	Cd	Pulsed	723 (398–1118)	9 (7–11)	ND	87 (64–108) PP	138 (124–151) Peak1 FUND PEAK; 473 (438–549) Peak2	Amorim et al. (2008)
Maylandia lombardoi	Cd	"Grunting"	220 ± 117	8 ± 4	ND	ND	226 ± 42 primary	Smith (2007)

(continued)

Table 3 (continued)

Species ($n = 35$) (current name)	Behavioral Context	Sound pattern	Bioacoustic traits: Sound duration (ms)	Pulse #; pulse rate	Pulse duration	Intra-call interval PP = pulse period; IPI = Interpulse interval	Frequency (Hz): "PEAK" = dominant or peak; "Main, Principle, Maximum intensity, Primary" = peak; Instantaneous; "MIDDLE" = middle "FUND" = fundamental "RANGE" = minimum to maximum	Literature cited
	Cd	Pulsed hypothesized "grunting" (no waveform)	Duration in analysis	ND	ND	(PP difficult to measure, no IPI data, recording noise)	Primary in analysis	van Staaden and Smith (2011)
	Cd	Pulsed	ND	ND	ND	(IPI short no data)	~180–500 PEAK, ~20–1200 RANGE (six species pooled)	Smith and van Staaden (2009)
Maylandia zebra	A	Pulsed	961 ± 295 (549–1430) male–male	9 ± 3 (5–14)	ND	126 ± 24 (90–161)	138 ± 15 (117–164) Peak1 (higher energy PEAK and FUND); 463 ± 35 (434–551) Peak2;	Simoes et al. (2008b)
	A	Pulsed	524 ± 153 (358–733) female–female	5 ± 1 (4–6)	ND	124 ± 27 (93–165) PP	143 ± 7 (134–152) Peak1 (higher energy PEAK and FUND; 480 ± 29 (445–525) Peak2	Simoes et al. (2008b)
	A (juvenile)	Single pulse	5 ± 0.25 SE	Non-pulsed	Non-pulsed	Non-pulsed	1611 ± 78 SE instantaneous frequency	Bertucci et al. (2012b)
	PAM	Pulsed	764 ± 407	17 ± 2	16 ± 5	55 ± 13 PP	ND	Danley et al. (2012)

	Cd	Pulsed	532 (384–786)	9 (7–14)	10 (8–11)	66 (60–74) PP	460 (399–509) PEAK	Amorim et al. (2004)
	Cd	Pulsed	672 (421–857)	9 (7–12)	ND	87 (68–113) PP	156 (129–221) Peak1 FUND PEAK, 489 (424–558) Peak2	Amorim et al. (2008)
Maylandia zebra	Cd	Pulsed: 1) Lead swim; 2) quiver display; 3) no display; 4) circle swim	567 ± 247 (214–1210); 1199 ± 647 (298–2622); 481 ± 381 (201–1276); 562 ± 157 (343–853)	7 ± 2 (4–12); 15 ± 8 (5–33); 5 ± 3 (3–12); 7 ± 1 (6–9)	ND	92 ± 20 57–120); 87 ± 19 (60–133); 100 ± 13 (79–116); 83 ± 21 (53–135) PP	Peak1 (higher energy PEAK and FUND) and 2: 133 ± 15 (117–164), 459 ± 52 (375–539) Peak1(higher energy PEAK and FUND and 2; 150 ± 31 (109–258), 489 ± 62 (398–586) Peak1 (higher energy PEAK and FUND) and 2; 129 ± 18 (117–164), 454 ± 48 (375–539) Peak1 (higher energy PEAK and FUND) and 2; 141 ± 0 (141–141), 471 ± 30 (422–492)	Simoes et al. (2008b)
Maylandia "zebra katale"	Cd	Pulsed	ND	ND	ND	(IPI long no data)	~180–500 PEAK, ~20–1200 RANGE (six species pooled)	Smith and van Staaden (2009)
Mchenga conophoros	A	Irregular interpulses and pulse clarity	ND	ND	ND	ND	ND	Lobel (2001)
	Cd	Pulsed	181 ± 59 (78–654)	10 ± 3 (5–30) 18 ± 2 (14–22) call duration/ pulse# **pulse rate**	7 ± 2 (3–10)	16 ± 6 (8–35) IPI	471 ± 50 (372–594) PEAK	Lobel (1998)

(continued)

Table 3 (continued)

Species (n = 35) (current name)	Behavioral Context	Sound pattern	Bioacoustic traits: Sound duration (ms)	Pulse #; pulse rate	Pulse duration	Intra-call interval PP = pulse period; IPI = Interpulse interval	Frequency (Hz): "PEAK" = dominant or peak; "Main, Principle, Maximum intensity, Primary" = peak; Instantaneous; "MIDDLE" = middle "FUND" = fundamental "RANGE" = minimum to maximum	Literature cited
Melanochromis auratus	Cd	"Grunting"	311 ± 179	ND	ND	ND	268 ± 158 primary	Smith (2007)
	Cd	Pulsed hypothesized "grunting" (no waveform)	Duration in analysis	ND	ND	(PP difficult to measure, no IPI data, recording noise)	Primary in analysis	van Staaden and Smith (2011)
	Cd	Pulsed	ND	ND	ND	(IPI short no data)	~180–500 PEAK, ~20–1200 RANGE (six species pooled)	Smith and van Staaden (2009)
Neochromis omnicaeruleus	Cd	Pulsed	In data analysis	8 ± 0.4 S.E.M.	ND	(PP in data analysis)	PEAK in figure	Verzijden et al. (2010)
Neolamprologus pulcher	A (with social behavior)	Pulsed (two-pulse)	896 ± 804 (with behavior)	2 ± 0.7	12 ± 4	(IPI <400 data in figure)	12,281 ± 3740 PEAK	Spinks et al. (2017)
	A	Pulsed (two-pulse)	918 ± 770 (male sounds)	2 ± 0.1	14 ± 2	ND	12,710 + 4304 PEAK	Spinks et al. (2017)
	A	Pulsed (two-pulse)	670 + 910 (female sounds)	2 ± 1	9 ± 1	ND	13,396 + 2202 PEAK	Spinks et al. (2017)
	A	Pulsed (two-pulse)	ND	ND	ND	ND	Often first pulse ~7000 – ~15,000, second pulse ~7000–>17,000 PEAK (no sample size)	Spinks et al. (2017)

Oreochromis mossambicus	A	Continuous pulse series and/or pulsed	246 (112–775)	Non-pulsed	Non-pulsed	Non-pulsed	Mean 40–60 (range < 300) ND	McPherson (2012)
	A	ND	50–500 (no sample size)	ND	ND	ND	120–1400 RANGE (no sample size)	Konstantinova et al. (1979) (as cited in Amorim et al. 2003)
	Cd, Cs	Pulsed	712 ± 458 (100–2834)	17 ± 9 (4–60)	12 ± 1 (9–15)	44 + 14 (22–137) PP	354 (207–524) PEAK; 38–1262 RANGE	Amorim et al. (2003)
	Cd	Pulsed hypothesized (no waveform) three sound types	ND	7–18 “double pulses”; 2–12; 4–6; (no sample sizes)	7–10; 6–12; 25–30; (no sample sizes)	35–100 PP; 7–95 PP; 100–250 PP; (no samples sizes)	200–259 FUND; 200–250 RANGE; 185–250 RANGE (no sample sizes)	Konstantinova et al. (1979) (as cited in Amorim et al. 2003)
Oreochromis niloticus	A (control group juveniles)	Continuous pulse series (double or triple pulses)	314 ± 79	2 ± 0.4	143 ± 24	No interpulse present	68 ± 33 Main PEAK: 35 ± 11 Peak1 FUND, 72 ± 13 Peak2, 121 ± 22 Peak3	Longrie et al. (2008)
	A (isolated juveniles)	Continuous pulse series (double or triple pulses)	285 ± 80	2 + 0.5	109 ± 13	No interpulse present	46 ± 13 Main PEAK; 45 ± 7 Peak1 FUND, 109 ± 17 Peak2, 173 ± 30 Peak3	Longrie et al. (2008)
	A	Pulsed	127 ± 20	2–4 range	114 ± 7	ND	57 ± 14 Peak1 Main peak	Longrie et al. (2009)
	A (female nest territoriality)	Pulsed	321 ± 101 SE	3 ± 1 SE	105 + 23 SE	ND	50 ± 14 SE PEAK	Longrie et al. (2013)
	A (female oral incubation of eggs vs intruders)	Pulsed	265 ± 84 SE	3 + 1 SE	107 ± 21 SE	ND	48 ± 16 SE PEAK	Longrie et al. (2013)

(continued)

Table 3 (continued)

Species ($n = 35$) (current name)	Behavioral Context	Sound pattern	Bioacoustic traits: Sound duration (ms)	Pulse #; pulse rate	Pulse duration	Intra-call interval PP = pulse period; IPI = Interpulse interval	Frequency (Hz): "PEAK" = dominant or peak; "Main, Principle, Maximum intensity, Primary" = peak; Instantaneous; "MIDDLE" = middle "FUND" = fundamental "RANGE" = minimum to maximum	Literature cited
Pelmatolapia mariae	Context not determined	Single pulse	~10 ms	Non-pulsed	Non-pulsed	Non-pulsed	~3000–8000 "most energy" with higher harmonics <20,000, <8000 PEAK	Kottege et al. (2015)
Petrotilapia nigra	PAM	Pulsed	422 ± 217	18 ± 9	10 ± 3	28 ± 5 PP	ND	Danley et al. (2012)
Pseudosimochromis babaulti	A and Cc Type1	Pulsed	590 (240–1470)	26 (8–40)	20 (10–20)	ND	193 (125–500) Main, 50–800 RANGE	Nelissen (1978)
Pseudotropheus cyaneorhabdos	Cd	"Grunting"	220 ± 62	8 ± 3	ND	ND	212 ± 49 primary	Smith (2007)
	Cd	Pulsed hypothesized "grunting" (no waveform)	Duration in analysis	ND	ND	(PP difficult to measure, no IPI data, recording noise)	Primary in analysis	van Staaden and Smith (2011)
	Cd	Pulsed	ND	ND	ND	(IPI short no data)	~180–500 PEAK, ~20–1200 RANGE (six species pooled)	Smith and van Staaden (2009)
Pseudotropheus johannii	Cd	"Grunting"	287 ± 172	10 ± 5	ND	ND	228 ± 56 primary	Smith (2007)

	Cd	Pulsed hypothesized "grunting" (no waveform)	Duration in analysis	ND	ND	(PP difficult to measure, no IPI data, recording noise)	Primary in analysis	van Staaden and Smith (2011)
	Cd	Pulsed	ND	ND	ND	(IPI short no data)	~180–500 PEAK, ~20–1200 RANGE (six species pooled)	Smith and van Staaden (2009)
Pseudotropheus "zebra gold"	Cd	Pulsed	668 (310–1022)	11 (4–20)	10 (9–11)	63 (52–77)	436 (389–480) PEAK;	Amorim et al. (2004)
	Cd	Pulsed	774 (558–1122)	13 (8–20)	ND	66 (53–78) PP	152 (135–202) Peak1 FUND PEAK, 477 (432–545) Peak2	Amorim et al. (2008)
Simochromis diagramma	Feeding and A "chew" sounds	Pulsed	2000–3000 (no sample size)	3 pulses/sec RATE (no sample size)	100 (no sample size)	ND	6000–10,000 PEAK, ~4000–20,000 (no sample size)	Nelissen (1975) (preliminary study to Nelissen 1978)
	A and Cc "brrr" sound	Pulsed	500–2000 (no sample size)	ND	ND	ND	70–300 RANGE (no sample size)	Nelissen (1975) (preliminary study to Nelissen 1978)
	Type2 "chewing"	Pulsed	2450 (1060–3800)	7 (3–11)	100 (50–150)	ND	8000 (6000–10,000) Main, 3000–6000 Lower and ~20,000 Upper Frequency	Nelissen (1978)
	A & Cc Type1	Pulsed	1110 (600–1700)	26 (16–37)	10 (10–10)	ND	200 (100–200) Main, 50–500 RANGE	Nelissen (1978)

(continued)

Table 3 (continued)

Species ($n = 35$) (current name)	Behavioral Context	Sound pattern	Bioacoustic traits: Sound duration (ms)	Pulse #; pulse rate	Pulse duration	Intra-call interval PP = pulse period; IPI = Interpulse interval	Frequency (Hz): “PEAK” = dominant or peak; “Main, Principle, Maximum intensity, Primary” = peak; Instantaneous; “MIDDLE” = middle “FUND” = fundamental “RANGE” = minimum to maximum	Literature cited
Tramitichromis cf. *intermedius*	Cd	Pulsed	199 ± 44 (120–304)	9 ± 2 (6–12); 21 ± 2 (17–33) call duration/ pulse# **pulse rate**	6 ± 1 (3–11)	15 ± 5 (8–34) IPI	388 (305–480) PEAK	Lobel (1998)
	Cd	Pulsed wild caught (captive born)	Nested mean 171	Nested mean 10	ND	ND	Nested mean 323 PEAK	Ripley and Lobel (2004)
Tropheus brichardi	Type2 “chewing”	Pulsed	2200 (80–5000)	4 (1–8)	90 (50–170)	ND	7850 (250–>20,000) Main, 1000–6300 Lower and 6300—>20,000 Upper Frequency	Nelissen (1978)
	A and Cc Type1	Pulsed	830 (250–2350)	32 (9–92)	20 (10–30)	ND	620 (800–900) Main, 200–2000 RANGE	Nelissen (1978)
Tropheus duboisi	Type2 “chewing”	Pulsed	1370 (110–3900)	5 (1–10)	80 (40–130)	ND	6606 (2500–12,500) Main, 630–3150 lower and 2150 - >20,000 upper frequency	Nelissen (1978)

	A & Cc Type1	Pulsed	460 (70–1470)	19 (3–33)	10 (10–10)	ND	470 (125–1250) Main, 63–5000 RANGE	Nelissen (1978)
Tropheus moorii	Type2 “chewing”	Pulsed	1060 (300–2100)	4 (2–10)	50 (40–80)	ND	5500 (800 – Above 20,000) Main, 630–8000 lower and 4000 - >20,000 upper frequency	Nelissen (1978)
	A & Cc Type1	Pulsed	400 (150–900)	20 (5–35)	20 (6–70)	ND	840 (50–1250) Main, 25–3150 RANGE	Nelissen (1978)

Statistics reported as mean ± SD (range) unless otherwise noted. *ND* no data

Table 4 Bioacoustic research topics

Research topic species	Results	Literature cited
HEARING CONSPECIFIC CALLS		
Astatotilapia burtoni	Females have hearing sensitive to male call frequency range	Maruska et al. (2012)
Labidochromis caeruleus	Hearing sensitive to tone bursts 100–1000 Hz and conspecific male call	Higgs et al. (2011)
Haplochromis nyererei	Males and females discriminate conspecific sounds from white noise bursts by change in activity level when responding to playback	Estramil et al. (2014)
Tramitichromis intermedius	Hearing peak matches the call dominant frequency	Ripley et al. (2002)
SOUND PROPAGATION DISTANCE		
Maylandia zebra	Courtship sound waveform pulse pattern barely discernable at 40 cm	Simoes et al. (2008b)
Maylandia fainzilberi, Pseudotropheus "zebra gold" × *M. zebra, P. emmiltos*	Sounds were recordable within one body length of fish (12 + 0.8 SD, 11–15 cm)	Simoes et al. (2008a)
Maylandia callainos, M. fainzilberi, M. zebra, M. emmiltos, Pseudotropheus "zebra gold"	Sounds with clear structure detectable at 1–2 body lengths (8.7–13.9 cm range for all species)	Amorim et al. (2008)
CALL ONTOGENY		
Maylandia zebra	Development of agonistic sound patterns in juveniles: Single to double pulsed; sound production first detected at >43 days	Bertucci et al. (2012b)
Oreochromis niloticus	First sounds in nest construction 210 days of age	Longrie et al. (2008)
Tramitichromis intermedius	Number of days of age to first courtship sound production 211 ± 3 SD	Ripley and Lobel (2004)
CALLING ACTIVITY PATTERNS		
Archocentrus centrarchus	Acoustic agonistic activity level varies through the reproductive cycle (mean sounds toward mate/day)	Schwartz (1980)
Herotilapia multispinosa	Calling activity rates (mean # agonistic "volley" sounds/15 min): Prespawning (highest # of calls), egg, larval, and free-swimming stages Relative # sounds/14 min; mean # growling reproductive and agonistic sounds/day	Brown and Marshall (1978)
Oreochromis niloticus	Diurnal calling peak, 24-hr acoustic monitoring	Longrie et al. (2013)
Tramitichromis intermedius	Calling peaks leading up to and just before spawning	Ripley and Lobel (2004)

(continued)

Table 4 (continued)

Research topic species	Results	Literature cited
CONTEXT SPECIFIC CALLS		
Maylandia zebra	Male courtship early calls longer duration, more pulses, shorter pulse period, higher frequency from later circle, and lead swim courtship calls	Simoes et al. (2006)
	Male–male agonistic sounds longer duration and pulse period than male courtship sounds	Simoes et al. (2008b)
Haplochromis nyererei	No difference between agonism and courtship call	
Tramitichromis intermedius	Difference between agonism and courtship calls: Courtship sound regular and distinct pulses	Lobel (2001)
FEMALE SOUND PRODUCTION		
Archocentrus centrarchus	Female 5–30 sounds/day; mean sounds and attacks/day over time	Schwarz (1980)
Hemichromis bimaculatus	Female agonistic sounds	Myrberg et al. (1965)
Maylandia zebra	Female agonistic sounds shorter duration with fewer pulses than male agonistic and courtship sounds	Simoes et al. (2006), Simoes et al. (2008b)
Neolamprologus pulcher	Female agonistic sounds	Spinks et al. (2017)
Oreochromis niloticus	Female agonistic sounds	Longrie et al. (2013)
Pelmatolapia mariae	Female sounds near in nest area evaluated with vector analysis	Kottege et al. (2015)
CONTESTS INFLUENCE CALLING		
Oreochromis mossambicus	Male–male contest winners produced more calls that were longer in pulse duration and lower in peak frequency	Amorim and Almada (2005)
Haplochromis nyererei	Dyadic contests elicit sounds	Verzijden et al. (2010)
COMPLEX CALL		
Hemichromis bimaculatus	Pulsed and “thump” sounds overlap	Rowland (1978)
Maylandia fainzilberi, Pseudotropheus “zebra gold” × M. zebra, M. emmiltos	Continuous waveform tonal “moan” with or without frequency modulation produced alone or precedes interpulsed sound (species data pooled)	Simoes et al. (2008a)
NON-PULSED WAVEFORM PATTERNS		
Cichlasoma portalegrense	Single pulse	Brown and Marshall (1978)
Hemichromis bimaculatus	Single pulse “thump” in bursts of 3–5	Myrberg et al. (1965)

(continued)

Table 4 (continued)

Research topic species	Results	Literature cited
Herotilapia multispinosa	Single pulse "thump" and "volley" in established contexts; "woof" unestablished	Brown and Marshall (1978)
Maylandia fainzilberi, Pseudotropheus "zebra gold" × *M. zebra* hybrid, *M. emmiltos*	Continuous waveform low amplitude, tonal, sometimes frequency modulated	Simoes et al. (2008a)
Maylandia zebra	Single pulse in juveniles	Bertucci et al. (2012b)
Neolamprologus pulcher	Single pulse broadband frequency	Spinks et al. (2017)
Oreochromis mossambicus	Continuous pulse series and/or Interpulsed (variable interpulses)	McPherson (2012)
Oreochromis niloticus	Continuous pulse series (double and triple pulsed)	Longrie et al. (2008)
Pelmatolapia mariae	Single pulse broadband frequency	Kottege et al. (2015)
PLAYBACK OF CONSPECIFIC SOUNDS or NOISE		
Archocentrus centrarchus	Sounds playback inhibited higher aggression in receivers toward conspecifics but this data was not confirmed in a later study	Schwartz (1974b, 1980)
Astatotilapia burtoni	Females prefer male calls to white noise	Maruska et al. (2012)
Hemichromis bimaculatus	Fishes respond significantly more to conspecific sound model playbacks over silent models	Rowland (1978)
Maylandia zebra	Territorial males respond to conspecific sounds but not temporal coding modifications	Bertucci et al. (2013)
Oreochromis mossambicus	Male agonistic sounds silence other males in a preliminary study	McPherson (2012)
Haplochromis nyererei	Females prefer males producing sounds versus silent males	Verzijden et al. (2010)
	Females were not attracted to male sounds alone requiring the visual presence of a male	Estramil et al. (2014)
CALL VARIATION and BODY SIZE		
Astatotilapia burtoni	Mean peak frequency of male calls inversely related to body size	Maruska et al. (2012)
Haplochromis nyereri	Noise playback reduced the intensity of courtship behavior	Slabbekoorn et al. (2012)
Maylandia callainos	Mean peak frequency of male calls inversely related to body size	Amorim et al. (2004)
Maylandia callaino, M. fainzilberi, M. zebra, M. emmiltos, and Pseudotropheus "zebra gold"	Peak frequency inversely correlated with body size	Amorim et al. (2008)

(continued)

Table 4 (continued)

Research topic species	Results	Literature cited
Maylandia zebra	Larger males produce lower frequency courtship sounds	Simoes et al. (2008b)
	Amplitude, temporal, and frequency call features correlated with body size	Bertucci et al. (2012a, b)
Haplochromis nyererei and H. pundamilia, Neochromis omnicaeruleus	Peak frequency correlates inversely with standard length	Verzijden et al. (2010)
INDIVIDUAL ACOUSTIC SIGNATURES		
Maylandia zebra	Instantaneous frequency, frequency modulation rate and pulse amplitude modulation rate that could serve as acoustic signatures for individuals	Bertucci et al. (2012a, b)
POPULATION CALL VARIATION		
Maylandia callainos and M. zebra	Variation in call parameters within Lake Malawi based on call means	Danley et al. (2012)
MULTIMODAL SIGNALING		
Maylandia callainos, M. lombardoi, Pseudotropheus cyaneorhabdos, P. johannii	Species combined audio and visual display	Smith and van Staaden (2009)
Maylandia zebra	Sound and visual signals reduce aggression	Bertucci et al. (2010)
Maylandia fainzilberi and *Pseudotropheus emmiltos*	Calls differed most between two sympatric species similar in color	Amorim et al. (2008)
Pundamilia nyererei	Phonotaxis alone insufficient for female attraction to male, visual cues also required	Estramil et al. (2014)
Tramitichromis intermedius	Wild born and captive cichlids hypothesized to use similar multi-modal signaling	Ripley and Lobel (2004)
REDUCED ACOUSTIC ACTIVITY DURING VISUAL DISPLAYS		
Melanochromis auratus	Sound production without visual displays	Smith and van Staaden (2009)
Maylandia zebra "katale"	Calling without "quiver" visual display	Smith and van Staaden (2009)
Oreochromus mossambicus	Calling activity intensified when territory was established	Amorim et al. (2003)
SILENT SPECIES?		
Astatoreochromis alluaudi	Lack of higher frequency register sounds in a monitored aquarium (>5000 Hz)	Spinks et al. (2017)
Cyphotilapia frontosa	Electric stimulation studies correlated with a vocal mechanism in another cichlid found no sound response from the muscles in this species	Longrie et al. (2009)

(continued)

Table 4 (continued)

Research topic species	Results	Literature cited
HYDRODYNAMIC SOUNDS		
Astatotilapia burtoni	Non-intentional sound production due to body motions proposed	Fernald (1975), Hirata and Fernald (1975)
Pseudotropheus emmiltos	Single pulse "dart" sounds are produced by sudden 180° swimming turns (spectrogram, sounds not described)	Simoes et al. (2008a)
ENVIRONMENTAL IMPACT ON SOUND PRODUCTION		
Oreochromis mossambicus	Hypothesized salinity effects on sound production influencing the swimbladder	Pujiyati et al. (2016)

(Lobel and Kerr 1999; Lobel and Mann 1995; Myrberg et al. 1978, 1986; Myrberg and Riggio 1985; Mann and Lobel 1995, 1997, 1998; Spanier 1979). However, the mechanism of sound production still needs to be studied across species.

3.1 Functional Morphology of the Cichlid Sound Mechanisms

Despite the recent research describing cichlid sounds and behavior, the morphological mechanism(s) responsible for these sounds still requires detailed study. In many sonic fish species, there are clear morphological adaptations and specializations dedicated to sound production (e.g., Bass and Ladich 2008; Kasumyan 2008). These sonic mechanisms involve the swimbladder (e.g., Alexander 1966; Fange 1966; Parmentier and Diogo 2006), different bones or fins (Fine et al. 1996; Parmentier et al. 2010), connective tissues (Parmentier et al. 2007), or in some cases multiple mechanisms (Kaatz 2002; Kaatz et al. 2017; Sörensen 1894–1895). In some species of fish, such as the rockfishes (Family Scorpaenidae), their sonic ability was initially hypothesized or inferred based on the identification of well-developed sonic muscles (Hallacher 1974), and later confirmed through acoustic recordings (Širović and Demer 2009). Even though it is now recognized that the occurrence of sounds in cichlids is widespread, the exact identity of the sonic mechanism is elusive with a few different hypotheses proposed or initially tested in the literature (Rice and Lobel 2003; Parmentier and Fine 2016).

The acoustic properties of fish sounds can be suggestive of the sonic mechanism: muscle-driven sounds typically have harmonic frequency structure, and variable call durations, while stridulatory sounds (produced by the grinding of hard surfaces) are broadband and shorter duration (Demski et al. 1973). However, these spectral and temporal properties of sounds are likely endpoints along a continuum, as there are many examples of muscle driven sounds that produce short duration pulses with little spectral structure, such as in red drum (Family Sciaenidae) (Guest and Lasswell 1978). Since most fishes are ectothermic, the frequency in sounds produced by muscles has a temperature-dependent response: warmer water temperatures increase the contraction speed of sonic muscles, which increases the frequency of the call (Connaughton et al. 2002; McKibben and Bass 1998). In the case of toadfishes (Family Batrachoididae), the contraction rate of the sonic muscle sets the fundamental frequency of the call (McKibben and Bass 1998).

The cichlid sonic mechanism is difficult to identify based only upon the acoustic properties of the cichlid sounds. The majority of cichlid sounds are relatively short duration (duration <1 s) and low frequency (dominant frequencies <1000 Hz). Based on the conceptual framework of Demski et al. (1973), these types of sound could be produced by either muscular or osteological mechanisms. Furthermore, there are aspects of the sounds, such as harmonic content (reviewed in Rice and Lobel 2003) and stereotypic acoustic features (Lobel 1998; Rice and Lobel 2003) that make the case even more ambiguous. Despite the number of publications documenting sounds produced by different cichlid species, comparatively few have examined the functional morphology. To date, two morphological systems have been hypothesized to be the source of cichlid sounds: pharyngeal teeth with associated musculature, which is then amplified by the swimbladder, and the buckling method involving abdominal musculature impinging directly on the swimbladder (Longrie et al. 2009).

3.2 Pharyngeal Teeth

The earliest hypothesis for the sonic mechanism in cichlids focused on the pharyngeal teeth (Lanzing 1974; Lanzing and Higginbotham 1976). The cichlid pharyngeal jaws have been suggested as a critical evolutionary innovation responsible for driving the ecological success and diversification of the family (Liem 1973, 1978, 1979; Liem and Greenwood 1981; Liem and Osse 1975). Early observations of cichlid noted that sounds associated with feeding behavior showed similar acoustic properties to communicative sounds (Lanzing 1974); however, some species show differences in the acoustic properties between these sound types (Longrie et al. 2009).

The shapes of cichlid pharyngeal teeth are intricate and elaborate (Casciotta and Arratia 1993; Lanzing and Higginbotham 1976), and show a diet-dependent phenotypic plasticity (Huysseune 1995; Smits et al. 1996a; Smits et al. 1996b; Trapani 2003). Many of the upper pharyngeal jaw teeth have “hooks,” whereas the bottom teeth are more of flat surface (Lanzing and Higginbotham 1976); for example, see Fig. 3. Lanzing and Higginbotham (1976) suggested that the divergent morphology of upper and lower pharyngeal jaw teeth form a “hook and anvil arrangement” and could be involved in the production of sounds. Sounds created by occluding teeth would presumably produce short duration, broadband sounds, with relatively higher

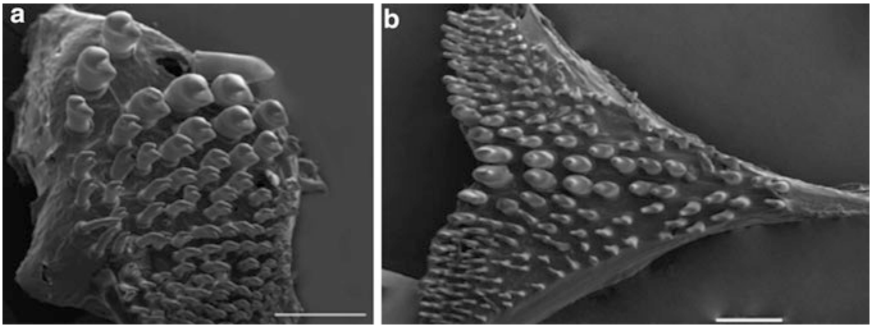

Fig. 3 Detail of the pharyngeal teeth from a *Tramitochromis intermedius* male. The upper and lower pharyngeal jaw teeth form a "hook and anvil arrangement." The magnification on the lower PJ is 15x and the magnification on the upper PJ is 19x. SEMs taken by A. Rice using a JEOL JSM-840 SEM

frequencies. A similar sonic mechanism has been suggested in jacks (Carangidae; Taylor and Mansueti 1960).

3.3 Pharyngeal Jaw Complex

One of the hypothesized evolutionary innovations and keys to the cichlid adaptive radiations in both the African Rift Lakes and the Neotropics is their highly developed pharyngeal jaw apparatus (e.g., Burress 2016; Liem 1973; Wainwright et al. 2012). The jaws are suspended and controlled by a suite of pharyngeal jaw muscles that are responsible for jaw occlusion, lateral, and anterior-posterior movement (Claes and De Vree 1991; Liem 1973). Intriguingly, the pharyngeal jaw muscles of cichlid fish have different physiological properties (Rice et al. 2001), which are also sexually dimorphic (Rice and Lobel 2002). This finding suggests the hypothesis that one sex is more morphologically adapted to produce sounds than is the other sex. Other sonic species of fish, where primarily the males produce the sounds, show a sexual dimorphism in sonic muscle morphology or physiology (Brantley et al. 1993; Walsh et al. 1987; Walsh et al. 1989) or brain regions controlling sound production (e.g., Bass and Andersen 1991; Bass and Baker 1990; Knapp et al. 1999). Thus, the corroborating evidence of physiological difference in pharyngeal jaw muscle performance, sexual dimorphisms in muscle physiology, along with the intricate movements of pharyngeal jaws sets the stage for in vivo physiological experiments to demonstrate the degree to which the pharyngeal jaw complex is involved in cichlid sound production (Rice and Lobel 2003).

Examples of sounds from one male *Tramitichromis intermedius* support the notion that the pharyngeal jaws are involved in sound production and that such sounds are amplified by the swimbladder. A typical courtship sound is illustrated in Fig. 4a showing both the series of pulses in a single call (Fig. 4a) and the detailed

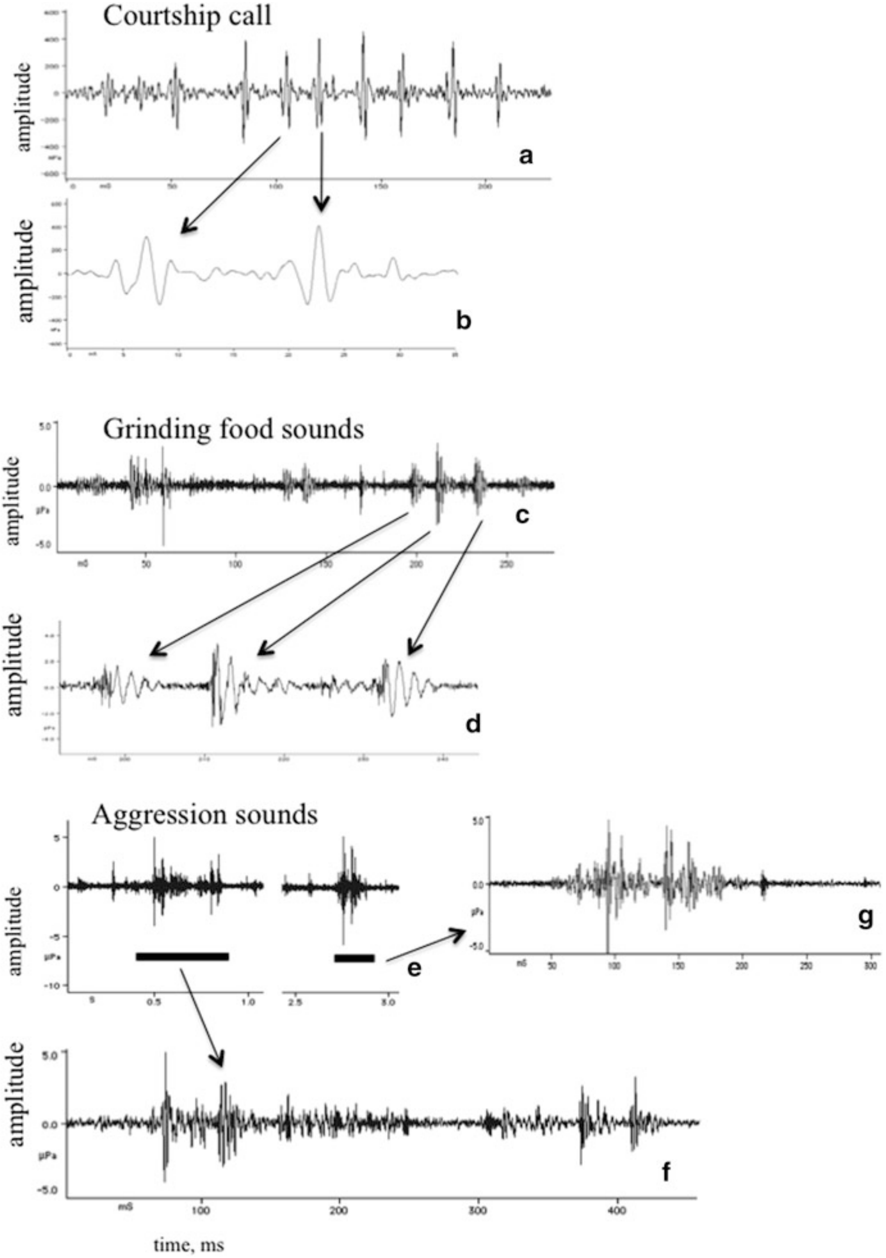

Fig. 4 Examples of courtship and grinding food sounds from one male *Tramitichromis intermedius* and aggressive sounds from *Copadichromis conophorus*. A typical courtship sound showing both the series of pulses in a single call composed of 10 pulses and overall duration of about 195.5 ms (**a**) and the detailed waveform structure of two pulses (**b**), pulse durations 6.69 and 7.33 ms separated by an interpulse interval of 8.54 ms. The same fish grinding consumed small sand-dwelling prey (**c**, **d**). In the audio–video recording, it was easily observable that the fish was

waveform structure of two pulses (Fig. 4b). A similar analysis involved sounds recorded while the same fish consumed small sand-dwelling prey. In the audio–video recording, it was easily observable that the fish was manipulating and grinding a hard-bodied prey in its buccal cavity. The series of food grinding sounds are shown with corresponding oscillographic patterns (Fig. 4c). Detailed waveform structure of two grinding sound pulses is shown in Fig. 4d. Courtship sounds are distinguished by distinct and consistently repetitive pulsed patterns with defined temporal meristics and repeatable pulse waveforms. Grinding sounds are highly irregular with inconsistent properties and appear much like simple noise type signals. Significantly, the two types of sounds from the same individual fish displayed the identical dominant frequency at 517 Hz indicating that amplification and resonance by the swimbladder were involved.

3.4 Fin-Girdle Muscles (Buckling Mechanism)

Research on *Oreochromis niloticus* raises the possibility of another sonic mechanism in cichlids termed “buckling” (Longrie et al. 2009). *O. niloticus* produces short duration, pulsed sounds in agonistic contexts (Longrie et al. 2009). This sound production coincided with posterior movement of the pectoral and pelvic girdles (Longrie et al. 2009). Electrical stimulation of the lateral body in anesthetized fish also resulted in sound production, with a decreased amplitude in fish with a deflated swimbladder (Longrie et al. 2009). Using the kinematic and electrostimulation data combined with morphological inspection, Longrie et al. (2009) suggest that the *vesica longitudinalis* muscle, which originates on the post-cleithrum, runs ventral to the swimbladder and inserts on the second anal fin pterygiophore is the candidate sonic mechanism (Longrie et al. 2009). This work raises interesting questions as to whether the *vesica longitudinalis* is involved in sound production more broadly across cichlid species, or whether it is an independent evolutionary innovation in tilapiine fish. It also raises the question of whether silent cichlids would represent a secondary loss of a vocal mechanism or independent origins of different vocal mechanisms.

Fig. 4 (continued) manipulating and grinding a hard-bodied prey in its buccal cavity. Oscillographic of the entire food grinding sequence of 227 ms duration. Courtship call and food grinding produce the same dominant frequency at 517 Hz. (**d**) Detail of the individual grinding sounds waveform, indicated by arrows. The first pulse is 8.17 ms duration; interpulse interval 5.74 ms, second pulse is 10.32 ms followed by 10.75 ms interpulse interval and third pulse is 7.17 ms. (e, f, g) Two bursts of an “aggressive sound” for comparison that was made by *Mchenga (Copadichromis) conophorus*: The first (left) is 351.2 ms duration and the second (right) is 168.7 ms

3.5 Evolutionary Implications

If cichlid pharyngeal jaws are involved in sound production, as preliminary evidence indicates, then we can expect that different pharyngeal jaw morphologies may produce different types of sounds. It remains to be determined if such different pulse waveforms reflect different types of sounds that are directly detectable by a fish. It is possible that the simplest type of acoustic signal produced is the specific sound of individual pulses, which are then frequently repeated. It may be the perceived sound of the pulse in combination with pulse rate timing that may contribute to species recognition. It is clear from prior studies that pulse number and/or repetition rate is closely correlated with the behavioral context of sounds.

Cichlids have attracted a great deal of attention as an adaptive radiation, particularly within the African rift lakes, with a spectacular diversity of behavior, ecology, and morphology (Albertson et al. 1999; Galis and Metz 1998; Kornfield and Smith 2000). It is no surprise then, that this lineage would show a widespread variety in sound production, and potentially sonic mechanisms. It is fascinating to investigate what is the cichlid sound producing mechanism(s). It has the potential to illustrate the evolution of acoustic diversity, especially among sympatric species. This research could potentially reveal the genetic mechanisms that are foundational to morphological specializations (Streelman et al. 2007), and has been proposed for the diversity of cichlid head and jaw morphologies (Albertson and Kocher 2006; Albertson et al. 2003).

4 Sound Characteristics

Many, but not all, cichlids produce a soft “purr” or “drumming” sound while performing courtship behavior, often accompanying the “quiver” display (Rowland 1978; Lobel 1998; Ripley and Lobel 2004; Brown and Marshall 1978). Fish sounds can be broadly categorized along a spectrum from continuous “long” sound to a series of short pulses or notes (Lobel et al. 2010). For cichlid species whose temporal patterns have been analyzed to date, most species consist of a series of regular pulses or notes with regular interpulse intervals (Table 3). Exceptions include in *H. multispinosa*, agonistic sounds are continuous, whereas in *M. conophoros* agonistic sounds are comprised of pulses with irregular interpulse intervals. Grunting and clicking species distinguished by Van Staaden and Smith (2011), varied in interpulse interval suggesting some species may have more continuous call patterns than others but the noise level of the recording environment precludes this conclusion. In the genus *Maylandia*, males have been documented to produce low amplitude, frequency-modulated sounds in addition to higher amplitude pulsed sounds (Simoes et al. 2008b). *Hemichromis bimaculatus* produced two different sound types in the same display (Rowland 1978). Single-pulse sound types were additionally produced by *Hemichromis bimaculatus*, *Herotilapia multispinosa*, *Maylandia zebra*

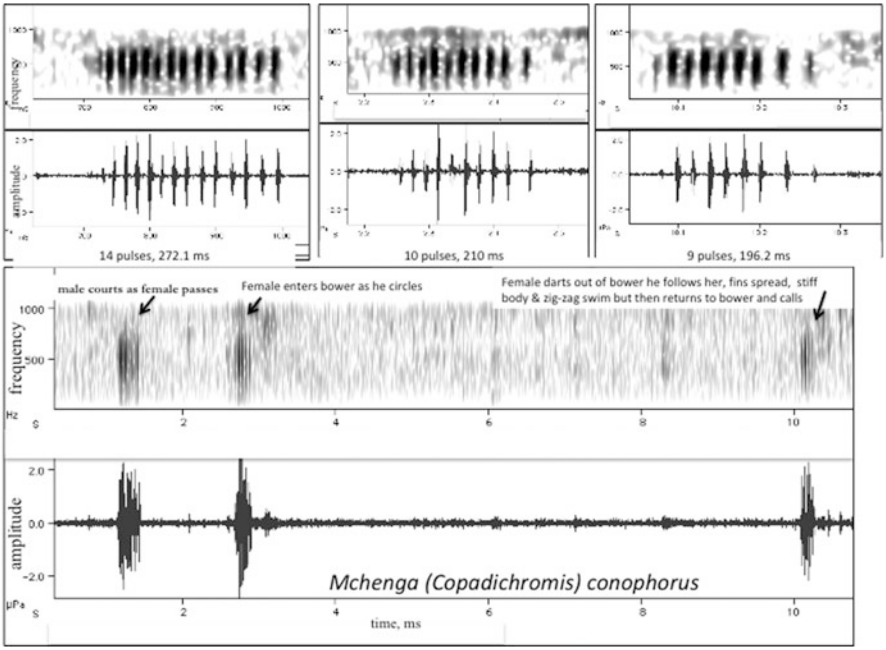

Fig. 5 Courtship sequence shown for *Mchenga (Copadichromis) conophorus* (Aug 23, 1990; 08:18:48–08:19:05 Hrs). Female enters bower and spawns then leaves the arena. See Fig. 7 for the fish recorded

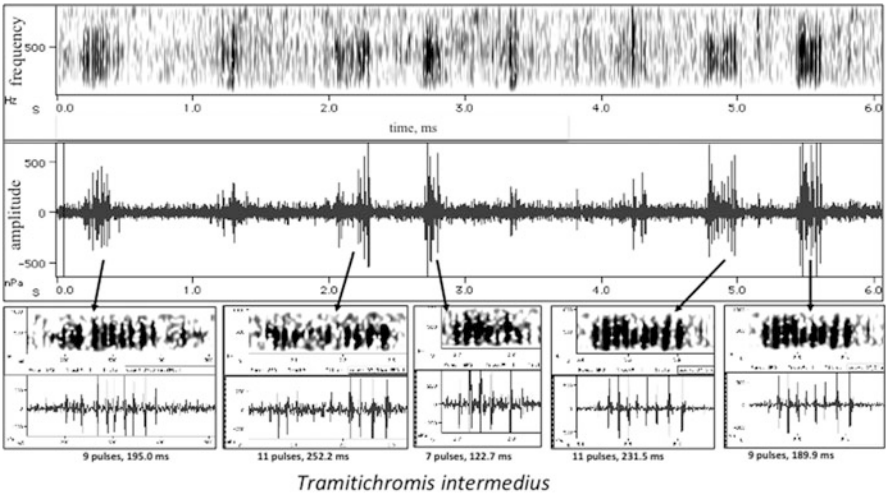

Fig. 6 Courtship sequence shown for *Tramitichromis intermedius* (Aug 22, 1990; 07:51–07:51:30 Hrs). A single male courting a single female as she swims casually passing-by, but she does not stop. See Fig. 8 for the fish recorded

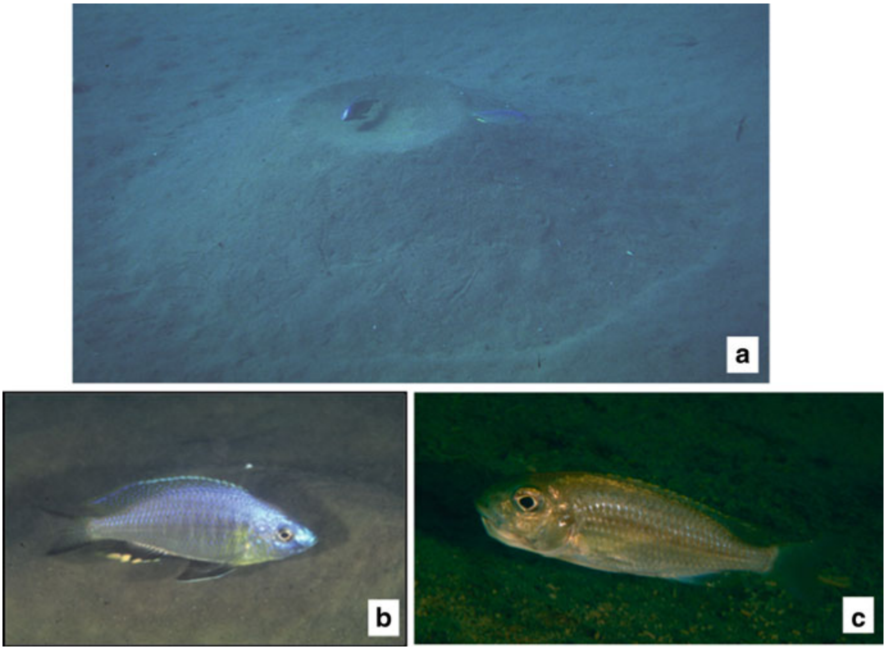

Fig. 7 (**a**), A male *Mchenga (Copadichromis) conophorus* defending his bower from an intruder male. (**b**) Male *M. conophorus* and (**c**) Female *M. conophorus* shown holding embryos in her mouth. Photographed at Cape McClear, Lake Malawi National Park offshore (depth 3–8 m) of the World Wildlife Fund Education Center and at Otter Point, August 5–27, 1990 (photos by P. S. Lobel)

juveniles, and *Oreochromis mossambicus.* However, some examples of sounds from these fishes appear to include occasional pulsed sections. An acoustic repertoire of a cichlid can range from one to four sound types per species. Typically, a male will display and produce sounds in the presence of a female pre-reproductively as a female approaches the spawning site. Examples of such sonic behavior while courting are shown for *Mchenga (Copadichromis) conophorus* (Fig. 5) and *T. intermedius* (Fig. 6). These same fish are shown in their natural habitat (Figs. 7 and 8).

4.1 Acoustic Patterns

The spectral and temporal sound measurements for cichlids are summarized in Table 3. Of the 39 cichlid species whose sounds have been acoustically detected with a hydrophone or analyzed to some extent, the three cichlids with few data are: *Amphilophus citrinellus*, *Chindongo elongatus*, and *Sarotherodon galilaeus.* Among the other 35 cichlid species whose sounds have been analyzed to some extent, six species have had pulse rate described and seven species have had call rate

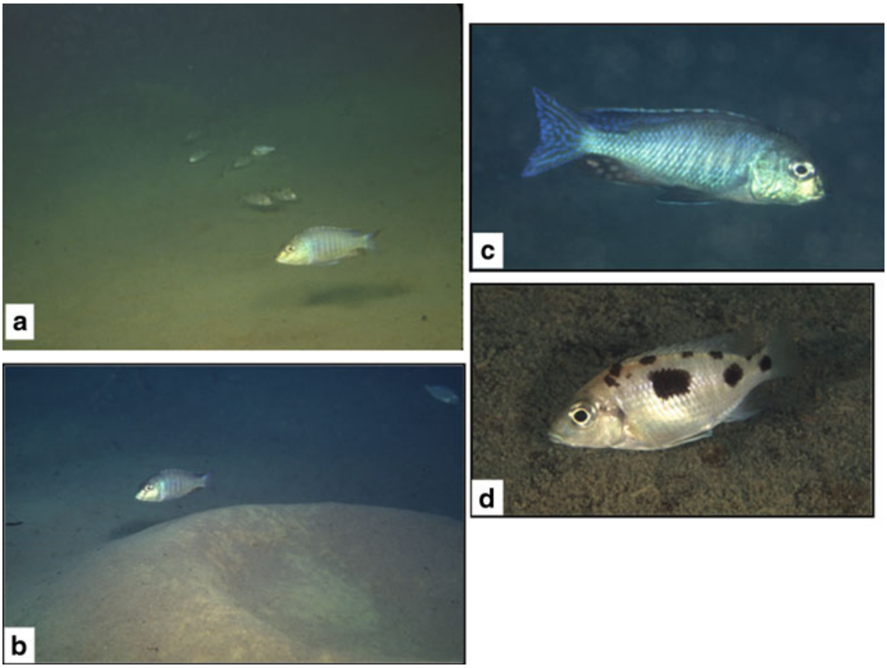

Fig. 8 (**a**) A male *Tramitichromis intermedius* with several females in background. (**b**) A male patrolling the rim of his bower. (**c**) A male in courtship colors. (**d**) A female. Photographed at Cape McClear, Lake Malawi National Park offshore (depth 3–8 m) of the World Wildlife Fund Education Center and at Otter Point, August 5–27, 1990 (photos by P. S. Lobel)

described. Additional acoustic traits have been reported for 30 species (Table 3) but not every species had all characteristics measured. *Pterophyllum* sp. has only had pulse rate (6 pulses/sec) and frequency described; *Amatitlania nigrofasciata* has only had rate (20 pulses/sec) and frequency described; two species, *Labidochromis caeruleus* and *Cichlasoma portalegrense*, have only had frequency described. *Pelmatolapia mariae* had sounds described in general but without temporal or frequency data listed (Table 3).

4.2 Typical Sound Characteristics

Pulsed sound types best characterize cichlid sounds and it is intriguing to contemplate whether this temporal information is meaningful in communication (e.g., Kihslinger and Klimley 2002). The number of species for which pulsed sounds (excluding chewing sounds) were statistically described were: duration ($n = 26$); pulse number ($n = 26$); pulse duration ($n = 19$); pulse period ($n = 10$); and interpulse interval ($n = 4$). Temporal sound traits for these sounds produced during agonism or courtship with statistical descriptions available for species including ranges (that exclude species with high frequency chewing sound types and single pulse sounds) for minimum to maximum range values are: call duration (ms) 277 ± 160 SD to 1319 ± 789 SD (51–4000; $n = 28$; 16 species; pulse number 6 ± 3 SD to 24 ± 19 SD (2–92, $n = 28$, 15 species); pulse duration (ms) 9 ± 5 SD to 21 ± 19 SD (3–70, $n = 17$, 13 species); pulse period (ms) 57 ± 24 SD to 118 ± 45 SD (7–250); $n = 17$; 6 species); and interpulse interval (ms) 21± 31 SD to 138 ± 122 SD (5–316, $n = 5$, four species). These values characterize the described sounds of cichlids that are produced in pulse series at a lower frequency range.

Most cichlids produce one sound type per call, which consists of a series of short pulses (Table 3). Not all contexts have been acoustically surveyed in all known acoustic cichlids therefore a statistic for call repertoire would be hypothetical. However, for the species with data, the reported maximum repertoire size for social contexts the conservative estimate for sounds of a certain origin or numerically described ranges from 1 to 4; $n = 35$ species. *Herotilapia multispinosa* had the largest repertoire (Brown and Marshall 1978). Non-Pulsed (single or continuous) are known from ten species (Tables 3 and 4) but have only been quantitatively described for three species for natural sounds with comparable range data for *H. multispinosa*, *O. mossambicus*, and *O. tilapia*. These sounds appear to be shorter in duration than pulsed calls. Their temporal duration ranges of minimum to maximum are 119 ± 94 SD ($n = 4$, three species) to 437 ± 237 SD ($n = 4$, three species).

A recent review has provided a lexicon for what could constitute different types of complex acoustic behaviors including variation across populations, across or within individuals, across or within contexts (Bolgan et al. 2018). Complex patterning within a call has been documented in two species of cichlids (Table 4). *H. bimaculatus* agonistic sounds include two sounds that overlapped on spectrograms, a pulsed sound and "thump" which is not sufficiently expanded to determine the pattern, although it lacks pulses on the spectrograms available (Rowland 1978). Male courtship sounds in three other species (*Maylandia emmiltos*, *M. fainzilberi* and a hybrid of *Pseudotropheus* "zebra gold' × *M. zebra*) consisted of a continuous waveform sometimes frequency-modulated sound followed by a pulsed sound. Increased complexity in vertebrate calls is well established to play a range of significant roles in both intra- and interspecific communication in frogs (Zelick et al. 1999).

Call rate per minute (aka calling rate) has been described for ten species: *Archocentrus centrarchus* (*Hemichromis bimaculatus* (Myrberg et al. 1965; Rowland 1978); *Herotilapia multispinosa* (Brown and Marshall 1978); *Maylandia callainos*, *Pseudotropheus* "zebra gold," *Pseudotropheus emmiltos*, *Maylandia fainzilberi*, and *Maylandia zebra* (Amorim et al. 2008); *Oreochromis mossambicus* (Amorim et al. 2003) and *Oreochromis niloticus* (Longrie et al. 2013). Sounds per minute is a readily comparable sound characteristic that can be compared across species and has been calculated for male courtship calls in six species. Among *Maylandia callainos*; *M. emmiltos*; *M. fainzilberi*; and *M. zebra*; *Pseudotropheus* "zebra gold" (Amorim et al. 2008); *M. emmiltos* had the highest call rate with 1.4 sounds/min and was statistically higher than the other species (Table 5). *Oreochromis mossambicus* call rate in courtship was 1.1 ± 07 sounds/min.

Table 5 Acoustic comparisons between sympatric cichlid species

Species call type	Temporal (ms) Traits that differed (no differences)	Frequency (Hz) Traits that differed (no differences)	Literature cited
Mchenga conophoros and Tramitichromis intermedius			
Male courtship	Pulse duration, pulse rate	Not tested	Lobel (1998)
	(call duration, pulse number, interpulse)		
Maylandia zebra, Maylandia callainos, and Pseudotropheus “zebra gold”			
Male courtship	Pulse number, pulse duration differed between some but not all species	Peak higher in *M. callainos*	Amorim et al. (2004)
	(call duration, pulse period)	(peak)	
M. zebra, M. callainos, and P. “zebra gold”			
Male courtship	Call duration, pulse number, pulse period differed between some but not all species	Peak differed between contexts	Simoes et al. (2006)
Maylanida faizilberi, M. zebra, M. callainos, and M. emmiltos and P. “zebra gold”			
Male courtship	Call rate, pulse number, pulse period differed between some but not all species	(peak)	Amorim et al. (2008)
	(call duration)		
Maylandia aurora, M. callainos, and M. zebra			
Nest associated (trill call)	Call duration, pulse duration, pulse period (pulse number)	Not tested	Danley et al. (2012)
Haplochromis pundamilia, and Haplochromis nyererei, Neochromis omnicaeruleus			
Male courtship	Pulse period	(peak)	Verzijden et al. (2010)
	Call duration, pulse number differed between some but not all species		
Maylandia callainos, M. lombardoi, Pseudotropheus johanii, and *P. cyaneorhabdos*			
Male courtship	Call duration, pulse number/call, number of calls/display	Primary	Van Staaden and Smith (2011)
	Pulse period distinguishes interpulsed “click” sounds of *M. callainos* from other species’ “grunting”		
	M. callainos differs from other species (discriminant function analysis)		
NO CALL DIFFERENCES:			
Petrotilapia nigra, Cyanotilapia afra, and *Labreotropheus fuellborni*			
Nest associated (trill call)	(described but not tested for differences: Call duration, pulse number, pulse duration, pulse period were similar)	Not tested	Danley et al. (2012)
Maylandia lombardoi and *Pseudotropheus cyaneorhabdos* (discriminant function analysis)			
Male courtship	(call duration)	(primary)	Van Staaden and Smith (2011)

Temporal Data The number of species for which temporal data was reported from reproductive and agonistic calls are: call duration $n = 26$; pulse number $n = 26$; pulse duration $n = 19$; pulse period $n = 10$; and between pulse interval $n = 4$. For these sounds minimum and maximum values for temporal traits (all data pooled) are: sound duration (ms) 255 ± 165 SD to 1226 ± 803 SD (27–4000; $n = 31$; 16 species); pulse number 6 ± 3SD to 23 ± 19SD (2–92; $n = 28$; 15 species); pulse duration (ms) 9 ± 5SD to 21 ± 19 SD (3–70; $n = 17$; 13 species); pulse period (ms) 57 ± 24 SD to 118 ± 45 SD (7–250; $n = 17$; 6 species); and interpulse interval (ms) 21 ± 31 SD to 138 ± 122 SD (5–316; $n = 5$; four species). The details are given in Table 3.

Frequency Data Frequency measurements describing cichlid sounds differ across publications with range, fundamental, maximum, center, or dominant (dominant synonyms are peak, principle, primary, and main) frequency values (Table 3). Frequency range measurements are subject to different methods, vary as a function of FFT used in the spectrogram, and these details are not always reported in cichlids. But, since many cichlids sounds are pulsed and broadband, frequency may not be the best way to describe these sounds. The number of species for which social context reproductive or agonistic sound frequency data was reported are: peak frequency $n = 29$ and frequency range $n = 18$. Frequency measurements describing cichlid sounds differ across publications with range, maximum, middle, or dominant (peak, principle, main) frequency values published for 31 species (Table 3). Frequency range measurements are subject to different methods and are not widely reported. Some examples for social contexts for minimum and maximum range values are: 95 Hz ±55 to 1385 Hz ± 1202 (25–5000 Hz; $n = 16$; 10 species). The minimum to maximum dominant frequency was: 493 Hz ± 1095 and the maximum was 1487 Hz ± 3555 (50–16,000, $n = 36$; 18, species).

Frequency range is low in *Oreochromis nilotucus* and *O. mossambicus* compared to some other cichlids. The sounds produced were described as very low, with most of the energy below 200 Hz (Longrie et al. 2008, 2009, 2013; McPherson 2012) and a mean dominant frequency below 68 Hz (46–68 Hz;) compared to other cichlids (Amorim et al. 2003; Longrie et al. 2013). The tonal sounds of several additional species, *Maylandia emmiltos*, *M. fainzilberi*, and *Pseudotropheus "zebra gold"* × *M. zebra*, are also very low among cichlids (Range 22–86 Hz Peak frequency), which have been recorded to date.

Frequency range is high with peak or main frequency well above 1000 Hz, for *Neolamprologus pulcher* (agonistic sounds, Spinks et al. 2017), *Pterophyllum (scalare?)* (Myrberg et al. 1965), and *O. mossambicus* (Lanzing 1974). High frequency (greater than 1000 Hz) sounds have also been reported from *Tropheus moorii, T. duboisi, T. brichardi, Simochromis diagramma, and Astatotilapia burtoni* (Nelissen 1978). These pulsed high-frequency range sounds seem to be different sound types from the typical pulsed lower frequency sounds of cichlids. Six of these species had sound ranges described for several sound characteristics and these are summarized by (mean ± SD): sound duration (ms) 370 ± 399 to 3660 ± 1141

(80–5000; $n = 5$; five species); pulse number 2 ± 1 to 8 ± 3 (1–11; $n = 6$; six species); pulse duration (ms) 42 ± 8 to 124 + 38 (30–170; $n = 5$; five species); and dominant frequency (Hz) 3667± 2021 to 12,833 ± 1768 (2500–16,000; $n = 3$; three species). We excluded the higher frequency chewing call types from our final characterization of cichlid sound call parameters analysis below. It is important to note that while understudied feeding sounds even if incidental can have a significant impact on social behavior suggesting their use as foraging cues as observed in a group foraging cyprinid (Scholz and Ladich 2006).

Fish Size and Dominant Frequency In general, among teleosts with simple swimbladders, larger fish produce lower frequency sounds than do smaller fish (Demski et al. 1973; Fine et al. 1977; Myrberg and Riggio 1985). This applies to cichlids (Myrberg et al. 1965; Rowland 1978) and also to pomacentrids, which have similar swimbladder structure (Myrberg et al. 1993; Lobel and Mann 1995). The hypothesis is that sound quality in terms of amplitude and frequency is in large part a morphologically determined signal related to swimbladder and body size. It is a basic principle of underwater physics that larger swimbladders resonate at lower frequencies than smaller ones (Clay and Medwin 1977; Urick 1983). This association could provide a reliable indicator of male size to the listening female fish that is selecting among potential mates.

Body size is an important variable affecting ultimate reproductive success of male cichlids and many other fishes (Bisazza and Marin 1991; Hert 1990; Magnhagen and Kvarnema 1989; Myrberg et al. 1986; Noonan 1983). Two studies have demonstrated that, in fact, the dominant frequency of the courtship sound from two pomacentrid species does decrease with increasing male size (Myrberg et al. 1993; Mann and Lobel 1995). A preference for females to mate with larger males, producing lower frequency courtship calls, has been demonstrated experimentally for the bicolor damselfish, *Stegastes partitus*. Female choice in this pomacentrid is also strongly influenced by the vigorousness of male courtship activity (Myrberg et al. 1986; Knapp and Warner 1991). Vigor is defined by the rate at which males display courtship-swimming motions and simultaneously produce courtship sounds although Knapp and Warner (1991) did not include bioacoustics. An individual cichlid's sounds differ in call parameters relating to body size (Amorim et al. 2004; Simoes et al. 2008b; Bertucci et al. 2012a, b; Verzijden et al. 2010; Maruska et al. 2012). Frequency patterns could contribute to individual sound differences (Bertucci et al. 2012a, b). However, the frequency may not vary significantly between species (Amorim et al. 2008). It is still an open question as to whether the specific acoustic structure conveys specific information or whether it is merely the occurrence and rapidity of sound production, but not details, that matter for fish mate selection. The simplest information that might be communicated by a fish's sonic behavior may be an individual male's location, readiness to spawn, and or his overall vigor (Lobel 2001).

4.3 Aggression and Courtship

The typical sound produced by a cichlid during aggressive and courting behavior is a series of rapid low frequency (typically 200–600 Hz) pulses. The "grunting" and "clicking" cichlid sound types described by Van Staaden and Smith (2011) were distinguished by discernibility of the duration of the interpulse interval. These acoustic traits could provide signature differences among individuals (Bertucci et al. 2012a, b). The territorial cichlid males responded to conspecific sounds but not temporal coding modifications (Bertucci et al. 2013). These preliminary data support the hypothesis that cichlid sounds are temporally structured in a way that contains information that could be used in the mate selection process. This type of acoustic coding has long been documented and is common in insects and amphibians and marine mammals, and has been proposed for fishes as well (Myrberg et al. 1978; Kihslinger and Klimley 2002; Spanier 1979). For example, pulse coding of species-specific sounds is a well-known feature of the mating behavior of *Drosophila* and other arthropods (Ewing 1989). Male field crickets with longer calling-bout durations are preferred by females (Hedrick 1986). Acoustic communication is a demonstrated feature in amphibian sexual selection (Ryan 1985; Zelick et al. 1999). It seems reasonable to consider that if insects and amphibians are using pulsed sounds in mate selection then the same is possible, even likely, for some fishes.

The following example illustrates typical courtship associated sounds for three cichlid species and emphasizes the comparative details of interspecific variation in single pulse patterns. It is possible that specific waveform structure of single pulses is a product of the sound producing mechanism. Waveforms of courtship sounds for *Maylandia zebra* (formerly *Pseudotropheus zebra*, Stauffer et al. 1997), *Mchenga (Copadichromis) conophoros,* and *Tramitochromis intermedius* are shown in Fig. 2.

Individual fish can vary the type of sound produced in different behavioral contexts. Courtship and aggressive sounds are hard to distinguish acoustically by listening when played to humans through a loudspeaker. Sounds differ between agonistic and courtship contexts for *Maylandia* species (Simoes et al. 2008b). However, in one other cichlid, *Pundamilia nyererei*, sounds produced in different contexts were the same (Verzijden et al. 2010). Acoustic contests in a laboratory setting between males did not show a correlation between male size, increased fighting intensity, and call number (Amorim and Almada 2005). Studies of *O. niloticus* demonstrated that in male–male contests winners were quick to court, courtship duration was extended and their calls were greater in number with longer pulse durations and lower peak frequencies than previous contest losers (Amorim and Almada 2005), traits that correlate with increased fitness in other vertebrate species. Dyadic contests elicited agonistic sound production in *P. nyererei* (Verzijden et al. 2010). These sounds are associated with aggressive behavior between males.

Mchenga (*Copadichromis*) *conophoros* aggressive sounds (Fig. 4e, f and g) are composed of irregular and longer duration pulses, which are clearly distinguishable from the regular and distinct pulses that are seen in typical courtship sound patterns.

5 Playback Experiments

Early evidence demonstrated the ability for individual male recognition by female *H. bimaculatus* (Nobel and Curtis 1939). For future research, playback of sounds will be crucial to discern if sounds elicit a behavioral response, which would support the notion that the sounds have specific temporal encoding information. There have been, so far, a limited number of experimental studies on cichlids, which are summarized in Table 4. Playback experiments have demonstrated that a cichlid will respond to conspecific sounds (Rowland 1978). Rowland (1978) conducted behavioral studies to observe the reaction of cichlids to physical models and to the playback of those sound recordings during repeat model experiments. He presented dummy fish with and without playback of the fish's courtship-display-like and aggressive-display-like sounds as well as presentations with white noise and silence. There was no difference to fish response between white noise and silent dummies, but fish showed a significant response to dummies playing back conspecific sounds over silent dummies. Cichlid sound playback in another study resulted in listeners becoming less aggressive (Schwarz 1974b). Schwartz (1974a, b) found that male *Archocentrus centrarchus* responded to conspecific sounds and that in this species acoustic cues inhibited aggression. This species does not apparently produce a courtship-associated sound (Schwarz 1980). A preliminary study of neighboring *O. mossambicus* nest territory holding males were found to produce agonistic "thump" sounds which are not the typically multi-pulsed call (McPherson 2012) and observations of playback suggest a possible chorusing interaction by the lead caller of played-back sound. Bertucci et al. (2013) found that male cichlids during agonistic encounters responded to sounds in general, but not to modification of variation in temporal patterns. Auditory plasticity influences female cichlid hearing and there is overlap between female hearing in reproductive condition and male courtship songs indicating the importance of sound in reproductive communication (Maruska et al. 2012). Two studies found that females preferred males with natural calls compared to males with (a) noise with male (Maruska et al. 2012) and (b) silent with male in playback experiments (Verzijden et al. 2010). Estramil et al. (2014) experimentally demonstrated the multimodal nature of cichlid sounds with females only responding to sounds if live males are present.

6 Species-Specific Sounds

Simple comparison of the pulse rate in the courtship calls of two sympatric species (but different genera) that live close together in Lake Malawi, *Mchenga (Copadichromis) conophoros*, and *Tramitichromis intermedius*, revealed statistically significant differences in pulse rate and pulse duration but not pulse number, call duration or inter-pulse duration (Lobel 1998). Lake Victoria cichlids (Verzijden et al. 2010) produce species-specific sounds. *Maylandia* spp. male courtship sounds differ in temporal acoustic traits (Amorim et al. 2008; Danley et al. 2012) and peak frequency (Amorim et al. 2004). Male courtship sounds of Lake Malawi cichlids differed among four congeneric and heterogeneric species with a more significant difference between congeners (Van Staaden and Smith 2011) and similar sounds for one pair of heterogeneric species. Male courtship calls of Lake Victoria cichlids, congeners, and heterogeneric species, are species specific (Verzijden et al. 2010). The importance of male calls to female listeners was shown experimentally to the female cichlid ear, with peak sensitivity occurring when females are in reproductive condition prior to the mouthbrooding phase (Maruska et al. 2012) in response to changing hormones demonstrating a peak in call sensitivity during reproductive conditioning. Yet, to date, no playback studies have examined the role of specific temporal or frequency trait differences among different species calls to the female listener. Studies examining contrasting differences in sound characteristics between the males of cichlid species are summarized in Table 5.

6.1 Sonic Diversity and Color Patterns

Nelissen (1975, 1977, 1978) provided a detailed analysis of the sounds of some Lake Tanganyika cichlids and found that several species displayed different acoustic repertoires. The number of sonic displays produced by a species was negatively correlated with the number of color patterns that species displayed with its behavior (Nelissen 1978). Species could be substituting between visual acoustic diversity and sonic diversity. The most sonically diverse species (*Tropheus* spp.) displayed the fewest color changes. The sonically least active species, *Simochromis* spp. maybe using color pattern displays to communicate. Another species, *Astatotilapia burtoni,* was intermediate. Increased sound activity with behavior was found for *Tropheus* spp., which is mainly nocturnal, compared to the diurnally active *Simochromis* (Nelissen 1978). A similar pattern is well known in coral reef fish communities where many nocturnal species (e.g., holocentrids, pempherids, and sciaenids) are also among the most sonically active. More recently, Amorim et al. (2008) found that among five Lake Malawi cichlid fish species of the *Maylandia (Pseudotropheus) zebra* complex, that the male courtship acoustic signals differed significantly in the number of pulses and in pulse period. They reported that the largest differences in acoustic variables were found between the two sympatric Mphanga Rocks species *P. emmiltos* and *P. fainzilberi*, that, in contrast to the other three species, look (to us at least) very similar to each other in color and pattern.

6.2 Silent Behavior and/or Non-acoustic Cichlids

Although many cichlids appear to make sounds with specific behavior, there have been several reported as being silent during certain behavioral interactions. This is an intriguing phenomenon and further study will be interesting. Ladich and Popper

(2001) refer to fish species that are not known to produce volitional sound as non-vocal. “Silent” is applied to fishes that have been examined for acoustic ability and found to lack it (Kaatz et al. 2010). Although many cichlids appear to make sounds with specific behavior, there have been 11 species reported as being silent during certain behavioral interactions (Table 6). *Neolamprologus pulcher* did not produce sounds during acoustically monitored social interactions (Pisanski et al. 2015, but see Spinks et al. 2017) although it did produce sounds when males were exposed to their image in a mirror (Spinks et al. 2017). The only evidence for possibly silent cichlid species is an anecdotal report found in Spinks et al. (2017) for *Astatoreochromis allaudi*, based on aquarium studies. *Cyphotilapia frontosa* lacked an acoustic response to electrical stimulation that did stimulate sounds in one other tested cichlid known to be a sound producer (Longrie et al. 2009). However, it should be emphasized that no behavioral studies of living social groups have yet been conducted for these species. The occurrence of these silent cichlid species raises the question as to whether this represents a secondary loss of this ability, or whether sounds in cichlids are independently derived. This exciting research is in its beginning phase of discovering which fish species may be making behaviorally relevant sounds. This is an intriguing phenomenon for further study.

Contexts that were well monitored and found to lack sound for all individuals tested in a species with other acoustic contexts included are listed in Table 6. Some examples are: *Hemichromis bimaculatus* courtship and spawning, brood care (Myrberg et al. 1965); *A. nigrofasciata* reproduction and male fighting (Myrberg et al. 1965); courtship, spawning, and guarding of fry in *O. niloticus* (Longrie et al. 2009); juveniles schooling and female during agonism, spawning, brooding, and fry release for *Tramitichromis cf. intermedius* (Ripley and Lobel 2004)*; Pterophyllum (scalare sp?) for* schooling adults and parents on nest or with eggs, larvae, or fry without intruders (Myrberg et al. 1965) courtship associated *A. centrarchus* during spawning for *H. multispinosa* (Brown and Marshall 1978). *Neolamprologus pulcher* did not produce sounds during acoustically monitored social interactions including male–male agonism and courtship (Pisanski et al. 2015, but see Spinks et al. 2017). Female *Tilapia mariae* did not produce sounds during male–female and male–male agonistic interactions (Kottege et al. 2015). Courted males of *Oreochromis mossambicus* were silent when displayed by vocalizing males (Amorim et al. 2003). Individuals of the subpopulation *Maylandia zebra* "katale" only produced incidental patterned sounds on the territory while clearing gravel, not during visual courtship displays (Smith and Van Staaden 2009; Van Staaden and Smith 2011). There are additional unpublished data reported by Spinks et al. (2017) supporting silence in another cichlid species, *Astatoreochromis allaudi*, based on aquarium studies. It is possible that there is individual variation in vocal activity (Van Staaden and Smith 2011); therefore, a statistically adequate number of individuals should be investigated before concluding the sonic status of a species or a specific behavioral context.Relatively low-intensity acoustic activity has, so far, been observed in three cichlid species (Table 4). Calling with visual courtship displays was rare or absent in some individuals of two tested species (*Maylandia zebra* “katale” and *Melanochromis auratus*) compared to other sympatric species (Van Staaden and

Table 6 Cichlids displaying behaviors unaccompanied by sounds

Species (current name, catalogue of fishes)	Behavioral context[a]: Silent, no sounds detected	Acoustic	Literature cited
Contexts with no sounds detected ($n = 11$ species)			
Amatitlania nigrofasciata	Prespawning, courtship, A (male–male fighting)	A (female caller and male), A (Nest defense female caller brooding)	Myrberg et al. (1965)
Archocentrus centrarchus	Reproductive (male and female): Cs, quiver, jerk, dig, nip substratem pseudoskim, aerate, jolt; Fin-flick, yawn	A	Schwartz (1980)
Hemichromis bimaculatus	Non-aggressive courtship; Cs; egg fanning; mate exchange over eggs or young; fin flicking over young	A (male and female); A (nest defense female caller parental period egg incubation, larvae, and free-swimming young); A (female returned to aquarium male caller), A (male–male conflict)	Myrberg et al. (1965)
Herotilapia multispinosa	Cs	Cd, A	Brown and Marshall (1978)
Maylandia zebra “katale”	Cd (visual courtship display without sound)	Male calls on territory while gravel clearing	Smith and Van Staaden (2009)
Oreochromis mossambicus	A (nearly always silent); males which could be acting as sneakers were silent while courted by vocal courting male	A (territorial male groups); Cd; Cs; Nest associated (male call in nest)	Amorim et al. (2003)
Oreochromis niloticus	Cd, Cs, and A Free alevins protection (female)	A, Nest associated (fin display, dig, hover), A mouth egg incubation (female)	Longrie et al. (2013)
Neolamprologus pulcher	Cd, A (male–male aggressive and submissive; female submissive) lower frequency sounds	None	Pisanski et al. (2015) (but see Spinks et al. (2017))
Pelmatolapia mariae	A (male–male, male–female)	Nest associated female caller paired male in area	Kottege et al. (2015)
Pterophyllum sp. (probably *scalare*)	School (adult group swimming); mated pair alone on nest with eggs, larvae, or free-swimming fry	A (nest defense egg and larvae, parent with free-swimming fry, parent–intruder aggression)	Myrberg et al. (1965)
Tramitichromis intermedius	Schooling (juveniles); A (female), Cf (female courtship), Cs (female), brooding, and fry release (females)	Cd	Ripley and Lobel (2004)

[a] *A* agonism, *Cd* male courtship display to female, *Cs* spawning
Female silence in courtship (“Cd”) is implied by the presence of a male calling during courtship but was only scored as a silent context when specifically examined

Smith 2011). However, reproductive behaviors were also uncommon in the small aquarium population tested (Smith and Van Staaden 2009). Intraspecific agonistic interactions of non-territorial males and females in *O. mossambicus* were rarely associated with inter-pulsed sound production (Amorim et al. 2003) while territoriality was the condition under which males began calling in greater abundance. In another study, territorial *O. mossambicus* males were found to produce distinct agonistic "thump" and pulsed courtship sounds on nest territories in the field (McPherson 2012). More studies are required to explore this aspect of cichlid bioacoustics.

7 Sound Detection and Hearing

The hearing abilities have not been measured in many cichlid species, compared to other taxa, and most of the work on the auditory system has examined ear or otolith morphology. The cichlid *Sarotherodon macrocephala* responds to underwater sound stimulation from 50 to 900 Hz with maximum sensitivity at 100 Hz (Fay and Popper 1975). This range of hearing sensitivity is typical for percoid type fishes without special morphological adaptations for hearing (e.g., ostariophysians, clupeids, Fay 1988; Popper and Fay 1973, 1993). The ears in both Old World *Sarotherodon macrocephala* and New World *Aequidens pulcher* are very similar to one another (Popper 1977). The otoliths of Cichlidae are diagnostic for the family (Gaemers 1984; Gaemers and Crapon de Crapona 1986). Sexual dimorphism in otoliths occurs in those haplochromine species that have a maximum male size greater than maximum female size (Gaemers and Crapon de Crapona 1986). The auditory sensitivity of the Malawi cichlid, *Tramitichromis intermedius* is correlated with the frequency range of sounds it produces during aggression and courtship (Ripley et al. 2002). The acoustic cichlid *Astatotilapia burtoni*'s hearing is sensitive to its own call acoustic traits (Maruska et al. 2012) as is the hearing in *Labidochromis caeruleus* (Higgs et al. 2011). The peak hearing sensitivity of *Tramitochromis intermedius* corresponds with the dominant frequency of its courtship calls (Ripley et al. 2002).

Auditory psychophysiological data support the notion that fishes, in general, have peak auditory sensitivity below 1000 Hz (Fay 1988; Popper and Fay 1993). The fish's central (brain) and peripheral (ear) auditory systems are fully capable of processing: 1) sound amplitude fluctuation with respect to both sensitivity and pattern discrimination and 2) sound source localization in azimuth and elevation (Fay 1988; Popper and Fay 1993). The response by females to pulsed courtship calls for mate selection has been demonstrated experimentally for a pomacentrid and is implicated in other fishes (Gerald 1971; Fine et al. 1977; Myrberg et al. 1978, 1986; Myrberg and Spires 1980; Schwarz 1985; Spanier 1979). That a cichlid can detect and learn response to sound has been demonstrated in *Oreochromis aureus*, which was behaviorally conditioned to associate a buzzer sound to being fed. Acoustic interaction between sexes is also suggested by results, which indicated that the courtship sound produced by male *Oreochromis mossambicus* (syn. *Sarotherodon*, *Tilapia mossambica*) facilitated oviposition in females (Marshall 1972). Auditory plasticity in male and female *Astatotilapia burtoni* has been examined and could influence how social sounds are detected through the reproductive cycle (Maruska and Fernald 2010).

Lateral line systems of fishes are sensitive to water displacement as well as near field and likely low-frequency sound. Both the lateral line and the ear are innervated by the VIIIth cranial nerve (see Webb et al. 2021). Various cichlid genera possess at least eight trunk canal patterns (Webb 1990). Another potential sensory adaptation, which is very poorly understood, may involve enlarged sensory pores in the mandible. These pores are apparently linked to the lateral line and presumably, may have a role associated with enhanced sound detection (Konings 1995). This feature has been identified in the genera *Aulonocara, Tramitichromis*, and related species (Konings 1995; Turner 1996). How these lateral line and sensory pore patterns may be related to a cichlid's response to sounds is not known. The suggestion is that these mandibular pores function to detect sounds or vibrations produced by invertebrate prey moving beneath the sand (Janssen 1990; Konings 1995). The role of lateral line cues in fish communication is an emerging topic of study (Butler and Maruska 2015, 2016; Weeg and Bass 2000; Weeg et al. 2005).

7.1 Background Noise Interference

Background noises due to pumps, filters, lights, and echoes in aquarium settings make it difficult to conduct critical experiments in small aquaria on how cichlid fishes produce and respond to sounds (Nelissen 1991). Acoustic recordings and playbacks made in an aquarium may be potentially misleading when interpreting specific acoustic characteristics of fish sounds because of reflections and reverberations against the walls (Akamatsu et al. 2002; Hawkins 1973). The type of aquarium wall materials may also have an impact on sound recordings (Parmentier et al. 2014).

Background noises (e.g., aquarium pumps and filters) sometimes appear as dark horizontal bands in sonograms (Nelissen 1978) and can mask part or all of a fish's sound, making analysis difficult (Rowland 1978). The effects of constant aquarium noise on a cichlid's development and behavior may also be a concern. Damage to fishes' hearing can result from excessive noise (Banner and Hyatt 1973; Cox et al. 1987; Ha 1985; Popper and Clarke 1976). Experiments have shown that environmental noise reduces behavioral activity levels in a cichlid and could therefore also impact its acoustic display activity (Slabbekoorn et al. 2012).

The influence of aquarium noises on fish hearing and communication is important to determine from three perspectives. First, how such noise affects acoustic recordings is an analytical issue. Second, it is a potential problem when interpreting behavior in an aquarium because we do not know how this noise may directly interfere by masking fish communication. Third, the direct effect on hearing and the development of hearing as fish are raised in captivity is an obvious concern. It is possible that fishes housed in high noise aquaculture and aquarium systems may have their hearing adversely impacted.

8 Future Directions

Two alternative (but mutually compatible) hypotheses have been proposed to explain rapid and extensive speciation of cichlids, one based on morphological plasticity and the other on sexual selection by female mate choice (Greenwood 1991). Morphological plasticity is inherent in cichlids and enables rapid anatomical changes, especially in the feeding mechanism of which the pharyngeal jaws are a key component (Liem 1973, 1991; Greenwood 1973, 1991). Alternatively, sexual selection is based upon female choice between variants in male features, most notably coloration (Dominey 1984; Seehausen et al. 1999) and bower (nest) height and shape (Stauffer and Kellogg 1996). The hypothesis debate is based, in part, upon the premise that anatomical changes in the pharyngeal jaws are not affected by sexual selection (Greenwood 1991). If, however, the pharyngeal apparatus is important for sound production as well as feeding, then some features of the morphology may be linked to sexual selection (as related to sound production) as well as trophic specialization. For female choice to function on this basis, different pharyngeal morphologies would be expected to produce sounds with different qualities. Preliminary observations of individual pulse waveforms among cichlids and pomacentrids reveal such differences. The evidence available to date indicates that sound production is an integral part of cichlid behavior, including courtship. However, before its role in the speciation process can be evaluated, the role of sound communication in mate selection needs to be determined. Darwin (1874; pp. 366–367) argued, “It is almost certain that in [fishes] sound producing instruments have, at least in some cases, been developed through sexual selection as a means for bringing the sexes together.” This hypothesis remains to be rigorously tested and although data is accumulating that suggests sounds do play an essential role in mate selection among cichlids, however, acoustics may not be the prime driver alone. Coincident signals of colors, fins and swimming, and odors may also be required to reinforce a female’s choice of a mate. Most simply, sound with behavior could serve to be an initial attention attracting display without any deeper content to the acoustic signal. These hypotheses are ready for experimental testing.

Acoustic signals are involved in much of the social and reproductive behavior of many animals, and the behavioral influence of sounds has been extensively studied in these terrestrial groups. In contrast, research, to date, on the acoustic communication of fishes has primarily focused on the description of sounds, sonic morphology, and definition of the contexts in which sounds are produced. Progress in the field of fish bioacoustics has lagged behind that of terrestrial systems mainly due to limitations of technology and the logistical difficulty of research in the underwater environment. Recent advancements have provided better tools to successfully conduct such studies and the number of fishes discovered making sounds has grown enormously in the last few decades (Rosenthal and Lobel 2006; Webb et al. 2008). Although it is now known that many fishes make sounds, only a limited number of studies have experimentally examined the behavioral significance of these sounds by using audio playback (Ladich 1997; Luczkovich and Keusenkothen 2007; Lugli 1997; Lugli et al. 2004; McKibben and Bass 1998; Myrberg et al. 1986; Myrberg and Riggio 1985; Rollo and Higgs 2008; Winn 1972; Yan and Popper 1991).

There is now ample evidence that cichlids, like many fishes, make distinct sounds associated with specific behaviors. The field of fish bioacoustics is making progress. However, to advance closer to the level of understanding that has been achieved in the studies of terrestrial animals, the next phase of research for fishes needs to focus on experiments using playback trials to determine on how sounds combined with visual and chemical cues are behaviorally relevant.

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The Evolution of Enhanced Cichlid Hearing: Functional Morphology and the Role of Ecoacoustical Factors

Tanja Schulz-Mirbach and Friedrich Ladich

Abstract In teleost fishes, the evolution of hearing enhancement and corresponding auditory structures remains largely elusive. We know little about the selective pressures acting on the evolution of improved hearing. Cichlids are marked by great species diversity; they have adapted to a variety of ecological niches, including different ecoacoustical conditions such as ambient noise levels or frequency spectra. This makes cichlids a perfect model for comparative approaches to investigate the relationship between ecological factors, acoustical behavior, and functional morphology of hearing in teleost fishes and to approach questions about the evolution of improved hearing. Functional acoustical studies show that cichlids evolved a considerable diversity in ancillary auditory structures and hearing abilities. This review summarizes what is known about the morphology of inner ears and swimbladders in cichlids and about their auditory abilities. The focus is on recent comparative studies designed to shed light on the functional morphology of hearing. These studies, however, still widely lack ecological and phylogenetic perspectives. We therefore suggest that future acoustical studies in cichlids should be embedded in a phylogenetic framework including ecological data. This would help gain insight into how hearing enhancement and auditory structures evolved in this group and potentially in other teleosts as well.

Keywords Auditory evoked potentials · Otophysic connection · Swimbladder extension · Inner ear · Sensory epithelium

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T. Schulz-Mirbach (✉)
Department Biology II, Ludwig-Maximilians-University Munich, Planegg-Martinsried, Germany
e-mail: schulz-mirbach@biologie.uni-muenchen.de

F. Ladich
Department of Behavioural and Cognitive Biology, University of Vienna, Vienna, Austria
e-mail: friedrich.ladich@univie.ac.at

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1 Introduction

Considering the great diversity of teleosts (ca. 30,000 species; Nelson et al. 2016), little is known about the functional morphology of hearing, i.e., the relationship between hearing abilities and the morphology of inner ears and ancillary auditory structures such as modified swimbladders (Braun and Grande 2008). Comparative studies of closely related taxa provide a powerful approach to elucidate this relationship (e.g., Ramcharitar et al. 2001, 2006b; Schulz-Mirbach et al. 2012). So far, studies on species differing in swimbladder morphology within the holocentrids, sciaenids, or the chaetodontids yielded, in part, conflicting results. Holocentrids (*Myripristis*) and chaetodontids (*Chaetodon*), with anterior swimbladder extensions and an intimate swimbladder-inner ear contact, showed distinctly enhanced hearing with a wider hearing bandwidth and better auditory sensitivities than species lacking such modifications (Coombs and Popper 1979; Nelson 1955; Tricas and Boyle 2015; Tricas and Webb 2016). In contrast, sciaenid species, with anterior swimbladder extensions, either show enhanced hearing or display similar hearing abilities compared to their counterparts that completely lack swimbladder modifications (Horodysky et al. 2008; Ramcharitar et al. 2006b). These outcomes highlight the need for more comparative investigations in other teleost families.

Cichlids have adapted to diverse ecological niches including an array of ecoacoustical conditions ("soundscapes") and show multiple social behaviors (Burress 2015; Seehausen 2015) such as parental care (Gonzalez-Voyer et al. 2008) and sound communication (Amorim 2006). In addition, former studies pointed to the potential diversity of swimbladder morphology in this group (Dehadrai 1959; Sparks 2008; Braun and Grande 2008). Hence, cichlids provide an excellent model for investigating the functional relationship between ecoacoustical conditions, hearing, and the auditory periphery (i.e., inner ears and ancillary auditory structures). Recent studies on cichlids from the subfamilies Etroplinae, Ptychochrominae, and Pseudocrenilabrinae point to a correlation between morphological modifications of the auditory periphery and enhanced auditory abilities (Schulz-Mirbach et al. 2012, 2014). The evolution of inner ears and hearing enhancement in fishes is poorly understood, partly due to the lack of ecoacoustical measurements. Again, cichlids could serve as a good model to uncover the underlying selective pressures and/or constraints. Investigating members of the Etroplinae and Ptychochrominae would also enable testing hypotheses about the effects of ambient noise conditions on the evolution of hearing enhancement (see Braun et al. 2012) as formulated by the "ecoacoustical constraint hypothesis" (Ladich 2014). This hypothesis posits that enhanced hearing most likely evolves in fishes living in stagnant waters such as backwaters of rivers and lakes characterized by low ambient noise levels. Under quiet conditions, enhanced hearing enables a fish to perceive faint sounds, which may be advantageous to detect approaching predators earlier and thus increases the likelihood for the fish to escape in time.

This chapter begins with a brief overview of how fish hear, providing general basic information on inner ear functioning and the effects of different swimbladder morphologies on fish audition. The second part of the review concentrates on recent comparative studies that have yielded detailed anatomical descriptions of the inner ears and swimbladders in four cichlid species including their hearing abilities. We illustrate new imaging techniques and underline that the in-depth study of key taxa builds an important database linking the morphology of auditory structures to inner ear physiology. Finally, we examine how morphological structures and hearing abilities might be embedded into a phylogenetic context, incorporating ecological factors, and pinpoint what questions could be addressed in future research. Specifically, we discuss the following questions regarding functional morphology and the evolution of hearing enhancement in cichlids:

1. How do differences in swimbladder morphology translate into different hearing abilities (Braun and Grande 2008; Schulz-Mirbach et al. 2012)?
2. Is there a high correlation between ancillary auditory structures (swimbladder size and presence of anterior swimbladder extensions) and inner ear morphology (Schulz-Mirbach et al. 2014)?
3. Have modified swimbladders and hearing enhancement evolved several times independently in Etroplinae and Ptychochrominae or within the Ptychochrominae (Braun et al. 2012)?
4. Are hearing abilities linked to ecoacoustical conditions in the respective habitats? Does the “ecoacoustical constraint hypothesis” (Ladich 2014) explain the evolution of hearing enhancement in etropline cichlids and members of the Ptychochrominae?
5. Has acoustic communication been a driving selective force for the evolution of hearing enhancement in cichlids?

1.1 General Structure and Function of the Inner Ear in Fishes

Inner ears in vertebrates serve both the senses of balance (vestibular sense) and hearing. In cartilaginous (Chondrichthyes) and bony fishes (Osteichthyes), inner ears together with the lateral line system form the octavolateralis system, enabling them to detect vibrational signals (Popper 1996). The lateral line system plays an important role in detecting water movement relative to the body of the fish, whereas the inner ears serve, among other functions (gravitational sense, detection of angular accelerations), to detect acoustic energy as water particle motion and in some taxa also in form of sound pressure changes (Popper 2011). Low-frequency vibrations (<200 Hz) at high intensities may, however, be detected by both sensory systems (Higgs and Radford 2012; Braun and Coombs 2000).

As in most vertebrates, the fish inner ear is composed of three semicircular canals and three otolith end organs, namely the saccule, the lagena, and the utricle (Popper et al. 2005; Popper and Schilt 2008). Each semicircular canal ends on one side in a dilation (= ampulla) that houses the sensory epithelium (= crista). The crista is

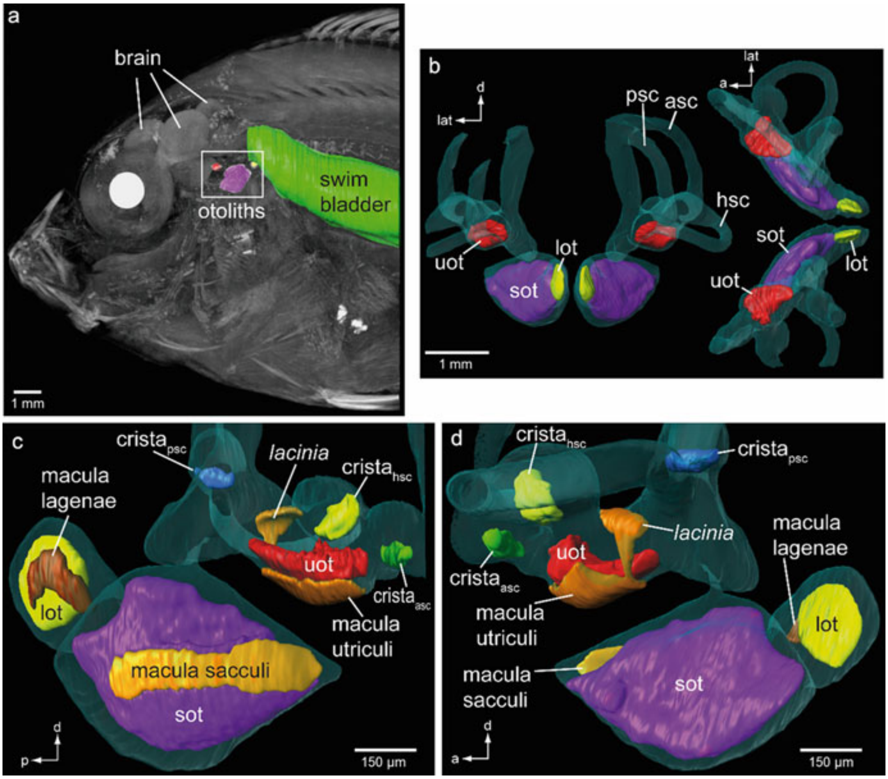

Fig. 1 (**a**) Position of the otoliths in the fish head and (**b**) position of the left and right inner ears relative to one another illustrated in the orange chromide *Etroplus maculatus*. (**c-d**) A higher magnification of the inner ear displays the extent to which maculae are overlain by the respective otolith. Ears are shown in posterior and dorsal views (**b**) as well as in medial (**c**) and lateral views (**d**). *a* anterior, *asc* anterior semicircular canal, *d* dorsal, *hsc* horizontal semicircular canal, *lat* lateral, *psc* posterior semicircular canal, *p* posterior; otoliths: *lot* lagenar, *sot* saccular, and *uot* utricular otoliths. Modified after Schulz-Mirbach et al. (2013a, b, 2014)

characterized by sensory hair cells having long ciliary bundles, all oriented in the same direction and overlain by a thick convex layer of a mucopolysaccharide gel (= cupula; Silver et al. 1998). The motion of the endolymphatic fluid in the semicircular canals provoked by, for example, head rotation (angular acceleration), bends the cupula and thus deflects the ciliary bundles (Popper 1996). In the three otolith end organs, the sensory epithelia (= maculae) are each overlain by a solid calcium carbonate biomineralisate (= otolith) in teleost fishes (Fig. 1; Popper et al. 2005). The otolithic membrane which connects the respective macula with the otolith transduces the otolith movement to the ciliary bundles of the sensory hair cells of the macula (Popper and Lu 2000). Sound and linear acceleration (body tilts, swimming along the antero-posterior, dorso-ventral, or along the lateral axes) are detected by all three end organs, whereby saccule and lagena are hypothesized to be the main auditory end organs (Popper and Schilt 2008). The gravitational force is assumed to be detected mainly by the utricle (Straka and Baker 2011; Flock and Goldstein 1978). In cichlids, the macula sacculi always extends anteriorly beyond the saccular otolith, as this otolith bears a sulcus acusticus which is open at the anterior end (Popper 1977; Schulz-Mirbach et al. 2014; Fig. 1c and d). Portions of the macula covered only by the otolithic membrane are hypothesized to be stimulated in a different manner than those parts overlain by the otolith (see Popper et al. 2005; Rogers and Zeddies 2008; Zeddies et al. 2011).

1.2 The Role of the Swimbladder in Hearing

In contrast to terrestrial tetrapods, fishes lack an eardrum (tympanum) to detect sound pressure fluctuations in the surrounding medium. Instead, they detect sound by sensing oscillations of the entire body including the sensory hair cells of the inner ears relative to the overlying inertial mass, namely the otolith. In this way, the inner ear detects particle motion within a sound field instead of sound pressure (Hawkins and Myrberg 1983; Ladich 2010, 2019). In the direct stimulation pathway, a sound source leads to the lagged movement of the denser otolith relative to soft tissues of the fish's body including the sensory epithelium. The otolith therefore acts as an accelerometer in the inner ear that stimulates the hair cells of the sensory epithelium; the relevant stimulus is particle motion emanating from the sound source (Hawkins and MacLennan 1976; de Vries 1950). Whereas all fishes are sensitive to the motion of media molecules, at least a third of all species possess accessory morphological structures, which enable them to detect sound pressure as well (Ladich 2010, 2016; Ladich and Schulz-Mirbach 2016; Hawkins and MacLennan 1976; see also Fig. 2 in Schulz-Mirbach et al. 2019). If fishes possess gas-filled cavities (e.g., swimbladder), sound pressure changes induce compression and decompression of the gas, resulting in the oscillation of the gas bladder walls (van Bergeijk 1967; Rogers et al. 1988). The resulting local particle motion is then transmitted to the inner ears most effectively when ears and swimbladder are coupled through anterior swimbladder extensions or the Weberian apparatus as found in otophysan fishes such as goldfish (*Carassius auratus*) and zebrafish (*Danio rerio*) (van Bergeijk 1967; Rogers et al. 1988). In these cases, the swimbladder acts as pressure-to-displacement transducer and the anterior parts of the swimbladder walls function as "internal tympana." Typically, species that possess ancillary auditory structures can detect frequencies up to several kilohertz, whereas fish lacking these structures can detect frequencies of only several hundred Hertz at higher sound intensities (for an overview see Fay 1988; Ladich and Fay 2013; Braun and Grande 2008). Accordingly, in fishes with ancillary auditory structures, sound can stimulate the inner ears via the direct (see above) and the indirect stimulation pathway.

Fishes that lack ancillary auditory structures tend to have a narrower hearing bandwidth and poorer hearing sensitivity (Fay 1988; Ladich and Popper 2004; Schulz-Mirbach and Ladich 2016; Ladich 2016). The general question arises

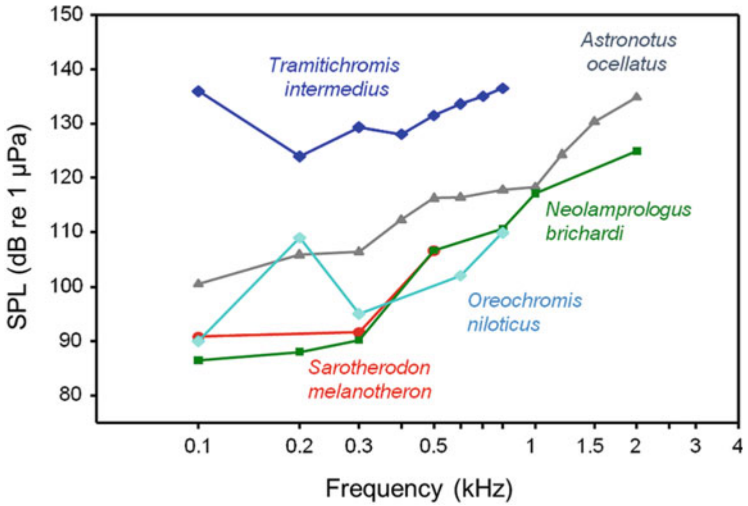

Fig. 2 Mean auditory thresholds of five cichlid species depicted in terms of sound pressure levels (SPLs). The thresholds of *S. melanotheron* were measured using a behavioral training method, whereas thresholds of the other species were obtained by AEP recording techniques using different set-ups. Redrawn after Tavolga (1974), Kenyon et al. (1998), Ladich and Wysocki (2003), Ripley et al. (2002), and Smith et al. (2004)

whether ancillary auditory structures (e.g., anterior swimbladder extensions, Weberian apparatus) and hearing improvements are associated with structural modifications of the inner ears as seen in otophysan fishes and to a lesser extent in certain holocentrids (Hawkins 1993), sciaenids (Ramcharitar et al. 2004; Ramcharitar et al. 2001; Ramcharitar et al. 2006b), chaetodontids (Webb et al. 2010), and cichlids (Schulz-Mirbach et al. 2012, 2014).

2 Hearing Abilities in Cichlids: Auditory Measurements

Until now, the hearing has been measured in 13 (Table 1) out of more than 1700 valid cichlid species (Nelson et al. 2016; Seehausen 2015). Except for the black chin tilapia (*Sarotherodon melanotheron*), whose auditory thresholds were determined behaviorally, all other species were investigated electrophysiologically using auditory evoked potential (AEP) recording techniques. Tavolga (1974) determined auditory thresholds in *S. melanotheron* using a classical conditioning method in which animals learnt to swim across a barrier in order to escape or avoid an electric shock after the onset of an acoustic signal. The AEP-technique records potentials elicited in the auditory pathway of an animal from the inner ears, the eighth cranial nerve and auditory nuclei in the brainstem, and higher centers in response to acoustic stimuli (Kenyon et al. 1998; Corwin et al. 1982; for a review of AEP-audiograms see Ladich and Fay 2013). Hearing measurements in cichlids and in fishes, in general,

Table 1 Overview of cichlid species whose inner ear and swimbladder morphology as well as hearing abilities have been studied (indicated with x)

Species	Ear morphology			Sb ext.	Aud. meas.	References
	Gross	SE	Oto			
Etroplus maculatus	x	x	x	Yes, AAS	x	Dehadrai (1959), Schulz-Mirbach et al. (2012, 2014), Ladich and Schulz-Mirbach (2013)
E. suratensis				Yes, AAS		Dehadrai (1959)
E. canarensis				Yes, AAS		Dehadrai (1959)
Paretroplus div. sp.				Yes, AAS	(x)	Braun et al. (2012), Sparks (2008)
Paratilapia polleni	x	(x)	(x)	Yes, (AAS)	x	Schulz-Mirbach et al. (2012)
Ptychochromis oligacanthus				Yes		Sparks (2008)
P. grandidieri				Yes		Sparks (2008)
Ptychochromoides vondrozo				Yes		Sparks (2008)
Katria katria				Short	(x)	Sparks (2008)
Oxylapia polli				Short		Sparks (2008)
Heterochromis multidens				Short		Sparks (2008)
Hemichromis guttatus	x	x	x	No	x	Schulz-Mirbach et al. (2012)
Sarotherodon melanotheron		x			x, behavioral	Popper (1977), Tavolga (1974)
Oreochromis niloticus			x	No		Saitoh and Yamada (1989), Smith et al. (2004), Casper et al. (2013)
O. mossambicus				No		Casper et al. (2013), Dehadrai (1959), Longrie et al. (2009)
Steatocranus tinanti	x	x	x	No (vestigial sb)	x	Ladich and Schulz-Mirbach (2013), Schulz-Mirbach et al. (2012, 2014)
Neolamprologus brichardi					x	Ladich and Wysocki (2003)
Astatotilapia burtoni	(x)				x	(Froese 1938), Maruska et al. (2012)
Tramitichromis intermedius					x	Ripley et al. (2002)
Maylandia benetos					x	van Staaden et al. (2012)
M. lombardoi					x	van Staaden et al. (2012)

(continued)

Table 1 (continued)

Species	Ear morphology			Sb ext.	Aud. meas.	References
	Gross	SE	Oto			
Pseudotropheus johannii					x	van Staaden et al. (2012)
Astronotus ocellatus					x	Kenyon et al. (1998)
Chaetobranchopsis sp.				Short		Sparks (2008
“Geophagus” steindachneri	(x)		(x)	Short		Sparks (2008)
Andinoacara pulcher		x				Popper (1977)

SE sensory epithelia (here: maculae), *Oto* otoliths, *Sb ext.* swimbladder extensions, *Aud. meas.* Auditory measurements

are still challenging because it is often unclear whether gas-filled cavities such as swimbladders have an auditory function: can they be regarded as ancillary auditory structures when they are not directly coupled to the inner ears (Schuijf and Hawkins 1983)? Unless auditory thresholds are evaluated in a set-up that enables separating particle motion from sound pressure (standing wave tube; Christensen et al. 2015; Hawkins and MacLennan 1976), it is not possible to confirm or to reject sound pressure sensitivity in species with a gas-filled cavity. Conversely, the presence of a gas-filled bladder itself affects and alters the sound field, making it difficult to compare species with and without swimbladders even in a standing wave tube set-up (Hawkins and MacLennan 1976). A standing wave tube is generally a steel cylinder with thick walls (ca. 1 cm) to avoid compliance effects equipped with an inertial shaker or projector at each end of the tube (see Hawkins and MacLennan 1976). Driving the shakers in phase (no phase shift) creates a sound pressure maximum in the center of the tank whereas driving the shakers out of phase with a phase shift of 180 ° results in maximum particle motion. Such a set-up enables to study fish subjected to either sound pressure or sound-induced particle motion. Any comparison of sound pressure level audiograms of species without clearly identified ancillary auditory structures and obtained by measurements in a sound field representing a (complex) mixture of sound pressure and particle motion must be interpreted with caution (Ladich and Fay 2013; Sisneros et al. 2016). Moreover, audiograms determined in different labs can differ due to different techniques. A case in point is goldfish: their auditory thresholds can differ up to 60 dB depending on laboratory and methodology applied (Ladich and Fay 2013; Sisneros et al. 2016). These technical difficulties have led investigators to describe auditory thresholds in terms of sound pressure levels (SPLs) and particle acceleration levels (PALs) (Schulz-Mirbach et al. 2012; Ladich and Schulz-Mirbach 2013). Sound pressure levels are measured by using a hydrophone whereas particle motion is evaluated using particle acceleration sensors (Wysocki et al. 2009) or by an array of several hydrophones (Hawkins and MacLennan 1976) or defined values of particle motion (in terms of displacement, velocity, or acceleration) are generated by a shaker-table set-up (Sand and Michelsen 1978; Radford et al. 2012).

2.1 Baseline Auditory Sensitivities

A comparison among cichlid species reveals that sound pressure level audiograms recorded under quiet lab conditions are either ramp-like, U- or W-shaped (Figs. 2, 3, 4 and 5). The main auditory sensitivities are below or at 0.5 kHz (Figs. 2, 3a and c, 5). A sensitivity maximum of 0.5 kHz is found in species having a close swimbladder-inner ear relationship as in *Paratilapia polleni* and the orange chromide (*Etroplus maculatus*; Fig. 6c and d; Schulz-Mirbach et al. 2012). In most of the studied species, the lowest sound pressure level-based auditory thresholds were between 70 and 100 dB re 1 μPa with the exception of *Tramitichromis intermedius* and *Astatotilapia burtoni*. Nonetheless, it remains unclear whether the low sensitivity in the latter two species points to interspecific variation or to methodological differences between labs (Ladich and Fay 2013; Sisneros et al. 2016). Interestingly, the behaviorally determined audiogram of *S. melanotheron* is

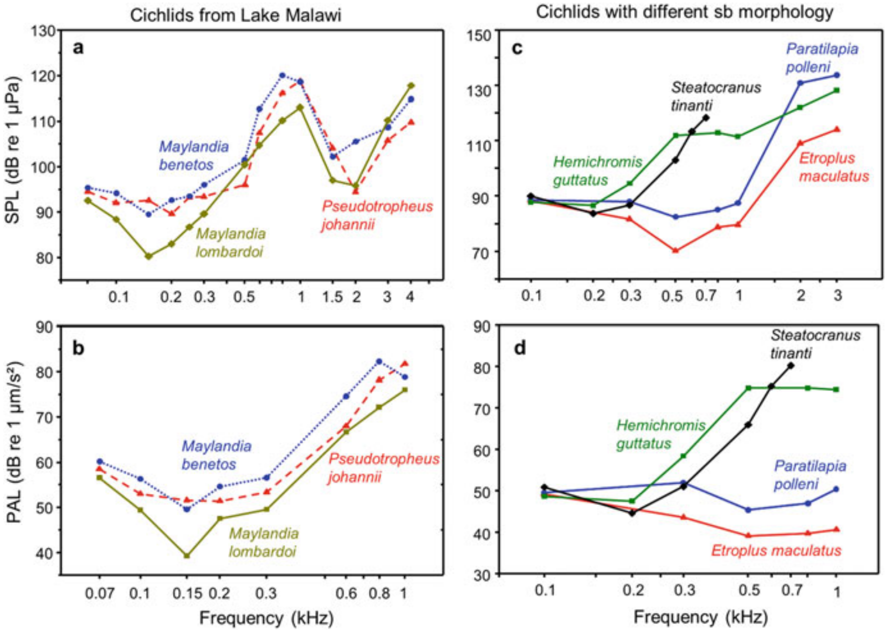

Fig. 3 Mean auditory thresholds of (**a–b**) three species from Lake Malawi and (**c–d**) South Asian (*E. maculatus*), Malagasy (*P. polleni*), and African species (*H. guttatus*, *S. tinanti*). Audiograms are depicted in terms of sound pressure levels (SPLs) in (**a**, **c**) and of particle acceleration levels (PALs) in (**b**, **d**). AEPs of species were measured using the same set-up in (**a–b**) and (**c–d**), respectively. Redrawn after van Staaden et al. (2012) and Schulz-Mirbach et al. (2012)

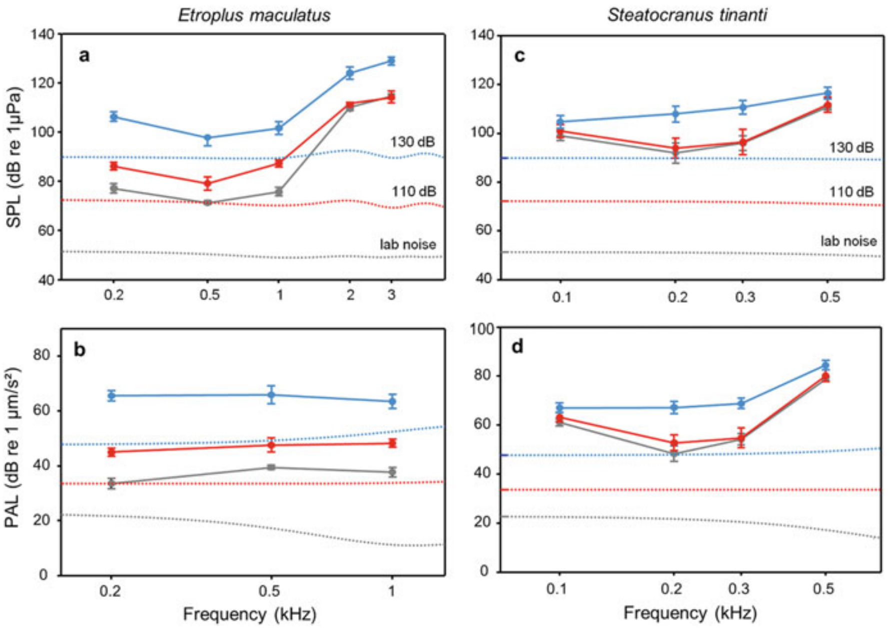

Fig. 4 Mean auditory thresholds of (**a–b**) *Etroplus maculatus* and (**c–d**) *Steatocranus tinanti* obtained under quiet laboratory and different masking noise conditions (white noise of 110 and 130 dB re 1 µPa). Both species were measured using the identical set-up. Different noise conditions are shown as cepstrum-smoothed spectra (*dotted lines*). PAL, particle acceleration level; SPL, sound pressure level. Redrawn after Ladich and Schulz-Mirbach (2013)

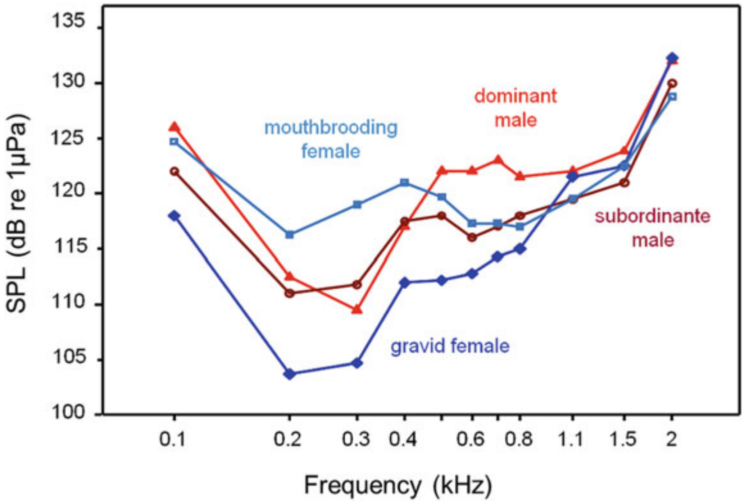

Fig. 5 Mean auditory thresholds of male and female *Astatotilapia burtoni* differ between social and reproductive phases. SPL, sound pressure level. Redrawn after Maruska et al. (2012)

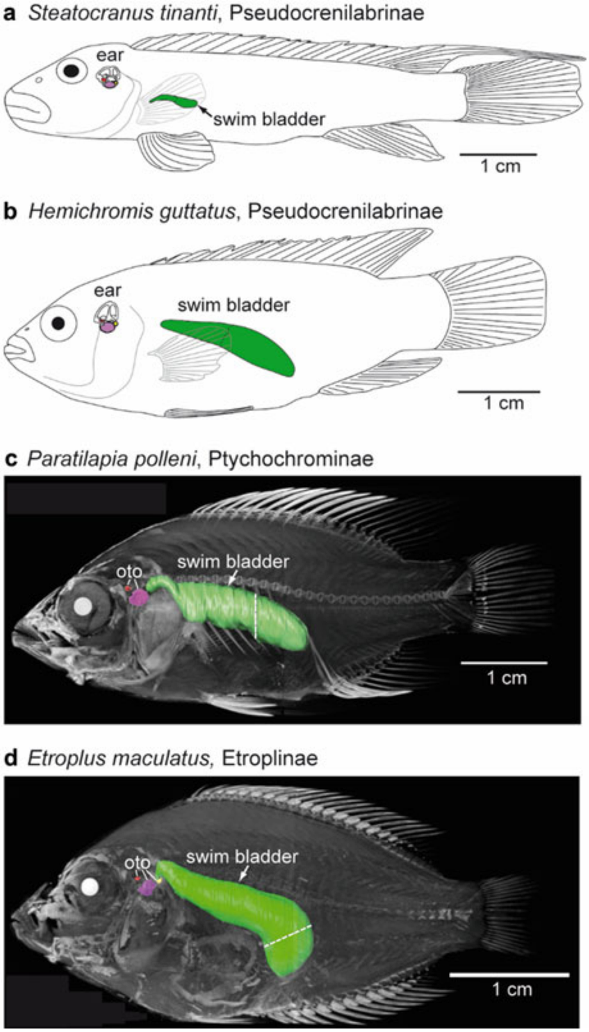

Fig. 6 Swimbladder morphology in four cichlid species. (**a**) *S. tinanti*: reduced to a tiny bladder. (**b**) *Hemichromis guttatus*: large swimbladder, without anterior extensions. (**c**) *Paratilapia polleni* and (**d**) *Etroplus maculatus*: swimbladder with anterior extensions contacting (*E. maculatus*) or coming close (*P. polleni*) to the inner ears. In all species, the swimbladder is divided into two parts by a diaphragm (***a–b**: black line; **c–d**: white line*). Fishes are represented by schematic drawings (**a–b**) or by 3D reconstructions based on microCT imaging (**c**, voxel size $x = y = 28\mu m$, $z = 25\mu m$; **d**, voxel size $x = y = 33\mu m$, $z = 25\mu m$). oto, utricular (*red*), saccular (*purple*), and lagenar otoliths (*yellow*). Modified after Schulz-Mirbach et al. (2012)

similar to the AEP-audiograms of *Neolamprologus brichardi,* the Nile tilapia (*Oreochromis niloticus*), and partly the oscar (*Astronotus ocellatus*), all showing a ramp-like audiogram (Fig. 2).

A comparative study on three species from Lake Malawi (*Maylandia benetis*, *M. lombardoi*, and the bluegray mbuna (*Pseudotropheus johannii*)) asked whether hearing abilities are adapted to ambient noise conditions in the lake in a species-specific manner and whether hearing correlates with the produced sounds and thus may facilitate sound communication. All three species displayed similar auditory sensitivities in the frequency range between 70 Hz and 4 kHz (van Staaden et al. 2012). They yielded a rather unusual W-shaped audiogram with main auditory sensitivity from 100 to 300 Hz and a second (high-frequency) "pressure" sensitivity at 1.5–2 kHz

(Fig. 3a). The maximum auditory sensitivity is within a frequency region of low ambient noise (noise window) and it was correlated with the main energy of pulsed communication sounds. This indicates that their hearing is adapted to ambient noise conditions and to the sounds produced by conspecifics. Lake Malawi cichlids do not possess an otophysic connection, which makes it difficult to explain their sensitivity at higher frequencies. It remains to be tested to which extent the swimbladder size and the distance between swimbladder and inner ears may explain potential pressure sensitivity at frequencies >1 kHz in these species.

Accordingly, other studies comparing species that differ in swimbladder morphology focused on whether swimbladder size or the presence of a close swimbladder-inner ear relationship correlate with hearing abilities (Schulz-Mirbach et al. 2012, 2014). *Etroplus maculatus* and *Paratilapia polleni*, which possess a (direct) coupling between the inner ears and the anterior swimbladder extensions, show enhanced hearing abilities and detect sounds up to 3 kHz. In contrast, the auditory sensitivity of the jewel cichlid (*Hemichromis guttatus*) and *Steatocranus tinanti*, which both lack such a functional coupling, decreases significantly above 0.3 kHz. *Hemichromis guttatus* and *S. tinanti* differ in the detectable frequency range depending on swimbladder size. *Steatocranus tinanti* (with vestigial swimbladder) can detect frequencies only up to 0.7 kHz. (Fig. 3c and d). The outcomes of these comparative studies on functional morphology are discussed in detail below (see Sect. 4).

It remains to be tested whether differences in sound pressure level audiograms in species with a large swimbladder but without an otophysic connection reflect true species-specific differences or whether part of the variation can be explained by methodological differences (Ladich and Fay 2013; Sisneros et al. 2016). Some cichlid species with large swimbladders that lack an otophysic connection may be (to some degree) sound pressure sensitive, whereas others displaying a similar swimbladder morphology are not (e.g., *T. intermedius*, *Oreochromis niloticus*). Enhanced hearing was therefore assumed for *H. guttatus*, also in the absence of direct connections, whereas a hearing specialization was clearly demonstrated in *E. maculatus* and *P. polleni* (Dehadrai 1959; Schulz-Mirbach et al. 2012). This assumption, however, requires further and more extensive testing in future studies by applying, for example, (swimbladder) elimination experiments (e.g., Yan et al. 2000; Poggendorf 1952).

Studies on fish hearing abilities other than those evaluating the detectable frequency range and the auditory sensitivities are scarce. The ability to discriminate frequencies was investigated by Tavolga (1974), who determined the critical band in audition in several fish species including the cichlid *Sarotherodon melanotheron.* The critical band is a narrow band of frequencies around a pure tone frequency that effectively masks the detection of this pure tone. Data seemed to indicate the absence of a critical band and thus of the ability to discriminate frequencies in this cichlid species, which contrasts to findings in the goldfish (Otophysa, Cypriniformes). In goldfish, characterized by distinctly enhanced hearing, the critical bandwidth lies between 0.1 and 0.2 kHz for a signal frequency of 0.5 kHz (Tavolga 1974). It remains to be tested if cichlids such as *E. maculatus* or *P. polleni* that possess enhanced hearing in terms of a wider detectable frequency range and improved auditory sensitivity are also able to discriminate frequencies.

2.2 *Extrinsic (Noise) and Intrinsic (Hormones) Effects on Hearing*

Baseline audiograms (see above) are usually determined under quiet laboratory conditions. In their natural environment, however, fishes encounter a wide variety of acoustical conditions that mainly depend on habitat type (e.g., stagnant waters versus rapids in a stream). Fast-flowing waters are typically noisier than stagnant ones such as lakes and backwaters of rivers (Ladich 2013). Moreover, noise levels also increase with wind speed (coastal surf), precipitation, or close to water falls (Ladich 2013). Consequently, several studies investigated the hearing abilities under natural ambient noise conditions (Lugli 2015; Amoser and Ladich 2005; Wysocki et al. 2007) or comparable white (Gaussian) noise spectra (Ladich and Schulz-Mirbach 2013; Ramcharitar and Popper 2004; Wysocki and Ladich 2005). In the presence of noise, auditory thresholds shift upwards, i.e., auditory thresholds are poorer than those obtained under quiet conditions—a phenomenon termed masking. The amount of masking depends on the spectral level of noise and on the auditory sensitivities of the tested species (Chapman and Hawkins 1973; Wysocki and Ladich 2005; Amoser and Ladich 2005; Vasconcelos et al. 2007; for a review see Ladich 2013).

Among cichlids, effects of masking were tested in *Etroplus maculatus* and *Steatocranus tinanti* using white noise levels at 110 and 130 dB re 1μPa that are frequently encountered in natural environments (Ladich and Schulz-Mirbach 2013; Wysocki et al. 2007). Auditory measurements in the presence of noise revealed that *E. maculatus* showed significant masking effects under both noise conditions. Auditory thresholds shifted up to 30 dB at the high noise level (130 dB) at all frequencies tested (0.2–3 kHz; Fig. 4a and b). At the low noise level (110 dB), masking occurred only in the most sensitive hearing range (0.2–1 kHz; Fig. 4a and b). In contrast, *S. tinanti* was affected only by the high level (130 dB) of white noise between 0.1 and 0.3 kHz (Fig. 4c and d). These differences in masking between *E. maculatus* and *S. tinanti* suggest an adaptation to different ecoacoustical conditions, i.e., different noise regimes (Lugli 2015; Braun et al. 2012). Decreased sensitivity to masking effects observed in rheophilic fishes such as *S. tinanti* could be explained by the high ambient noise levels these fishes encounter in their habitats (see Lugli et al. 2003). Thus, in rheophilic species, there was no selection pressure on improved hearing or retaining a larger swimbladder for better hearing would have even been disadvantageous due to increased buoyancy (Ladich 2014). In contrast, it may have been a major selective advantage in *E. maculatus* and other species which permanently or partly thrive in quiet habitats to evolve enhanced hearing abilities (Ladich and Schulz-Mirbach 2013; Ladich 2014).

Apart from masking, the effects of long-term exposure to high noise levels were investigated in fishes (Ladich 2013; Popper 2014; Popper et al. 2014). Cichlids and other fish taxa serve as a model to investigate the potential harmful effects of anthropogenic noise on hearing (e.g., Amoser et al. 2004; Smith et al. 2004). Amoser and Ladich (2005) demonstrated that exposure to high noise levels (158 dB) results in temporary hearing loss (temporary threshold shifts, TTS). It took 3 days for goldfish and up to 14 days for the Pictus cat (*Pimelodus pictus*; Otophysa, Siluriformes) to fully recover their hearing abilities after noise exposure. Among cichlids, the potential harmful effect of anthropogenic noise was studied in the genus *Oreochromis*. Smith et al. (2004) exposed *O. niloticus* to high levels (130–170 dB re 1µPa) of white noise for seven and 28 days. In contrast to goldfish, no long-term hearing loss was observed (except after 28 days of exposure at the highest noise level at 0.8 kHz). The comparison between otophysan fishes and *O. niloticus* indicates that species without ancillary auditory structures and enhanced hearing are less affected by anthropogenic noise. Nonetheless, when exposed to high levels of continuously and intermittently played back white noise (approx. 120 dB), *Haplochromis piceatus* (no hearing enhancement), and zebrafish (Otophysa, Cypriniformes, enhanced hearing) responded in a species-specific way. Noise exposure significantly reduced swimming speed in the first minute in both species, but only the zebrafish showed a distinct startle response with the onset of sound exposure whereas *H. piceatus* spent more time in the bottom-area of the test tank (Sabet et al. 2016). The underlying reasons for these behavioral differences may also be a complex mixture of differences in lifestyle (“pelagic” versus benthic) and anxiety levels; hence, it is not easily possible to correlate the species-specific behavior with the different hearing abilities of the two species (Sabet et al. 2016).

Pile driving and other impulsive sounds have the potential to injure or kill fish (Popper 2014). To further investigate swimbladder and tissue damage, Halvorsen et al. (2012) exposed different species with distinct swimbladder morphologies to pile driving sound (186 and 216 dB re 1 $\mu Pa^2 \cdot s$ sound exposure level, SEL). The three species were the physostomous Lake sturgeon (*Acipenser fulvescens*; “non-teleost” Actinopterygii, Acipenseriformes), which retains the connection between swimbladder and gut through the pneumatic duct, the physoclistous *O. niloticus* with no connection between swimbladder and gut, and the hogchoker (*Trinectes maculatus*; Pleuronectiformes), which has no swimbladder. At the loudest SELs, *O. niloticus* showed the highest number and the most severe injuries per fish among all three species whereas *T. maculatus* showed no visible injuries. Accordingly, the Mozambique tilapia (*Oreochromis mossambicus*) exposed to 960 pile driving sounds of 216 dB re 1 µPa exhibited barotraumas such as swimbladder ruptures, herniation, and hematomas to several organs (Casper et al. 2013). However, sensory hair cell damage was found in only one out of eleven specimens exposed at the highest SEL. Both studies demonstrated that high-level impulsive sounds result in serious tissue damage, but the specific effects on inner ears and hearing abilities warrant further investigation.

As demonstrated for the plainfin midshipman (*Porichthys notatus*, Batrachoidiformes), hormones influencing the reproductive state such as 17β-estradiol are likely to affect hearing abilities, especially in vocal fishes (Forlano et al. 2016). In the sound-producing cichlid species *Astatotilapia burtoni*, the auditory sensitivity depends on the male social status and female reproductive state (Fig. 5; Maruska et al. 2012). Receptive (gravid) females were more sensitive to low-frequency male courtship sounds than females during the mouth-brooding phase. Auditory thresholds were negatively correlated with circulating steroid levels in females and positively correlated with those in males, underlining the importance of steroids in reproductive state-dependent hearing (steroid-induced auditory plasticity; Maruska et al. 2012). Cichlids show a great diversity of reproductive strategies (Seehausen 2015). Comparative studies on closely related species differing in their mating and brooding behavior such as lamprologine species from Lake Tanganyika (Reddon et al. 2016) may therefore be promising to investigate the effects of hormones on hearing abilities.

3 Diversity of Swimbladder and Inner Ears in Cichlids

3.1 Morphology of the Swimbladder and Ancillary Auditory Structures

A comparison of *Steatocranus tinanti*, *Hemichromis guttatus*, *Paratilapia polleni*, and *Etroplus maculatus* (Fig. 6) revealed that all four species possess an euphysoclistous swimbladder with a transverse diaphragm (including a sphincter) dividing the organ into an anterior and a posterior chamber (Schulz-Mirbach et al. 2012). Except in *E. maculatus*, the swimbladder of all species had a more opaque and thicker walled anterior chamber and a translucent and very thin-walled posterior chamber. In *E. maculatus*, the whole swimbladder was thick-walled (stiff) and silvery whitish. Further histological investigations of the swimbladder wall in Etroplinae and other cichlids could reveal important insights into the physical properties of the swimbladder and thus potential interspecific differences in the motion of the swimbladder walls in a given sound field. This would be especially interesting for members of the genus *Paretroplus*, in which very thin tubes connect the anterior swimbladder extensions to the main body of the swimbladder (Sparks 2008). In the following description, we focus on the distance between the swimbladder and inner ears in different cichlid species.

The rheophilic *Steatocranus tinanti* (Fig. 6a) has a small, vestigial swimbladder without anterior extensions located in the anterior body cavity distinctly removed from the inner ears. In some specimens, the anterior chamber of the swimbladder is asymmetric (Schulz-Mirbach et al. 2012). In contrast to *S. tinanti*, *Hemichromis* *guttatus* (Fig. 6b) has a large swimbladder with two small slightly asymmetric anterior bulges but without anterior extensions (Schulz-Mirbach et al. 2012).

So far, only a few cichlid taxa were shown to possess distinct anterior swimbladder extensions. These are most complex (in contrast to simple anterior swimbladder horns) in Etroplinae. Some members of the subfamilies Pseudocrenilabrinae and Cichlinae, *Heterochromis multidens*, and species of the Neotropical genera *Chaetobranchopsis* and *Geophagus* are reported to possess anterior extensions which approach the posterior skull but neither contact nor penetrate it (Sparks 2008). Nonetheless, a detailed anatomical examination of the swimbladder and its role for auditory abilities in these groups remain elusive. Within the Malagasy Ptychochrominae, anterior extensions are very short in *Katria* or *Oxylapia*, but in *Ptychochromis* and *Ptychochromoides* these extensions come close to or terminate at the posterior skull (Sparks 2008). The most pronounced swimbladder-inner ear relationship is found in the ptychochromine genus *Paratilapia* (Figs. 6c, 7a and b), whose two tube-like swimbladder horns are enveloped by extensions of the septum transversum and the parietal peritoneum connecting the horns to the exoccipital foramina (Sparks 2008; Schulz-Mirbach et al. 2012). Their swimbladder horns thus come close to the inner ears but neither penetrate the skull nor directly contact the inner ears.

Dehadrai (1959) was the first to identify the modified swimbladder morphology in Etroplinae by comparing *Etroplus maculatus*, *E. suratensis*, and *E. canarensis* with *Oreochromis mossambicus*. The anterior swimbladder extensions in the three etropline species that came close to the inner ears, whereas the large swimbladder in *O. mossambicus* lacked these extensions (see also Longrie et al. 2009). More recent studies by Sparks (2008) and Braun et al. (2012) confirmed that etropline species, especially species of the genus *Paretroplus*, are characterized by anterior swimbladder extensions penetrating the posterior skull (exoccipitals) through large foramina (Braun et al. 2012). In *Paretroplus damii* and *P. menarambo*, the posterior neurocranium shows large bullae (Sparks 2008), while in *E. maculatus* the posterior skull has large and less complex-shaped foramina (Schulz-Mirbach et al. 2013b).

A detailed anatomical investigation of *E. maculatus* revealed that the swimbladder extensions show a unique bipartite structure composed of a gas-filled portion and a pad-like part (Figs. 6d, 7c and d; Schulz-Mirbach et al. 2012, 2013b). No internal bullae are present within the neurocranium. The gas-filled part does not penetrate the skull but contacts the lagena via connective material attached to a thin bony lamella (minimum 3µm) that partly envelops this otolith end organ. The swimbladder pad closes the large exoccipital foramen and almost contacts the posterior and horizontal semicircular canals and a recessus located posterior to the utricle. The gap between neurocranium and extension is sealed by a ribbon of connective material stretching from the dorsal and lateral sides to the ventral sides of the swimbladder extension. The swimbladder pad is penetrated by a large blood vessel and by the glossopharyngeal, vagal, and posterior-lateral line nerves. Four pad components can be identified: (1) parts of the swimbladder wall that made up the

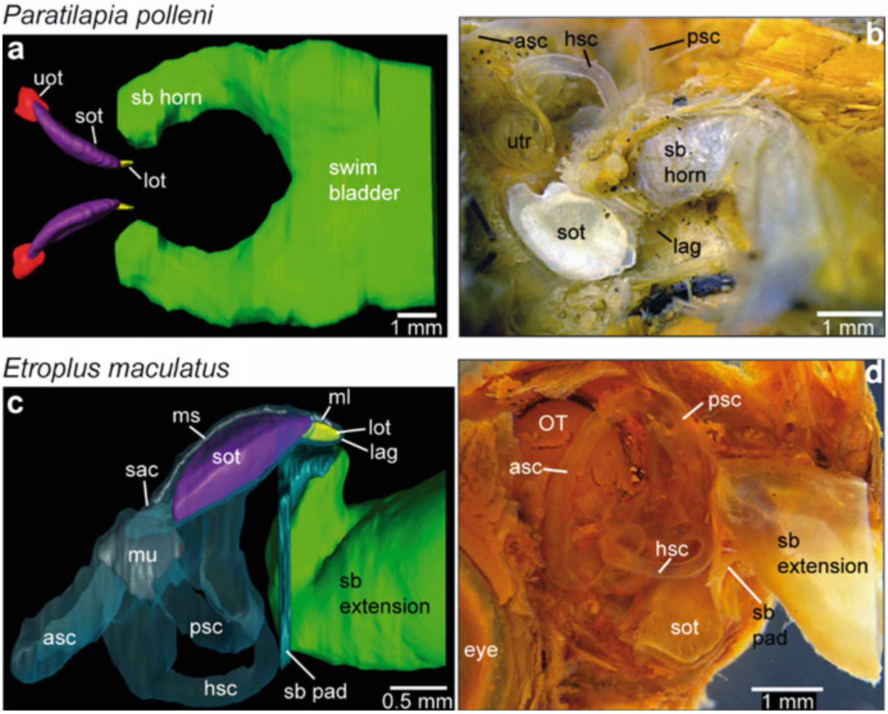

Fig. 7 Relationship between swimbladder and inner ears in (**a–b**) *Paratilapia polleni* and (**c–d**) *Etroplus maculatus*. In *P. polleni* the anterior swimbladder extensions are simple horn-like structures terminating at the posterior skull and approaching yet not contacting the lagenae. In *E. maculatus* these extensions comprise a gas-filled part that contacts the lagena via a thin bony lamella and a pad-like structure that comes close to the posterior and horizontal semicircular canals. (**a**) and (**c**) show 3D reconstructions in ventral view based on high-resolution microCT imaging (**a**, isotropic voxel size 15μm; **c**, isotropic voxel size 9.8μm). In (**b**; ventro-lateral view) and (d; lateral view) the left ear and left swimbladder extension are exposed in dissected, formalin-fixed, and iodine-stained specimens. *asc* anterior semicircular canal, *hsc* horizontal semicircular canal, *lag* lagena, *lot* lagenar otolith, *ml* macula lagenae, *ms* macula sacculi, *mu* macula utriculi, *OT* optic tectum, *psc* posterior semicircular canal, *sac* saccule, *sb* swimbladder, *sot* saccular otolith, *uot* utricular otolith, *utr* utricle. Anterior is to the left. Modified after Schulz-Mirbach et al. (2012) and Schulz-Mirbach et al. (2013b)

postero-ventral region; (2) connective material connecting the extension to the exoccipital foramen, reaching from the supraoccipital crest to the ventral portion of the pad; (3) connective material contacting the lagena and closely approaching the horizontal and posterior semicircular canals; (4) connective material building up the ventro-lateral part.

3.2 Inner Ear Morphology

Gross Ear Morphology

Cichlids show the general inner ear structure reported in many other “percomorph” fishes: a utricle and the three semicircular canals define the upper inner ear, and a large saccule together with a smaller or distinctly smaller lagena comprise the lower inner ear (Froese 1938: Bloyet’s haplo (*Astaotilapia bloyeti*) Popper 1977: the blue acara (*Andinoacara pulcher*), *Sarotherodon melanotheron*; Saitoh and Yamada 1989: *Oreochromis niloticus*; Schulz-Mirbach et al. 2013b, 2014). Interspecies comparisons (Schulz-Mirbach et al. 2012, 2013a, b, 2014) revealed subtle to distinct differences in overall ear morphology (Fig. 8), partly correlating with hearing abilities (and skull shape) of the respective species.

The head in the rheophilic *Steatocranus tinanti* is significantly flatter than in *Etroplus maculatus* and *Hemichromis guttatus* (Fig. 6a versus b–d). Accordingly, the inner ear is dorso-ventrally compressed in *S. tinanti* (Fig. 8a), showing shorter vertical semicircular canals than the ears in *H. guttatus* (Fig. 8b) and *E. maculatus* (Fig. 8c). The saccule is also more elongated in *S. tinanti*, while it is taller in *H. guttatus*. In *E. maculatus*, the saccule shows a pointed tip that is firmly attached to the skull bone via connective tissue. The inner ears of *E. maculatus* display a distinctly thinner connection between the saccule, the semicircular canals, and the

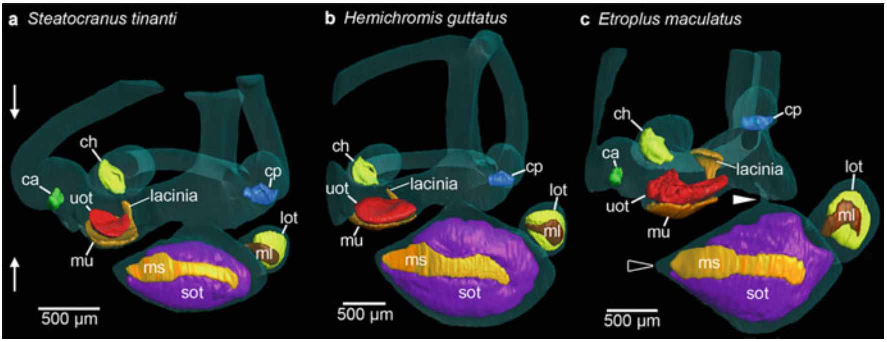

Fig. 8 The ear morphology in three cichlid species differing in swimbladder morphology and hearing abilities. The inner ear is dorso-ventrally compressed in the rheophilic (**a**) *Steatocranus tinanti* (indicated by white arrows), whereas the ears, especially the semicircular canals, are taller in (**b**) *Hemichromis guttatus* and (**c**) *Etroplus maculatus*. In *E. maculatus*, a thin connection links the upper and lower parts of the ear (*white arrowhead*), and the tip of the saccule (*open arrowhead*) is firmly attached to the skull bone. 3D reconstructions are based on microCT scans (isotropic voxel size 4μm). Ears are shown in medial view with anterior to the left. *ca* crista of the anterior semicircular canal, *ch* crista of the horizontal semicircular canal, *cp* crista of the posterior semicircular canal, *lag* lagena, *lot* lagenar otolith, *ml* macula lagenae, *ms* macula sacculi, *mu* macula utriculi, *sac* saccule, *sot* saccular otolith, *uot* utricular otolith, *utr* utricle. The high resolution prohibits reconstructing the entire ear (small region of interest); thus, anterior and posterior semicircular canals were only partly reconstructed. Modified after Schulz-Mirbach et al. (2014)

utricle than those of *H. guttatus* and *S. tinanti*. Moreover, in *E. maculatus* the left and right lagenae are closer to each other.

Sensory Epithelia (Maculae) and Otoliths
The first data on orientation patterns on the maculae of cichlids were provided by Popper (1977). His examination of the macula sacculi of *Andinoacara pulcher* and *Sarotherodon melanotherodon* showed a typical "percomorph" shape, i.e., a wide anterior part (ostium) with two horizontal orientation groups of ciliary bundles, and a narrower posterior portion (cauda) with two vertical orientation groups (Fig. 9). Accordingly, the (saccular) otoliths also generally resemble the "percomorph" type (see Nolf 1985, 1993). Saccular otoliths in cichlids are elongated oval or fusiform to rhomboid with a medial furrow (sulcus acusticus) that is open anteriorly and closed posteriorly (heterosulcoid sensu Schwarzhans 1980). The contour of the sulcus corresponds to the outline of the macula sacculi except for the anterior-most portion of the macula, which is not overlain by the otolith (Schulz-Mirbach et al. 2014; Popper 1977). Saccular otoliths of *Oreochromis niloticus* were figured by Saitoh and Yamada (1989) and saccular otoliths of a number of further cichlid species were illustrated and described by Gaemers (1984) without, however, referring to the corresponding maculae sacculi. Other studies used cichlid otoliths as a model to investigate the effects of hydrostatic pressure (Correia et al. 2012) or microgravity on otolith growth (Anken et al. 2002; Beier et al. 2004; Brungs et al. 2011).

The macula lagenae in cichlids was first studied in *Andinoacara pulcher* and *Sarotherodon melanotherodon* (Popper 1977). In these species, the macula lagenae has a broad ventral part and a short narrow dorsal arm; two orientation groups of ciliary bundles are mainly oriented in dorso-ventral to antero-posterior direction in the posterior half of the macula and into ventro-dorsal direction in the anterior portion. The corresponding lagenar otolith houses the macula lagenae in the fossa acustica (sensu Assis 2003), except for the antero-dorsal most portion, which is only overlain by the otolithic membrane (Popper 1977).

As outlined above, most studies either focused on the morphology of the otoliths or the macula sacculi and macula lagenae. In the following, we describe the outcomes of a comparative study (Schulz-Mirbach et al. 2014) in more detail because this is relevant for further functional interpretation. All three types of maculae and the corresponding overlying otoliths in *Etroplus maculatus* (Etroplinae), *Hemichromis guttatus* (Pseudocrenilabrinae), and *Steatocranus tinanti* (Pseudocrenilabrinae) showed that the species differed distinctly in the 3D shape and orientation patterns of ciliary bundles of the maculae and in otolith morphology (Figs. 8a and b versus c, 9; Schulz-Mirbach et al. 2014). The lagenar otolith in *E. maculatus* was thin, large, and flat and the utricular otolith large with a "crystallized" appearance when compared to those in *H. guttatus* and *S. tinanti* (Fig. 8; Schulz-Mirbach et al. 2014). Quantification of the otolith area, namely the area of the macula-oriented face of the otolith, revealed that *S. tinanti* has smaller saccular and lagenar otoliths than the other two species. The lagenar otolith was distinctly smaller than the saccular otolith in *S. tinanti* and *H. guttatus*, whereas this size difference between the two otolith types was less pronounced in *E. maculatus*. The three

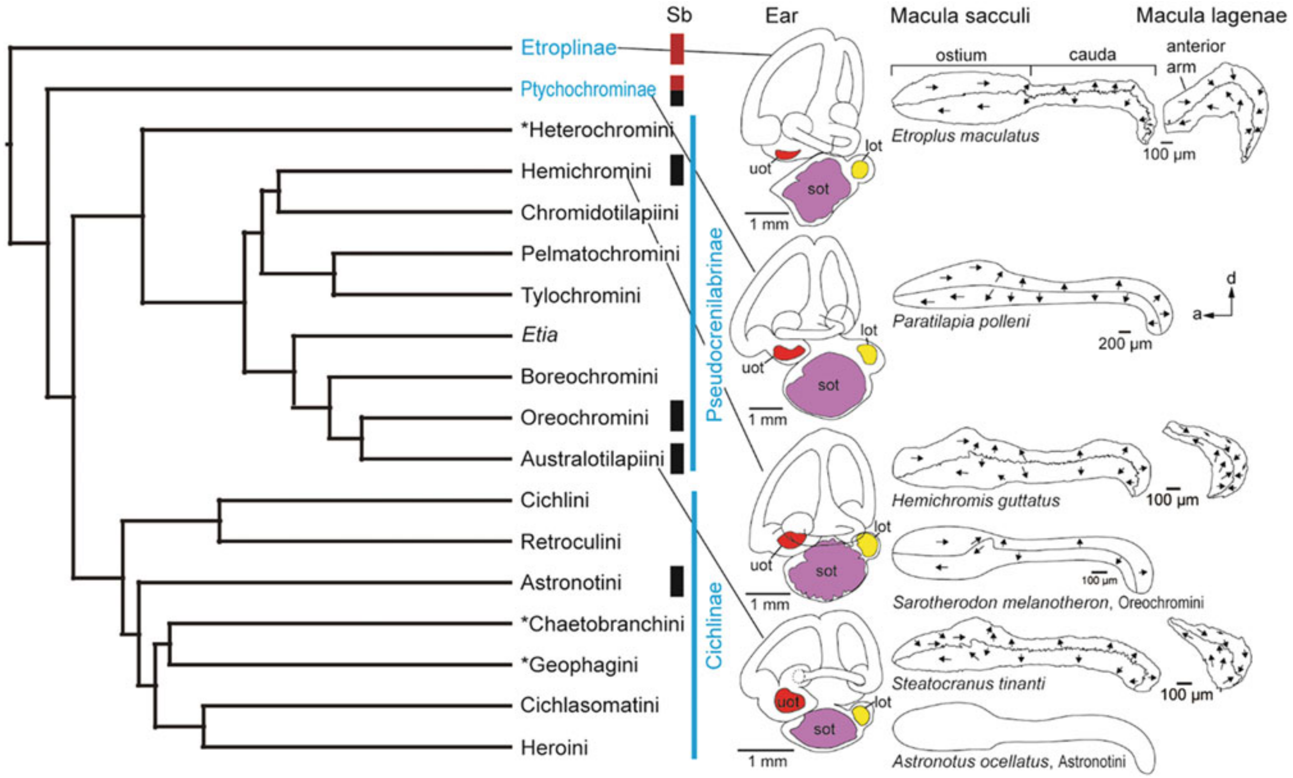

Fig. 9 Inner ear morphology and maculae in cichlids related to their phylogenetic position (phylogenetic hypothesis according to McMahan et al. 2013). Despite the diversity of swimbladder (sb) morphology in cichlids (*black boxes*: swimbladders without anterior extensions; *red boxes*: swimbladders with extensions; see Schulz-Mirbach et al. 2012), 2D orientation patterns of ciliary bundles on the macula sacculi are similar in Etroplinae (possessing ancillary auditory structures), Pseudocrenilabrinae, and Cichlinae (maculae of *Andinoacara pulcher* were described by Popper 1977). In contrast, the macula lagenae is distinctly different in Etroplinae compared to the studied members of Pseudocrenilabrinae and Cichlinae; in Etroplinae, the anterior arm of the macula lagenae is

oriented anteriorly instead of antero-dorsally. So far, only one macula sacculi of *Paratilapia polleni* has been studied. Drawings of the ears refer to *Etroplus maculatus*, *Paratilapia polleni*, *Hemichromis guttatus*, and *Steatocranus tinanti* (from top to bottom). Illustrations of maculae and inner ears are modified after Popper (1977) and Schulz-Mirbach et al. (2012). In *Astronotus ocellatus*, only the contour of the macula sacculi was available (see Popper and Hoxter 1984). The asterisk (*) marks taxa reported to possess (short) anterior swimbladder extensions (see Sparks 2008). Drawings of maculae and inner ears are shown from medial view with anterior to the left. Lagenar otolith (lot, *yellow*); saccular otolith (sot, *purple*); utricular otolith (uot, *red*). Modified after Schulz-Mirbach and Ladich (2016) species also differed distinctly with regard to the weight of all three otolith types. Otoliths were lighter in *S. tinanti* than *H. guttatus* and *E. maculatus*. In contrast to the saccular otolith, the lagenar otolith of *E. maculatus* weighed less than that in *H. guttatus*. The utricular otolith was heaviest in *E. maculatus* and lightest in *H. guttatus*.

While most parts of the maculae were overlain by the respective otolith, some regions were covered by otolithic membrane only; these were the anterodorsal-most part of the macula sacculi, the anterior-most region of the anterior arm of the macula lagenae, and the lateral extension (= lacinia) of the macula utriculi. In all three species, the macula utriculi were bowl-shaped with a distinct lacinia. In *E. maculatus*, the lacinia was considerably larger and extends from lateral to dorsal, forming a roof-like structure dorsal to the utricular otolith. The orientation pattern of ciliary bundles on the macula utriculi was radial on the cotillus ("ventral floor" of the macula utriculi) and opposing in the striola region (anterior-most region of the macula utriculi); on the lacinia, ciliary bundles showed an opposing orientation pattern in *E. maculatus*, but were arranged rather antiparallel in *S. tinanti* and *H. guttatus* (Schulz-Mirbach et al. 2014).

The macula sacculi of *E. maculatus* showed a larger ostium (anterior portion) that was distinctly separated from the cauda (posterior portion) by a "neck," whereas in the other two species it showed a gradual transition from the ostial to the caudal region (Fig. 9). The posterior tip of the cauda in *E. maculatus* was more distinctly bent in ventral direction. The orientation pattern of ciliary bundles on the macula sacculi was the same for all three species and resembled the "dual" pattern described by Popper and Coombs (1982). The dual pattern consists of two horizontally oriented groups on the anterior part of the ostium, two vertical groups on the posterior part of the ostium and on large parts of the cauda, and again two horizontal groups on the posterior-most portion of the cauda. In all three species the sulcus acusticus was heterosulcoid, i.e., divided into an ostial (anterior) and a caudal (posterior) part and open anteriorly and closed posteriorly.

The macula lagenae in *E. maculatus* displayed a large anterior arm that was bent anteriorly, while the anterior arm was much smaller and antero-dorsally oriented in *H. guttatus* and *S. tinanti*. Two major orientation groups of ciliary bundles were present on the macula lagenae in all three species, and ciliary bundles showed a slightly opposing to antiparallel pattern. While the macula lagenae were uniformly vertically oriented in *S. tinanti* and *H. guttatus*, it was bent up to 90° in the anterior-most portion in *E. maculatus*. This resulted in a sensory epithelium with two "perpendicularly" arranged planes and thus differently oriented ciliary bundles, which were arranged in 3D on this macula.

4 Hearing in Cichlids: Functional Morphology and Evolution

4.1 Relationship between Swimbladder Morphology and Hearing Abilities

Major differences in swimbladder morphology that reduce the distance between swimbladder and inner ears seem to affect auditory sensitivities in cichlids (Braun and Grande 2008; Schulz-Mirbach et al. 2012). Cichlids whose swimbladder extensions directly or indirectly touch the inner ears show distinctly better auditory sensitivities and/or a broader hearing bandwidth than species lacking these structures. Furthermore, swimbladder size influences auditory abilities beyond the presence or absence of anterior extensions. The extensions in *Etroplus* and *Paratilapia* result in better auditory sensitivity at frequencies above 0.3 kHz (Schulz-Mirbach et al. 2012). Large swimbladders appear to increase the maximum detectable frequency range, while anterior extensions increase the auditory sensitivity in a mid-frequency region at 0.5 and 1 kHz.

Anterior swimbladder extensions are well known from several members of other teleost groups such as the clupeiform family Clupeidae (e.g., Blaxter et al. 1981), the "percomorph" families Sciaenidae (Ramcharitar et al. 2001, 2004, 2006b), Gerreidae (only shown for the silver mojarra, *Eucinostomus argenteus*; Parmentier et al. 2011a), and Chaetodontidae (Webb et al. 2006, 2010), the beryciform family Holocentridae (Hawkins 1993; Parmentier et al. 2011b), and the gadiform family Moridae (Deng et al. 2011; Paulin 1988; for an overview see Braun and Grande 2008). Even though some taxa show "complex" swimbladder extensions (in contrast to simple anterior swimbladder horns)—among them the blue antimora (*Antimora rostrata*; Moridae; Deng et al. 2011) or the shoulderbar soldierfish (*Myripristis kuntee*; Holocentridae; Parmentier et al. 2011b)—no other examined species possess a structure similar to the tissue pad in *Etroplus* and perhaps all Etroplinae. The function of the tissue pad is unknown. It might enhance the transmission efficiency from the swimbladder to the inner ears. It also provides a larger contact region to the membranous labyrinth than the air-filled swimbladder extension alone. This larger area may improve the transmission of the pressure oscillations in the swimbladder wall to the "perilymph" surrounding the inner ear (Schulz-Mirbach et al. 2013b).

The adaptation to a rheophilic mode of life in *S. tinanti* (Schwarzer et al. 2012) may have led to the reduction in swimbladder size characteristic of many bottom-dwelling fishes, e.g., gobies, sculpins, and some catfishes. This may explain their limited hearing abilities. A comparative study on catfishes demonstrated a significant effect of swimbladder size on hearing abilities (Lechner and Ladich 2008). Loricariid and callichthyid catfishes with small encapsulated bladders displayed significantly lower auditory sensitivities at higher frequencies than representatives of catfish families with large, free swimbladders (Ariidae, Doradidae, Pimelodidae, etc.). If low auditory sensitivity in *S. tinanti* is correlated to small swimbladder size, then the opposite may be assumed for *H. guttatus*. This species detects frequencies up to 3 kHz, indicating that the large swimbladder helps detect higher frequencies despite the lack of a swimbladder-inner ear connection (Schulz-Mirbach et al. 2012). Improved hearing including sound pressure detection in the absence of a direct connection was also observed in other families such as in damselfishes (Pomacentridae; Myrberg and Spires 1980).

The proximity of the swimbladder to the inner ears and swimbladder size probably plays an important role in efficient sound transmission to the inner ears, i.e., the closer the swimbladder comes to the inner ears, the higher the auditory sensitivities at frequencies above 0.3 kHz (except for two out of eight frequencies in *H. guttatus* and *P. polleni*: at 2 and 3 kHz; Schulz-Mirbach et al. 2012). These findings in cichlids are therefore partly consistent with those in holocentrids and sciaenids. A discrepancy exists between holocentrids, sciaenids, and cichlids in the effect of the swimbladder-inner ear relationship on hearing sensitivity (see above; Hawkins 1993; Horodysky et al. 2008). This may be partly explained by the fact that in holocentrids, for example, swimbladder morphology and auditory sensitivities have not been investigated in the same species (Nelson 1955; Coombs and Popper 1979). Moreover, differences in the set-ups for AEP measurements make comparisons difficult (Sisneros et al. 2016).

Different selective pressures may act on swimbladder size and the development of anterior swimbladder extensions (Schellart and Popper 1992) because the overall size may be closely linked to the function of the swimbladder as an organ for buoyancy control (Alexander 1966) whereas anterior extensions are most likely directly correlated to hearing enhancement. Discussions of swimbladder modifications with respect to hearing enhancement must take into account its multiple functions including sound production in some vocal fishes (Ladich and Popper 2004; Ladich and Bass 2011; Ladich and Fine 2006; Fine et al. 1995). The swimbladder in some bottom-dwelling fishes such as toadfishes (e.g., the oyster toadfish, *Opsanus tau*) plays a major role in sound production but perhaps only an inferior one in hearing (Edds-Walton et al. 2015; Yan et al. 2000); others such as gobies, sculpins, or the cichlid *S. tinanti* have mostly or completely lost their swimbladders and show low auditory sensitivity. Loricariid and callichthyid catfishes seem to show a trade-off between reduced swimbladder size and hearing enhancement. While swimbladder size in these fishes was decreased to reduce buoyancy as an adaptation to a bottom-dwelling lifestyle, they retained tiny paired encapsulated gas bubbles connected to the inner ears which still function as ancillary auditory structures (Lechner and Ladich 2008).

Swimbladder morphology in cichlids may also depend on its function as a sound-producing organ. So far, sound-generating mechanisms in cichlids are widely unknown even though numerous species are vocal (see Lobel et al. 2021). Whereas swimbladder drumming muscles serve in sound production in toadfishes, cods, or some catfish families, such a structure has never been described in cichlids (Ladich and Fine 2006; see Lobel et al. 2021). Lanzing (1974) and Rice and Lobel (2002) proposed that *Oreochromis mossambicus* and *Tramitichromis intermedius* generate sounds with a pharyngeal jaw mechanism. In *Oreochromis niloticus*, contractions of hypaxial muscles situated ventro-lateral to the swimbladder seem to be involved in sound production by compressing the rib cage and the swimbladder (Longrie et al. 2009). Future studies should investigate whether sound communication, among other factors, boosted the evolution of swimbladder diversity in cichlids.

4.2 Relationship between Inner Ear Morphology and Hearing Abilities

Modified swimbladders and enhanced hearing in cichlid fishes may correlate with modifications of inner ear structures, especially with respect to the sensory epithelia (maculae) of the otolith end organs. Artificially flattened maculae (i.e., in 2D) of *E. maculatus* exhibited an orientation pattern of sensory hair cells that was similar to those found in *S. tinanti* and *H. guttatus* as well as in several other teleosts without swimbladder extensions (e.g. the shortfin molly, *Poecilia mexicana*, Cyprinodontiformes; Schulz-Mirbach et al. 2011). For example, similar orientation patterns of ciliary bundles on the macula sacculi have been described for the cichlids *Sarotherodon melanotheron* and *Andinoacara pulcher* (Popper 1977) and members of the order Gobiiformes (e.g., the dusky frillgoby, *Bathygobius fuscus,* and the eye-bar goby, *Gnatholepis anjerensis*; Popper 1981). These findings are largely congruent with the results of a study on ciliary bundle orientation patterns in sciaenids with swimbladder extensions. That study reported similar orientation patterns in species with and without anterior swimbladder extensions (Ramcharitar et al. 2001), except for the silver perch (*Bairdiella chrysoura*; Sciaenidae; Ramcharitar et al. 2004). Hence, there does not necessarily exist a direct relationship between ancillary auditory structures such as anterior swimbladder extensions, enhanced auditory abilities, and more "complex" orientation patterns of ciliary bundles—at least based on orientation patterns of artificially flattened maculae. It would be, however, interesting to test if, to what extent, and in which taxa auditory structures may show a concerted evolution. In the case of a close swimbladder-inner ear relationship resulting in enhanced hearing, one may hypothesize that the swimbladder and the ears evolve as an integrated module instead of two independent modules; the latter would be expected for taxa that lack an otophysic connection (Schulz-Mirbach et al. 2019).

In *Etroplus maculatus* the swimbladder extensions "contact" the lagenae instead of the saccules, which could explain the typical "percomorph" dual-orientation pattern of ciliary bundles on its macula sacculi. However, if this interpretation were correct, one would predict an altered orientation pattern and additional orientation groups on the macula lagenae—but the analysis of artificially flattened maculae did not support this assumption (Schulz-Mirbach et al. 2014). When considering the natural 3D curvature of the maculae, however, the orientation patterns of ciliary bundles on the macula lagenae in *E. maculatus* did show a more complex pattern: the ciliary bundles on the anterior-most portion of the macula lagenae formed additional orientation groups (Schulz-Mirbach et al. 2014). Such a 3D arrangement of ciliary bundles was found in the anterior region (ostium) of the macula sacculi of silver perch (Ramcharitar et al. 2004), the ostium of the bowfin (*Amia calva*; "non-teleost" Actinopterygii, Amiiformes; Popper and Northcutt 1983), and in the macula lagenae of the deep-sea dwelling the longnose tapirfish (*Polyacanthonotus challengeri*; Notacanthiformes; Buran et al. 2005). The wider range of directions of ciliary bundles based on the 3D curvature of the respective macula should theoretically translate into a wider range of directional stimuli being detectable, and hence ought to play a crucial role in sound source localization (Schulz-Mirbach et al. 2014; Ramcharitar et al. 2004).

Two (not mutually exclusive) hypotheses may explain the modified morphology of the utricle (large and 3D-arranged lacinia of the macula utriculi and heavier utricular otoliths) in *E. maculatus*. First, the modified utricle may improve gravity and linear acceleration perception because it plays an important role in the sense of balance (e.g., Riley and Moorman 2000; von Frisch and Stetter 1932). Second, the utricle may also be involved in enhanced auditory abilities. For example, Popper and Tavolga (1981) interpreted the distinctly enlarged utricle in ariid catfishes such as the hardhead sea catfish (*Ariopsis felis*; Otophysa, Siluriformes)—together with a unique structure of the macula utriculi that runs as a ribbon along the equatorial region of the corresponding otolith—as a potential adaptation facilitating low-frequency hearing. However, not all ariids possess a pronounced sensitivity to low frequencies (Lechner and Ladich 2008). Likewise, the tripartite macula utriculi in Clupeiformes (connected to intracranial extensions of the swimbladder) was hypothesized to be crucial for ultrasound detection (Denton and Gray 1979). Even though all clupeiform fishes show this modification, only representatives of the subfamily Alosinae seem to be able to detect ultrasound (Mann et al. 1997, 1998, 2001, 2005). Altogether, these results highlight the need for neurophysiological experiments in *E. maculatus* and other cichlids to test the potential role of the utricle in enhanced auditory abilities.

Sciaenids with anterior swimbladder extensions exhibit an enlarged anterior region of the macula sacculi, the ostium (Ramcharitar et al. 2001, 2006a; Ladich and Popper 2001). The presence of such an expansion in *E. maculatus* suggests a functional relationship between the macula sacculi and enhanced auditory abilities as proposed for sciaenids (Ramcharitar et al. 2001). Interestingly, *E. maculatus* also has a dilated anterior portion of the macula lagenae (Schulz-Mirbach et al. 2014). Those two findings point to a distinct role of both the saccule and the lagena for sound perception in *E. maculatus* and probably in Etroplinae in general.

4.3 Evolution of Hearing Enhancement in Cichlids

Several not mutually exclusive hypotheses have been formulated to explain the evolution of hearing enhancement in teleost fishes (for a review see Ladich and

Schulz-Mirbach 2016). The ecoacoustical characteristics of a habitat might impose certain constraints on whether and how hearing improvement may evolve (see "ecological constraints hypothesis;" Ladich 2014). As outlined above, the ambient noise level(s) fish encounter in their habitat may restrict the evolution of enhanced hearing: fish might benefit most from improved auditory sensitivities in a quiet environment with low levels of background noise. According to the "shallow water hypothesis" (Rogers and Cox 1988), water depth is another important trigger for enhanced hearing in terms of the ability to detect higher frequencies. Only higher frequencies of several kHz can travel larger distances in shallow waters. Low-frequency sound does not propagate in shallow waters due to its long wavelength (cut-off frequency phenomenon). Accordingly, this physical constraint may have contributed to the evolution of sound pressure sensitivity (Rogers and Cox 1988). This, coupled with specialized auditory structures such as the Weberian apparatus in Otophysa (Fink and Fink 1996), is hypothesized to have evolved to expand the hearing bandwidth to several kHz instead of several hundred Hertz (Ladich and Fay 2013). Apart from the potential effects of certain habitat conditions, enhanced hearing may have evolved in the context of interactions with con- or heterospecifics. One driving selective force may have been the ability to more effectively avoid predators. Ultrasound detection in some clupeid species is assumed to have evolved in response to the ultrasonic clicks that one of their predators (dolphins) uses during foraging (Mann et al. 1998). Acoustic communication and the ability to detect conspecific sounds may have additionally boosted the evolution of improved hearing, especially in vocal species. Nonetheless, numerous studies provide evidence that a coevolution of vocal communication and hearing enhancement is rather unlikely (for an overview see Ladich and Schulz-Mirbach 2016; Ladich and Popper 2004). Finally, in some cases, hearing enhancement might simply have evolved as a by-product, as hypothesized for Southeast Asian labyrinth fishes (Anabantiformes) such as the Siamese fighting fish (*Betta splendens*; Ladich and Popper 2001). In this group, the air-filled labyrinth organs initially evolved for air-breathing in oxygen-depleted habitats (Bader 1937), and secondarily resulted in the improved hearing because these organs are located close to the ears (Yan 1998).

In cichlids, Braun et al. (2012) addressed questions related to the ecoacoustical constraints hypothesis while focusing on Malagasy Etroplinae (*Paretroplus*) and Ptychochrominae. Preliminary results based on investigating auditory structures and hearing measurements embedded in a phylogenetic context indicate that ancillary auditory structures and hearing enhancement evolved several times independently in Malagasy and South Asian cichlids. Further studies should clarify why these morphological modifications along with improved hearing have evolved in Etroplinae and some members of the Ptychochrominae, i.e., what specific selective forces or constraints led to hearing enhancement in these fishes.

Another important aspect to study is whether modifications of the inner ears and the swimbladder, especially a (close) swimbladder-inner ear relationship as found in Etroplinae or *Paratilapia polleni*, evolved in a concerted or a mosaic manner. Does, for example, a swimbladder-inner ear connection evolve as a single module (phenotypic integration) or as two (independent) modules (see Tsuboi et al. 2014; Lehoux and Cloutier 2015)?

5 Suggestions for Future Research

We want to end our chapter with research questions and hypotheses that future studies may focus on. As far as possible, we also briefly line out which methods or approaches might be applied to tackle the respective questions.

1. Habitats inhabited by cichlids with different hearing abilities should be characterized with regard to ambient noise conditions, i.e., noise levels and spectral profiles. Based on these data, auditory thresholds and the degree of masking should then be evaluated to determine whether species-specific hearing abilities represent an adaptation to the respective ecoacoustical conditions encountered in the respective habitats. Comparative morphological and physiological approaches could use species pairs of each cichlid subfamily that originate from different ambient noise regimes, i.e., a rheophilic member versus a non-rheophilic (deep-bodied) member that also differ in swimbladder morphology (reduced versus normal-sized and/or with anterior extensions). Such studies might also include the marine Pholidichthyidae as an outgroup, as this family has recently been identified to represent the sister group of the Cichlidae (Wainwright et al. 2012; Betancur-R et al. 2013; Broughton et al. 2013).
2. Disentangling the amount of pressure and particle components of sound a species can detect remains a major challenge in fish bioacoustics (Popper and Fay 2011; Sisneros et al. 2016; Fay 2011; Hawkins and MacLennan 1976). A recent study using a modified standing wave tube set-up successfully determined the sensitivity to particle motion and pressure changes in the West African lungfish (*Protopterus annectens*; Christensen et al. 2015). This approach might also be promising to test hearing abilities in more detail in different cichlid species. This would be especially important in those cichlids that possess large swimbladders without an otophysic connection and that show distinct differences in the hearing bandwidth. It is, for example, unclear how re-radiated particle motion from the swimbladder might be transmitted to the ears in *Hemichromis guttatus* (which clearly detects frequencies up to 3 kHz) compared to *Neolamprologus brichardi*, which detects frequencies at most up to 2 kHz (Fig. 3c versus 2).
3. To gain deeper insights into hearing abilities in general, more acoustic measurements on a wider range of species covering the enormous diversity in cichlids are needed. These should go beyond hearing bandwidths and auditory sensitivity to evaluate the ability of acoustic scene analysis (= ability to discriminate between different sound sources; e.g., Fay 2011). Future approaches should also take into account the potential effects of different reproductive phases or social status when evaluating auditory abilities in cichlids (Maruska et al. 2012; Forlano et al. 2016).

4. In order to better determine the contribution of the swimbladder to hearing, in-situ measurements of the physical properties and oscillation mode of the swimbladder walls (see Fine 2012; Fine and Parmentier 2015) during the sound presentation in living animals are warranted. For example, Webb et al. 2010) has used microCT imaging for imaging swimbladders in live specimens of the chaetodontid genera *Chaetodon* and *Forcipiger*. Moreover, we know little about how differences in swimbladder size and shape influence hearing abilities in fishes (Popper et al. 2003; Lechner and Ladich 2008; Zebedin and Ladich 2013). Again, cichlids could provide a good model for such experiments because they cover a considerable range of diversity in swimbladder morphology. A recent study using hard X-ray phase contrast imaging on *E. maculatus* and *S. tinanti* successfully visualized the in-situ motion of the swimbladder walls and the otoliths (Schulz-Mirbach et al. 2018). This approach might be useful to elucidate the factors underlying species-specific differences in hearing abilities.
5. Future studies should also approach two additional questions. Is sound production (sound spectra) correlated to hearing sensitivities in the presence of ambient noise? Was acoustic communication therefore a driving force in the evolution of the diversity of hearing abilities in cichlids? Most species produces sounds with main energies below 0.3–0.5 kHz (Amorim 2006; van Staaden et al. 2012; see Lobel et al. 2021), which seems to be correlated to a main auditory sensitivity below 0.5 kHz (Figs. 2, 3a and c, 5). Other species, however, emit sounds with main energies between 3 and 20 kHz, which contrasts with auditory sensitivities known so far (Spinks et al. 2016; Nelissen 1978; Amorim 2006).
6. The aforementioned approaches should be embedded in a phylogenetic framework by, for example, using phylogenetic PCA (e.g., Burress 2016), especially when analyzing morphological characters of the swimbladder or the inner ears. Comparative investigations should focus on closely related taxa that have adapted to a variety of different ecological niches, that display diverse reproductive and foraging behaviors, and whose phylogenetic relationships are well understood, such as the cichlids in Lake Tanganyika (see Weiss et al. 2015). Such analyses would no doubt improve our understanding of the evolution of macula shape and size (including the morphology of the overlying otolith) and of the orientation pattern of ciliary bundles on the respective macula.
7. Ontogenetic studies comparing cichlid species with and without ancillary auditory structures (e.g., *Hemichromis guttatus* versus *Etroplus maculatus*) could specifically test for temporal and/or spatial differences in the transcription of those genes involved in inner ear development (the three otolith end organs) and in the formation of the anterior swimbladder extensions.
8. What role does developmental/phenotypic plasticity play, for example, regarding the length of the anterior swimbladder extensions? This would be especially interesting in taxa with short to medium-sized anterior extensions that are not linked to the posterior skull such as in the Malagasy genera *Ptychochromis* and *Ptychochromoides* (Sparks 2008). Future studies should also consider that the auditory abilities of a species may show a plastic response in adults depending on social status or reproductive phase, as documented for *Astatotilapia burtoni*

(Maruska et al. 2012). If plasticity is demonstrated, is physiological plasticity also identifiable for inner ear structures such as the number of ciliary bundles on the macula sacculi (see Coffin et al. 2012: *Porichthys notatus*)? Finally, the analysis and comparison of transcriptomes of the saccule of different social/reproductive phases could provide information on the genetic processes underlying this plasticity (Faber-Hammond et al. 2015: *Porichthys notatus*).

On the one hand, we still lack profound knowledge of the diversity of auditory structures and hearing abilities in cichlids. On the other hand, the studies conducted so far indicate that cichlids could serve as an important model to shed new light on the underlying reasons for the evolution of hearing enhancement and the emergence of ancillary auditory structures in teleost fishes.

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Parental Care in Cichlid Fishes

Sigal Balshine and Maria E. Abate

Abstract Cichlid fishes are champion caregivers that protect, clean, aerate, and sometimes even feed their young. This tropical fish family's extensive species radiation combined with great diversity in care habits make cichlids immensely useful models for studying the evolution of parental care. In this chapter, we review the diverse ways that care is provided (~1/3 of species guard young on the ground and 2/3 mouthbrood) and the variation in sex of the caregiver (42% of species have biparental care, 58% show the derived state of female-only care). Substrate guarding, the ancestral form of care, is especially common among New World cichlids. In contrast, mouthbrooding, dominates in African clades. We also describe two forms of expanded (allo) care: (1) brood mixing where parents care for non-descendant young; and (2) cooperative breeding with joint care by an entire social group. Such cooperative breeding, arguably one of the most socially complex breeding systems, has arisen at least 5X among cichlids, all within a single clade, the Lamprologines of Lake Tanganyika. Using one well-studied cooperative species, *Neolamprologus pulcher,* as an example, we review the various possible explanations for the evolution of cooperative care. We conclude by discussing some exciting future directions for the study of parental care in cichlids.

Keywords Costs and benefits of care · Sex of the caregiver · Mouthbrooding and substrate guarding · Cooperative breeding · Brood mixing

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S. Balshine (✉)
Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton, ON, Canada
e-mail: sigal@mcmaster.ca

M. E. Abate
Department of Biology, Simmons University, Boston, MA, USA
e-mail: abate.maria.e@gmail.com

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1 Introduction

Cichlids a large fish family, (currently over 1700 scientifically described species), have one of the most rapid rates of speciation known among vertebrates (Brawand et al. 2014; Kocher 2004). These tropical freshwater fishes have diversified so quickly that the some of the lakes they inhabit have been called “Darwin’s dream ponds.” The family’s explosive adaptive radiation has captured the attention of evolutionary biologists worldwide (Meyer et al. 1990; Brawand et al. 2014). In addition, because many cichlid species are commercially fished and are used worldwide in fish farming facilities, knowledge of their reproduction and care habits have economic importance for aquaculture and fisheries (Pauly 1976; Trewavas 1982; Kocher et al. 1998). However, it was their extensive and protracted investment in young that first drew the attention of behavioral scientists to these fishes (Baerends and Baerends-van Roon 1950; Wickler 1962). Cichlid parental behavior and their beautiful colors also created a high interest in these species among the public and the aquarium trade (Loiselle 1985a). The pioneering behavioral research of many early ethologists combined with information from aquarists, inspired field biologists to venture into the wild to study cichlids and generated comprehensive surveys and information on their parental care and mating behavior in various lakes, rivers, and regions of the world (Trewavas 1935, 1983; Wickler 1965, 1966, 1967; Lowe-McConnell 1969; Fryer and Iles 1972; Ribbink et al. 1980, 1983; Kuwamura 1986; Goldschmidt et al. 1990; Keenleyside 1991; Barlow 2000).

Over 30,000 species of teleost fishes exist on our planet (Nelson et al. 2016), and the vast majority of these do not provide care for offspring (Gittleman 1981; Gross and Sargent 1985; Reynolds et al. 2002; Mank et al. 2005). In contrast, *every* cichlid species provides parental care, and the bonds between parents and offspring can be long lasting, often involving sophisticated communication and signaling (Breder and Rosen 1966; Fryer and Iles 1972; Keenleyside 1991; Sefc 2011). The incredible diversity in cichlid parental care behavior and how this diversity came about is the topic of this chapter. Our intension is not to create an exhaustive review or analysis of all the available empirical or theoretical literature about cichlid parental care; instead, we concentrate on particular species or studies that showcase typical aspects of cichlid parental care behavior. We begin by describing the major classifications of care habits observed among cichlids.

2 Parental Care Strategies

The ways that cichlids care for their young varies dramatically across the different species. Some species defend young for just a few days in simple structures, others will care for young in elaborately prepared structures or even inside the parent’s body for weeks or even months (Figs. 1 and 2). Some cichlid species will feed their young by producing extra mucus, or by lifting up leaves, detritus, or rocks and

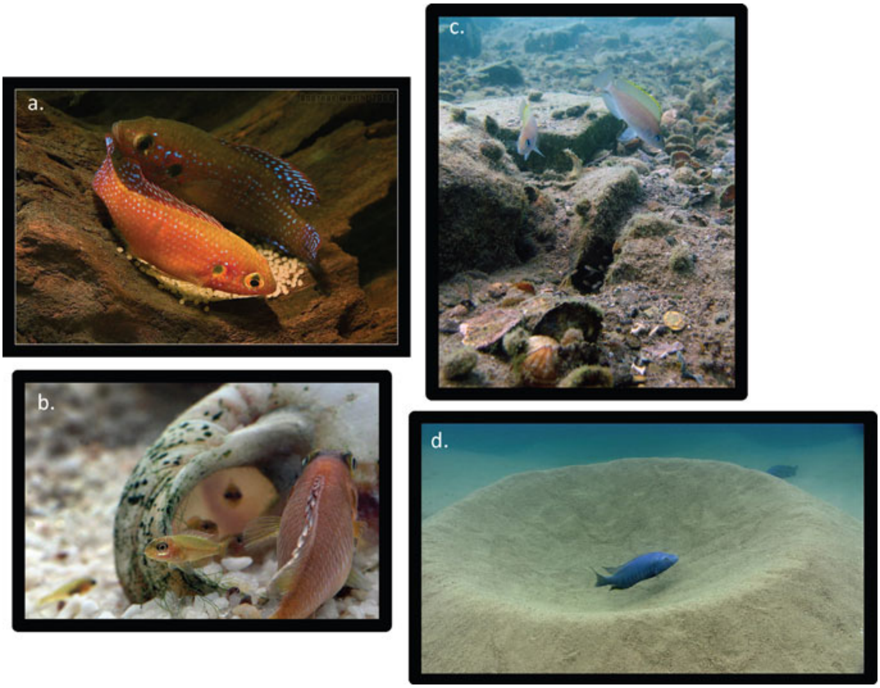

Fig. 1 Substrate guarding cichlids spawn and care for young (**a**) on flat rock or a stone surface on the ground as in this spawning pair of jewel cichlids, *Hemichromis lifalili* from the Congo River; (**b**) in empty snail shells as observed for this *Lamprologus ocellatus* from Lake Tanganyika; (**c**) in a pit or tunnel used by this biparental pair of defending *Neolamprologus caudopunctatus* from Lake Tanganyika; or (**d**) in a sand bower (a volcano-shaped mound) created by the male *Nyassochormis micocephalus* from Lake Malawi. Photographic credits: Frank Mueller, and Alex Jordan

exposing the aquatic insects underneath them for their young to eat (Hildenmann 1959; Townshend and Wootton 1985a, b; Wisenden et al. 1995; Schütz and Barlow 1997; Balshine and Sloman 2011).

2.1 Gamete Provisioning

All female cichlids provision their eggs with nutrient rich, yolk stores but the degree of egg provisioning varies dramatically within and across species. This results in wildly different egg sizes across species and also differences in terms of yolk content, albumen, hormones, and nutrient composition. For example, the African *Tropheus brichardi,* from Lake Tanganyika, has the largest eggs of any cichlid (6.3 mm in length), while neotropical *Mikrogeophagus ramirezi* of the Orinoco River Basin in South America has the smallest (0.9 mm in length) (Kolm et al. 2006a; Ron Coleman's Cichlid Egg Project, http://www.cichlidresearch.com). Egg

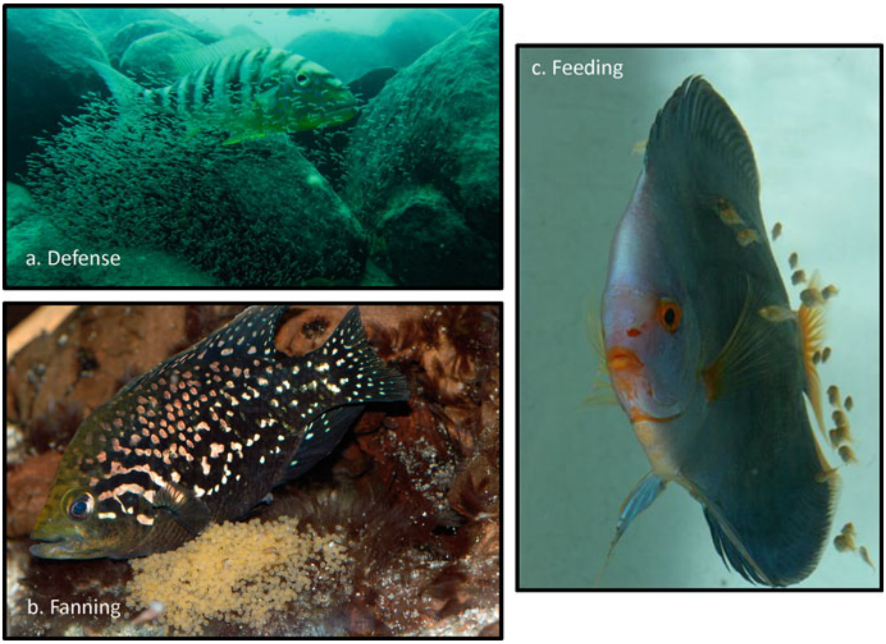

Fig. 2 The different ways or forms that cichlids provide parental care. (**a**) A male *Boulengerochromis microlepis* vigorously defending its hatched free-swimming young; this is the largest cichlid in the world and is endemic to Lake Tanganyika. (**b**) A female cichlid from Madagascar *Paratilapia polleni* fanning her eggs. (**c**) A parent blue diamond discus, *Symphysodon discus* from the Amazon basin with young feeding on the abundant mucus produced. This mucus is produced for about three weeks after spawning and is the main source of food for the offspring. Photographic credits: George J. Reclos and Chaim Shohat

size determines hatchling size and developmental duration and egg size also can vary within and across females as well as between populations (Coleman and Galvani 1998). For example, St. Peter fish, *Sarotherodon galilaeus,* make larger eggs at the start of the breeding season when food is more plentiful and smaller eggs at the end of the season when food is in shorter supply (Balshine-Earn 1996). In other species, such as the convict cichlid, *Amatitlania nigrofasciata* (= formerly *Archocentrus nigrofasciatus; Cichlasoma nigrofasciatum*), egg size and mass increases through the breeding season (Townshend and Wootton 1984). Egg size is influenced by many factors, including environmental conditions, clutch size, and the mother's phenotypic quality (Smith and Fretwell 1974; Christians 2002; Kindsvater et al. 2011). In general, young that hatch from larger eggs, have a higher probability of survival and show faster growth and this is especially true if the young are born in challenging environments, where food is scarce (Coleman and Galvani 1998). In the mouthbrooding cichlid, *Simochromis pleurospilus*, young that hatch from large eggs are faster swimmers, spend less time feeding, and are able to spend more time hiding from predators compared to young hatching from small eggs (Segers and Taborsky 2011). Phylogenetic analyses have shown that across different lakes, cichlid lineages colonizing rocky shore and pelagic niches evolved larger eggs and smaller clutches when compared to benthic lineages from these same lakes (Duponchelle et al. 2008).

The duration of care varies among cichlids from between 10 to 90 days (Konings 1998; Keenleyside 1991). For example, *Lamprologus callipterus* completes care in less than two weeks while *Neolamprologus tretocephalus* provides parental care for up to 20 weeks (Nagoshi 1983, Kuwamura 1986). Parental care duration has co-evolved with egg size, with larger eggs taking longer to hatch (Trewavas 1983; Fishelson 1995). Species that care for longer durations usually have only a few, extremely large eggs, while species that care for only a few weeks tend to produce many, small eggs (Shine 1989; Sargent et al. 1987). However, a phylogenetically based comparative test of this idea by Kolm and co-workers (2006a) showed that clutch size, not egg size was most closely related to the duration of care; smaller clutches had longer care. Their study was based on a rather small sample of only 25 cichlid species, so additional analyses with more species would certainly be worthwhile to ascertain with greater certainty how widespread and robust this pattern is.

2.2 Nest Preparation

The preparation of a territory or the nest where the eggs will be released, fertilized, and cared for is another form of care. Many cichlid species merely clean off a flat rock or stone surface (e.g., *Hemichromis lifalili*, Fig. 1a) and use this cleaned off area as a nest. Other cichlids will use an existing structure such as an empty gastropod shell (e.g., *Lamprologus ocellatus,* Fig. 1b) or an overhang on a rock (e.g., *Neolamprologus furcifer*) and look after their young in these ready-made structures or shelters (Nagoshi 1983; Kuwamura 1986). Some cichlid species extensively modify an existing structure or will even create new structures *de novo* (Taylor et al. 1998). For example, *Neolamprologus caudopunctatus* (Fig. 1c) *and N. pulcher* (Fig. 5) dig out the sand under rocks to create a safe area to spawn in (Kuwamura 1986; Balshine et al. 2001). Both *Lamprologus callipterus* and *Cyathopharynx furcifer* of Lake Tanganyika are master builders, constructing remarkable nests. Male *L. callipterus* do this by transporting and collecting hundreds of empty gastropod shells into large piles where females spawn (Takamura 1987; Sato 1994), and *C. furcifer* dig a crater shaped nest up to 2 meters in diameter (Karino 1997; Schaedelin and Taborsky 2006; Balshine and Sloman 2011). Many sand-dwelling cichlids of Lake Malawi (e.g., *Lethrinops, Cyrtocara and Oreochromis* spp.) also prepare elaborate bowers shaped like pits, volcanoes, or castles (Fig. 1d, McKaye 1991; Kellogg et al. 2000; Kidd et al. 2006).

The building of such nesting structures in which the eggs are deposited can be costly to the parent in terms of energy, time, and predation risk (McKaye 1983, 1984; Gauthier and Thomas 1993). Such costs are better born by particular individuals with particular traits, and the nest or burrow can become much more than the place where young are looked after. Because these bowers or display sites can reflect the quality of individual builders (Schaedelin and Taborsky 2006; Martin and Genner 2009), females sometimes assess and base their mate choices on nest quality; commonly showing strong preferences for males that build big, elaborate, or particularly well-constructed nests (Kellogg et al. 2000; Genner et al. 2008; Young et al. 2010). The nest or bower can be thought of as an extension of the individual's phenotype (Dawkins 1982; Soler et al. 1998; Östlund-Nilsson 2001; Schaedelin and Taborsky 2006; Schaedelin and Taborsky 2009; Jordan et al. 2016). And yet at its essence, the construction and preparation of a nest, cavity, or burrow constitute a basic but important aspect of care, providing excellent fortification for young against predators and adverse environmental conditions (e.g., low dissolved oxygen). A good quality nest strongly influences the survival probabilities of young (Clutton-Brock 1991). However, adults too can enjoy protection from adverse conditions by remaining in the nest or burrow. Often, the nest is an area where adults will sleep, hide, and look after their young. An example of such is the complex "brood chamber" of *Neolamprologus pulcher* which is used as a place to breed and to hide, and so the brood chamber typically contains several entrances that help to provide easy access to safety and maximizes protection from predation for adults as well (Balshine et al. 2001; Heg and Taborsky 2010). In general, the topic of how nest quality and nest building effort precisely influences the survival and growth of cichlid young still requires much empirical testing, and comparative analyses of how nest building elaboration correlates with brain size and specific brain regions, as has been shown in birds and Malawian cichlids (Day et al. 2005; York et al. 2019) would be another fruitful area for future research.

2.3 Defense

An important aspect of cichlid parental care is vigorously defending young from predators, often inside a nest or crevice within a larger defended territory. In many species of cichlids, parents will continue to guard free-swimming young and remain near these young long after they have hatched (Fig. 2a). A good example comes from *Cyphotilapia frontosa* where the offspring are cared for by the parent for three months (Balon 1981; Barlow 2000). As the offspring grow they become more mobile and will swim or drift around the territory searching for food and even go off the territory altogether but always with their parents close by. The parents continue to guard these young and will signal danger if a predator is nearby, by fluttering or flickering of their pelvic, dorsal, or anal fins in rapid bursts or jolting their head or fins (Smith 1992; Shennan et al. 1994). These repetitive rapid fin movements by parents cause the young to swim down and hide among the substrate, or to return to the safety of their parent and hide underneath their body or re-enter their mouths when danger is detected (Baerends and Baerends-van Roon 1950; Cole and Ward 1969; Perrone 1978). Mouthbrooding cichlids vigorously protect their young by keeping them in their mouths for the entire development duration (see Sect. 3.2). Such internal brooding is an extremely effective method of protection because the only way a predator can capture or kill the young is by injuring or killing the parent or by forcing the parent to eject or drop its young (McKaye and Kocher 1983).

2.4 Embryo Directed Behavior (Cleaning and Fanning)

Another important care behavior is the cleaning of eggs; parents will often consume diseased or dead eggs from the brood, to reduce and prevent disease spread (Brown and Marshall 1978). Many cichlids will hover under or above their fertilized eggs or attached young and conspicuously use their pectoral fins to move water over the young in the nest (Fig. 2b). Such fanning behavior brings oxygen to the developing fish embryos and may also remove waste substances from the nest (Reebs and Colgan 1991, 1992; Hale et al. 2003). Egg respiration depletes the oxygen layer around the egg, and CO_2 can become more abundant (Reebs and Colgan 1992). So, such fanning behavior by parents can strongly increase the probability that young will survive. Species inhabiting deep crevices with less oxygen, need to fan more than those that rear in the open (Kramer 1987; Reardon and Chapman 2009; Friesen et al. 2012). Some researchers have argued that fanning quality or quantity can be viewed as courtship or mate attraction signal in fishes (Lindström and St. Mary 2008). However, for a number of reasons fanning is highly unlikely to act as a sexual ornament in most cichlids. First, cichlid parents do not fan before receiving eggs. Second, while mixed broods are found in some species (e.g., convict cichlids, Wisenden and Keenleyside 1992), cichlid parents usually provide care for one brood at a time and caring parents do not continually attract mates. Third, the female often fans the eggs alone. Fanning has not been particularly well studied in cichlids and its role in influencing offspring survival and mate choice in some polygamous species certainly deserves further attention. Note, cichlid species that care for the young in their mouths (see Sect. 3.2) do not fan their young but instead churn (or turn) them inside their buccal cavities to ensure that they receive sufficient oxygen.

2.5 Provisioning of Young

Some cichlid species will even actively feed their young. This is an extremely unusual behavior among fishes. Leaf lifting is one way that a parent can provision offspring; parents use their mouths to lift up a submerged leaf or a twig off the surface of a river, stream, or lake-bed, and thereby expose a food supply of aquatic insects for their young to forage on. This behavior has been observed in aquaria and in the field for several South neotropical species, e.g., *Cribroheros alfari* (= formerly *Cichlasoma alfari), Cryptopheros panamensis* (= formerly *Cichlasoma panemense),* and the convict cichlid (Townshend and Wootton 1985a, b; Wisenden et al. 1995). Other cichlid parents will use their bodies to dig into the substrate, commonly making rapid beats with their pectoral fins that stir up food sources for the young that swarm the area as soon as the parents start this fin digging behavior (Williams 1966; Wisenden et al. 1995). However, the most extreme example of offspring provisioning among cichlids comes from a number of Amazonian species where both parents produce excess epidermal mucus secretions during the parental care period. After hatching, the young then feed off this mucus (Fig. 2c). This type of provisioning exerts a considerable physiological demand for parents (Buckley et al. 2010) and the feeding strategy was first described by Hildenmann (1959) for *Symphysodon discus*. Mucus provisioning has since also been observed in *Amphilophus citrinellus* (= formerly *Cichlasoma citrinellum*) and *Etroplus maculatus* and *E. suratensis* (Noakes and Barlow 1973a; Ward and Wyman 1977) and convict cichlids (Abate *aquarium observations*). The mucus is a source of nutrients, antibodies, and microbial symbionts, and can contain several different hormones thought to speed up development (Schütz and Barlow 1997; Chong et al. 2004, Sylvain and Derome 2017).

3 Where Does Care for Young Occur?

Cichlid care strategies are classified by both the *location* where the parents take care of their young and by *which sex* provides the parental care. Cichlids look after their pre- and post-hatched young on the ground or inside their mouths (i.e., the buccal cavity). Cichlid species that care on the ground are called *substrate guarders* or substrate brooders (Fig. 3a), while cichlid species that carry their young in their mouths are called *mouthbrooders* (Fig. 3b, c, e). In this section, we describe these two major forms of cichlid care in more detail.

3.1 Substrate Guarders

Many cichlid species (~40% of all cichlid genera) care for eggs in nests on the ground in the open (Fig. 1a), in crevices such as empty snail shells (Fig. 1b), in deeply dug burrows, pits, or long tunnels (Fig. 1c), or on the roofs of rocky caves. Such care is known as substrate guarding or brooding. The term substrate “brooding” is somewhat misleading because unlike birds, cichlids do not physically transfer heat to the embryos. But substrate guarding could also be considered a misnomer because these species do many things for the young beyond defense. A female will deposit a small batch of adhesive eggs in the nest which either the male alone, the female alone, or most typically both parents have prepared ahead of time. Then the male fertilizes the eggs one or a few at a time. The female lays more eggs and the whole procedure is repeated until the entire brood is deposited and fertilized (Fig. 1a). The eggs will develop for several days (exact duration is temperature and

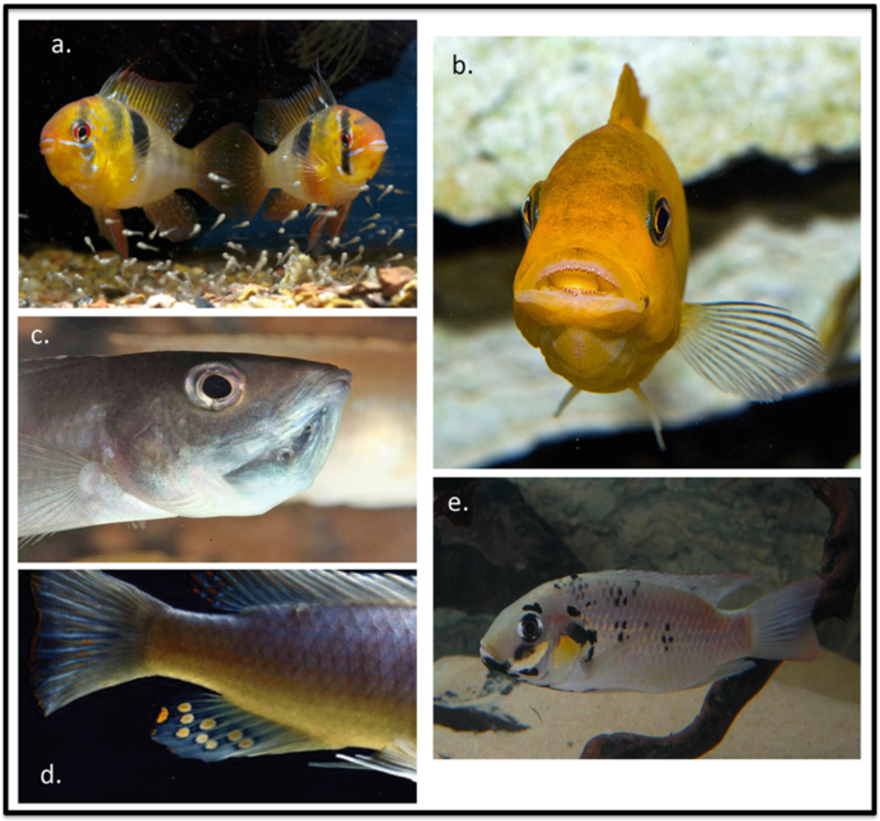

Fig. 3 (**a**) Substrate guarding of young on the ground is usually performed by two parents in the dwarf cichlid *Mikrogeophagus ramirezi* from South America. (**b**) A mouthbrooding *Cyprichromis leptosoma* female from Lake Tanganyika holds her young in her mouth for several weeks even after they have hatched. (**c**) Another mouthbrooder, a female *Pseudotropheus saulosi,* from Lake Malawi. (**d**) Egg spots on a male's anal fin (**e**) *Sarotherodon melanotheron,* the black-chinned tilapia, a cichlid from West Africa is one of the only known male mouthbrooders. Photo credit: George J. Reclos; Ad Konings and Walter Salzburger

species dependent) before hatching. Following hatching the small embryos or wrigglers are not yet free swimming and remain attached to the nest by sticky mucus threads found on the embryo's head region (Peters and Berns 1982; Courtenay and Keenleyside 1983). Parents will fan, clean, and turn the eggs and the hatched young (Keenleyside 1991; Stiassny and Gerstner 1992, Fig. 2b). Parents also use their mouths to taste eggs, receiving chemical cues that facilitate the removal of dead or diseased eggs, and to turn eggs, which is thought to move lipids around and enhance optimal embryo development (Keenleyside 1991; Sopinka et al. 2009). The hatched young continue to absorb the nutritious yolk sac for several days while stuck on the nest surface before their adhesive threads dissolve and they are able to swim freely at which point they will move out of the nest, cave or pit with their parents hovering in attendance close by (Barlow 2000, Fig. 2a, 3a).

Sometimes the eggs or the young will be transferred by the parents to different sites within the territory and such relocating of young occurs under both field and laboratory conditions (e.g., Nicaraguan cichlid, *Hypsophrys nicaraguensis* (= formerly *Cichlasoma nicaraguense*), Abate *aquarium observations; Neolamprologus pulcher,* Balshine *aquarium observations*). Substrate guarding parents will use their mouth for such transfers, carefully moving one or a few young at a time. The reasons why parents move the brood around are not well understood but it has been hypothesized that it serves an antipredator function (Keenleyside 1991). Once hatched, the free-swimming young remain together in a group, protected by one or both parents (Fig. 2a, 3a) and these young usually remain fairly close to the ground, darting further down and into the substrate itself if danger arises. Either a single parent or both parents together will protect the young from the fertilized egg stage all the way to the free-swimming development stage. Both the largest cichlid in the world *Boulengerochromis microlepis* (up to 80 cm SL, Fig. 2a) and the smallest cichlid *Neolamprologus multifasciatus* (~2.5–4 cm SL) practice this type of care known as biparental substrate guarding (Brichard 1989).

3.2 Mouthbrooders

In the majority of cichlid species (~60% of all cichlid genera), parents take newly fertilized eggs into their mouths where they are held for days, weeks, or months; these species are called mouthbrooders (Fig. 3b–e). This kind of care is called mouthbrooding, or buccal incubation, even though as mentioned earlier no heat is transferred to the eggs. Spawning usually occurs on the ground. More often than not, it is the female alone that picks up these fertilized eggs (but see Sect. 4.1). In many mouthbrooding species, the male will release sperm on the eggs which are on the ground and then the female picks up fertilized eggs; however, in some cichlid species, the eggs are fertilized inside the buccal cavity (Mrowka 1987; Fitzpatrick et al. 2009). Females in these species lay and immediately pick up unfertilized eggs in their mouths. The territorial male then presents his anal or pelvic fins, which have conspicuous ovoid spots that are egg-like in shape and color, known as egg spots or egg dummies (Fig. 3d; Hert 1989). As the female snatches or nibbles at these egg spots or dummies on the male's anal fin, his nearby genital papilla discharges sperm that is picked up by the female, and fertilization occurs inside her mouth (Mrowka 1987; Egger et al. 2011). The function of these egg spots remains a highly debated issue (Wickler 1962; Hert 1991; Egger et al. 2011; Theis et al. 2012). Mouthbrooding parents incubate and churn the young in their buccal cavity until they are fully developed, and usually do not feed at all or very little during mouthbrooding (Balshine-Earn 1995a, b). Mouthbrooding duration varies between individuals and species and can range from days to months (Kolm et al. 2006a); parents can also adjust the incubation duration according to the predation risk to their offspring. For example, in the presence of predators of young, *Ctenochromis horei* parents will retain their young inside their mouths for 22 days, an extension of four days compared to the care duration in predator-free areas (Taborsky and Foerster 2004).

The main advantage of mouthbrooding is that like live bearing, it offers exceptional protection from predators (Keenleyside 1979; Blumer 1982), and as well parents can shield young in their mouths from other surrounding environmental stressors like low oxygen levels or high salinity (Stickney 1986). Mouthbrooding also affords parents the ability to carry offspring away from danger with relative ease or to more suitable developmental habitats (i.e., areas that are shallower and warmer). Finally, mouthbrooding releases parents from requiring a suitable nesting substrate for embryo development. The main disadvantage of mouthbrooding is that the number of young that can be efficiently cared for is severely restricted by the size of the parent's buccal cavity (Balshine-Earn 1997). As a consequence, this space limitation means that mouthbrooding cichlids often have much smaller clutches compared to substrate guarder cichlids (Lowe 1955).

Mouthbrooder eggs are not sticky and the cleaning and oxygen delivery to eggs all occurs inside the parent's buccal cavities (Fishelson 1995). Churning, an oral rolling or chewing motion, moves the brood around inside the parent's mouth and this action begins as soon as the eggs (or hatched young, *see below*) are picked up (Baerends and Baerends-van Roon 1950). This vigorous movement is thought to provide oxygen and like the hygienic duties of substrate guarders are thought to promote young's normal growth and development (Fryer and Iles 1972). Most mouthbrooding cichlids pick up the eggs in their mouths immediately, and this behavior is termed immediate or advanced mouthbrooding (Keenleyside 1991).

3.3 Delayed (Primitive) Mouthbrooding

In contrast to the more common cichlid care form of advanced mouthbrooding, some species of cichlids wait a few days before taking the young into their mouths and these species are therefore called delayed mouthbrooders. These unusual cichlids combine elements of substrate guarding with mouthbrooding. In delayed mouthbrooders the adhesive eggs are laid and fertilized on the ground, and then the eggs are guarded in a nest usually by both parents until they hatch a few days later (Keenleyside 1991). Once the young hatch, they are picked up and orally cared for by one or both parents for a few weeks. Once the young are able to swim freely, they can be released by the parent to forage on their own but young will return quickly to the parents if a predator appears or if the parent signals alarm (Loiselle 1985a, b; Timms and Keenleyside 1975; Mrowka 1984). Delayed mouthbrooding is the dominant form of care found in many neotropical cichlid genera including *Aequidens*, *Geophagus*, *Gymnogeophagus,* and is also common in some African taxa such as *Chromidotilapia*. In Lake Tanganyika, we find the reverse pattern to delayed mouthbrooding, with one sex looking after the eggs in their buccal cavity, but then this is followed by a period of biparental substrate guarding by both parents where they closely follow the free-swimming young after they have been released from the mouth of one of the parents. An example of this type of care is found in the Tanganyikan cichlids, *Perrisodus microlepis*, and *Haplotaxodon microlepis* (Fig. 3c) where females mouthbrood alone for nine days, but then both parents jointly guard the free-swimming young, and will remain with the young for several weeks until the young are about 3 cm in total body length (Yanagisawa 1985, 1986; Yanagisawa and Nshombo 1983).

Both immediate and delayed mouthbrooding can inflict a significant physiological cost (Yanagisawa and Sato 1990). Mouthbrooding parents must fast or at the very least decrease their food intake during care (Yanagisawa and Ochi 1991). There is evidence that young inside the buccal cavity can consume some food derived from the parent foraging; however, caring parents often have empty guts and always have less in the digestive tracts than do non-caring parents (Yanagisawa and Ochi 1991). Weight loss has been measured in caring mouthbrooding parents, and this loss is associated with slower growth and reduced future fecundity (Balshine-Earn 1995a, 1996).

4 Who Looks After Young? The Sex of the Caregiver

Which sex provides care to the young varies among cichlid species. In this section, we provide a description and examples of the sex roles associated with biparental and with uniparental care, and we then address the evolutionary transitions between these care strategies in Sect. 5.

4.1 Biparental Care

After the eggs have been laid and fertilized, cichlid parents commonly jointly care for the young by guarding and tending them (Fig. 1a). If both parents provide care then typically a pair bond will form between the male and female, the pair remain together for at least 1–7 days before the first spawning event. In some cichlid species, mated pairs remain together, caring together over many breeding cycles (Stiver et al. 2006); and in other species, the pair bond lasts for only one reproductive cycle until the young are independent (Barlow 1991). Biparental care is extremely common among the cichlids of Central and South American, as well as those from Madagascar and West Africa (82% of these cichlid genera are biparental, Fig. 4a, b).

In most biparental cichlids, either sex is capable of providing all aspects of care but males and females normally play different roles and the care duties are not shared equally, especially so at the early stages of development (Itzkowitz 1984; Keenleyside 1991). The female typically will remain extremely close to the young (<1–2 body lengths away), providing direct brood care (fanning the young, and

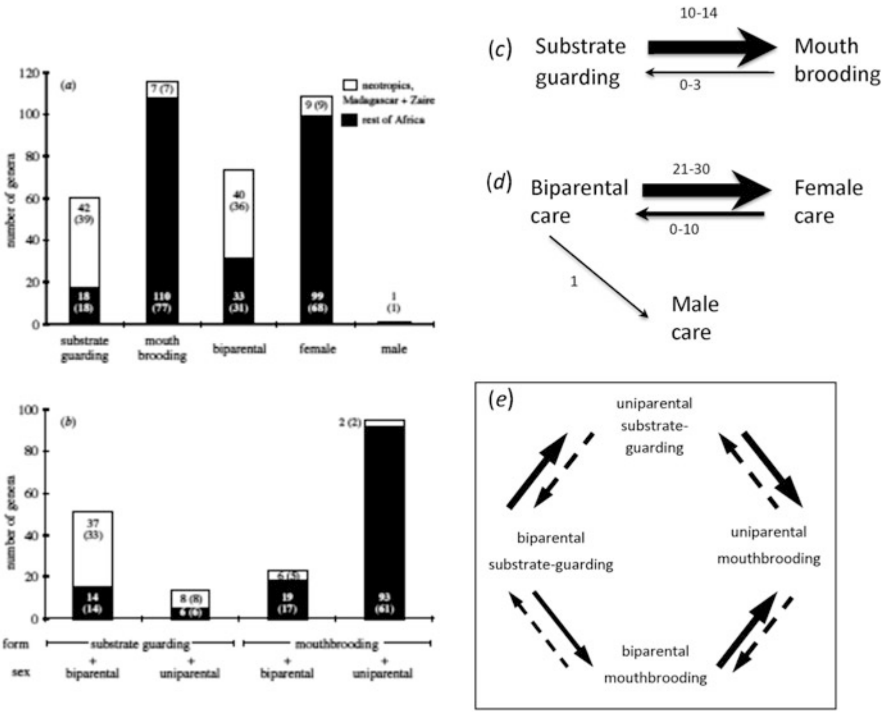

Fig. 4 (**a**) Number of cichlid genera providing care either by substrate guarding or by mouthbrooding as well and the sex of the caregiver ($n = 173$ genera). (**b**) Numbers of cichlid genera combining both the form of care and sex of the caregiver ($n = 170$ genera). Shading of the bars indicates the major biogeographic groupings of genera from the major clades, ancestral genera from Madagascar, Asia, and Zaire, and the sister clades from South America and Africa. Numbers in the bars indicate the number of genera extrapolated from the available data given in parentheses. Taxa which could not be assigned a parental care state were not included in this analysis. (**c**) Transitions between substrate guarding and mouthbrooding, and (**d**) transitions between biparental, female-only and male-only care. Arrow widths are proportional to the number of transitions. (**e**) A stepping stone model of parental care evolution for cichlids. Taken from Goodwin, Balshine, and Goodwin et al. (1998) Proceedings of the Royal Society, 265, 2265–2272

performing hygienic duties) while the male commonly defends the territory boundaries from predators and conspecifics (Nagoshi 1983, 1985, 1987). However, females also regularly chase away brood predators and in some cases can be even more aggressive than the male (Desjardins et al. 2008; Sowersby et al. 2017, 2018). When Keenleyside (1991) compared 21 different cichlid species, he found that in 16 of these species the female spent more time close to the eggs and fanned and cleaned the eggs more than the male parent did. In many biparental caring species, the caring female will in fact flee less frequently from disturbance and return to the brood faster than will the caring male (Carlisle 1985; Barlow 1976). It is possible that the division of labor observed among cichlids depends more on differences in body size and less on sex. Male are typically larger (Kolm et al. 2006b; Gonzalez-

Voyer et al. 2008), and the parent with the largest body size is likely to provide the best protection of the territory and young. Evidence for the idea that the larger sex will defend more comes from a sex-role reversed cichlid called *Julidochromis ornatus* found in Lake Tanganyika (Awata et al. 2006). In this species both parents look after the eggs and young on the ground, the care roles are labile and dependent on relative size. In 80% of the pairs observed, the females were larger and the males spent more time with offspring but the opposite was true for the 20% pairs where the male was larger. The sex differences in care were most exaggerated when the body size differences between the pairs were greatest (Awata et al. 2006). In most biparental cichlid species, once the young are large enough to swim freely, both parents will equitably share guarding duties (Smith-Grayton and Keenleyside 1978; Wisenden and Keenleyside 1994).

Some biparental caring cichlids are mouthbrooders. Perhaps one of the best-known examples of a species with this type of care is Galilee St. Peter's fish (*Sarotherodon galilaeus),* a tilapiine species, widely distributed throughout North Africa and the Middle East. This species has labile care. The female lays batches of eggs on the ground which are fertilized by the male and then the pair circles around the mound of fertilized eggs for ~10–15 min before either the male or female alone or usually both parents will pick up the eggs and orally care for them for about 2–3 weeks or until the young are able to swim freely and feed themselves (Ben-Tuvia 1959; Fishelson and Heinrich 1963; Iles and Holden 1969; Balshine-Earn 1995a; Balshine-Earn and Earn 1998). Another variant on this biparental mouthbrooding theme comes from Lake Tanganyika where the cichlids of the Eretmodini and Limnochromini tribes practice female-to-male shift mouthbrooding. *Eretmodus cyanostictus* and *Tanganicodus irsacae* are two such cichlid species in which eggs are first taken into the female mouth for 9–14 days, and then at this halfway point through the developmental period, the female carefully transfers the young, one at a time, from her mouth into her partner's mouth for additional buccal brooding by the male (Kuwamura 1986, 1997; Kuwamura et al. 1989; Neat and Balshine-Earn 1999; Morley and Balshine 2002, 2003). Several *Xenotilapia* species have similar parental care patterns where maternal mouthbrooding is followed by a period of paternal mouthbrooding, and then interestingly both parents together will continue to guard the free-swimming offspring in the water column (Kuwamura 1997; Konings 1998; Yanagisawa 1986).

4.2 Male Care

Although exclusive paternal care, also known as male-only care, is the most common form of care observed across teleost species (Blumer 1982; Gittleman 1981; Gross and Sargent 1985; Gross 2005), there are only two cichlid species with exclusive male-only care. Both of these species are paternal mouthbrooders from West Africa and are part of the same genus, *Sarotherodon* (Trewavas 1983). The first species is *Sarotherodon occidentalis* (Loiselle 1985a, b) and little is known about this species (Trewavas 1983). The second species, the black-chinned tilapia, *Sarotherodon melanotheron* (Fig. 3e), is somewhat better studied with reproductive information from both field and laboratory studies. Black-chinned tilapia breed in the brackish estuaries, lagoons, and swampy river deltas of the West African coastline (from Sengal to Zaire, Trewavas 1983), where these fish encounter rapid fluctuations in water levels, oxygen concentrations, salinity, and temperature (Pauly 1976). Males and females are roughly the same size (Balshine-Earn 1995b) but can be easily distinguished externally by their operculum color; males have a bright brassy yellow spot while females have dark red or purple spot on their operculum (Aronson 1951). According to Barlow and Green (1969), males grow faster and have larger heads than females, a trait that could help in paternal mouthbrooding. Females establish the territory and court males in what appears to be a role reversed lek (Ellis 1971; Trewavas 1983). Pairs together build a nest, but the female is more active in pit digging and in courtship (Heinrich 1967). The female deposits 20–80 eggs in a nest in small batches and the male fertilizes each batch of eggs before taking the fertilized eggs into his mouth where they hatch and develop (Barlow and Green 1969; Aronson 1949).

The pair bond dissolves shortly after spawning ceases. The male broods the eggs for about 2 weeks (range 7–20 days, Aronson 1951; Balshine-Earn and McAndrew 1995). In the laboratory, females were more competitive and better at monopolizing mates than were males. Males were choosier about mates showing a strong preference for large females, while in contrast females did not discriminate between males based on body size (Balshine-Earn and McAndrew 1995). Slower male reproductive rates and more competitive females have been taken as support for sex role reversal in the black-chinned tilapia (Balshine-Earn and McAndrew 1995). However, the parental behavior of black-chinned tilapia has never been studied in the wild. Given that paternal care is so common across all other groups of fishes, it is worth thinking about why male-only care is so rare among cichlids (Breder and Rosen 1966) and more importantly why it has evolved in these two West African species. Does living in brackish lagoons and estuaries make for a particularly harsh or fluctuating environment? How might such unpredictable or challenging environmental conditions influence the benefits and costs of care for males versus females? These questions clearly deserve further attention.

4.3 Female Care

Although male-only care is exceedingly rare, female-only care is extremely common among cichlids, especially so among the mouthbrooding cichlids of the African great lakes of the Rift Valley, Lakes Malawi, Victoria, and Tanganyika (Fig. 4a, b). Females provide care alone in 62% of all cichlid genera and in 99% of all mouthbrooders genera. In fact *all* of the cichlids (~1000–1500 species) of Lakes Victoria and Malawi are maternal mouthbrooders (Fryer and Iles 1972; Nelson et al. 2016). Most of these female-only caring species have a lek-style polygynous breeding system where males construct nests or court females from small clustered breeding arenas (or leks) that are devoid of any resources for offspring care or the spawning female (Barlow 2000, Fig. 1d). Females assess and choose males to spawn with, releasing a few eggs before picking up the eggs in their buccal cavity (Fig. 3b, c). Females also suck up sperm from males either from the ground or while nuzzling or snatching at the male's anal or pelvic fins (Mrowka 1987) which are often covered with egg spots, small circles that mimic the color and shape of the female's eggs (see description above, Hert 1989, and Fig. 3d). A spawning female can lay eggs with a number of different males and males will court and spawn with as many females as possible, providing no care or resources beyond sperm for the offspring (Fitzpatrick et al. 2009). Females alone care for the eggs and hatched young, churning the eggs and efficiently protecting the young inside of their buccal cavities (Keenleyside 1991). By holding young in their mouths, females not only provide a safe haven for young but can sometimes even nourish them with the little algae or other limited food they manage to acquire while mouthbrooding (Yanagisawa and Ochi 1991). Females will continue to follow and guard the free-swimming young long after continual mouthbrooding has ceased, and these mothers will allow young to retreat into their buccal cavities at night or whenever danger threatens (Barlow 2000).

5 Evolution of Care in Cichlids

Most fish do not care for the young; only ~20% of teleost families show parental care (Baylis 1981; Gross and Sargent 1985). Why care has evolved in some fish species and not others has been an area of active research. As in other taxa, care in cichlids should evolve whenever the fitness benefits (i.e., increased offspring survival) outweigh the costs (Clutton-Brock 1991). The main benefit of care is that it improves offspring survival and can make development more efficient or optimal. The three costs of parental care are (1) decreased survival, (2) lost feeding opportunities, and (3) lost mating opportunities for parents. For example, the caring parent will defend young vigorously from predators, a behavior that certainly reduces offspring mortality, but is costly to parents who take great risks while defending and can be injured or even killed while protecting young (Ghalambor and Martin 2001; Clutton-Brock 1991).

Of the 20% of fish families that provide care for young, 50% show male-only care, 30% show female-only care while biparental care is rare (only about 20% of all caring families have biparental care, Blumer 1979; Gross 2005). Cichlids stand apart from other fish taxa for a number of reasons connected to their parental care behavior. First, *all* the species in this large fish family provide parental care. Second, they care for a relatively prolonged period. And third, many cichlid species have biparental care. With over 200 genera (~2000 estimated species, Nelson et al. 2016) and great variation in the way care is performed (substrate guarding versus mouthbrooding) and in the sex that provides care (biparental versus female-only versus male-only care), cichlids provide a particularly well-suited model system for testing theories about the evolution of vertebrate parental care (Blumer 1982; Keenleyside 1991; Balshine-Earn and Earn 1998; Goodwin et al. 1998; Kolm et al. 2006a, b; Gonzalez-Voyer et al. 2008). Moreover, the use of cichlids to understand how parental care evolves has been strongly bolstered by the existence of extensive, robust knowledge of the evolutionary relationships between cichlid species (Meyer et al. 1990; Albertson et al. 1999; Kocher 2004; Salzburger et al. 2005; Brawand et al. 2014). The explosive and fairly recent radiation of cichlid species (especially in the African Great Lakes) has resulted in intense research focus on understanding taxonomic relations in this freshwater fish family and a tsunami of species-level phylogenies exist for this family (López-Fernández et al. 2010; Dunz and Schliewen 2013; Meyer et al. 2015; Takahashi and Sota 2016; Ivory et al. 2016). Molecular phylogenies together with the interspecific variation in care patterns afford us an exceptional opportunity to study the evolution of parental care and to explore various related life-history traits (Goodwin et al. 1998; Reynolds et al. 2002; Klett and Meyer 2002; Kolm et al. 2006a, b, Gonzalez-Voyer et al. 2009).

Caring cichlid parents do not simply defend young, but they also clean, fan, incubate, and sometimes feed these young (see 15.2). All of these activities take parents considerable time and energy which is not spent on feeding and maintaining themselves (Cooke et al. 2006). These lost opportunity costs associated with care particularly those associated with feeding and energy stores mean that parents suffer suppressed growth and reduced future fecundity as a result of providing parental care (Smith and Wootton 1994; Balshine-Earn 1995a). The time until the next breeding attempt is known to be greater as a result of providing care (Balshine-Earn 1995a). In addition, there are lost future mating opportunities associated with caregiving because caring parents are usually not searching for new mates; and energy reserves need to be built up again after care ends before parents can mate and start to care once again (Maynard Smith 1977; Keenleyside 1983).

Higher offspring survival is a benefit of care that is enjoyed equally by both the male and female parent. However, the costs of providing care rarely impact males and females in the same way. Thus, the cost-benefits ratio of providing care to males versus females determines which sex will provide parental care (Maynard Smith 1977). For example, in an area where there are many predators of young but few predators of adults, two parents standing guard or taking turns defending will result in higher offspring survival. Such high predation environments can select for biparental care, especially if there are also few re-mating opportunities for either sex. However, as the environment changes as a result of food shortages, decreased predator abundance, or changes in the number of available mates; then it may pay one sex to desert their mate and their young resulting in uniparental care (Maynard Smith 1977; Lazarus 1990). Manipulation of modern-day environmental conditions will not commonly reveal these costs of care because parents and offspring have mostly co-evolved to specific levels and types of care. Hence, the measurements of these costs and benefits of care under current conditions will not necessarily shed light on identifying the costs and benefits when care first evolved in the past. However, in some cichlids, care is still labile, so that both parents can provide care together or alternativly only one sex can care alone (Keenleyside 1985; Balshine-

Earn 1995a). In these cichlid species with labile care, experimental manipulations of the costs or benefits of care have confirmed that sex differences in costs and benefits of care determine whether it is male, female, or both that provide care (Keenleyside 1983; Dupuis and Keenleyside 1982; Balshine-Earn and Earn 1998; Smith and Wootton 1995). For example, when additional mating opportunities were experimentally provided (increasing the costs of care), we observed more desertion by the sex that can benefit from this extra mating, resulting in increased uniparental care. This behavioral plasticity helps inform about the conditions that may have selected for the evolution of uniparental or biparental care.

Based on geographic distribution and on embryonic morphological traits, it has long been argued that biparental substrate guarding is the ancestral care state for cichlids (Lowe-McConnell 1959; Iles and Holden 1969; Peters and Berns 1979, 1982, Fig. 4). Mouthbrooding is thought to have evolved in particularly high-risk environments, although some researchers have argued that sperm competition, as a way to keep eggs away from competitors, may have driven the evolution of oral incubation (Fitzpatrick et al. 2009). Researchers have pointed out that once the evolution of mouthbrooding occurred, the egg and larval attachment systems (i.e., the sticky head glands) so important in substrate spawning species, became superfluous and were lost secondarily. In some mouthbrooders, an intermediate condition is found where the adhesive stalks are present but not fully functional (Lowe-McConnell 1959; Iles and Holden 1969; Kraft and Peters 1963). Indeed, many substrate guarding species seem preadapted to mouthbrooding as they will orally move their young from one excavated pit to another and will often collect stray young in their mouths and spit them back into a defended school (Keenleyside 1979, 1991). Once mouthbrooding evolved as a way to care for the young, it increased parents' mobility during care and promoted greater protection of the young. Mouthbreeding also allowed spawning to occur in one region and juvenile growth to occur in another because parents could efficiently transfer young to shallow nursery grounds (Lowe-McConnell 1959). The obvious cost of mouthbrooding is the physical space limit set by the buccal size and the fact that a caring parent cannot feed as easily or at all when holding onto a mouth full of young (Smith and Wooton 1994, 1995; Balshine-Earn 1995a; Reardon and Chapman 2009). Most substrate guarders have many small eggs that develop relatively quickly, while in contrast, most mouthbrooders have a few extremely large eggs that have much longer development durations (Peters and Berns 1982; Noakes and Balon 1982). Phylogenetically based comparative analyses have confirmed that substrate guarding was ancestral to mouthbrooding in cichlids and that there have been multiple (10–14) evolutionary events, or independent transitions from substrate guarding to mouthbrooding over time (Trewavas 1983; Goodwin et al. 1998, Fig. 4a, b and c, Klett and Meyer 2002).

The evolution from substrate guarding with infrequent oral collection of eggs, to permanent mouthbrooding would probably have required several modifications to morphological and physiological systems, such as an expansion of the buccal cavity, denser gill-rakers to prevent embryo loss from the mouth cavity, and the abiliity to endure fasting (Fryer and Iles 1972; Keenleyside 1991). It is likely that shifts to mouthbrooding occurred slowly and infrequently. In contrast, transitions in the sex of the caregiver would have been far less constrained (because both sexes are capable of defense) as such shifts were likely to be influenced by ecological factors, such as predator and food abundance (Townshend and Wootton 1985a, b), and the operational sex ratio (Balshine-Earn 1996; Balshine-Earn and Earn 1998). All of these ecological factors can change relatively quickly. Game theoretical modeling and manipulative experiments of the costs and benefits of care (Keenleyside 1985; Balshine-Earn and Earn 1997, 1998), all confirm that uniparental care can arise as a result of mate desertion after spawning is complete. Empirical tests manipulating these costs and benefits in two normally biparental species, the mouthbrooding St. Peter fish and substrate guarding neotropical convict cichlid, showed that uniparental care emerges when the operational sex ratio is heavily biased to one sex and when the clutch size is small enough that one fish can incubate the young on its own (Keenleyside 1985; Balshine-Earn and Earn 1997, 1998).

Phylogenetically based comparative analyses of parental care have reconstructed historical transitions in interspecific patterns of care in cichlids. These studies have confirmed that biparental care was the ancestral care state to uniparental care (Goodwin et al. 1998, Fig. 4d). Also, these comparative analyses corroborate that sex of the caregiver typically evolved in a stepping stone fashion with single jumps between parental care states being most likely (Fig. 4e). Finally, these comparative studies confirm that which sex provides care (both sexes versus the female alone) appears to have been much more evolutionarily labile in cichlids than the form of care (mouthbrooding versus substrate guarding). There have been at least 21–30 transitions to maternal care from biparental care and one transition to paternal care from biparental care identified in cichlids (Fig. 4d; Goodwin et al. 1998; Klett and Meyer 2002; Reynolds et al. 2002; Sefc 2011). Transitions in the opposite direction from uniparental maternal care to biparental care appear to be far more rare. However, interestingly in the *Xenotilapia* lineage, Kidd and co-workers (2012) uncovered 3–5 multiple independent transitions from maternal care to biparental care, suggesting that parental care evolution is incredibly labile and that there is by no means one stable endgame strategy. Another comparative study found the evolutionary transition from biparental care to female-only care resulted in an increase in sexual selection acting on males that in turn led to greater male abandonment, creating a feedback loop producing and stabilizing uniparental care (Gonzalez-Voyer et al. 2008).

The topic of the evolution of nest building among cichlids is almost untouched and our knowledge of nest building behaviors has certainly lagged behind other aspects of parental behavior (but see Kidd et al. 2006, and York et al. 2015 for exciting research on bower building). For example, the costs and benefits of building nesting structures that protect offspring have not yet been fully elucidated or manipulated experimentally. We also know little about how nests of varying quality influence offspring survival. As mentioned above, bower building in Lake Malawi cichlids has been well studied. York et al. (2015) showed that the macrohabitat (or depth), sensory ability (opsin expression) and feeding behavior (jaw morphology) varies between cichlid species that dig pit versus species that build castle style bowers. However, this type of bower nest building is done primarily to court females and does not affect offspring survival. Females go to these display sites to mate but then care for the young on their own elsewhere. Studies like these, highlight how the watershed of new molecular phylogenies now available for cichlids, can be combined with modern neurophysiological and molecular techniques to address fundamental questions about parental care, its evolutionary pathways and trajectories (Kolm et al. 2006b; Gonzalez-Voyer et al. 2008; York et al. 2015). In the future, it will be useful to examine the degree to which nest building behaviors have converged across different cichlid taxa, how environmental conditions influence nest building, and also which nest types were ancestral, and which structures are evolutionarily derived.

6 Alloparental Care

Some cichlid species exhibit alloparental care, also known as allocare; a form of care where individuals provide parental care to non-descendant young (Kramer 2010). Allocare has been well studied in birds, mammals, and insects (Riedman 1982; Hogendoorn et al. 2001; Lyon and Eadie 2008; Wong and Kölliker 2013). In cichlids, allocare exists in two forms: brood mixing and cooperative breeding. The term brood mixing is applied when young are separated from their genetic parents and are raised by other caregiving parents. Cooperative breeding occurs when a number of sexually mature individuals communally raise young together (brood amalgamation or creching, Ribbink et al. 1980), or when one or more sexually mature subordinate adults help raise young of dominant breeding individuals within a shared territory (Taborsky and Limberger 1981; Koenig and Dickinson 2004). In this section we review the various explanations for these forms of alloparental care in cichlids and address the questions: how and why do cichlids form mixed broods; and why has cooperative breeding involving helpers evolved?

6.1 Brood Mixing

Brood mixing is a widespread phenomenon found in caregiving fishes (Wisenden 1999; Tariel et al. 2019) and is especially common among cichlids. The mixing of broods can occur before or after the non-descendant young are free-swimming; and has been found in both substrate and mouthbrooding cichlids; it also occurs within as well as between species (McKaye and McKaye 1977; Kellogg et al. 1998; Wisenden 1999; Sefc 2011; Schaedelin et al. 2013). Because cichlids have extended uni- or biparental care durations lasting between 2 and 12 weeks, with parents defending free-swimming young that actively roam, this provides an increased timeframe for brood mixing to occur (Keenleyside 1991).

There are three distinct routes to brood mixing: (1) brood parasitism, where a parasitic species dumps its young on a reluctant hetrospecific species that is caring for its own young; (2) extra-pair young are deposited with their half siblings and raised by one parent and one foster parent; and (3) individuals willingly adopt or kidnap and then care for non-descendant young. Brood mixing has often been claimed to be a misdirected or maladaptive behavior, but accumulating evidence from parentage and behavioral studies suggests that foster parents can benefit from brood mixing. Next, we describe the three routes to brood mixing, and then we explain (see Sect. 6.1.1) how fostering can sometimes increase reproductive success for the adopting parent.

Brood Parasitism The most famous case of brood mixing via brood parasitism involving cichlids was first described by Sato (1986) who discovered that the cuckoo catfish, *Synodontis multipunctatus*, from Lake Tanganyika parasitizes the caregiving behavior of a number of mouthbrooding cichlid species. The catfish's conspicuous eggs act as a sign-stimulus and stimulate the cichlid mother to take them into her buccal cavity. The cost to the duped mother is great since the catfish young hatch earlier and grow much faster than her own young. Moreover, the catfish also have a specialized jaw morphology that facilitates the consumption of the cichlid hatchlings inside their mother's mouth (Cohen et al. 2019). Some cichlid species have fared better in the host-parasite arms race with catfishes. For example, in Lake Malawi, *Ctenopharynx pictus*, *Copadichromis pleurostigmoides and Ramphochromis* spp. are all cichlids that have evolved a mutualistic defense with the bagrid catfish, *Bagrus meridionalis*. The cichlid parents will inject their young into catfish broods and will often abandon them to the guarding catfish parents (McKaye 1985). The cichlid young will even feed on the foster catfish's mucus. However, in this example, the catfish benefits from the arrangement as their own young are attacked less often in the center of the mixed-species brood and can have even higher survivorship, especially when the cichlid mothers remain at the periphery of the mixed-species flock and defend the flock along with the catfish, which occurs in about half the cases (McKaye et al. 1992).

Adoption of Half Siblings Another pathway to being an adoptive parent occurs in biparental cichlids when a mate cheats, producing young with two or more mates but then takes on care for all its offspring together. Mixed broods of full siblings and half siblings have been found in a large number of cichlid parentage studies, and the use of genetic markers has shown that many socially monogamous, biparental cichlids have extra-pair mating (Coleman and Jones 2011; Sefc et al. 2008; Lee-Jenkins et al. 2015). Parents often care for broods of young that are a mixture of full and half siblings. For example, only half of the offspring in the broods of the Lake Tanganyikan cichlid, *Variabilichromis moorii* (= formerly *Neolamprologus moorii*), are sired by the male that guards over them, with some broods having as many as 11 male sires (Sefc et al. 2008; Zimmermann et al. 2019). Guarding *V. moorii* males do not adjust their level of defense according to paternity perhaps because 1) they do not know that they have been cuckolded; 2) they do not know how often they have been cuckolded; or 3) they can be relatives of the cuckolders (Bose et al. 2019;

Zimmermann et al. 2019). In a convict cichlid population in Costa Rica, Lee-Jenkins et al. (2015) showed that mixed broods are extremely common (79% of 48 broods studied); based on the genetic patterns uncovered these researchers suggested that some mixed broods might occur when a female transfers her early free-swimming young to her bigamous male and his other female.

What are some of the factors that can influence the rate of mixed brood formation? Female biparental caring cichlids are known to perform such farming out or young-dumping behavior (Yanagisawa 1985; Taborsky 1994) when male desertion occurs (Wisenden and Keenleyside 1992). For many biparental species, desertion by one parent means that the young will not survive to independence; and this is especially true under conditions of high predation (e.g., Yanagisawa 1985; Keenleyside and Mackereth 1992; Wisenden and Keenleyside 1992). Farming out can also free up energy for the parent's future reproductive investment (Balshine-Earn 1995a). Young that are farmed out may be able to survive if they can receive protection from their bigamous father and his mate at his other nest site or territory. However, whether or not the presence of a bigamous male actually improves the survival of his farmed out young over an unrelated male parent remains unknown and needs to be empirically tested. Finally, farming out is not restricted to a deserted female. In the socially monogamous *Perissodus microlepis* from Lake Tanganyika, farming out is performed by deserted females but most often it is practiced by a paired male evading his parental care duties (Ochi et al. 1995; Yanagisawa 1985), and the young *Perrisodus* will even be farmed out to the guarded broods of other species (Ochi and Yanagisawa 1996).

Adoption of Free-swimming Non-Descendant Young Sometimes adults look after their own broods as well as the young from other parents. The earliest accounts of adoption of obviously foreign young in nature were by Burchard (1967), who observed both *Tilapia melanopleura and T. maria* fostering young of the predator *Hemichromis fasciatus*. There are several ways by which non-descendant (foreign) free-swimming young may mix with genetic young (Wisenden 1999). The first is *farming out*; as described above, a parent sometimes will actively transfer offspring to other parents for foster care (Yanagisawa 1985). Pairs of *P. microlepis* have been observed traveling more than 100 meters to dump their young with another pair (Ochi and Yanagisawa 2005). Also, upon experimental or natural male removal, deserted females will regularly gather up their young and dump them into the schools of nearby foster parents of intact pairs (Yanagisawa 1985). Farming out is common in Lake Tanganyika mouthbrooding and biparental species (e.g., Yanagisawa 1986). For example, in *Neolamprologus caudopunctatus,* 66% of broods contained non-descendant young and some of those young came from parents living 40 meters away (Schaedelin et al. 2013). Farming out may be a way to evade parental duties and decrease the time between broods and also possibly spreads out or minimizes predation risk for the young (Ochi et al. 1995; Roy Nielsen et al. 2008).

Another route to brood mixing is via accidental *offspring inclusion* whereby stray or abandoned young independently disperse to or enter any encountered broods

(Taborsky 1994). Chaotic movements and disruptions during territorial disputes or predator attacks can facilitate accidental acceptance of non-descendant young and create mixed broods (Ribbink et al. 1980; Keenleyside 1991). Since, cichlids, like many other fish species, have young that tightly associate, this shoaling tendency may also play a role in enhancing the probability for these random mixing events causing mixed broods to form.

Another possible but rare avenue to brood mixing is active *kidnapping*. The one documented example of kidnapping comes from the Midas cichlid, *Amphilophus citrinellus* (=*Cichlasoma citrinellum*) in Nicaragua. A male took advantage of a territorial dispute between two pairs, rushed in, and kidnapped some young (McKaye and McKaye 1977). Some scientists argue this could be viewed as a form of accidental offspring inclusion (Wisenden 1999), but there was a proactive and deliberate action on the part of the foster parent, precluding this explanation.

6.1.1 Why Should Foster Parents Adopt Free-Swimming Non-Descendants?

To explain why brood mixing occurs, a number of different hypotheses have been put forward. The random mixing hypothesis (Wilson 1975) stresses the haphazard nature of a non-descendant individual coming into contact with another brood. According to this theory, the young actively disperse and move into groups of non-siblings. Foster parents do not defend against or cull these non-descendants either because they lack the means to recognize kin (Kempenaers and Sheldon 1996; Coyne and Sohn 1978; Myrberg 1975) or because of the cost of misidentifying offspring as foreign is too high (Lotem 1993). While some cichlids may not be able to recognize non-descendant young (e.g., *Perissodus microlepis,* Zimmermann et al. 2019), others are clearly able to recognize their young or other kin by visual and chemical cues (e.g., Noble and Curtis 1939; Myrberg 1966; Noakes and Barlow 1973b; McKaye and Barlow 1976; Le Vin et al. 2010; Keller-Costa et al. 2015).

In contrast, the *facultative adoption hypothesis* suggests that foster parents can and do recognize non-descendants as unrelated, but they still adopt them because the benefits of doing so outweigh the costs (McKaye and McKaye 1977). For example, if a female is mated to a high-quality male, she might end up caring for his young with another female; however, the costs of fostering these young, are outweighed by the high-quality traits or resources acquired by having a quality mate (Stiver and Alonzo 2011). Alternatively, if the foster parents are related to the farming-out genetic parents, the foster parents will also pass on some of their genes through these non-descendants (Bose et al. 2019). Studies indicate that the adoption of free-swimming non-descendants in fishes is an effective anti-predation strategy (e.g., McKaye and McKaye 1977; Wisenden and Keenleyside 1994). This idea was first proposed by Sverre Sjölander (1972) based on observations of mixed broods of different cichlid species under high predation risk from the jewel cichlid (*Hemichromis guttatus*). Free-swimming young are attacked often and are commonly eaten by predators (such as juvenile or adult cichlids, characins, catfishes); and while undefended an entire brood can be completely consumed quickly (Barlow 1976; Nagoshi 1987; Alonzo et al. 2001; Snekser and Itzkowitz 2009; Wisenden 2020). For example, Wisenden et al. (2015) observed that broods of foraging convict cichlid were attacked by predators at least once every 10 minutes at one of his study sites.

How precisely does a larger brood, augmented with non-descendant young, decrease the risk of predation for the foster parent's young? Being part of a larger group means that individuals benefit from diluting the predation risk, or that the young might enjoy increased vigilance or create a more effective confusion effect as the coordinated movements of many individuals decrease the chance of a successful attack by a predator (Krause and Ruxton 2002). Larger broods are also known to be more vigorously defended by parents (Lavery and Keenleyside 1990) Moreover, the peripheral location of the adoptees (selfish herd effect) and their often smaller size (selfish shepherd effect) makes them more vulnerable to predation, providing further protection for the foster parent's young (Wisenden and Keenleyside 1992, 1994; Fraser and Keenleyside 1995; Lee et al. 2016). Hence parents can improve the survival of their own young by accepting non-related young that will increase the antipredator benefits of group living. How many non-descendants to adopt may depend on a cichlid parent's current brood size and its ability to defend many young (Lee et al. 2016).

The *facultative adoption hypothesis* provides an explanation for adoption based on adult fitness, but the young too are also under selection and should not be treated as passive vessels when studying brood mixing. The chance of mortality increases dramatically when an individual strays away from their parents (Lee-Jenkins et al. 2014); and when predation risk is high, cichlid young stay close to their parents, and care lasts longer (Wisenden 2020). But can cichlid young even tell who their own parents are? When exposed to visual cues alone, free-swimming convict cichlids (<10 mm SL) in groups oriented toward any adult exhibiting parental behaviors of darkened pelvic fins and rapid turns (Lavery et al. 1990; De Gannes and Keenleyside 1992). Several different laboratory studies using convict cichlids have tested for recognition of family versus non-kin olfactory cues; and overall, the results suggest the ability to make the correct choice and move towards kin depends on age (and size) of young and if the young was alone or in a group (Abate and Kaufman 2006; Wisenden and Dye 2009; Lee-Jenkins and Godin 2013; Wisenden et al. 2014). In cichlid species, the ability for free-swimming and older young to respond to predator cues and develop antipredator competence can be influenced by a number of factors, including size, perceived predation risk, and social learning (e.g., Abate et al. 2010; Stratmann and Taborsky 2014; Al-Shaer et al. 2016; Fischer et al. 2017; Meuthen et al. 2018; Wisenden 2020). We now need brood mixing studies that consider the ability to perceive both kin recognition cues and predator cues while taking into account the perspective of the free-swimming cichlid young as well as their parents.

6.2 Evolution of Cooperative Breeding

In some cichlid species, it is not just a breeding pair that provides care for offspring but the entire social group works together to raise young. This cooperative breeding is an evolutionary conundrum because it is hard to understand why individuals should ever help others raise their young, especially if this assistance comes at the expense of one's own ability to pair up, reproduce and raise offspring. The first cichlid (and the first fish) described to exhibit such cooperative breeding behavior was the freshwater African cichlid, *Neolamprologus brichardi,* (Coeckelberghs 1975; Taborsky and Limberger 1981). *Neolamprologus brichardi* and its sister or the subspecies *N. pulcher* remain the best-studied cooperative breeding cichlid (Fig. 5a); this species complex has emerged as a model organism for the study of the evolution of cooperation (Wong and Balshine 2011a). To date over 150 papers have been published on this one cichlid species. However, there are thought to be as many as 20 cooperatively breeding cichlid species (Heg and Bachar 2006), all

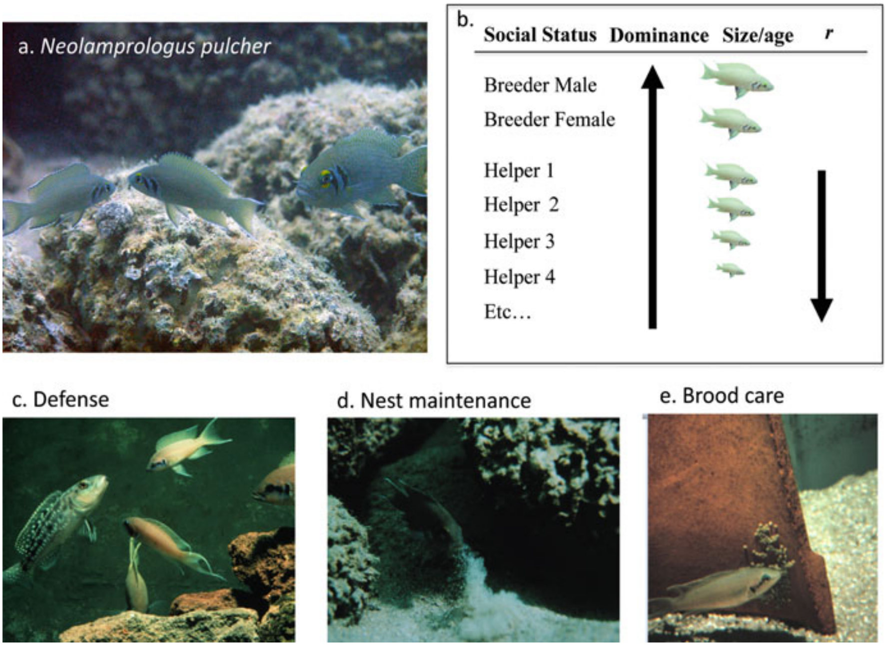

Fig. 5 (**a**) The group living, cooperative breeding *Neolamprologus pulcher*; two helpers and a breeder from Lake Tanganyika. Photo credit: Julie Desjardins. (**b**) The social structure of *N. pulcher* groups is organized into a size/age-based dominance hierarchy where the largest individual in each social group is the breeding male, then the breeding female and the subordinate helpers too also exist along a size-based dominance hierarchy. Smaller helpers are more closely related to the breeding pair. *r* = relatedness to dominants. Taken from Wong & Balshine 2011a. Each member of an *N. pulcher* social group shares workload duties including (**c**) defense; (**d**) territory maintenance; and (**e**) brood care. Photo credits: Michael Taborsky

belonging to the same tribe, the Lamprologini of Lake Tanganyika. Interestingly, cooperative care appears to have evolved 5 times independently in this clade with some degree of radiation following the transition (Dey et al. 2017). About 25% of all Lamprologines (approximately 20 of 82 species) are cooperative caregivers. Why has cooperation evolved in these species and in this clade but not in any other cichlids, remains an open question.

Most of these 20 cooperative breeding species are socially monogamous, biparental, and have a non-piscivorous diet and these factors may have contributed to the evolution of sociality (Dey et al. 2017). For the sake of brevity and because it is by far the best known and best studied cooperatively breeding cichlid, here we provide a detailed description of how and why *N. pulcher* cooperates in raising young.

N. pulcher is found in social groups of 3–20 individuals living together on Lake Tanganyika's rocky substrates at depths of 3–45 m (Taborsky and Limberger 1981; Balshine-Earn et al. 1998; Wong and Balshine 2011a). Social groups co-defend a small and shared territory (mean area = 3150 cm^2) made up of rocks over sand or in the crevices of larger boulders, these rocks and crevices are used as both breeding substrate and shelter (Balshine et al. 2001). Many social groups, each one defending a single shared territory, are found clustered closely together on the lake bottom. These clusters of territories are called colonies or sub-populations and the size of these colonies ranges anywhere from 2 to >100 social groups (Stiver et al. 2004, 2007; Hellman et al. 2016). Although density (group size and territory size) can vary across and within a colony, at one study area, Kasakalawe Point, the mean distance between two territories was on average 1.6 m, and the average distance between colonies was 22.3 m (Stiver et al. 2007).

Each social group is made up of a dominant breeding pair and several smaller individuals called helpers (Taborsky 1984, 1985; Fig. 5b). The breeding male is always the largest individual in a social group, the breeding female is usually the next largest fish while the helpers are always subordinate, and are generally smaller than the breeders. The fish in each social group can recognize each other and are organized into a single size-based dominance hierarchy that is reasonably stable over time (Fig. 5b, Fitzpatrick et al. 2008; Wong and Balshine 2011a, b; Dey et al. 2013, 2015). The hierarchy reflects a queue for breeding status. If a dominant breeder dies or is eaten, both male and female subordinate helpers can ascend through the ranks and inherit a dominant breeding position in the territory (Balshine-Earn et al. 1998; Balshine and Buston 2008). Subordinates can also leave their social group (disperse) either to take over a dominant breeding position in another group or to become a more dominant helper (moving into a higher rank in the queue) in another social group (Stiver et al. 2004, 2006). Females more commonly take the inheritance route to reproduction whereas males more typically disperse to take over new groups (Balshine-Earn et al. 1998; Bergmüller et al. 2005; Balshine and Buston 2008; Stiver et al. 2004, 2006, 2007; Hellmann et al. 2015, 2016).

The entire *N. pulcher* social group will together defend the territory against predators, conspecific neighbors, and heterospecific space competitors (Fig. 5c). The group also collectively maintains the territory and the shelter system, which also acts as the brood chamber. Individuals maintain the territory and the shelters within the territory by digging out the sand underneath the rocks/shelter and removing debris to ensure free access to the underground tunnel system (Fig. 5d). In addition, all group members may participate in brood care by cleaning and fanning eggs, and the young (Fig. 5e, Taborsky and Limberger 1981). Territory defense, territory maintenance, and brood care are commonly combined into a single index that is used to quantify individual variation in what is called effort, helping, allocare or work (Wong and Balshine 2011a). Direct brood care such as fanning and cleaning eggs can only be quantified in the laboratory, but brood chamber visits are often used as a proxy for direct brood care in field studies. In the field, the breeding female will be the most active individual in the social group performing the highest amount of "work," while the breeding male is the least active, with the subordinate helpers showing an intermediate level of work and female helpers are more active than male helpers (Balshine et al. 2001; Stiver et al. 2005; Desjardins et al. 2008).

Do Helpers In Fact Help? Essentially, the assistance that subordinate helpers provide should have a load-lightening effect for dominant breeders (Zöttl et al. 2013a). There is growing correlative as well as experimental evidence from both the laboratory and field showing that the presence of helpers is indeed beneficial to breeders (Balshine et al. 2001; Brouwer et al. 2005). In the field, larger groups have more offspring (Balshine et al. 2001), and in comparison to intact groups, the experimental removal of helpers, dampens offspring survival (Brouwer et al. 2005). However, larger groups of *N. pulcher* inhabit larger, higher quality territories with more shelter (Balshine et al. 2001), so increased offspring production could simply be the result of enhanced territory quality and not helpers number per se. Also, the removal of a helper from a group disrupts the social hierarchy (Wong and Balshine 2011b), and so such helper removal manipulations could influence subsequent group stability and breeder investment in young. What is needed now to firmly answer the question of whether the helpers truly increase the reproductive success of dominant breeders, is to experimentally reduce helping while keeping these non-helping helpers in the group and then track the survival of young. This type of experiment might be possible via hormonal manipulation that knocks back allocare or by placing helpers in a transparent tube, behind a barrier or one way mirror so they cannot help but are still part of the group and can be observed by other group members to not help.

Why Do Helpers Help? A great research effort has been leveled at answering this question, but we still do not fully know why *N. pulcher* helpers of both sexes help and this remains an area of active research. One rather simple explanation is that what we call 'helping' or brood care in *Neolamprologus pulcher* is in fact parental care. We know that both male and female subordinate helpers sometimes breed within their social groups in the field (Hellmann et al. 2015, 2016) and will also do so in the laboratory (Dierkes et al. 1999; Heg et al. 2008b; Zöttl et al. 2013a, b). Subordinate helpers might in fact be directly and immediately enhancing their own selfish interests by caring for their own offspring. So, there may be no conundrum of why helpers help. Help could potentially reflect selfishness if it is directed only towards their own young. However, most *N. pulcher* helpers do not reproduce and most helpers will rear the breeders' offspring (Hellmann et al. 2015, 2016). So, additional explanations must be sought for what appears to be altruistic acts by helpers.

A popular and long-standing explanation for cooperation is Hamilton's concept of inclusive fitness (1963, 1964); this theory posits that individuals can accrue fitness benefits indirectly by helping their kin breed. The relatedness among individuals in a *N. pulcher* social group varies widely among dyads and groups. In general, the average relatedness between helpers and breeders is low and decreases with helper age. Across groups, the average $r = 0.03$ between helpers and the dominant breeding male and is $r = 0.14$ between helpers and the breeding female (Stiver et al. 2005; Dierkes et al. 2005; Hellmann et al. 2015, 2016; Fig. 5b). These low levels of within-group relatedness are probably generated by rapid breeder turnover, especially for breeder males who often do not remain in the breeding position for more than three months (Stiver et al. 2004). Low relatedness levels may arise from helper emigration and immigration (Stiver et al. 2004, 2007; Bergmüller et al. 2005; Heg et al. 2008). It of course remains possible that more closely related helpers within a social group help more, especially given that there is evidence for kin recognition in *N. pulcher*. Le Vin and co-workers (2010) showed that subordinate helpers preferred to associate with related kin over unrelated non-kin, but did not show a preference for associating with familiar kin over unfamiliar kin, suggesting that there was preference for kin and not familiarity when making decisions about who to affiliate with (but see Jordan et al. 2010). Despite *N. pulcher's* clear ability to recognize kin, field studies and experimental manipulations in the laboratory, have shown that more related helpers, in general, do not help more (Stiver et al. 2005; Zöttl et al. 2013a). In an elegant laboratory study, Zöttl et al. 2013b manipulated the kinship of subordinate female helpers and examined the consequences on their helping efforts. These researchers found daughters and sisters were not more likely to be accepted as helpers than non-related female helpers but that non-related helpers helped more following a simulated cannibalism event. These results strongly suggest that kinship has a negligible effect, if any, on helping decisions in *N. pulcher*. However, a critical experiment that still needs to be conducted would be to explore if when given a binary choice subordinate helpers choose to help related over unrelated individuals.

If kin selection is not linked to cooperation, then there is likely to be a direct benefit associated with helping in *N. pulcher*. Some researchers have argued that helping is a form of rent, paid out to dominant breeders in return for being allowed to remain in the group territory and receive protection from the breeding pair (Zöttl et al. 2013b). This *pay-to-stay* hypothesis (Gaston 1978) was tested by three studies, two in the field by Balshine-Earn et al. (1998) and Fischer et al. (2014) and in the laboratory by Bergmüller and Taborsky (2005). In both early experiments the researchers showed that if *N. pulcher* helpers are prevented from helping, they will subsequently increase their helping efforts over and above previous levels. However, the breeders did not punish these absent or lazy helpers on their return—a key prediction of the pay-to-stay hypothesis. However, in the second field study, idle helpers in small groups did receive more aggression from breeders and were more likely to be evicted (Fischer et al. 2014). A very recent paper provides some further evidence that unhelpful *N. pulcher* helpers are punished for not helping (Naef and Taborsky 2020), and so it is likely that helping and cooperation evolved, or is currently maintained, as a means of being allowed to remain in the safety of the social group and enjoy the protection from a dominant breeding pair and its shelter system. Zöttl et al. (2013b) and others have argued that because unrelated female helpers help more, help can be viewed as a commodity which can be traded or exchanged for protection and group acceptance.

Another idea is that helping evolved because it acts as a *signal of prestige or quality* (Zahavi 1995). Individuals of higher quality could signal their higher quality by helping more and by doing so would gain higher social prestige, increased social rank, more resources, better territories, mating opportunities and social allies (Woolfenden and Fitzpatrick 1978; Lotem et al. 2003). Wong and Balshine (2011a) argue that help or allocare is unlikely to have evolved in *N. pulcher* because of its signaling function since in this species, groups are organized into strong size-based dominance hierarchies and body size is a much more obvious and reliable trait on which to assess individual quality. Zahavi (1995), Grafen (1990) and Gintis et al. (2001) who all modeled this idea, uniformly agree that there is no need for help to evolve as a signal if an easier way to observe and track individual quality differences exists. There are two key predictions for this signal of prestige hypothesis. First, helpers should be less helpful without an audience (Wright 1997), a prediction that has yet to be formally tested in *N. pulcher*. Second, more helpful individuals should enjoy higher probabilities of being chosen as a mate, inheritor, or collaborator (Zahavi 1995). Although there is evidence that more helpful female helpers are more likely to inherit top breeding positions (Balshine and Buston 2008; Wong and Balshine 2011a), several confounding variables (e.g., body size and relatedness) remain to be ruled out in these field based experiments before we can firmly conclude that inheriting a breeding position is the benefit to the helper.

A final explanation for why helping might have evolved is called *group augmentation*, which is the idea that helping enhances group size which in turn increases individual survival and future reproduction (Brown 1987). Kokko et al. (2001) showed that group augmentation could operate and select for increased help if: (1) helpers can inherit breeding positions within the group; (2) some offspring reared as a result of help, remain in the group; (3) helping is costly and these costs accelerate as more help is provided; (4) costs of helping are less than the benefits accrued by inheriting a large group; and (5) other group members cannot fully compensate for help not provided (Kokko et al. 2001). Most of these assumptions hold true in *N. pulcher* (although see Zöttl et al. 2013a). Helpers can inherit breeding positions, do sometimes remain in their natal group, helping is costly and helpers appear to not fully compensate for removed helpers (Balshine-Earn et al. 1998; Grantner and Taborsky 1998; Brouwer et al. 2005; Stiver et al. 2005, 2006; Zöttl et al. 2013a). However, we do not know if there are survival costs associated with helping, nor do we know the lifetime reproductive success associated with inheriting a large versus a small group. The key predictions of the group augmentation hypothesis are that: (1) helping increases breeder productivity; (2) increased breeder productivity translates into more young being recruited into the group and

(3) there are benefits of living in larger groups. There is evidence supporting all three of these predictions in *N. pulcher* (Taborsky 1984; Balshine et al. 2001; Heg et al. 2004, 2005; Brouwer et al. 2005), but again, several confounding variables still need to be ruled out before we can conclude firmly that helping works this way (Wong and Balshine 2011a). Predation pressure and threats from other social groups can select for group living and set the stage for the evolution of cooperation (Bruintjes et al. 2016). Groenewoud et al. (2016) used a cross population study of *N. pulcher* to show that cooperative defense and communal construction of a shelter system provides considerable protection from predators. Similarly, Tanaka et al. (2016) showed that predation pressure delays and dampens dispersal behavior. In summary, although a great deal of research has focused on *Neolamprologus pulcher*, to ascertain which of the adaptive explanations is responsible for helping, many of the critical tests supporting each proposed mechanism, still need to be conducted or further flushed out. Most evidence to date suggests that cooperation in *Neolamprologus pulcher* evolved as a result of the mutually beneficial trading of help by subordinates in exchange for access to the protection of a social group. However, future manipulative experiments that increase or decrease the level of care will need to be combined with long-term field studies aimed at measuring the inclusive fitness of helping for helpers and breeders.

7 Future Directions

Four scientific advances will invigorate future cichlid parental care research. First, is the massive recent advances in computational and statistical phylogenetics which have made more cichlid phylogenies available, which in turn have enable more phylogenetically based comparative studies of the evolution of parental care (e.g., Sturmbauer et al. 1994; Goodwin et al. 1998; Klett and Meyer 2002; Kolm et al. 2006a, b; Gonzalez-Voyer et al. 2008; Fitzpatrick et al. 2009; Kidd et al. 2012). Some of these new studies are revealing surprising findings. For example, Gonzalez-Voyer et al. 2008 used a comparative study on Tanganyikan cichlids to test whether parental care was a cause (the traditional view posited by Trivers 1972) or consequence of sexual selection (an alternative proposed by Kokko and Jennions 2003, 2008). While confirming the link between sexual selection and parental care, surprisingly Gonzalez-Voyer et al. (2008) phylogenetically based results suggest that sexual selection determines parental care patterns and not the reverse. New cichlid phylogenies with better species coverage and more resolution, based on more molecular markers, continue to be generated; and these will refine our ability to conduct even better and broader comparative analyses, and will continue to provide us with new directions for our critical tests of correlative trait evolution while offering better estimates of how often various care strategies arose.

Second, is the recent bioinformatics and genomics revolution led by high-throughput technological advances. These technologies have rapidly expanded the available molecular data and led the prompt acquisition of whole genome sequences across a range of organisms. Entire genomes for a handful of cichlids have already have been sequenced (Brawand et al. 2014; Wagner et al. 2013) and many more will be available (W. Saltzberger *personal communication*). This growth of genomic studies facilitates a brave new world for scientists interested in how different species or genera with similar parental care behavior have either conserved or divergent genes, gene networks and gene regulation associated with care. To date genome-wide studies are showing that the emergences of genetic variation and proliferation of cichlid species in such short time scales relied on both neutral (non-adaptive) and adaptive processes, like selection (for more details, see Wagner 2021). As with the evolution of species themselves, the evolution of care among cichlids, will probably depend on multiple evolutionary mechanisms. Future research will hopefully be able to shine a light on which regions of the genome (coding or regulatory regions) or which gene duplication events were necessary drivers in the evolution of care. Large-scale genomic databases are certainly exciting new tools and the analysis of this molecular data (see Parsons et al. 2021) should lead to deeper insights in our understanding of parental care evolution in cichlids as well as link the underlying physiological mechanisms and genetic architecture to parental care behavior.

Third, is the growing interest in exploring the parental behavior using neurophysiological and neuroanatomical techniques. Neuroscientists are increasingly applying modern neurobiological tools to test how cognitive development is affected by parental care (Liu et al. 2000; Keebaugh et al. 2015) and to uncover the neural mechanisms and epigenetics underlying behavior. To explore the brain in relation to social behavior, scientists are increasing turning to many new non-model study organisms, including cichlids (Pollen et al. 2007; Gonzalez-Voyer et al. 2009; Tsuboi et al. 2016; O'Connor et al. 2016); and this approach is bound to help shed light on the evolution of parental care.

Fourth, because care strategies like brood mixing involve cooperation and conflicts between different players (e.g., in the case of brood mixing, genetic parents, foster parents and their respective young), the use of dynamical game theory may be extremely valuable in elucidating which care strategies are most likely to emerge under different environmental conditions (e.g., Quiñones et al. 2016). Furthermore, to test the theoretical models and our general understanding of parental care, we need even more rigorous empirical experiments that manipulate different ecological factors such as density, predation, and relatedness.

Niko Tinbergen (1963) argued that to truly understand a behavior, we need to study its ontogeny, underlying causation, fitness function and evolutionary history. To date, cichlid behavioral scientists have concentrated their efforts mainly on understanding the function and evolutionary history of parental care. A great deal of work is still needed before we recognize the molecular or genetic signature underlying care behavior or how epigenetic factors, the social environment, learning or transgenerational effects impact parental care behavior in cichlids (Kasper et al. 2018). Our understanding of the proximate mechanisms (genetic and neurobiological) that control parental behavior in cichlids is still very much at its infancy. For example, new brain imaging techniques (fMRI and CT) should be able help us identify which brain areas or centers are involved in parenting behavior (see Pollen et al. 2007, for a similar study with mating systems). In addition, a variety of nanopeptides, hormones and blockers are now readily available for fishes and these should provide the means of manipulating parental care levels in experiments (e.g., Dey et al. 2010; O'Connell et al. 2012; Oliveira et al. 2002; see Félix and Oliveira 2021). Such neuro-endocrinological manipulations should go a long way in helping us achieve a more comprehensive understanding of the evolution of parental care. In combination, these techniques associated with ever changing theory will constitute the new frontiers for the research of cichlid parental care.

Finally, while many of the above suggestions for future work rely on sophisticated and technologically advanced methodologies, it is important to remember that descriptive studies on parental care habits along with parentage data (based on genetic markers, e.g., Lee et al. 2016) on more model species are urgently needed. We are still missing basic information on many cichlid species especially those from less studied regions and from smaller lakes and rivers. Some areas such as the neotropics and African crater lakes are evolutionary hotbeds and hold many scientific insights about behavior (Schliewen et al. 1994; Barluenga et al. 2006). The lack of basic data about cichlid parental care behavior, its function, evolution, ontogeny and underlying physiology, under conditions of global change (Bose et al. 2019a, b) is not only a barrier for comparative studies, but such data is absolutely necessary to guide good management practices for cichlid conservation and will help direct sustainable fishing or aquaculture practices into the future.

8 Summary and Conclusions

In cichlids, care is provided by either one parent alone (uniparental care) or by both the male and female together (biparental care). Cichlids care for their young by egg provisioning, nest building, defending, fanning and cleaning embryos as well as feeding the hatched young. Buccal guarding (or mouthbrooding) is the most common form of care among cichlids and evolved from guarding on the ground (substrate guarding), the ancestral form of parental care. Many morphological and physiological changes would have had to occur to support the shift from guarding young on the ground to guarding them in the mouth. In contrast, many fewer evolutionary innovations would have been needed for the shift to female-only or male-only care from biparental care. Accordingly, evolutionary shifts in which sex provides care appears to have been far more labile across cichlids, with 21–30 transitions to uniparental care from biparental care.

Cichlids exhibit alloparental care in two ways, either via brood mixing or cooperative care. Brood mixing can come about via three routes that range in the willingness of the foster parents to adopt. Predation risk appears to be a major driving force of brood mixing, an idea that should be tested in more species to establish its broad significance. Approximately 20 cichlid species, all from one Tanganyikan clade, have evolved group parental care, known as cooperative breeding and the comparative evidence suggests there have been 5 separate transitions towards cooperative breeding (Dey et al. 2017). To better understand care evolution and the mechanisms responsible for care, we must not only evaluate parental effort following experimental manipulation of factors that influence the costs and benefits of care like paternity assurance, trade-offs between current versus future reproduction, brood size and age, parent age and condition, but we must also find ways to experimentally alter the amount of care provided and explore the fitness consequences of such manipulations. The variation observed in cichlid care habits, combined with the sheer number of species, the robust phylogenetic information available for this group and the relative ease with which these fishes can be studied and experimentally manipulated under both controlled laboratory and ecologically valid field conditions, all render this family of fishes an experimental and comparative study goldmine. Finally, the plethora of new molecular and physiological tools now available, means we can begin to uncover the neurobiological, genetic and molecular signatures associated with parental care evolution. These approaches will ensure that these amazingly diverse tropical fishes remain a major evolutionary test bed and will continue to be used to further our knowledge about the evolution of care long into the future.

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Cichlids as a Model System for Studying Social Behaviour and Evolution

Alex Jordan, Barbara Taborsky, and Michael Taborsky

Abstract The complex social behaviour of cichlids has fascinated scientists and hobbyists alike for almost 100 years. In this chapter, we review the breadth and complexity of cichlid behaviour, particularly with respect to social interactions. We present the case that cichlids are one of the best model systems for understanding both the mechanisms and evolution of behaviour. This is due to the fact that cichlids can be observed without being greatly disturbed, both in the aquarium and field and because of the unique opportunity to experimentally manipulate their environment and behaviour. We first give a brief account of the diversity of social systems in the cichlids and the diverse research in this area, from the very early work of authors like Curtis, Noble, and Baerends, to modern studies into the dynamics and structure of social behaviour in these fish. In Sect. 2, we explore the causal factors leading to the evolution of social complexity, discussing the occurrence and evolution of different social systems across ecological and life-history contexts. We investigate the behavioural complexity displayed by cichlids in Sect. 3, including a brief treatment of the different modalities of behavioural interactions. In Sect. 4, we discuss the immense potential for using cichlids as model species in studying social and behavioural evolution, before ending in Sect. 5 with exciting future directions for research employing the latest technical advances in both the laboratory and field.

Keywords Social organisation · Behavioural diversity · Mating · Communication · Plasticity

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A. Jordan (✉)
Max Planck Institute of Animal Behavior, Konstanz, Germany
e-mail: ajordan@ab.mpg.de

B. Taborsky · M. Taborsky
Division of Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland
e-mail: barbara.taborsky@iee.unibe.ch; michael.taborsky@iee.unibe.ch

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1 The Beautiful Complexity of Cichlids

For the unacquainted, fish may be considered to be simple, anonymous, vacant, or unthinking entities; the apocryphal tale of the goldfish and its three-second memory is testament to this common perception. When we consider vast schools of sardines moving through the water, following relatively simple interaction rules, and moving as a cohesive unit, it is not hard to see how the idea of simplistic fish behaviour has emerged, especially when compared to the subtle and varied behaviour of primates and other mammals. In fact, pelagic species that live in open water may often have low-complexity behavioural repertoires, as they exist in fission-fusion groups in which the primary ecological pressures—feeding and avoiding predation—require highly conserved and stereotypical behavioural patterns that promote aggregation. These pressures may lead to a specialised form of social interaction, that of collective behaviour, in which synchrony and conformity are prioritised as strategies to avoid predation, hunt, or share information (Gordon 2014). In many of these species, even mating is typified by relatively anonymous synchronised release of gametes into the water column (Takemura et al. 2010). While large groups of almost identical animals moving and behaving in synchronisation are certainly capable of producing complex emergent behavioural patterns, at the level of the individual agents—be they mammals, birds, or in our case fish—there is a relatively small behavioural rule set by which they act (King et al. 2018).

But then consider the cichlids. These fish commonly live in stable social groups with repeated interactions and show highly developed behavioural responses to encounters with mates, social partners, rivals, and competitors, including heterospecifics (Taborsky 1984; Martin and Taborsky 1997; Balshine-Earn et al. 1998). In addition, the cichlids also have highly developed socio-cognitive abilities, including memory of past social interactions, facial and kin recognition, and commodity trading (see Félix and Oliveira 2021). Almost every aspect of the interaction between cichlid fishes consists of a wonderful array of postures, colour changes, fin movements, and reciprocal behaviours. Ethograms for cichlids range from 20 to 50 discrete behaviours, spanning aggression, courtship, social affiliation, and punishment. The ‘language’ of cichlid behaviour has fascinated both naturalists and ethologists for almost 100 years, with early researchers like Breder (1934), Noble and Curtis (1939), Baerends and Baerends-van Roon (1950), and El-Zarka (1956) publishing some of the first studies on the amazing diversity and complexity of cichlid behaviour. More recent syntheses have further cemented the evidence for cichlids as some of the most fascinating and complex animals on the planet (Keenleyside 1991; Barlow 2000).

The social systems of cichlids also include a vast range of levels of social organisation. The so-called ‘sardine cichlids’ of the genus *Cyprichromis*, for instance, live in vast pelagic fission-fusion shoals and resemble the ecology, behaviour, and social systems of pelagic marine species (Ochi 1996). Nevertheless, even these Cyprichromine species show more social structure than basic fission-fusion, at least during mating and lekking, during which males may defend open-water

3-dimensional ‘territories’ and be spatially isolated from shoaling females and non-breeding males (Konings 2015). The ‘mbuna’ (algae scrapers) of Lake Malawi, as well as some Lake Victorian haplochromines, Lake Tanganyikan *Tropheini*, and the *Geophaginae* in the Americas have itinerant feeding behaviour and often forage in large groups, but may also have temporary territories during breeding periods or defend semi-permanent feeding territories (Kohda 1991; Yanagisawa and Nishida 1991; Genner and Turner 2005). These territories are commonly held by males, who may court passing females from a flat rock or an area cleared of debris. Males are highly territorial during these periods and may form dear-enemy relationships with neighbouring males. After breeding, the mouthbrooding females re-join itinerant fission-fusion shoals. Finally, there are a great many substrate spawning cichlids, best represented in the tribe Tanganyikan Lamprologines and West African and South American riverine species that live in long-term social units. The Lamprologines, in particular, show the greatest variety of social systems known in any group of fish (Kuwamura 1986). These cichlids may live in pairs, harems, or even social groups numbering up to 50 individuals, and they display many of the social attributes once held to be the realm of mammalian societies, especially primates (Heg and Bachar 2006). This includes, for instance, reciprocal trading of different commodities among group members, such as access to defended resources against help in brood care and territory maintenance (Taborsky 1985; Heg and Taborsky 2010; Zoettl et al. 2013b; Naef and Taborsky 2020).

The value of studying cichlids in the context of evolutionary biology has long been recognised (Kornfield and Smith 2000) and progress in understanding the morphological, genomic, and ecological processes involved in speciation continues apace (e.g. see Wagner 2021 and other chapters in this volume). Yet our understanding of how behaviour evolves is still relatively poor, not only in cichlids, but across taxa and disciplines. Cichlids represent an incredibly powerful system in which to interrogate and explore behavioural evolution (Rossiter 1995). In this chapter we will demonstrate the value of cichlids as models for understanding the evolution of social behaviour, highlighting the progress in this area and outlining future avenues for further work.

2 Cichlid Social Groups

In this section we summarise the major forms of social organisation in cichlids, presenting evidence for the potential causative factors leading to different social structures. We go on to explain in detail the life-history consequences of different social arrangements across cichlids, with a particular focus on the Lamprologine cichlids of Lake Tanganyika.

2.1 Ecology: Defendable, Stable Resources

When considering the evolution of social behaviour, it is helpful to consider how the physical structures that individuals live in and around, and the resources they use, can affect the frequency and nature of interactions among group members. The link between the behaviour—especially social behaviour—and physical structures is perhaps best exemplified by the nests of social insects, where the structure is both a cause and consequence of social behaviour. Yet this link is true for many other relationships between space, structure, and behaviour. In cichlid species that utilise ephemeral and mobile food resources, such as plankton blooms, or those that live in streams or rivers where food is brought in by currents, there is no single area in which individuals will permanently gather to access food. As such, fish species that utilise transient, ubiquitous, or unpredictable food resources may be less likely to develop complex social behaviours, as scramble competition may be the best response to such environments. There is also little benefit in the defence of ephemeral food patches. The primary benefit of living in groups when food is transient more likely comes through processes such as predation dilution and increased vigilance. In such cases, groups, when they do form, are more likely to exist as fission-fusion shoals without stable membership or group sizes, and are likely to be itinerant in their search for food resources. In cichlids, the vast majority of Haplochromines do not have stable feeding territories and these and many other cichlids instead form large shoals of females and non-breeding males that continually move within a larger general feeding area. An exception to this itinerant lifestyle is resident groups of juveniles, young-of-year, or conglomerates of similar size heterospecifics, typically numbering between about 50 and a few hundred individuals (*Perissodus microlepis, Neolamprologus caudopunctatus, Lepidilolamprologus attenuatus*), which form apparently locally stable groups for unknown lengths of time (Jordan and M. Taborsky pers. obs.). These groups may arise from a single brood that has moved from the parental breeding territory (or may stay within or above it), but can also form as apparently ad-hoc groups of different species brought together through a common resource (e.g. a semi-stable current-carrying plankton plumes). Similarly, the Lake Tanganyikan genus *Cyprichromis* forms massive pelagic groups numbering in the thousands, which aggregate around structures such as vertical rock walls. Similarly, large heterospecific groups of *Simochoromis* and *Tropheus* aggregate on algae-covered stone outcrops in shallow water, although the degree of site attachment in these and other fission-fusion shoaling species is difficult to judge.

In contrast, when resources are static and defendable, permanent, stable home ranges occupied by small groups, pairs, or single individuals are more common. One form of site attachment comes in the form of defended feeding territories. For example, some species that feed on Aufwuchs (‘turf’ or algae-covered stones), which they defend as feeding territories either permanently or during mating and breeding. In Lake Malawi, *Pseudotropheus elongatus* adult males, females, and large juveniles defend a feeding territory (Ribbink et al. 1983), while in the

Tanganyikan *Tropheini*, single individuals defend ‘algae gardens’ either for feeding themselves or additionally to attract mating partners (Kotrschal and Taborsky 2010). Some *Eretmodini* form lifelong, stable pairs that jointly defend an algae patch as an all-purpose territory (Taborsky et al. 2014) while in *Neolamprologus obscurus*, the territory serves as both a breeding resource and a food catchment area (Tanaka et al. 2016). These territories may be permanently defended, or defence may be temporary, as in the case of *Gnathochromis pfefferi*, which defends a breeding territory during the morning and a separate feeding territory during the afternoon (Barlow 2000). Despite these examples, defence of a permanent feeding territory is relatively rare, perhaps due in part to the intractability of defending the ephemeral food resources used by many cichlids.

More common are territories based around shelters and breeding sites, which are more temporally and structurally stable resources (e.g. Brown 1964), especially in substrate brooding cichlids. In New World and riverine cichlids this may take the form of a submerged log or rock, while in Old World and lake cichlids it may be a crevice among the rocky shore, empty snail shells, or a chamber dug out from under stones and boulders. Among social groups, competition for these shelter sites can be intense, and inter-group rivalry can create physical borders between group territories. For example in the shell-dwelling *N. multifasciatus*, neighbouring groups continually dig out sand from within their own territories and deposit it on or over the edge of their borders (Sato and Gashagaza 1997; Jordan et al. 2016). This is often directly deposited into the territory of another group, in which the behaviour is perpetuated, leading to the development of sand drifts along the territory boundaries. These boundaries create clear physical partitions among social units of this species, which are reflected in the social structure (Fig. 1). A paucity of suitable shelter sites may also lead to increased sociality by delaying dispersal decisions. For example in *N. pulcher*, dispersal of juvenile helpers is limited by predation risk (Taborsky and Limberger 1981; Taborsky 1984; Heg et al. 2004a). Experimental provisioning of potential territories to wild communities does not cause subordinate group members to leave their group and establish their own territories when these territories were placed at the edge of a colony, but territories placed within the colony were readily claimed and inhabited by both *N. pulcher* and the syntopic *N. savoryi* (Heg et al. 2008). Moreover, when attractive positions were experimentally created within neighbouring territories, some individuals chose to switch groups after intensifying exploration of such groups (Jungwirth et al. 2015). Laboratory experiments revealed that dispersal decisions are influenced by both availability of alternative breeding sites and the quality of the home territory (Bergmüller et al. 2005). Nevertheless, habitat saturation is not essential to delay dispersal; when alterative dispersal options are experimentally presented, even unrelated subordinates may prefer to stay with dominants (Taborsky 1985; Heg 2010). This may be related to the tendency for helpers to join large groups and groups containing more dominant individuals, even though joiners incur greater aggression and reduced chances of inheriting the territory in these groups (Jordan et al. 2010a; Reddon et al. 2011a), suggesting a primary function of group membership is protection against predation (Taborsky 1984).

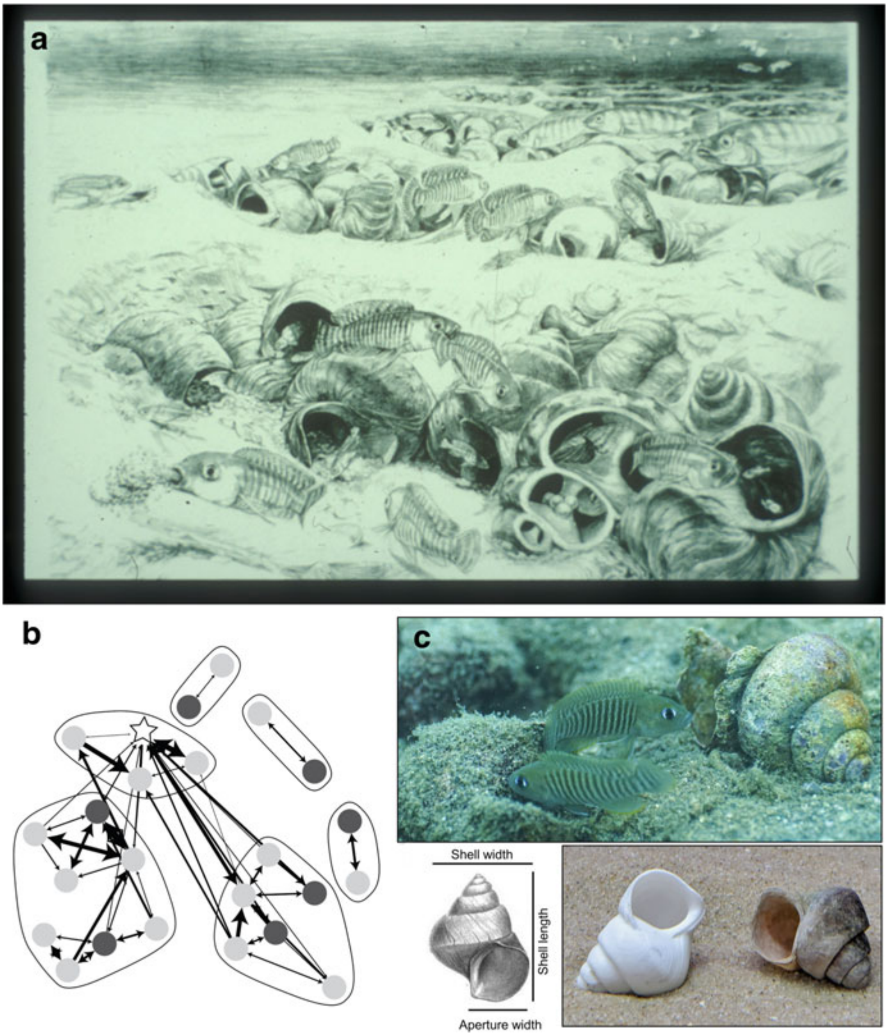

Fig. 1 The shell-dwelling Tanganyikan cichlid *Neolamprologus multifasciatus* lives in large communities composed of hundreds of social groups, typically containing between 2 and 10 members, but in some cases up to fifty individuals. (**a**) in these communities, groups rear young within shells, defend against predators, perform courtship and aggressive displays, and forage for food (illustration by Uwe Kohler), (**b**) these groups are composed of individuals that perform repeated social interactions, and are highly amenable to social network analyses like those performed in Jordan et al. (2016), (**c**) within these groups, individuals compete over resources, including empty *Neothauma* snail shells, the structure of which mediates preferences, as revealed using scanning and 3D printing of shells in Bose et al. (2020)

2.2 From Fission-Fusion to Long-Term ‘Closed’ Groups

The temporal social dynamics of animal groups can have far-reaching consequences for the behaviour of individuals within them. One of the major differences among animal groups is the degree to which individuals can move among groups and the residence times within each group (Jordan et al. 2010a). On the one extreme are fission-fusion systems, in which groups may form and dissolve in a matter of seconds. A classic example is that of guppy shoals in Trinidad, which may be composed of a hundred or so individuals, but in which each individual may only remain for a brief time before joining another shoal (Croft et al. 2006). The social environment in which an individual exists is therefore highly transient, and the likelihood that two individuals will have repeated interactions is reduced. This can also be true for very large schools; marine species such as sardines can number in the thousands, effectively eliminating the possibility for repeated social interactions among the same social partners. In these large schools, the role of the individual is relatively diminished, and all individuals are likely to react and behave in a collective manner (Parr 1927).

In cichlids, this type of fission-fusion social system is found among many pelagic species that have itinerant feeding territories based on local plankton (e.g. *Cyprichromis*), or which travel over rocky substrates grazing on algae (Malawian mbuna, *Petrochromis spp., Geophagus spp.*). Moreover, many species transition between group states, forming fission-fusion shoals either at specific life stages (e.g. non-reproductive *Lamprologus callipterus* and *Boulengerochromis microlepis*), or depending on their reproductive state (e.g. non-reproductive ‘subordinate’ males joining shoals of females in *Astatotilapia*). This form of social arrangement is best represented in the pelagic and above-littoral zones, where no natural cover exists and shoaling is an effective behavioural strategy to reduce predation risk. In Lake Tanganyika there are relatively few cichlids in the pelagic zone (e.g. the largest of all cichlids, *B. microlepis*, and members of the genera *Hemibates* and *Bathybates*), but this niche is mostly populated by two non-cichlid species, the endemic clupeids, *Limnothrissa miodon* and *Stolothrissa tanganicae*, known locally as ‘kapenta’, as well as their primary predators, the Nile perch species *Lates angustifrons*, *L. mariae, L. microlepis and L. stappersi*. In the open-water areas above rock and sand in Lake Tanganyika, shoaling and schooling cichlids in fission-fusion schools are common, and best represented by solitary or small groups of *Cunningtonia, Opthalmotilapia, Cyathopharynx, Cyphotilapia*, or very large schools of *Cyprichrominii* (Rossiter 1995).

At the other end of the social spectrum are groups in which membership is stable over long periods, where individuals form pairs, harems, or larger social groups (Fig. 2). These social structures are most commonly associated with rocky and intermediate rock/sand habitats including crevices, exposed rocky surfaces, sand patches interspersed with rock, as well as vast beds of fossilised *Neothauma, Paramelania,* and *Lavigeria* snail shells. The physical structures in these habitats are used as spawning and shelter sites by many Lamprologine species (Gashagaza

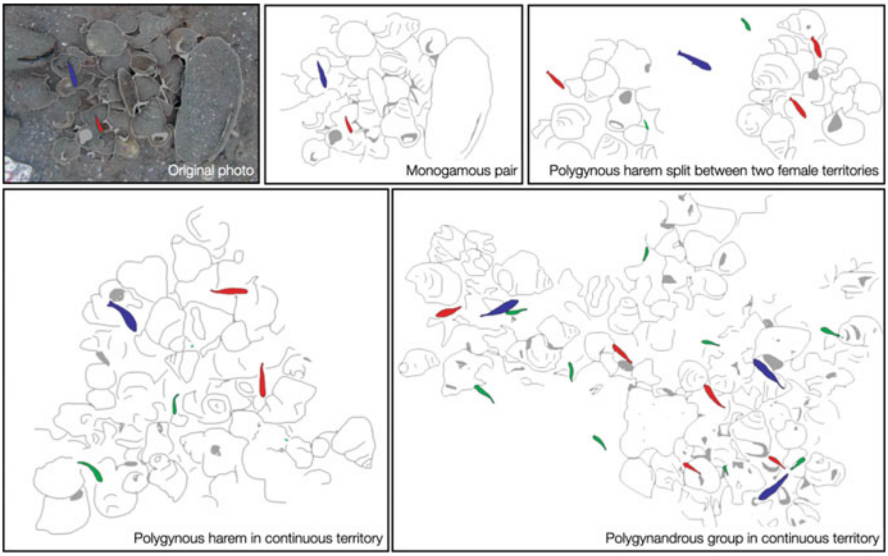

Fig. 2 Social organisation can vary greatly within and among species depending on factors like resource availability and predation risk. At Chikonde Bay, Zambia, *N. multifasciatus* lives in social groups ranging from pairs up to polygyndrous groups. Outlines of shell territories in grey, males in blue, females in red, and juveniles in green (Figure by Alex Jordan)

et al. 1995), and also serve as feeding sites (Hori 1983; Kuwamura 1992; Kohda and Yanagisawa 1992; Tanaka et al. 2018b). In Lake Tanganyika, almost 65% of cichlid species are associated with these rocky habitats (Rossiter 1995), and it is the species in these regions that have received the most attention by behavioural researchers. Work on the species *Neolamprologus pulcher* has shown that aggression prevents free movement of individuals among groups, as individuals attempting to join groups may be repelled by resident members if their help is not needed (Zoettl et al. 2013b). When movement among groups does occur, it is preceded by an extended period of prospecting behaviour, in which an individual will frequently visit a group over a period of weeks or months before finally being accepted (Bergmüller et al. 2005; Zoettl et al. 2013a; Jungwirth et al. 2015). Much like many mammalian social systems, these ‘closed’ groups are characterised by iterated social interactions, well-established social dominance hierarchies, and varying degrees of intra-group relatedness (Taborsky 2016b).

The distinction within cichlids of these two generalised life-history strategies was long ago described as the ‘school’ and the ‘territorial society’ social states and were considered to be labile as a function of development or breeding status (Baerends and Baerends-van Roon 1950). *Lamprologus callipterus* represents a particularly striking example of this lability, with packs of non-breeding individuals forming large schools of itinerant collective hunters, some of which then ontogenetically shift to become territorial as breeders occupying shell beds (Sato 1994; Schuetz et al. 2010). Within the Great Rift Lakes, predation risk can be a major determinant of social structure in both fission-fusion and more stable groups. In Lake Tanganyika, the historical presence of large piscivorous species has promoted collective anti-predator behaviour in many pelagic species. However, fission-fusion groups are less well-represented in Malawi and Victoria, which have until recently lacked such large predators (Coulter et al. 1991; Rossiter 1995). In stable group-forming species, predation pressure can also lead to changes in group structure (Groenewoud et al. 2016). At a more general level, the debate about the role of predators inhibiting or promoting speciation is long-standing (Worthington 1937, 1940; Fryer 1959, 1965; Jackson 1961).

While many social groups form to decrease the risk of predation or increase the likelihood of successful resource defence, groups may also form to overwhelm the defence of territory holders. In species such as *Petrochromis spp., Simochromis spp.*, and *L. callipterus*, foraging groups may be able to overwhelm the territorial defence of other species (Kohda and Takemon 1996). In these species, groups move into a territory to feed on algae cover or benthic invertebrates, and while they are attacked by residents, their numbers are too great for the group to be repelled and the per capita risk of attack is greatly reduced, so that individuals within these groups can successfully exploit the feeding territories of other species. This strategy has been called the ‘Saint Ignatius strategy’ due to the increased likelihood that an aggressive act from a territory owner will befall a social partner or ‘friend’ (Paradis and Williams 2014), constituting a form of risk dilution accrued to individuals in groups or aggregates. As pointed out by Barlow (1974a, b, 2000), these groups are functionally similar to groups of coral reef herbivores, such as the T-shirt surgeon fish (*Acanthurus triostegus*), which move through feeding territories of other fish in large roving bands.

An extended form of sociality occurs when stable arrangements of heterospecifics form around defended resources, as observed for instance in herbivorous (algae-feeding) cichlids in Lake Tanganyika (Kohda 1991). In these cases, it has been argued that hierarchy and social relationships may form between members of different species in much the same way as for conspecifics, i.e. through repeated interactions based on site attachment and resource defence. Indeed, size-dependent heterospecific hierarchies were observed between two *Tropheus* species, as well as up to five species of *Petrochromis*. Alternatively, these heterospecific interactions may take on a different valence and become cooperative, as in algae grazing *Petrochromis polyodon* and *Tropheus moori*. While these species have overlapping territories containing algae mats, they are rarely aggressive towards one another, potentially because *P. polyodon* feeds primarily on unicellular algae while T. moori feeds on filamentous algae, and so competition is reduced. Cooperation occurs as mutual defence of the territory, and benefits may arise to *T. moori* also from feeding being facilitated by the scraping action of *P. polyodon* (Kohda 1995). Although we are not aware of scientific documentation of this phenomenon, a form of cooperative hunting is also observed between *Lepidiolamprologus elongatus* and some species of Mastacembalid eel in Lake Tanganyika, in which heterospecific pairs form and hunt through rocks and shell beds (A Jordan and M Taborsky pers. obs.)

2.3 Reproduction

There are two main modes of reproduction in cichlids that have a great influence on the likelihood of social systems and behaviours developing. Substrate brooding, in which eggs are laid on an external surface and guarded where they are laid in situ, and mouthbrooding, where eggs and fry are taken into the buccal cavity and reared therein for a period up to a few weeks. Tanganyika is unique among the African Great Lakes in possessing indigenous representatives of both groups; the endemic cichlids of Lakes Malawi and Victoria are all maternal mouthbrooders (Fryer and Iles 1972; Greenwood 1974; Ribbink et al. 1983). These two groups show fundamental differences in their breeding mode and ecology. Substrate spawning usually involves strong territoriality, a firm pair-bonding, and guarding of eggs and young (Kuwamura 1986; Nagoshi and Gashagaza 1988). In contrast, mouthbrooding is most commonly performed by only one sex, typically the female, and does not involve strong territoriality (Yanagisawa and Nishida 1991).

Mouthbrooding is common (Fig. 3) and widespread in the Cichlidae in both Old and New World species, and while it is most commonly performed by females, it may be performed by either sex (Kuwamura 1986), or even by both as in *Microdontochromis rotundiventralis* (Yanagisawa et al. 1996) and *Eretmodus cyanostictus* (Grüter and Taborsky 2005; Steinegger and Taborsky 2007; Taborsky et al. 2009). The existence of the pharyngeal jaws has relaxed selection on the mouth as a food processing unit in the cichlids, facilitating the development of a buccal cavity in which fry can be reared. This mode of parental care means that outside the actual event of fertilisation, cichlid parents do not need a substrate in which to defend eggs or need to provide shelter to young. The mouth provides all the protection the young need, even supplying a mobile shelter into which fry can retreat at a moment's notice of danger from the parent. Because of this, once they have mated, individuals that are carrying eggs or fry can immediately re-join fission-fusion shoals and do not need a substrate in which to protect and shelter the brood. The evolution of mouthbrooding can thus be considered a pre-adaptation for lacustrine living because it immediately releases care-giving species from an obligate association with the benthos. Mouthbrooding is considered a causative factor in the success of cichlids in the vast African Rift Lakes, where hundreds of species have radiated from a small number of founding species. Because there is no need for long-term territories in mouthbrooding species, it is frequently only the male that defends a bower or breeding site at which courtship and mating occur. These are transient territories, typically assembled in leks, that last only as long as the male owners are in breeding condition, during which time they may sire broods with numerous females before returning to a transient feeding life stage. This type of breeding system occurs, for example in the Lake Tanganyika cichlids *Cyatopharynx furcifer* (Schaedelin and Taborsky 2006, 2010), *Ophthalmotilapia ventralis* (Immler and Taborsky 2009) and *Simochromis pleurospilus* (Kotrschal and Taborsky 2010).

Not all mouthbrooding species are lek-breeding and promiscuous, however. There are species that form permanent or semi-permanent social bonds

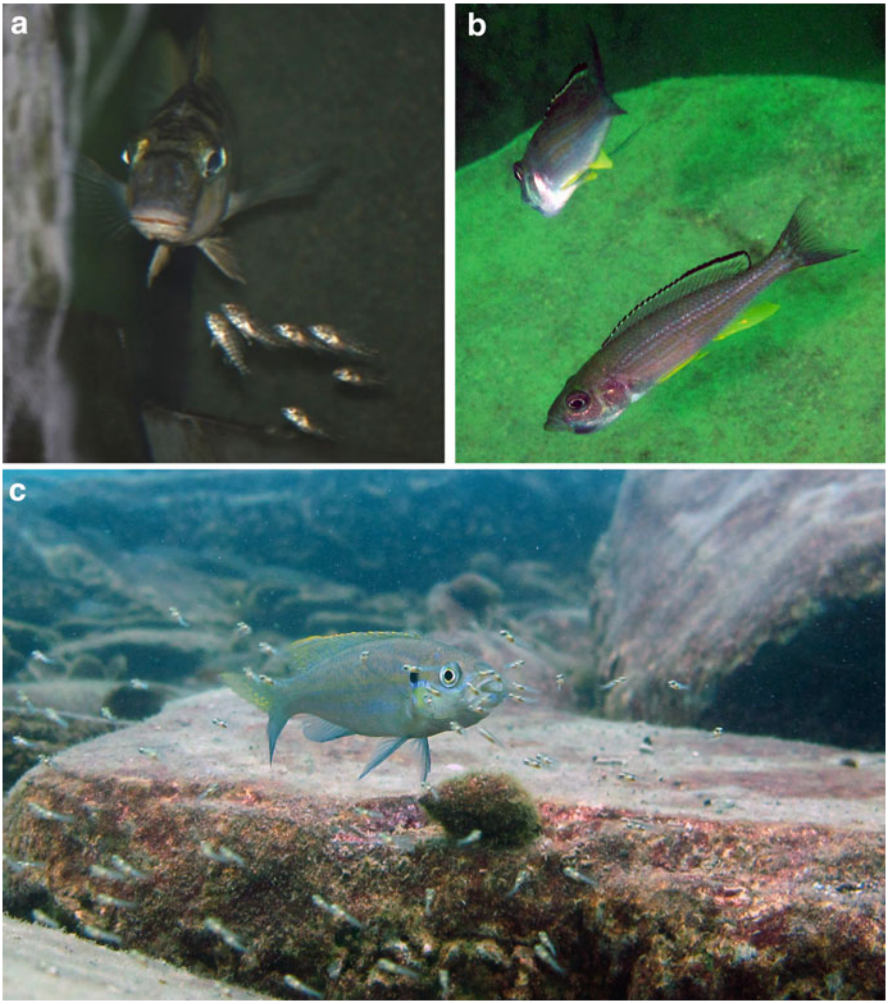

Fig. 3 Mouthbrooding in cichlids. (**a**) a female *C. pleurospilus* recalling her young into the buccal cavity due to perceived threat (photo F.H.I.D. Segers), (**b**) female *Cyprichromis coloratus* form large shoals while mouthbrooding eggs and young (photo Alex Jordan), (**c**) both male and female *Perissodus microlepis* provide care of young, here young retreat from the substrate into the mouth of the guarding parent (photo Alex Jordan)

co-occurring with more complex mouthbrooding behaviour such as biparental mouthbrooding. A female-to-male shift of young is known in several monogamous mouthbrooding cichlids of Lake Tanganyika; e.g. *Eretmodus cyanostictus, Tanganicodus irsacae, Asprotilapia leptura, Xenotilapia flavipinnis, X. boulengeri, X. longispinis, X. spilopterus* (Kuwamura 1986; Yanagisawa 1986; Grüter and Taborsky 2005; Steinegger and Taborsky 2007; Sefc 2011). The transfer of young may be a mechanism to reduce the period of time that females spend without feeding, potentially allowing them to return to breeding condition more quickly. This explanation would only be evolutionarily stable if the pair-bond remained stable over an extended period, during which the male's fitness was defined by his association with the female and he was certain of paternity. A lack of pair fidelity (arguably true for *E. cyanostictus* in which pairs are stable for circa 1.5 breeding cycles; Taborsky et al. 2009) would reduce the male's payoffs from parental investment and leave biparental mouthbrooding at risk of being lost in evolutionary time. Accordingly, in *E. cyanostictus*, there is intensive sexual conflict over the burden of parental care around the time when the females signal the male that she is ready to transfer the young (Steinegger and Taborsky 2007). Another Tanganyikan species, *M. rotundiventralis* also displays biparental mouthbrooding, although parents only swap a portion of the brood, apparently to aid in intrabuccal feeding of the young rather than reduce the care period (Yanagisawa et al. 1996). Maternal mouthbrooders employ either a semalcavous or iterocavous strategy—either releasing fry permanently after a fixed period of mouthbrooding, such as *Stomatepia pindu*, a West African Crater Lake cichlid or allowing fry to re-enter the buccal cavity when danger appears, as in many Rift Lake species including *Haplotaxodon microlepis* and species of the subfamily of *Tropheini* and the genus *Xenotilapia* (Kuwamura 1986).

The alternative parental care system, substrate or crevice brooding (Fig. 4) is the ancestral state and requires a territory in which to spawn and protect eggs and fry (Kuwamura 1986). As outlined earlier, these territories often constitute a stable defendable resource from which repeated social interactions can arise, either with stable neighbours in a permanent breeding territory or shorter-term defence of a shelter during the breeding phase. Mixed strategies also exist, for example in the genus *Geophagus* from Brazil, where both substrate spawning and mouthbrooding are used. In *G. jurupari* pair first spawns on a rock or hard surface, after which the larvae will be taken up into the mouth by one parent for mouthbrooding (Reid and Atz 1958; Lowe-McConnell 1969). The fry will then be transferred to the other parent as in the examples described for other biparental mouthbrooders. In most other species, a pair will guard a flat rock surface, a cleared patch of sand or gravel, a leaf, a crevice, or a burrow, and they will clean and defend the area for a period prior to spawning (Perrone and Zaret 1979; Kuwamura 1986). The female will attach her eggs to the substrate, at which point they will be fertilised by the male (see Balshine and Abate 2021). After spawning, the pair or a single parent will guard the fry while they remain within the territory. Alternatively, as in the case of the world's largest cichlid, *Boulengerochromis microlepis*, parents may defend their mobile offspring for over a year. In the latter species parents have been sighted with juveniles approaching 10 cm in length (Büscher pers. comm.). This relationship has been suggested to reduce the feeding rate of parental *B. microlepis* to such a degree that death of the parents through starvation might sometimes occur (Konings 2015), though no formal evidence has been gathered on this conjecture.

Fig. 4 Substrate spawning in cichlids. (**a**) *Neolamprologus caudopunctatus* defend a large swarm of fry, (**b**) the black adult *Varibilichromis moori* defends its bright yellow offspring, (**c**) a female *N. multifasciatus* cautiously watches as *Lamprologus callipterus* forages near her territory (photo by Jakob Guebel) (**d**) tiny juvenile *Lepidiolamprologus attenuatus* within a shell, (**e**) a pair of *N. caudopunctatus* perform head down threat displays, potentially to signal danger to their fry (hidden in cave) or ward off potential predators (all photos Alex Jordan)

2.4 Social Group Demography and Dominance Hierarchies

For most cichlids, there is a simple division in social states. While not breeding, they exist as solitary, free-ranging individuals, or they form schools or loose shoals. During breeding, pairs, harems, leks, or colonies may form, during which time social interactions (Fig. 5) with neighbours, rivals, mates, and potential mates may be more frequent and for a time, iterated, which creates opportunities for sexual selection, e.g. in *L. callipterus* (Taborsky et al. 2018). However, these groups are not stable and membership changes frequently, preventing the formation of long-term social relationships.

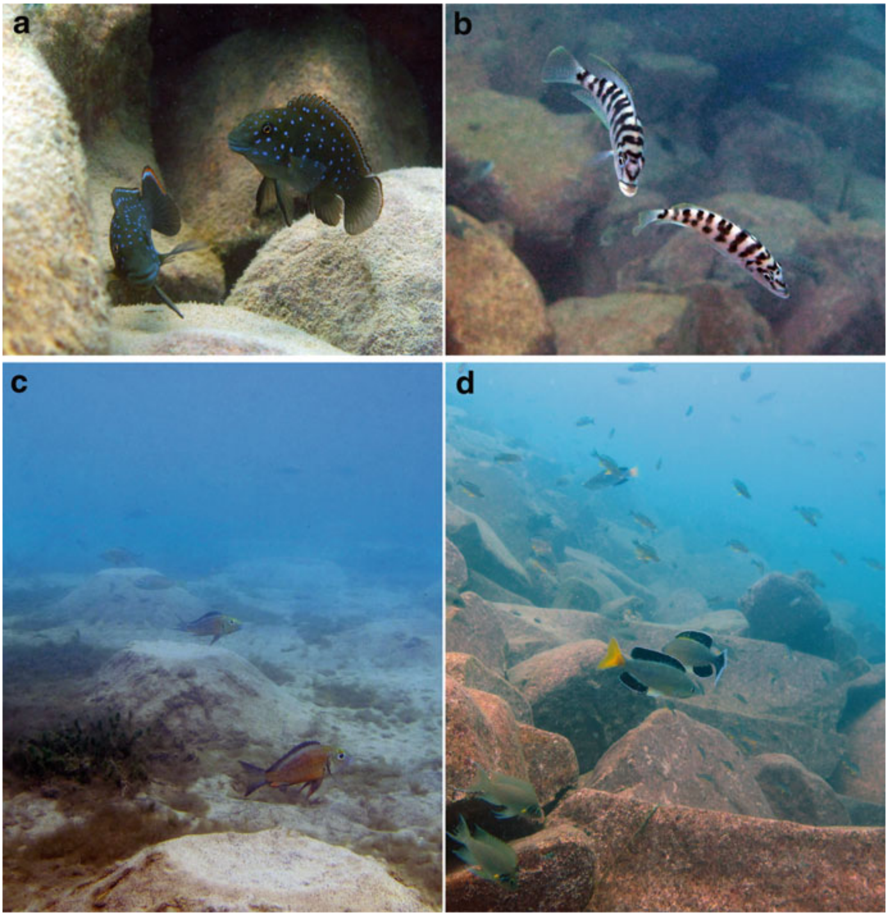

Fig. 5 Social interactions are ubiquitous among cichlids. (**a**) a pair of *Eretmodus cyanosticus* displays in shallow water, (**b**) *Altolamprologus fasciatus* form long-term stable bonds, (**c**) male *Callochromis macrops* display to one another atop their breeding cones, (**d**) male *Cyprichromis coloratus* display to one another by circling with erect fins (all photos by Alex Jordan)

In contrast, some species of cichlids form long-term social groups. When examining group structure, demography, behaviour, and social relationships, one of the best studied species among vertebrates is *N. pulcher* (Taborsky 2016b). The northern phenotype of this species has been originally described as *N. brichardi*, but DNA sequence data suggested merging these populations into one species (Duftner et al. 2007). These fish belong to the Lake Tanganyikan Lamprologines, a tribe containing species with many of the most varied social arrangements of cichlids, or arguably any vertebrate group. In *N. pulcher*, social units typically consist of a dominant pair of breeders and on average between five and six subordinate individuals of various sizes (Taborsky and Limberger 1981; Balshine et al. 2001), known as 'helpers' due to their aid in maintenance, territory defence, and brood care of juveniles to which they may or may not be related (Taborsky 1984; Dierkes et al. 2005). The number of helpers within a group may vary as a function of local ecological conditions; in the north of the lake, there is a small proportion of groups without helpers (~5%), whereas in the south of the lake breeding units lacking helpers are extremely rare (Taborsky and Limberger 1981; Heg et al. 2005b). These differences in demography and social complexity within groups are likely driven by predation risk and the associated benefits of having groups with multiple helpers (Heg et al. 2004a; Groenewoud et al. 2016). In *N. pulcher*, breeder males often move between and defend multiple 'groups' or harems of females and subordinate helpers, in which the males move between groups but females and juveniles do not (Limberger 1983; Desjardins et al. 2008; Wong et al. 2012; Jungwirth et al. 2016). These groups frequently occur in larger colonies consisting of anywhere from a few groups to several hundred (Heg et al. 2008). In other, closely related species such as the rock and shell-dwelling Lamprologines, family structure is similar in that juveniles are frequently found in long-term association with breeding pairs, e.g. in *N. savoryi* (Heg et al. 2005a), *N. obscurus* (Tanaka et al. 2015) and *Julidochromis ornatus* (Heg and Bachar 2006; Awata et al. 2010), but in no other species is the behavioural interaction among individuals as well characterised as in *N. pulcher*.

Within groups of *N. pulcher* there is a strict dominance hierarchy based on body size (Dey et al. 2013). This species has indeterminate growth and is long-lived for its size (up to 8 years in the field, and over 10 years in the aquarium (Jungwirth et al. 2020), but growth rate depends on social rank, group composition, and probably also on cooperative effort, which is energetically costly (Taborsky 1984; Grantner and Taborsky 1998; Taborsky and Grantner 1998; Riebli et al. 2012). Like in most cichlids, size is the primary predictor of contest outcomes, with larger individuals assuming higher positions in the social hierarchies within groups of *N. pulcher* and other species (Hamilton et al. 2005; Jordan et al. 2010a, b; Reddon et al. 2011b; Dey et al. 2013). Similarly, in *Astatotilapia burtoni* the dynamics of social interactions have been well studied, with larger males more likely to win in aggressive contests, and the transition from dominant to subordinate status in this species being characterised thoroughly in both behavioural and physiological studies (Maruska 2015). Differences in size and growth rate may maintain boundaries between social positions in cichlids (Heg 2010), potentially facilitating social niche specialisation (Bergmüller and Taborsky 2007). The presence of multiple age and size classes within groups may also reduce conflict among members, which may lead to the formation of larger groups (Bergmüller and Taborsky 2010). Because cichlids have indeterminate growth, these size differences persist rather than converging on a single maximum adult size, maintaining the capacity for a group to support different social niches. In *N. pulcher*, the differentiation of social roles, for instance, starts in the earliest life stages at an age of only a few weeks (Kasper et al. 2017). The process of behavioural differentiation probably develops from small asymmetries arising among siblings of a brood over time, resulting in individuals taking up different roles within a social group, thereby reducing direct competition between them (Bergmüller and Taborsky 2010).

2.5 Cooperation

Cooperation is one of the most complex forms of social behaviour, encompassing group hunting, cooperative reproduction, and group defence (Dugatkin 2002). During these group behaviours, individuals may appear to forgo their own selfish interests in favour of actions that benefit the group, but on closer inspection group behaviours are typically explicable from the direct fitness benefits accrued to the individual (Clutton-Brock 2009). Cooperative breeding is less straightforward to explain, especially in contexts where relatedness is low. Why would an individual forgo its own reproduction to aid the rearing of juveniles to whom it is barely related?

Cichlids provide a wealth of insight into cooperative breeding. This process is characterised by the joint care of young produced primarily by dominant group members and is widespread in animals, including invertebrates, birds, and mammals (Brown 1983; Stacey and Koenig 1990; Solomon and French 1997). Cooperative breeding is primarily explained by the fact that when groups have high within-group relatedness, aiding the reproduction of others in the group accrues benefits through inclusive fitness (Hamilton 1964; Griffin and West 2003; Bourke 2011). However, in cichlids and other fish, the generally lower relatedness within fish groups precludes inclusive fitness as an explanation for cooperative breeding. Within fish, cooperative breeding has been described in roughly 25 species of cichlids and a few other species (Taborsky 1994; Heg and Bachar 2006). Like many other advanced social behaviours, cooperative breeding occurs primarily among the cichlids from Lake Tanganyika, where about one-third of biparental substrate brooders in this lake breed cooperatively (Taborsky 1994; Heg and Bachar 2006).

The behaviours involved in cooperation are varied and explained in detail in Sect. 3, but centre around the need to both defend the young and defend and maintain the breeding shelter and territory (Taborsky 2016b). The trade-offs for these cooperative behaviours are significant—helpers grow more slowly than individuals living outside of reproductive groups, due both to their subordinate status within the group (Taborsky 1984; Heg et al. 2004b) and the time and energetic costs of helping behaviours such as digging and defence (Grantner and Taborsky 1998; Taborsky and Grantner 1998). By restraining growth, helpers can accrue resources to later boost growth after leaving the territory. Most importantly, helpers benefit through increased survivorship in established groups via access to safe shelter sites and larger groups having higher persistence and offering greater protection from predation (Taborsky 1984; Heg et al. 2004b, 2005a). In fact, the benefits of living in groups are apparently so high in this species that almost no individuals live singly in the south of the lake (Stiver et al. 2004). When given a choice, solitary individuals prefer to join groups composed of larger individuals, which offer the greatest potential protection from predation (e.g. Fig. 6), even though by doing so they accept a lower social rank (Jordan et al. 2010b).

The benefits for subordinates to live in groups do not explain why they engage in costly alloparental care. Why not just reap the benefits of group life without investing in the care of others' offspring? This might be explained by group augmentation benefits, as larger groups provide more safety (Heg et al. 2004b, 2005a) and if helpers protect offspring, irrespective of their origin, they may augment the group size for better protection (Kingma et al. 2014). Nonetheless, in *N. pulcher* the apparently most important cause of the helpers' altruistic brood care behaviour is the reciprocal trading of the subordinates' brood care against the benefits they gain from dominants by protection and resource access (Quinones et al. 2016). In other words, subordinates pay rent to be allowed to stay (Fig. 7) in a dominant's territory (Taborsky 1985; Bergmüller and Taborsky 2005; Bruintjes and Taborsky 2008; Fischer et al. 2014). Interestingly, this can render greater fitness benefits to subordinates than helping kin (Jungwirth and Taborsky 2015). In accordance with this, unrelated helpers show higher helping levels than related ones (Stiver et al. 2005; Zoettl et al. 2013b; Quinones et al. 2016), and within groups, helpers may specialise in performing different duties according to their body size (Bruintjes and Taborsky 2011).

3 Behavioural Complexity

From courtship displays and pair-bond reinforcement, social group dominance, submission, and affiliation displays, to communication of danger from parent to offspring, cichlid social communication encompasses a massive range of contexts, information types, and behavioural mechanisms. It was the wealth of behaviours observed in captive cichlids that captured the attention of the early researchers like Noble and Curtis (1939), Baerends and Barends-van Roon (1950), and El-Zarka (1956), who created ethograms rivalling those of mammals in their complexity and behavioural sophistication. Next, we explore a range of contexts and modalities in which cichlids are known to exchange information through behavioural signals.

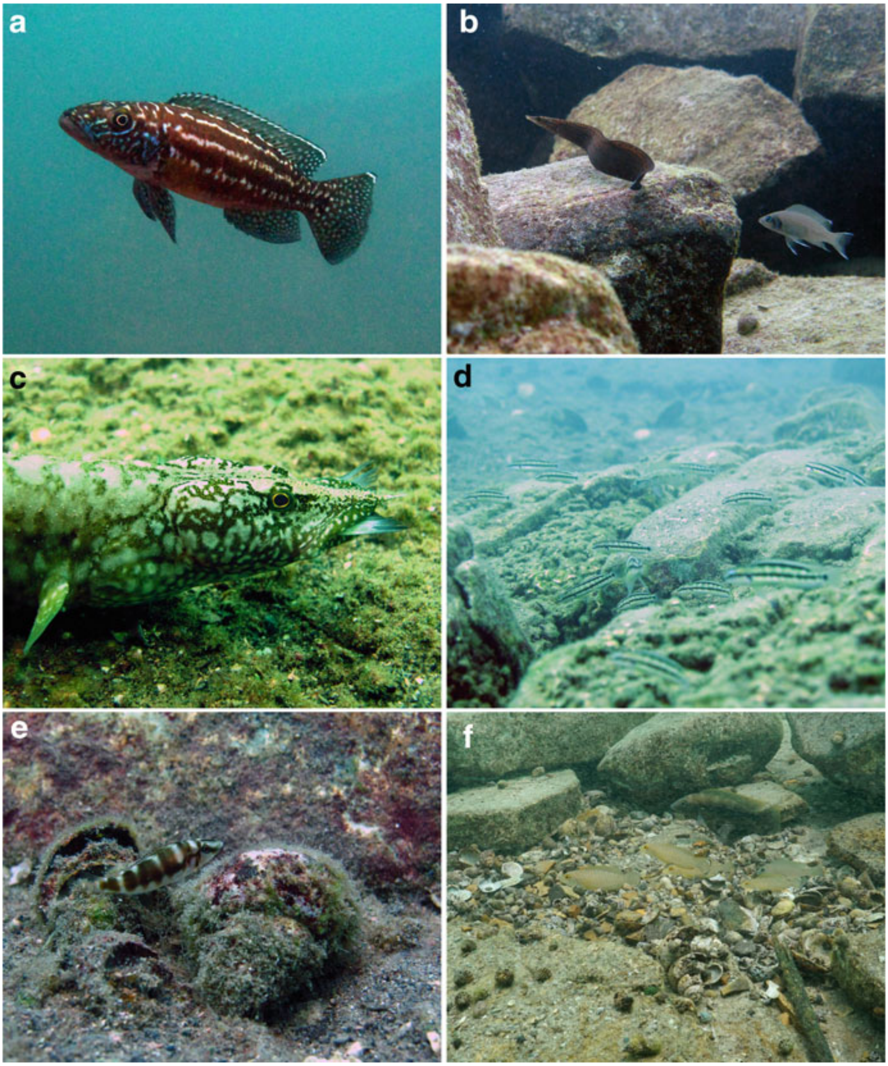

Fig. 6 Cichlids often form social groups to increase protection against predation, which comes in many forms. (**a**) a 20 cm *Lepidiolamprologus kendalli* is fully capable of preying on adults of other species, (**b**) *N. pulcher* chases a *Mastacembalid* eel out of its territory, (**c**) a large *Mastacembalus frenatus* eats a large cichlid prey, (**d**) small *Telmatochromis vittatus* prey on eggs within the nests of social cichlids, (**e**) laterally compressed *Altolamprologus* species are efficient hunters of fry of other species, (**f**) even social groups have trouble defending against marauding bands of *L. callipterus*, which can overwhelm the defence of territory holders, here *L. tetracanthus* (all photos by Alex Jordan)

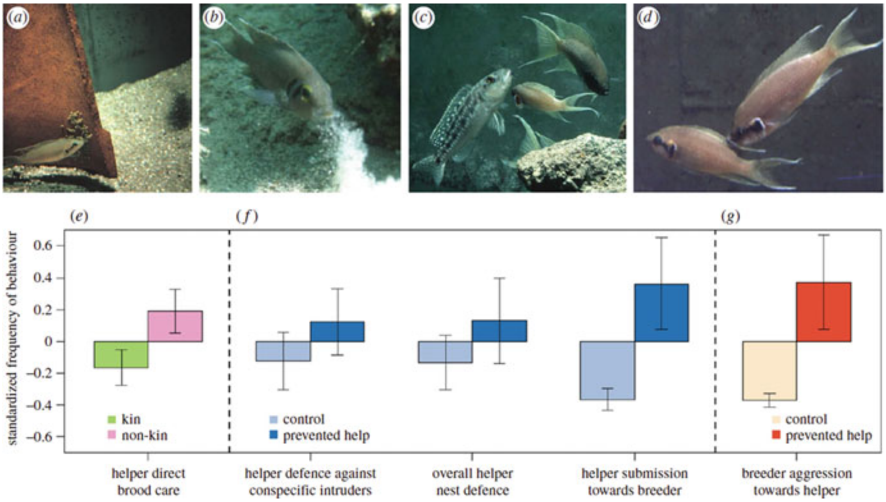

Fig. 7 Cooperative and aggressive behaviours of *N. pulcher* reflect a 'pay-to-stay' mechanism, by which subordinate helpers pay rent for being tolerated in the territory of dominant breeders. Helpers show brood care by cleaning the eggs of breeders (**a**), by performing nest maintenance such as digging out sand from shelters (**b**), and by defending the territory against predators, such as *Lepidiolamprologus elongatus* (**c**). These helping behaviours are prompted by aggression from the breeders. In (**d**), a breeder (right) shows aggression towards a subordinate, and the subordinate responds with submissive behaviour (tail quiver). Panels (**e–g**) summarise the results of experimental manipulations from several studies. Bars show the mean of the standardised frequency of behaviour, with error bars denoting the standard error of the standardised behaviour frequencies. (**e**) Unrelated helpers (purple) provide more help than related ones (green; Zöttl et al. 2013). (**f**) After subordinates have been prevented from giving help (dark blue), they compensate by increasing their previous help and submission level (light blue), presumably in an attempt to appease the breeder (Bergmüller & Taborsky 2005; Fischer et al. 2014). (**g**) Aggression levels in the group are normally very low (cream), but they increase considerably when subordinates are experimentally prevented from helping (red; Fischer et al. 2014; from Quinones et al. 2016)

3.1 Social Interactions Generate Selection for Behavioural Complexity

For a great many group-living animals, social information conveyed among individuals is simple and driven by cues rather than directed signals that have evolved as a mode of communication. An example is the escape response within a group of animals, which can spread among a group by relatively straightforward social contagion of a retreat response in one or a subset of individuals rather than through a complex communication such as vocalisation or other signalling (Krause et al. 2002; Ward and Webster 2016). Importantly in this case, although the cue does communicate information to social partners, the retreat behaviour itself has evolved to avoid predation rather than to communicate to other individuals that danger is nearby. Nevertheless, the escape response may still be used as a source of social information about the presence of predators or the level of risk.

Avoiding predation is the primary functional explanation for group formation in many species (Pitcher 1986) including largely anonymous, collective behavioural processes that do not rely on complex signalling (Treherne and Foster 1981). In the wild, cichlid communities are dense and composed of numerous social groups and different species (Rossiter 1995). A rapid retreat response from one individual of any species in these groups can promptly propagate throughout a community, especially in shell-dwelling communities (A Jordan pers. obs.). Similarly, producer-scrounger feeding aggregations may form through social cues, with some group members waiting for others to find a food item or patch and using that social information to move in and begin feeding themselves (Giraldeau and Caraco 2018). This is the common feeding mode of *L. callipterus*, which use social information to detect and exploit rich food patches in a producer-scrounger situation. Again, the cue leading to information spread within the group, feeding behaviour, has not evolved for the purpose of communication. The key point is that although these mechanisms can provide information to members of a group, they have not evolved as signals and do not require specialised behaviour to communicate information.

It is when more complex types of information must be passed among individuals that the stage is set for selection to produce more advanced communication behaviours. This is especially true when the identity of signaller and receiver interact to modulate the meaning and salience of information, providing further selective pressure on socio-cognitive capacities and increased behavioural sophistication. Hierarchy in particular can be a powerful mediator of social behaviour, affecting the nature and frequency of interactions (Rodriguez-Santiago et al. 2020), as well as social (King et al. 2008) and collective movement decisions (Nagy et al. 2010). Indeed, when studying animals living in groups, it is always necessary to consider the effect of social influence on the behavioural output of any one individual. In groups of the shell-dwelling cichlid *N. multifasciatus,* for example a behavioural change in one individual can rapidly spread through the group, changing the overall social structure of the group as a function of an initial behavioural change in only one member (Jordan et al. 2016). Perhaps because of this interdependence within their groups, communication in social cichlids has developed into some of the richest and most sophisticated in the animal world.

3.2 Communication Modalities

A major question in cichlid research has been the adaptation of sensory and signalling systems to prevailing environmental conditions. In particular, much research effort has concentrated on the evolution of colour diversity in response to the light environment and how this process has affected the African cichlid radiation (Seehausen et al. 1999, 2008). More generally, the communication modality that has received far and away from the greatest research attention in cichlids is the visual system (Korzan and Fernald 2007; Chen and Fernald 2011), a research trend common for most fish species (Rosenthal and Ryan 2000) that we explore in greater depth below. However, just as for other fish, cichlids also incorporate auditory (Amorim et al. 2003, 2008, 2015; Miguel Simões et al. 2008; Maruska and Fernald 2012), chemosensory (Barata et al. 2007; Keller-Costa et al. 2015; Bayani et al. 2017), and mechanosensory communication (Butler and Maruska 2015) in their social interactions.

In cichlids, 29 species have been described as sound producers (Longrie et al. 2013). Auditory communication has been examined primarily in the context of the physiological mechanisms underlying hearing and sound production, a logical trend given the long and successful history of morphological comparative studies in cichlids. Swimbladder and ear morphology have been compared within cichlids and in comparison to non-cichlids (Braun and Grande 2008; Schulz-Mirbach et al. 2012; Ladich 2016) and behavioural studies have demonstrated the role of auditory communication among cichlids, for example during courtship displays (see Lobel et al. 2021). In *Oreochromis mossambicus* both male–male contests and male–female courtship are accompanied by sound production (Amorim et al. 2003). Similarly, in *A. burtoni* males produce sound during their courtship display, and females prefer to associate with males when the presentation of these males is accompanied by courtship sounds compared to noise controls (Maruska and Fernald 2012). These sounds, which often are produced through chewing or body vibration (Longrie et al. 2013), seem to play a role in social communication. Yet we are at a relatively early stage in our understanding of the context in which these signals are produced and their effect on the behaviour or the recipient.

Chemosensory and olfactory communication play a major role in aquatic environments and are known to be important in social affiliation also in other freshwater species such as stickleback (Ward and Hart 2003). In cichlids, this sensory modality is also used in numerous social behavioural contexts. Both courtship and aggressive contests may involve increased rates of urination prior to and during interactions, and the urine composition may be modified according to the social context (Hirschenhauser et al. 2008). For instance, the urine of dominant males may contain higher concentrations of chemical cues than that of subordinate males (Miranda et al. 2005; Barata et al. 2007). Indeed, urination during contests may be a direct form of signalling to rivals, as suggested in *N. pulcher* where aggressive propensity is communicated via urine-borne chemical compounds (Bayani et al. 2017). Morevoer, chemical cues are importantly involved in recognition mechanisms, for instance, in kin recognition of *N. pulcher* (Le Vin et al. 2010).

Cichlid social communication also appears to rely on the mechanosensory system (see Webb et al. 2021), the role of which has recently been examined in contest behaviour in *A. burtoni* and discussed in general terms by Butler and Maruska (2015). Since the early studies of Baerends it has been noted that cichlids perform behaviours such as ‘tail-beating’ during male–male agonistic encounters, and during these behaviours the physical displacement of water may provide a signal of the opponent’s size or strength (Baerends and Baerends-van Roon 1950). By ablating the lateral line system, and thereby disrupting the mechanosensory system, Butler and Maruska (2015) provided evidence that detection of these water-borne vibrations is necessary for contest resolution in *A. burtoni*, demonstrating that this modality may be required for effective resolution of social conflicts.

3.3 Aggressive/Agonistic/Territorial Interactions in Cichlids

Such is their willingness to engage in territorial disputes that cichlids are notorious among aquarium hobbyists for their quarrelsome nature. Many a pet store purchase has ended in disaster when too many, or too few, cichlids are housed in aquaria. Of course, this behaviour is not restricted to captivity; in their natural habitat territoriality and aggressive behaviours are some of the most commonly observed in wild cichlids. The form and expression of aggressive behaviour in cichlids are highly conserved across species and involves stereotypical interactions that progress through clear stages of escalation. Two males engaged in a territorial dispute will generally initiate disputes with a frontal display with the head pointing downward and the opercula, branchiostegal membrane, and fins spread. Upon escalation, the males may proceed to fast approach, tail-beating, circling, chasing, butting, biting, and mouth-fighting as the conflict intensity increases. Baerends and Baerends-van Roon (1950) divide territorial and aggressive behaviour into three different categories: chasing, intraterritorial fighting, and boundary fighting. 'Boundary fighting' involves a series of stereotyped signals and colour changes to signal to any potential intruders, but may also be used in interactions with neighbours and rivals. Typically, the resident will face towards the intruder with fins spread and may perform a jerking swimming pattern. The opercula may then be spread and the pair may engage in back and forth swimming behaviour such that the advance of one individual is met with a retreat by the other, and then vice-versa. Early researchers interpreted this behaviour in stickleback as a compromise between aggression and fear, each being represented behaviourally in turn (Leiner 1929). If the boundary is breached, response to territorial incursion involves lateral displays in which the medial fins are erected and the branchiostegal membrane extended. This is associated with exaggerated swimming toward the intruder, potentially providing a mechanosensory signal. This 'intraterritorial fighting' will be escalated if the intruder does not leave, at which point overt butting and biting of the flanks will occur. If the intruder reciprocates this behaviour, the pair will engage in continuous circling behaviour in which each attempt to perform lateral rams and bites towards the other, or opponents will lock their jaws and try to push or turn the body of the opponent, until one performs submissive behaviour and leaves the territory. Once this dominance has been established, 'chasing' behaviour may occur. As the name implies, chasing constitutes a directed aggressive act from a socially dominant individual toward a fleeing subordinate individual, typically as a mechanism to further remove an intruder from a territory, and may include attempts at physical damage through biting during the chase. Aggressive displays or behaviour may also be responded to with submissive behaviours, which may themselves be diverse and nuanced, but on which little empirical work has been conducted. Engaging in physical contests can be costly because rivals expend energy and time, risk injuring themselves (Briffa and Sneddon 2007), and especially in high predation environments like Lake Tanganyika, may increase exposure to predation through the reduction in attention (A. Jordan pers. obs.). As such, memorising dominance relationships and performing submissive behaviour rather than reciprocal aggression can be adaptive by reducing the costs of unwinnable contests (Barnard and Burk 1979).

As discussed earlier, resource defensibility is a key factor in determining social behaviour and territoriality in animals (Brown 1964), and has a particularly strong effect on antagonistic interactions in cichlids. This effect can operate on two levels and timescales—it can lead to fixed among species differences and labile within species differences. This latter effect is exemplified in the transition from free-ranging, non-aggressive, and shoaling behavioural phenotypes during non-breeding periods to the highly aggressive and territorial behaviour displayed by the very same individuals during breeding. In *Oreochromis mossambicus*, the distribution of male territories shifts from non-uniform ranges with flexible boundaries in non-breeding states to highly ordered and uniform territory ranges once all males enter breeding condition (Barlow 1974a, b). This change in territory packing is a consequence of the shift in aggressive behaviour towards other males and has consequences on the social and spatial structure of the population generally (Chase and Seitz 2011). In many other species of cichlids, the change from a non-breeding to a breeding state is accompanied by massive increase in territoriality and aggression. The mechanisms underlying this behavioural transition are well understood, particularly in the African riverine mouthbrooder *A. burtoni*, where social status changes are associated with a range of gene expression, endocrine, and morphological shifts. The details of the mechanisms underlying these social changes are discussed by Félix and Oliveira (2021).

3.4 Courtship and Mating

Here we discuss the range of communication and behaviour expressed during reproduction, which is by definition a social act. As in all taxa, there is a great difference in the behaviour of species that first form pairs, harems, or cooperative groups prior to breeding, and those which come together only in the act of courtship and mating itself. In pair-bond forming species, reproduction, and cohabitation may involve almost the entire behavioural repertoire, while in those species that only couple during mating, lekking, and male courtship are the most common behaviours (Schuetz et al. 2010; Haesler et al. 2011; Schütz et al. 2017). The majority of teleost parental care systems, male-only (paternal) brood care is extremely rare in cichlids, which has important ramifications for the operational sex ratio and mating behaviour. Primarily it means that female choice for male ornaments and courtship is more common where paternal investment after copulation is low because the operational sex ratio is biased towards a greater number of males who must compete for mating opportunities. In Haplochromines, for instance, where males form temporary leks and eggs are incubated by the female, sexual dimorphism is far more pronounced than in pair-bonding and group breeding species, where sexes may closely resemble one another. In *L. callipterus*, the sexual size dimorphism has reached its extreme, with males outsizing females on average 12 times by weight, which is the greatest sexual dimorphism known among animals with males exceeding females in size (Schütz and Taborsky 2000, 2005). Interestingly, in this species there is also an extreme intrasexual dimorphism between large, bourgeois nest building males and tiny reproductive parasites, which reach only 2.5% of the mass of nest males (Sato et al. 2004). This intrasexual size dimorphism is fixed for life, representing a sex-linked Mendelian single locus genetic polymorphism. The dwarf males in this species do not court, but surreptitiously enter the territory of a nesting male to fertilise a large proportion of the deposited eggs using highly specialised behavioural and gametic traits (Taborsky 2001; Wirtz-Ocana et al. 2013; Ocana et al. 2014).

In species without post-zygotic paternal care, males typically first choose a site from which to court passing females. This may be a flat stone, a patch of gravel cleared of debris, or a purpose-built bower constructed from sand. These structures can be discrete, like in *O. ventralis*, where only a thin layer of fine sand is deposited on a horizontal stone surface (Immler and Taborsky 2009); but they may alternatively be impressive in their construction, like in the bower building cichlids of Lake Malawi and Lake Tanganyika (McKaye et al. 1990; Schaedelin and Taborsky 2006). In *Cyathopharynx furcifer*, for instance, a fish only 15 cm in length, males construct sand craters of more than 40 cm in diameter, moving on average over 5 ½ kg of sand and spending 80% of their time transporting sand when constructing these craters, mouthful per mouthful (Schaedelin and Taborsky 2006). On average, the males expend 18 hours net building time to complete such crater, which involves a total swimming distance of >8 km for transporting the required amount of sand (Bucher 2004). Each male builds a crater matching in size to his own competitive power. Females assess males according to their individual crater building activity. These elaborate sand structures exemplify individual-specific extended phenotypes that are evaluated by females during mate choice (Schaedelin and Taborsky 2009).

In general, if males monopolise spawning sites they tend them carefully and defend them vigorously against conspecific rivals and heterospecifics while waiting for passing females. Such territory can take many forms, from a depression in the sand as in many Tilapia type species, a constructed bower as in many Tanganyika Ectodines (see above), or simply a volume of water defended against other males as in some *Cyprychromini*. When a female is nearby, males dart out rapidly from their territory and perform a series of fin extensions, quivering, and body arching towards the female, attempting to entice her back to their territory. If the female shows interest, the male will repeatedly attempt to lead her, swimming in front of the female with quick and exaggerated swimming movements oriented towards their spawning site. Arriving at the spawning place, the male and female may engage in repeated circling, which is the time when gametes are released and taken up into the mouth of the caring parent. In many species the male will then present its egg dummies with quivering body movements. Egg dummies are brightly coloured spots or tassels that somewhat resemble the species eggs. They can be positioned either on the anal fin and also on the dorsal fin or on extended filaments of their pelvic fins (Wickler 1962; Hert 1989; Salzburger et al. 2007). Responsive females will touch the dummies with their mouth as if attempting to take them up. This is probably the moment when they collect the sperm that males deposit on the bottom of their spawning site (Immler and Taborsky 2009). In *O.ventralis*, the eggs are fertilised in the mouth of the female, and she usually collects several ejaculates from different males in a sequence. This provides opportunities for post-mating sexual selection to take effect, as sperm compete for fertilisation in the female's mouth without the direct influence of their producer. The owner of the bower is therefore not necessarily the father of the resulting offspring (Immler and Taborsky 2009; Haesler et al. 2011).

Typically, in lekking mouthbrooders, the social interactions encompassing the male-female pairing are brief—a transient sexual relationship is formed immediately prior to fertilisation of the eggs, during which aggression from the male is reduced. Once fertilisation is complete however, the female is often chased vigorously from the territory (Seitz 1940). Hence, the social system in many mouthbrooding cichlids is rather simple, with interactions among adults confined to territorial aggression among males and the brief interaction between male and female during gamete deposition and uptake. For pair-bonded, haremic, and social species, the process of courtship and mating is more nuanced and long-term, and is associated up with the process of social behaviour and territory defence more generally. Often, the pair-bond will form long before the act of spawning, and may begin with one or both sexes constructing, cleaning out, or defending a permanent or semi-permanent territory. Courtship itself may be similar to that of mouthbrooders with only temporary associations, with a series of fin extensions, quivers, and leading behaviours prior to spawning. Nevertheless, there are species-specific sequences and structures of behaviour that offer a fascinating window into the evolution of courtship itself, as well as being potential pre-zygotic barriers to hybridisation. While the details of parental care in cichlids are dealt with elsewhere in this volume, it is during and after this phase that many other types of social interaction are also displayed. Between the members of the pair, behaviours that resemble aggression, but which are performed at a slower speed or in a constrained fashion are common. Affiliative behaviours such as 'hook swimming' and 'soft-touch' (Sopinka et al. 2009) are often performed by subordinates towards dominants, or by females towards males. These forms of display are often performed after the return of one individual from territorial defence or having briefly left the territory, and may function as a form of pair reinforcement. As for other social signals, there is considerable variation among species in the form and function of these affiliative and submissive behaviours, and uncovering the causes and consequences of this variation offer much scope for future research. Finally, reproductive behaviours themselves may be used as a subtle social signal to deceive or manipulate partners. In *Julidochromis spp*. females may perform 'pseudospawning' behaviour, a behaviour frequently shown by many cichlids preparing for the synchronous release of gametes during spawning. This behaviour of *Julidochromis* females was interpreted as 'pretending' to lay eggs along the substrate to confuse males regarding the number of offspring they have actually sired with that female, and thus providing more paternal effort and defence toward her brood

(Kohda et al. 2009). This is reminiscent of the situation in dunnocks, a small songbird with similar polyandrous mating patterns, where females solicit matings with group males differing in rank, which may increase the propensity of males to care for the brood (Davies et al. 1996).

3.5 Signalling Danger (Predation)

Cichlid parents are highly attentive and may provide care long into the development of their offspring. This is often provided within the spawning territory of the parents, where the fry are afforded some degree of protection from predation. As the cloud of fry ascends from the substrate in order to feed, one parent, both parents, or in the case of cooperative breeders, parents and helpers will remain vigilant for approaching predators. If a threat is detected, the parents will quickly signal to the fry using, for instance, a series of fin flicks and subtle body movements. One of the most used signals is an abrupt raising and lowering of the dorsal and pectoral fins, which Liebig (1920) described in *Cichlasoma biocellatum* as serving to either attract or repel the fry, depending on the speed of the motion. The same behaviour in *H. bimaculatus* was interpreted by Fischer (1924) as a signal to attract young to food sources, and subsequent authors studying *Nannacara taenia* (Stoye 1933) and *Aequidens latifrons* (Breder 1934) interpreted these purely as warning signals to the fry, which would rapidly descend to the substrate. Other species will take offspring back into the mouth if a dangerous predator appears after the initial release in a process described as iterocavous mouthbrooding. Examples of this strategy include species within the South American *Geophagus steindachneri*, the African cichlids *Pseudocrenilabrus multicolour* and the *Tropheini*. These species rapidly take fry into their buccal cavity at the sign of danger or will signal to fry using pelvic fins and head down posture, at which point fry rapidly swim back into the mouth.

3.6 Helping and Cooperation

Intra-group social communication is best studied in cooperatively breeding cichlids, where different group members may assume divergent roles, depending on size, status, and sex. A variety of potentially sex-specific (Mitchell et al. 2009) aggressive, affiliative, and submissive behaviours are involved in the establishment and maintenance of dominance relationships among group members (Taborsky 1984; Hamilton et al. 2005; Dey et al. 2013). Sex can also affect dominance acquisition among same-size subordinates (Riebli et al. 2012), and growth patterns (Hamilton and Heg 2007). Cooperative behaviours in such groups often involve keeping predators at bay by aggressive defence behaviour (Fig. 3c), providing shelters (e.g. by digging out cavities under stones that can serve for breeding; Fig. 3b), cleaning eggs and larvae with the mouth (Figs. 2b, 3b), and fanning eggs for oxygen supply. Tasks may be shared unequally between group members, depending on current demands (Taborsky and Limberger 1981; Taborsky 1984; Desjardins et al. 2008). In the cooperative breeder *N. pulcher*, if several demands appear concurrently, helpers may specialise in territory maintenance, whereas female breeders focus on direct brood care and both breeders heavily engage in defence (Taborsky et al. 1986). Large, piscivorous predators are attacked most often by male breeders, followed by female breeders and large helpers. Defence against dangerous predators is often shared and strategic risk sharing among group members is suggested by significant positive correlations between group size and the per capita attack frequencies of breeders and large helpers against experimentally deployed large predators (Heg and Taborsky 2010). Among helpers, large individuals may either specialise in defence behaviour (Taborsky and Limberger 1981) or in digging while smaller helpers defend the breeding shelter against egg predators (Bruintjes and Taborsky 2011), depending on ecological challenges and the negotiation process between breeders and helpers (Naef and Taborsky 2020). When helper-sized fish cooperatively dig out a common shelter, they apparently apply direct reciprocity decision rules to decide about their digging effort (Taborsky and Riebli 2020).

In this species, social behaviours such as aggression and submission among group members make up the bulk of the behavioural time budgets of both breeders and helpers, with aggression and submission dominating the time and energy budgets of breeders and helpers, respectively (Taborsky and Grantner 1998). Among the cooperative behaviours, territory maintenance takes up a considerable proportion of the behavioural time budget of helpers and female breeders. In addition to digging, territory maintenance also includes the removal of stones, shells, and particles as well as cleaning the spawning site. The energetic investment of territory maintenance involves a six-fold increase of energy expenditure compared to the routine metabolic rate, which is comparable to the energetic costs of flying in birds (Grantner and Taborsky 1998). During breeding, digging is responsible for nearly 20% and 25% of behavioural metabolic costs in helpers and female breeders, respectively, with expenses varying among different stages of the breeding cycle (Taborsky and Grantner 1998).

4 Cichlids as a Model for Studying Social Behaviour

Understanding the ecological and evolutionary pathways leading to social behaviour is a long-standing challenge in biology. A major difficulty lies in isolating the sources of selection that may favour the evolution of particular social systems, especially when comparisons are confounded by variation across ecological, geographical, or life-history parameters. The controversy around the social-brain-hypothesis reveals the difficulties in associating variation in a putative mechanism of complex sociality (brain size) with one or other causative factor, in this case group size or dietary breadth (DeCasien et al. 2017; Powell et al. 2017). Ideally, we would have a system in which there is variation in the trait, or traits of interest, with minimal variation in other potentially confounding factors. When considering social evolution and social behaviour, cichlids—and in particular Lake Tanganyikan Lamprologine cichlids—offer just such a system.

4.1 Phylogeny and the Evolution of Sociality

A major strength of cichlids as a study group is their well-resolved phylogeny, which has been leveraged to understand many aspects of morphological and genomic radiation. Within and across the African Great Lakes (Old World) and Neotropical regions (New World), there is a great diversity of social systems and social behaviour, and since the early work of Baerends and Baerends-van Roon (1950), the utility of comparative behavioural studies in cichlids has been recognised. However, the inherent difficulties of quantifying behaviour at anything approaching the detail and objectivity achieved, for example in morphological studies, have constrained comparative behavioural studies to use broad categories and classifications (e.g. Gonzalez-Voyer et al. 2008). This can limit the resolution of behavioural comparisons and cause disagreement over the categories themselves (Dey et al. 2017; Tanaka et al. 2018a). Of particular importance in this debate, and a major challenge for researchers is the assignment of species into categories of social structure and mating patterns using quantitative, rather than qualitative descriptors (Lein and Jordan 2021).

The primary source of this difficulty is that although cichlids have a dazzling variety of mating patterns, many of these do not fall easily into discrete mating system categories as originally proposed (Emlen and Oring 1977). Moreover, for many species, mating patterns and social arrangement are a function of resource availability and other ecological factors, and variation in social arrangement and behaviour within species living in different locations is commonplace (e.g. Groenewoud et al. 2016). One difficulty in ascribing species-level categories or social descriptors can be found when species themselves are ill-defined, for example in *Telmatochromis temporalis*. Like in many cichlids, the taxonomic status of this species is subject to some disagreement: while the populations on rocks have consistently been described as *T. temporalis* (Sato and Gashagaza 1997; Konings 2015), populations found on shell beds have been described as both the same (Hanssens and Snoeks 2001) or later as different species (Hanssens and Snoeks 2003). Takahashi (2004) describes behavioural and molecular differences between morphs, suggesting they constitute two separate evolutionary lineages, and goes on to demonstrate differences in social structure between the ‘normal’ and ‘dwarf’ morph with respect to number of females in a male’s territory as a function of body size. Although there is apparent directional selection on larger body size in both morphs through increased access to mates, this is countered in shell-dwelling morphs by the need to enter the shell, leading to their smaller average size (Takahashi and Koblmüller 2011).

This difference between rock and shell-dwelling morphs is not restricted to this species—both *N. pulcher* and *N. multifasciatus* occur in rock and shell-dwelling populations, with distinct, but as yet unquantified, differences in their social arrangements. In the well-studied Kasakalawe population of *N. pulcher*, group territories are clearly separated, inhabiting rock territories interspersed in sand patches (Balshine et al. 2001; Heg et al. 2005b). In contrast, the shell-dwelling *N. pulcher* population at Mwina exists in massive aggregations of hundreds of interacting individuals making it difficult to distinguish social units (A Jordan & M. Taborsky pers. obs.). Similarly in *N. multifasciatus*, the effectively endless availability of shells in the Chikonde population is correlated with very large group sizes of 50 or more individuals, whereas other populations in areas of lower shell abundance (e.g. Mbita Island, Ndole Bay), as well as the rock-dwelling populations, contain many more pairs or polygynous harems (A. Jordan pers. obs.). Other ecological factors can similarly influence social structure; a comparison between populations of *N. pulcher* reveals that social organisation and behaviour is strongly affected by predation risk and associated ecological factors (Groenewoud et al. 2016). In areas with high predation risk, groups more often contained more large than small members, whereas in areas of low predation this trend was reversed. These examples demonstrate that social structure can vary in subtle ways that extend beyond social categories such as asocial, group-living, monogamous, or polygynous. Given our increasing understanding of the fitness consequences of variation in social structures (Ward and Webster 2016), as well as the controversy that can arise over these broad categories, a more standardised and quantitative assessment of variation in social structure is clearly needed. As we outline in the section on future directions, the advent of automated tracking of large groups of cichlids that is now possible may generate far greater insight into the interactions, identities, and social structure of both captive and wild cichlid groups (Lein and Jordan 2021). With robust descriptors of social interactions and group dynamics in quantitative space, differences in both social arrangement and behaviour can be mapped directly onto phylogenies to generate testable hypotheses about social evolution. This in turn will allow us to interrogate what the social, ecological, neurobiological, and physiological pressures and constraints on behaviour may have been over evolutionary time.

A particularly powerful system for studying sociality in cichlids is that of the tribe Lamprologini, which contains species with similar ecological niches, but a breadth of social systems, including almost all cooperatively breeding fish species described to date (Taborsky 1994; Sato and Gashagaza 1997; Heg and Bachar 2006). The diversity in social behaviour among a group of species that shares many other aspects of life history allows for a powerful comparison of the forces shaping behaviour without confounding differences in geography, morphology, and ecology. This is well-represented in the 15 or more ‘shell-dwelling’ Lamprologine cichlids. Aside from their close phylogenetic relatedness, these dwarf species are also very similar in terms of their ecology. All 15 species known exclusively use fossilised shells of the genus *Neothauma* for shelter from predators and brood chambers; all face similar predators, predominantly from the related genus *Lepidiolamprologus*; all have overlapping dietary niches, although some feed benthically and some from the water column (Ota et al. 2012); all are morphologically similar (i.e. they are small) as a consequence of needing to be able to enter shells; all practice some level of paternal care by fanning oxygen into the shell thus ventilating the eggs until these hatches and subsequently defending offspring from being eaten; and all occur at similar depth ranges, often on vast shell beds, and many are found syntopically in mosaic communities.

Despite their similar ecological lifestyles, there is a striking divergence between species in terms of the social strategies that are adopted. The species *N. multifasciatus, N. brevis* and *L. ocellatus* exemplify this divergence in the social system, but are members of a much larger group in which comparisons are possible. *N. multifasciatus* is the smallest cichlid species known (m: 30 mm SL, f: 20 mm SL) and lives in depths as shallow as 10 metres on beds of *Neothauma* shells, which it excavates in small funnel-shaped depressions of the sandy lake bed, and which are inhabited by stable social groups of up to 30 or more individuals (typically around 2–3 adult males and 4–5 females; Kohler 1998, Jordan et al. 2016). The second species, *N. brevis* is substantially larger (m: 60 mm SL, f: 40 mm SL) than *N. multifasciatus* and forms temporary breeding pairs that inhabit often only a single shell on the widely shell-scattered open sand habitat. In the similar-sized species *L. ocellatus*, by contrast, large males hold small harems of 2–3 females and defend a territory of approx. 1–3 m^2 in diameter against intruders. Similar to *N. brevis*, theses shells get partially covered with sand (Konings 2015). These three species exemplify the range of social complexity, but there are many other dwarf shell-dwelling Tanganyika cichlids that differ somewhat in their social organisation while maintaining many other aspects of ecology and life history, including *N. multifasciatus, N. similis, N. brevis, N. calliurus, N. pulcher, N. ornatipinnis, L. ocellatus, L. callipterus, L. caudopunctatus, Telmatochromis vittatus, T. temporalis,* and *Lepidiolamprologus meeli* (Sato and Gashagaza 1997).

Variation in social organisation in populations that face similar ecological pressures, such as the shell-dwelling cichlids, provides a powerful comparative system for understanding social evolution but must be combined with an understanding of the behaviours expressed by individuals within the respective social units. We now move on to discuss behaviour at the level of the individual, before examining how an understanding of both social structure and individual behaviour can provide fundamental insight into the evolution of sociality generally.

4.2 Plasticity, Behavioural Development and Individual Differences

While there is an amazing diversity of social behaviours displayed among cichlid species, behavioural expression among individuals can be equally diverse. It has been clear since the concept of selection was introduced by Darwin that consistent variation among individuals is required for behavioural evolution to occur. This variation is the raw material upon which selection can act. The behaviour may be consistently expressed for shorter or longer periods, and be more- or less-varied among individuals, depending on the mechanistic basis of the behaviour being expressed. Variation in behaviour generally results from an interaction between genetic determination and environmental/social effects reflected in phenotypic plasticity. The relative importance of these sources of variation can greatly differ, ranging from highly conserved, more, or less fixed action patterns with a putative genetic basis such as honeybee cleaning of cells (Oxley et al. 2010), to more complex and highly variable behavioural traits such as observed in social interactions (Chervet et al. 2011), the mechanisms of which remain the focus of much ongoing research.

To date there is only limited evidence of genetic polymorphisms governing differences in cichlid social behaviour, with the prominent exception of alternative male reproductive tactics. The Tanganyikan cichlid *L. callipterus* exhibits two divergent, genetically determined male morphs. Giant males build nests consisting of up to hundreds of empty snail shells, and they court females that lay their eggs inside these shells. Tiny 'dwarf' males sometimes manage to enter a snail shell in which a female is spawning to fertilise eggs from the tip of the shell, thereby parasitizing the effort of the giant nest owners (Taborsky 2001; Sato et al. 2004; von Kuerthy and Taborsky 2016). Only males are affected by this genetic polymorphism, which is inherited via the male Y-chromosome or some other sex-specific genome region (Ocana et al. 2014). Furthermore, the yellow and red male colour morphs of the West African riverine rainbow krib (*Pelvicachromis pulcher*) seem to be genetically determined (Heiligenberg 1965; Martin and Taborsky 1997) and are linked to male mating tactics. Red males always defend a territory holding one or several females, whereas yellow males may either mate monogamously or become 'satellite males' or helpers, which do not have a female partner on their own but help red males in territory defence and brood care while taking a share in siring offspring (Martin and Taborsky 1997).

While these examples of male genetic polymorphisms in morphology and social behaviour are impressive, they might be rare in cichlids (Taborsky 2008). In contrast, individual differences in social behaviour shaped by experience seem far more widespread, with important effects often lasting for life. Phenotypic plasticity refers to the ability of a genotype to express different phenotypes depending on the environmental conditions it experiences and is a specific case of a more general gene-by-environment interaction. It allows organisms to adapt quickly to changes in the environment and thus it may help these organisms to survive rapidly changing conditions. This seems particularly important in the context of social interactions. In general, as plastic adjustments can take effect much faster than evolutionary change, plasticity may rescue populations exposed to changes in their environment before a strategy to cope with a stressor can evolve (Chevin and Lande 2010).

Recently, there has been a rapid increase in our understanding of how the diversity of social behaviour observed in a single cichlid species originates from plasticity. Plasticity can affect social behaviour at two temporal scales; (1) long-term effects, where the social environment a fish experiences during its development shortly after birth shapes social behaviour irreversibly ('developmental plasticity') and (2) short-term adjustments of the phenotype, which are typically reversible ('flexibility'). Such flexibility is shown, for instance, if the current dominant fish of a social group is temporarily removed and a previously subordinate group member may switch to claiming the dominant status. Once the former dominant fish is reinstalled in its territory, the previous ascender may fully reverse back to a subordinate state. In *A. burtoni* males, switching from a non-aggressive, subordinate state to a dominant hierarchy position is accompanied by a drastic change in behaviour, in which ascended dominants show high aggression against any other male. The behavioural change is accompanied by the expression of a bright colour pattern interspersed with strongly contrasting black stripes and bars (Maruska and Fernald 2018).

Developmental plasticity, however, is more difficult to explain than such fully flexible adjustments, because irreversible changes made early in life have consequences for the entire life including adulthood at a time when the future social conditions cannot be anticipated with certainty. This means that if the environment in which a fish develops is a poor predictor of the future, an individual is bound to live with a somewhat maladapted phenotype. Therefore, the lifelong effects of developmental plasticity should only occur if the future can be predicted with some reliability (Burgess and Marshall 2014). The challenge of studying the effect of developmental plasticity on fitness is that all life stages and environmental conditions encountered during the course of an individual's life have to be considered to test for pleiotropic and other negative effects. Often this is only possible in captive studies under controlled experimental conditions.

The cooperatively breeding cichlid *N. pulcher* is an ideal species to study the developmental plasticity of social behaviour. Its natural habitat in Lake Tanganyika represents a predictable world: group sizes of social units may remain stable over years (Heg et al. 2005a) and, while predation risk differs between separate populations (Groenewoud et al. 2016), it is predictable within populations, where it partly depends both on group size and the distance to neighbouring territories (Jungwirth and Taborsky 2015). In the aquarium, the social environment after birth can be easily manipulated experimentally. This may be done, for instance, by rearing young in groups containing either the parents with or without helpers or the same-aged siblings only (Arnold and Taborsky 2010; Taborsky et al. 2012). Similarly, social complexity in early life can be manipulated by keeping young in large groups with parents and many helpers, or in small groups in which the breeder pair only has one helper (Fischer et al. 2015). In both studies using such experimental variation of rearing conditions, individuals reared in a social setting with more adults and helpers being present were better able to solve contests efficiently later in life and they were more likely accepted as subordinates in a territory by large fish. As such effects persist throughout life (Fischer et al. 2017), this suggests that offspring reared in more complex social environments had developed a better social competence during early life (Taborsky and Oliveira 2012).

Apart from causing quantitative differences in social behaviour, developmental plasticity may also give rise to lifelong behavioural specialisation. As outlined

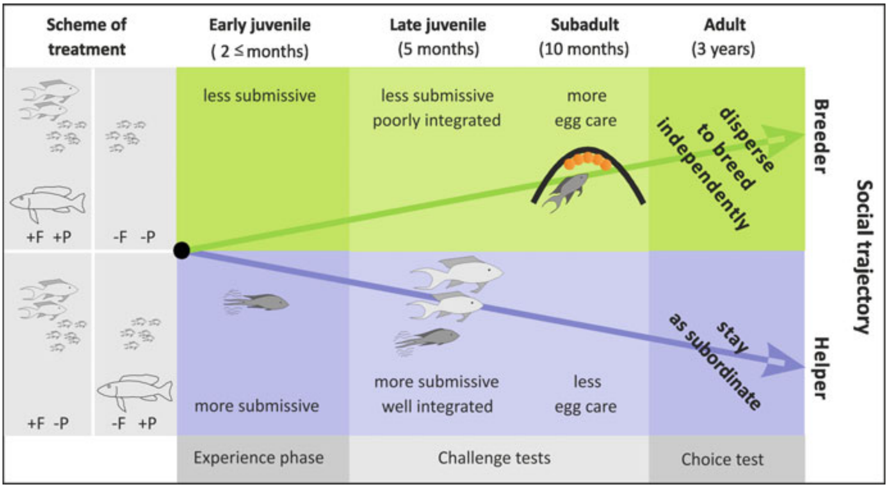

Fig. 8 In *N. pulcher*, the early social environment and predation risk interact to induce a specialisation in one of two social trajectories, (1) individuals that have a higher propensity to act as brood care helper, which disperse early for independent breeding, and (2) individuals that show a higher propensity to exhibit submissive behaviour, which remain philopatric. On the left side of the graph, in grey, a schematic representation of the early-life treatments is provided, with the respective fish symbols representing the presence (+) or absence (-) of adults (F) and predators (P). (From Fischer et al. 2017)

above, in *N. pulcher* subordinate group members may help their dominant breeder pair by participating in territory defence and maintenance as well as by cleaning and fanning eggs and larvae (Taborsky and Limberger 1981). Some subordinates help only a little but appease aggressive breeders by intensive submissive displays (Fischer et al. 2014). These two alternative tactics used to appease dominant breeders are not applied very flexibly. Instead, some individuals specialise in helping and others in showing submissive displays (Kasper et al. 2017, 2018a). The specialisation of subordinate group members in either a submissive or a helper type arises as a consequence of the early environment in which young *N. pulcher* grow up during their first weeks of life. When the two key selective forces of *N. pulcher*, predation risk and social environment, were manipulated in a full-factorial rearing experiment (Fig. 8), they interactively shaped the propensity to show rather more submission or more helping behaviour (Fischer et al. 2017). Interestingly, the propensity to delay dispersal from the natal family unit or to disperse early for independent breeding was also driven by the early experience in predation risk and social environment.

For a social cichlid, the most extreme manipulation of the social rearing environment is to be reared in full social isolation. *Pelvicachromis taeniatus* are socially monogamous cave-breeding cichlid from West Africa. After a period of extensive, biparental brood care, juvenile *P. taeneiatus* live in groups until they reach sexual maturity. When young of this species are reared in complete social isolation, their social behaviours clearly carry the signature of early social deprivation. Compared to normal, group-reared conspecifics, isolation-reared fish are more aggressive towards conspecifics and, consequently, they are less likely to join a juvenile shoal (Hesse and Thünken 2014). Additionally, these fish are more likely to inspect a predator without a companion (Hesse et al. 2015) and show deficits in sexual behaviour (Hesse et al. 2016).

It remains to be answered why social experience made in the earliest life stage can have such strong and lasting effects on social behaviour. An important factor is the temporal structure of the environment animals live in, which appears to be relatively stable, at least in some cichlids. Developmental plasticity can only be adaptive in environments that are predictable to some degree, that is where current conditions predict future conditions. In such environments cues that young pick up from their social environment may inform them about the intensity and type of competition, they will encounter in the future. This includes cues about local density, sex ratio, or the age and size structure of populations. In addition to this inadvertent information, direct experience from social interactions with siblings, parents, or other group members may significantly contribute to later-life social performance, which may occur by improved opportunities to learn how to behave adequately in different social situations (Taborsky 2016a).

4.3 The (Co-)Evolution of Social Structure and Behaviour

As we have outlined, cichlids show an incredible variation in both social structures and social behaviours, which exists within and among species, populations, and individuals. While this variation might seem daunting, it presents an unparalleled opportunity to explore the degree to which social organisation and social behaviour are linked. Some questions arise naturally—are species (or populations) showing more complex social organisations also behaviourally more complex? Are animals living in larger or socially more diverse groups cognitively more sophisticated? Does stable social structure reflect the existence of stable and defendable resources? Other questions are more nuanced but no less fascinating—can the same neurobiological template produce both social and non-social animals? What effect do the various forms of gene-by-environment interaction (e.g. juvenile experience, social niche availability, food abundance) have on subsequent social behaviour? Is biparental care the basal state required for subsequent evolution of more complex sociality?

For these and a wealth of other questions related to social behaviour, there is very likely a cichlid system well-suited to finding an answer. At the level of sheer numbers, this may not be surprising given almost half of all vertebrates are fish, and one in every 10 species of fish are cichlids. For instance, there are almost 10 times as many species of cichlids as there are primates. Yet cichlids have a number of attributes above sheer species diversity that make them particularly well-suited to studying questions of social behaviour and evolution:

1. Cichlids have some of the best studied, and best resolved phylogenetic relationships of any taxonomic group. Any evolutionary comparison requires a robust scaffolding on which to make comparisons and examine transitions in the traits of interest. With a long history of comparative work that has developed into cutting-edge studies employing genomic and transcriptomic approaches, the opportunity for quantitative comparative work in cichlids is nearly unmatched.
2. Cichlids have a great diversity of social organisations. Within the broad family Cichlidae, the spectrum of sociality ranges from species living as solitary pelagic piscivores to lurking ambush predators mimicking decaying fish, through polyandrous harems of crevice spawners, to cooperative breeders with social organisations approaching the complexity of the most highly social insects, birds, and mammals. This diversity in social structure allows for comparisons at many levels, including life-history and ontogenetic effects, the fitness consequences of living in groups, and the evolutionary trajectories of social systems.
3. A major limitation of many comparative studies is the unavoidable inclusion of confounding variables in the comparative framework. Within cichlids, and especially those in Lake Tanganyika, syntopic populations encounter near identical environments, occurring in mosaic communities and in some cases even living within the same nests (e.g. *L. callipterus* with *T. vittatus* and *L. calliurus*). While there are many communities in which similar species overlap in spatial and temporal distribution, the shell-dwelling communities of Lamprologines are one of the best examples of this shared ecology—abiotic factors are shared, most animals are of similar size, have the same predators and therefore risk regime, and compete over similar physical resources. This overlap in ecology means that many alternative sources of selection on social behaviour can be ruled out, at least within the same populations. Moreover, where variation in ecological factors does exist, for example among nearby populations, this can usefully be used to test hypotheses about the effects of this variation on social behaviour.
4. The rich and varied behavioural repertoire of cichlids provides the raw material for many lines of inquiry concerning the evolution of, and variation in, behaviour. Examining why individuals may behave in different ways under different social or environmental contexts, what the immediate or long-term consequences of these behavioural differences may be, and how relevant sensory information is integrated into behavioural decisions, are all fascinating and timely questions that the rich diversity of cichlid behaviour can help to answer.
5. The ability to work with cichlids in both lab and field, using largely equivalent experimental designs, is a particularly powerful feature of the system. Using cichlids, creating aquarium experiments with realistic social and physical arrangements is relatively straightforward, especially in rock and shell-dwelling species that are typically highly site-specific and defend relatively small areas that can be recreated in captive settings. But the exceptional benefit of cichlids as a study system in behaviour is that these laboratory-based experiments can be directly translated to field settings. For many species, high site-specificity and territoriality mean that researchers are able to return to the same locations and study the same, individually identifiable subjects for extended periods. Thus, the

degree of control and replication typically only found in lab studies can be extended to the field. Obviously, this does not apply for all species, but it pertains for many species including most of the *Lamprologini* of Lake Tanganyika, which remain in the same location for much of their life.

6. Cichlids are typically small and therefore highly amenable to captive breeding and experimentation. Their popularity as aquarium species is testament to this relative ease of care, and their famed parental care behaviour in both mouthbrooding and substrate spawning species leads to high population growth under appropriate conditions. Most species have generation times in the order of 4–6 months, making them suitable for some experimental breeding designs, and the ability to hybridise among species that might vary in a trait of interest also opens up the potential for backcrossing to explore the genetic basis of certain behaviours. In the age of CRISPR-Cas9 gene-editing technologies, the large size and accessibility of fertilised zygotes has already been used to produce genetically-modified lines of *A. burtoni*, and is also being explored in Lamprologines (see below).

5 The Past, Present, and Future of Cichlid Behavioural Research

The study of social behaviour in cichlids has a long history, with reports on the reproductive and social behaviour of jewel cichlids (*Hemichromis bimaculatus*) and the Mozambique Tilapia (*Oreochromis mossambicus*) already well established by the 1950s (Breder 1934; Noble and Curtis 1939; Baerends and Baerends-van Roon 1950). These early studies provide a richly detailed account of a great many aspects of cichlid social interactions, territoriality, courtship, and parental behaviour, which was the origin of modern studies into cichlid behaviour. Since then, cichlid behavioural studies have continued apace, spanning continents and taxonomic groups. These behavioural analyses can be performed in both lab and field, with many studies asking how behaviour changes in different contexts (e.g. Jordan et al. 2016; Groenewoud et al. 2016). Cichlids are also a prime example for advanced cognitive skills in fish (Fernald 2017; Bshary and Brown et al. 2014), including the ability to successfully infer relationships without direct physical contact with individuals (Grosenick et al. 2007; Hotta et al. 2015a, b), the ability to recognise familiar individuals (Kohda et al. 2015) and discriminate them from unfamiliar individuals (dear-enemy effect; Balshine et al. 2017; Weitekamp and Hofmann 2017), and the ability to deceive other conspecifics (Chen and Fernald 2011).

In addition to studies of cognition, cichlids are emerging as a prime system in which to study the structure and function of brain regions associated with social interactions across vertebrate species (O'Connell et al. 2011; Félix and Oliveira 2021). Within the vertebrate brain, two neural circuits are most commonly examined in studies of social behaviour–the Social Behaviour Network (SBN; Goodson 2005;

Newman 1999) and the mesolimbic reward system. The social decision-making network (SDMN) is a higher-order integration of these circuits and is associated with stimulus salience and the regulation of adaptive social behaviours including reproduction, aggression, and parental care. Over the past decades, numerous studies of cichlids, covering a wide array of different aspects including the mechanistic basis of behaviour have been conducted; for example, in *Astatotilapia burtoni* (Greenwood et al. 2008; Maruska and Fernald 2018; O'Connell et al. 2011), *Oreochromis mossambicus* (Almeida et al. 2019), and *N. pulcher* (Kasper et al. 2018a, b; Taborsky et al. 2013). This work is being extended to other cichlid groups, in which representative histological brain atlases are currently being constructed for a number of Lamprologine cichlids (*N. pulcher*: D. Antunes et al., unpublished data; *N. multifasciatus, N. similis, N. brevis, L. ocellatus, L. ornatipinnis, L. meeli, T. temporalis* 'dwarf morph': Lein et al., in preparation). Not only will this vastly expand the number of candidate species, but it will also facilitate studies into patterns of neural activity in response to social stimuli through quantification of immediate early gene (IEG) expression levels (e.g. transcription factors c-Fos, EGR-1) in candidate regions of the SDMN using similar approaches to numerous neuroethological studies involving fishes (Desjardins et al. 2015; Maruska et al. 2013; Roleira et al. 2017; Teles et al. 2015, 2016; Weitekamp and Hofmann 2017). Cichlids are also amenable to CRISPR gene editing and other genetic tools that allow selective manipulation of candidate neural circuits involved in social interactions (Juntti 2019), providing experimental potential to examine candidate mechanistic pathways underlying social behaviour.

In the modern era, cichlid behavioural studies are already taking on a new and exciting aspect with the advent of visual tracking and computational ethology (Rodriguez-Santiago et al. 2020) alleviating many of the difficulties in studying cichlids in the wild or in large social groups. Computer tracking of groups numbering up to thousands of fish is now possible, bringing the analysis of large groups of cichlids under natural conditions within reach (Francisco et al. 2020). In concert with this, approaches such as behavioural decomposition may soon allow an unsupervised machine learning approach to analysing different behavioural states (Fig. 9; Nuehrenberg and Jordan 2019). This technique is already being employed with great success in model organisms such as *Drosophila* and mouse, demonstrating that the behaviour of freely interacting animals can be recorded and analysed using automated processes in incredibly high detail, which can be used also to infer social relationships (Berman et al. 2014). Given the variety of cichlid behaviour, the ease with which these behaviours are expressed under lab conditions, and the strong foundation of cichlid ethology developed over the past 70 years or so, it is easy to foresee that these techniques will translate extremely well to cichlid behavioural research. These approaches have the potential to revolutionise the study of social behaviour in cichlids, and harness the benefits of a rich ethological history combined with cutting-edge technological approaches. Indeed, the future of research on the evolution of social behaviour in cichlids is bright.

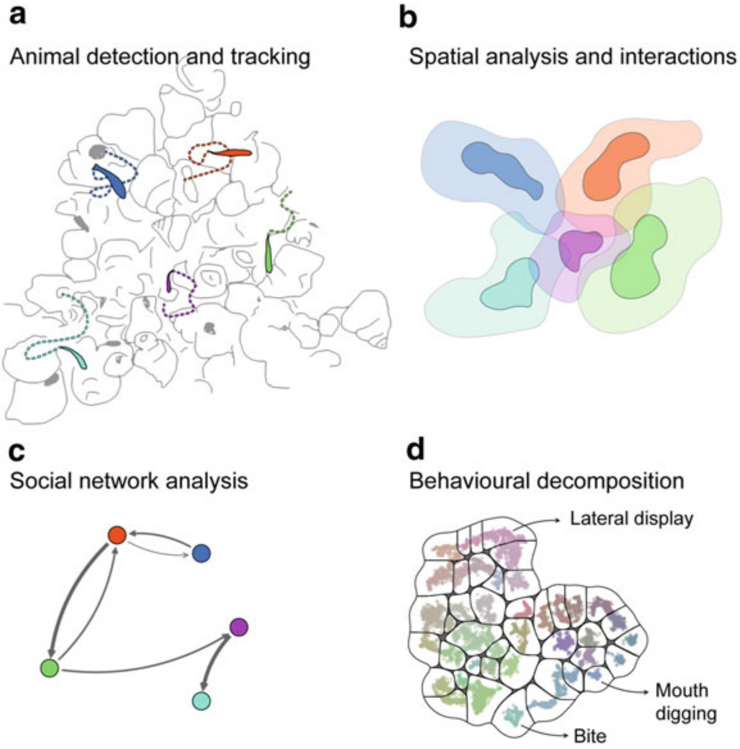

Fig. 9 Future directions for cichlid research will (**a**) utilise the increasing power of automated tracking and machine learning to track cichlid movement, posture, and interactions, (**b**) perform high-resolution spatial analyses, including interactions with environmental structures, (**c**) analyse social networks, and (**d**) use behavioural decomposition techniques, which use kinematic analyses to describe behavioural categories and can be represented in representations like this t-SNE embedding, to complement traditional ethological observations (Figure by Paul Nuehrenberg and Alex Jordan)

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Integrative Neurobiology of Social Behavior in Cichlid Fish

Ana S. Félix and Rui F. Oliveira

Abstract Social behavior encompasses the interactions between individuals of the same species, fundamental to their survival and reproduction. The study of these kinds of behavioral patterns and the unraveling of its underpinnings is a fascinating research area. However, to fully understand social behavior it is essential to integrate the various components underlying social interactions. From a mechanistic point of view, we ought to grasp specifically how the brain controls behavior, through the concerted action of its neural circuits, cells, genes, and molecules, and also how the social environment feedbacks and impacts the brain. On the other hand, this pursuit of knowledge on the proximate factors, which determine social behavior, is pivotal to achieve valuable insights on its ultimate causes. Performing comparative studies across different species, taking into consideration developmental, ecological, or life history features, have been a growing concern. A considerable amount of literature has been published on these matters using cichlids as model systems. Cichlids can give an important contribution to the field due to their amazing diversity and complexity of behavioral patterns and mating strategies. Here, we review the current state of knowledge on the neural basis of social behavior specifically focusing on studies carried out with cichlid fish.

Keywords Social decision-making network · Social brain hypothesis · Social cognition · Nonapeptides · Steroids · Neurogenomics

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A. S. Félix
Instituto Gulbenkian de Ciência, Oeiras, Portugal

ISPA – Instituto Universitário, Lisbon, Portugal

R. F. Oliveira (✉)
Instituto Gulbenkian de Ciência, Oeiras, Portugal

ISPA – Instituto Universitário, Lisbon, Portugal

Champalimaud Neuroscience Program, Lisbon, Portugal
e-mail: ruiol@ispa.pt

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1 Introduction

The aim of this chapter is to provide a comprehensive review of the neurobiology of social behavior in cichlids. First, we begin by presenting cichlid fishes as emerging vertebrate models for the study of social behavior, highlighting some of their remarkable features that can be explored to acquire new sights in the field. Next, the Social Decision-Making Network, a neural network that involves a set of core brain areas interconnected with each other that together control social behavior and are modulated by steroids and nonapeptides, is introduced and its application to cichlid research is discussed. The third section examines the social brain hypothesis proposed to explain animal cognition and the relation between sociality and brain size. An overview of the notable cognitive adaptations for social living in cichlids is also included. The following section discusses the neuroendocrine regulation of social behavior, by exploring how steroids and nonapeptides act in the brain and influence behavior and conversely how social behavior affects hormones. Finally, the neurogenomics of social behavior, namely the discovery of the specific genes and pathways that regulate behavior acquired with high throughput genomic tools, is addressed and several studies in cichlids are reported.

2 Cichlids as Models for the Study of Social Behavior

The family Cichlidae is distinguished as the most species-rich vertebrate family, with some estimates at more than 3000 species distributed widely in the American, African, and Asian continents (Kocher 2004). Cichlids are the subject of particular interest because of their explosive and diverse speciation since around 2000 species evolved in a short period of time (Kocher 2004; Seehausen 2006). Also, the parallel evolution of adaptive phenotypes, either in closed and distant related lineages, and all the underlying mechanisms involved along the process of evolution are central themes in cichlid research (Henning and Meyer 2014).

Besides phenotypic diversity such as color patterns, body shapes, or head morphology, these fishes are characterized by diverse social systems (see Jordan et al. 2021). Mating systems include (1) monogamy, when a male and a female form a mating pair establishing a pair bond, e.g., *Tropheus moori* (Egger et al. 2006) and *Pelvicachromis taeniatus* (Langen et al. 2013), (2) polygamy, when a mate has several partners but with possible selection of the partner at each spawning, e.g., *Neolamprologus brichardi* (Limberger 1983), (3) polygyny, when males mate with several females but females only mate with one partner, e.g., *Lamprologus callipterus* (Sato 1994), (4) polyandry, when a female mates with several males but a male spawns with only a female, e.g., *Julidochromis transcriptus* (Kohda et al. 2009), or (5) promiscuous, when males fertilize eggs from several females and the eggs of one female can be fertilized by several males, e.g., *Mchenga eucinostomus* (McKaye 1983). Another appealing facet is their reproductive strategies (Taborsky

2001) as they can monopolize mates or resources by defending spawning sites or nests in lek-systems, e.g., *Lethrinops c.f. parvidens* (Kellogg et al. 2000), perform sneaking fertilizations by parasitic males, e.g., *Oreochromis mossambicus* (Oliveira and Almada 1998a) and adopt mutualistic cooperative breeding systems, e.g., *N. brichardi* (Taborsky 1984a). There are cases where fertilization occurs externally, e.g., *Pseudocrenilabrus multicolor* (Mrowka 1987) or orally by females that suck the male sperm into the buccal cavity where they keep the eggs, e.g., *Thoracochromis wingatii* (Wickler 1962). Then parents can incubate fertilized eggs in nests, e.g., *L. callipterus* (Sato 1994), caves, e.g., *P. taeniatus* (Thünken et al. 2007) or in their mouths as female mouthbrooders, e.g., *Tropheus moori* (Egger et al. 2006), or male mouthbrooders, e.g., *Xenotilapia flavopinnis* (Kuwamura et al. 1989). Finally, parental care systems range from biparental, e.g., *P. taeniatus (Langen* et al. 2013*)*, to unipaternal, e.g., Saint Peter's fish, *Sarotherodon galilaeus* (Balshine-Earn 1997) or unimaternal, e.g., Pseudocrenilabrus *multicolor* (Mrowka 1987). *There* are also species that can display several of these forms of care, e.g., *S. galilaeus* (Schwanck and Rana 1991; Balshine-Earn 1997; see Balshine and Abate 2021). Figure 1 presents a phylogenetic comparative analysis among some of the Lake Tanganyika cichlids, which integrates behavioral traits (form of care and sex of the care provider) as an example of this behavioral diversity.

In addition to this vast and unique repertoire of social behavior, the advantage of having five cichlid genomes and transcriptomes available, namely *Oreochromis niloticus, Neolamprologus brichardi/pulcher*, *Maylandia zebra*, *Haplochromis nyererei*, and *Astatotilapia burtoni* (Brawand et al. 2014) and the recent development of powerful tools applicable to cichlid species, such as high-throughput sequencing (e.g., RNA-seq), transgenics (Juntti et al. 2013; Golan and Levavi-Sivan 2013; Ma et al. 2015) with particular emphasis on CRISPR/Cas9 mutagenesis technique (Juntti et al. 2016), has projected cichlids to the spotlight. In the near future, we expect exciting developments within cichlid research and in particular in social behavior.

3 The Cichlid Social Brain: Social Complexity and Brain Evolution

Traditionally, social behavior repertoire was considered to be determined by specific and differential brain areas or mini-circuits. However, a growing body of literature recognizes that social behavior is regulated by a broader and dynamic brain network. Newman (1999) was the first to introduce the concept of the Social Behavior Network (SBN) in mammals, which states the existence of a set of brain areas that together control social behavior. The SBN is composed of six nodes: the Medial Extended Amygdala (meAMY/BNST), the Lateral Septum (LS), the Medial Preoptic Area (POA), the Anterior Hypothalamus (AH), the Ventromedial and Ventrolateral Hypothalamus (VMH) and the Midbrain Periaqueductal Gray and

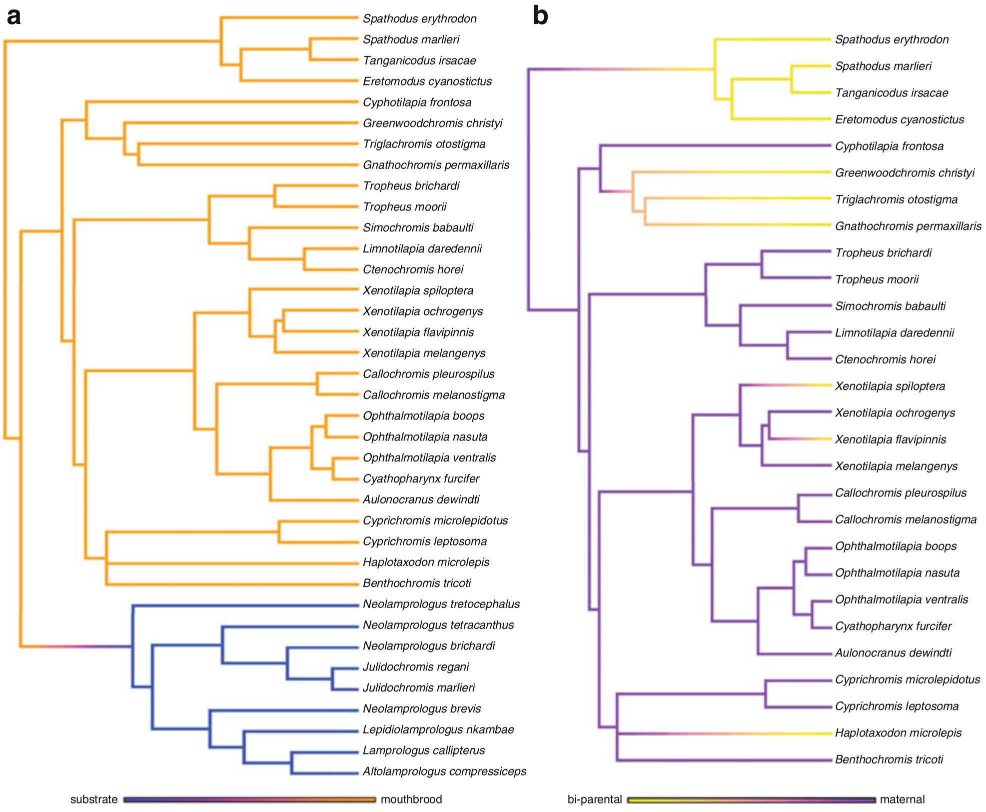

Fig. 1 A molecular phylogeny of some of the Lake Tanganyika species with possible character transitions in (**a**) the form of care (substrate guarding in blue and mouthbrooding in orange) and (**b**) the sex of the care provider (biparental care in yellow and maternal care in purple). Adapted from Tsuboi et al. (2015)

Tegmentum (PAG/CG). It is important to bear in mind that other unspecified areas are also relevant for characterizing social conducts yet each one of the SBN areas is a core node, reciprocally interconnected with the others, containing sex steroid hormone receptors and has an established role in the activation or regulation of several types of social behavior. Diverse studies using brain lesions, electrical manipulation, neuropharmacological manipulations, and immediate early gene expression have provided solid evidence for the common involvement of these specific areas on reproductive, parental, or even agonistic behavior. SBN is thereby defined as an integrated neuroanatomical network in which the dynamic activation patterns of the nodes are responsible for multiple behaviors modulated by social environment and sex steroids. For instance, a sequence of temporal behavioral responses such as sniffing, mounting, ejaculation, or grooming (the typical repertoire of male rodents' reproductive behavior), would be the result of the activation of this circuit, modulated either by external factors (environment) or by intrinsic components (sex steroids). Also, the key determinant factors of species and sex are responsible for ascertaining the brain's organization and connectivity across a common central network, which in turn are shaped by hormones throughout development and over the lifetime. As a consequence, a vast array of social behavior patterns which are species-specific arises, as well as pronounced dissimilarities among males and females within the same species (Newman 1999).

Goodson (2005) suggested the extension of this model to nonmammalian vertebrates. He presented evidence to show that birds and teleost fishes also have an SBN, and particularly an amazing evolutionarily conservation of the mechanisms that regulate social behavior in vertebrates. Furthermore, he introduced neuropeptide modulation, namely arginine vasotocin (AVT, the mammalian homologue of arginine vasopressin) and isotocin (IT, the homologue of oxytocin), as important components of the SBN by enabling additional plasticity and diversity in social behavior.

However, an individuals' adaptive response is an integration of internal physiological cues and external stimuli being evaluated. The evaluation of the salience of a stimulus is assumed to be regulated by the Mesolimbic Reward System (via dopaminergic signaling) and is pivotal for social behavior. In that sense, O'Connell and Hofmann (2011) proposed that social behavior would be concurrently regulated by two neural circuits: the SBN and the Mesolimbic Reward System, constituting the Social Decision Making Network (SDMN). The mesolimbic reward system is a composite of eight areas: the Striatum (Str), the Nucleus Accumbens (NAcc), the Ventral Pallidum (VP), the Basolateral Amygdala (blAMY), the Hippocampus (Hyp), the Ventral Tegmental Area (VTA), and the LS and the BNST/meAMY, overlapping nodes of the SBN. With their study, they provided a comparative analysis of these two networks in five major vertebrate lineages: mammals, birds, reptiles, amphibians, and teleost fishes. Based on hodology, neurochemical profiles, development, gene expression, presence of steroid hormone receptors, and behavioral functional studies, the authors presented putative brain homologies. Their aim was achieved—to provide a useful resource to study the neural substrates responsible for social behavior in vertebrates and a relevant framework to make systematic species comparisons.

Although the SDMN model is consistent and strongly supported in mammals, its application to nonmammalian species is questioned. Some of the proposed homologies are not straightforward or are only partial, and functional studies are lacking, particularly for the mesolimbic reward system, raising concerns in its extrapolation to other taxa, such as cichlids (Goodson and Kingsbury 2013). One example of such is the POA node, where the anamniotes correspondent comprises vasopressin–oxytocin nonapeptides neurons, whereas in amniotes those cells are within the paraventricular nucleus of the hypothalamus (PVN). Thus, some propose the mammalian node as POA/PVN, thereby including these peptidergic neurons, so important in behavioral modulation (Goodson and Kingsbury 2013). The same authors endorse the SDM as a workable framework that is not yet an evidenced and confirmed model.

3.1 Comparing Teleost Fishes and Mammals: SDMN Brain Homologies

The teleost SBN is presumably constituted by the supracommisural part of the ventral pallium (Vs), the ventral (Vv), and lateral (Vl) parts of ventral telencephalon, the POA, the ventral tuberal nucleus (vTn), the anterior tuberal nucleus (aTn), all localized in the forebrain, and the PAG, lying in the midbrain (O'Connell and Hofmann 2011). The Mesolimbic Reward System is assumed to be composed of the central (Vc) and dorsal (Vd) parts of the ventral telencephalon, the medial part of the dorsal telencephalon (Dm), the lateral part of the dorsal telencephalon (Dl), the posterior tuberculum (TPp) in the midbrain, and also the Vv/Vl and the Vs, concurring nodes of the SBN (O'Connell and Hofmann 2011). Figure 2 represents a schematic diagram of the SDMN in teleosts and Table 1 summarizes the putative mammalian correspondence for each teleost brain nucleus.

The fact that the teleost telencephalon undergoes an eversion during development—instead of an invagination like all other vertebrates—renders homology determination an arduous task (Wullimann and Mueller 2004). Nevertheless, grounded on neuron connectivity, neurochemical profiles, development, gene expression, presence of steroid hormone receptors, and functional studies, O'Connell and Hofmann (2011) present the following brain homologies:

- The Vs is the putative homologous region of the meAMY/BNST, due to conserved expression patterns of developmental genes, hodological features, and neurochemical studies (reviewed in O'Connell and Hofmann 2011). Goodson and Kingsbury (2013) though point to chemo-architectural evidence to consider that the postcommissural nucleus of the ventral telencephalon (Vp) is combined

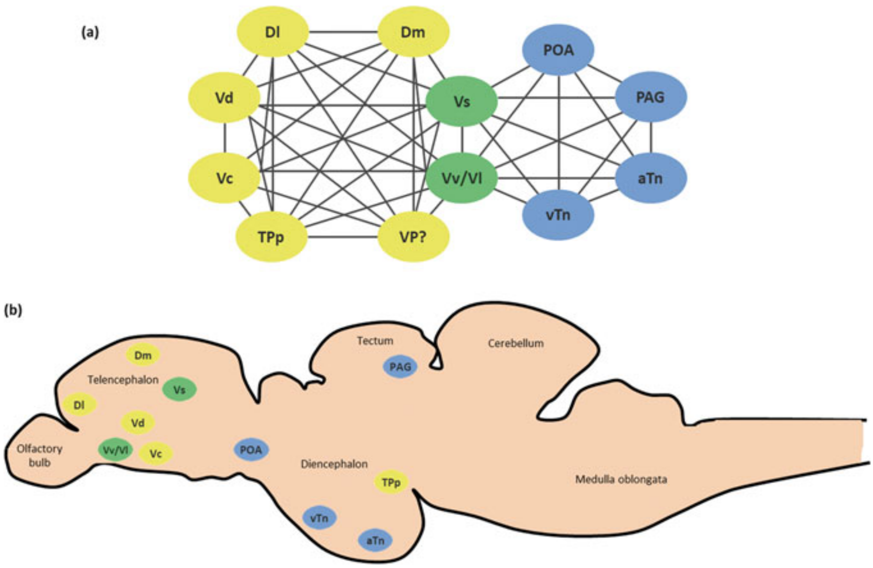

Fig. 2 (**a**) Representation of the interaction between hormones and the Social Decision-Making Network (SDMN) within teleosts social behavior: putative nodes of the Mesolimbic Reward System in yellow—dorsal (Vd) and central (Vc) part of the ventral telencephalon, medial part of the dorsal telencephalon (Dm), lateral part of the dorsal telencephalon (Dl), posterior tuberculum (TPp), and the Social Behavior Network in blue—Medial Preoptic Area (POA), ventral tuberal region (vTn), anterior tuberal nucleus (aTn), and Midbrain Periaqueductal Gray (PAG). Ventral and lateral (Vv/Vl) parts of ventral telencephalon and supracommisural part of the ventral pallium (Vs), overlapping nodes of the SBN and the Mesolimbic Reward System, are in green. A homologous for the mammalian Ventral Pallidum (VP) node has not yet been identified. (**b**) Schematic diagram of a sagittal section of a teleost brain representing the SDMN brain nodes

with the Vs and suggests that the Vs/Vp is even homologue to the entire subpallial amygdala.

- The Vv and Vl are comparable to the mammalian LS region since cholinergic neurons were only detected here. This area is reciprocally connected to other nuclei and it contains sex steroid receptors (see Wullimann and Mueller 2004; O'Connell and Hofmann 2011 for more details). Its relationship with reproductive behavior is supported by some studies—the Vv and the Vs ablation of *Carassius auratus* impairs male ejaculation while stimulation of the Vv in females' *Oncorhynchus nerka* elicits digging and spawning (Kyle and Peter 1982; Satou et al. 1984). However, besides the fact that the Vv presents some similarities with other regions, the Vv/Vl are exclusive of subpallial origins while LS has important pallial components involved in the process information between the SDM and the mesolimbic system. Thus, relevant questions arise with this homology (Goodson and Kingsbury 2013).
- The teleost POA is localized in the hypothalamus along the third ventricle and is divided into three subregions accordingly to cell size: parvocellular, magnocellular, and gigantocellular. Like in mammals, it is reciprocally connected

Table 1 Putative mammalian correspondence for each teleost brain nuclei of the Social Decision-Making Network (SDMN)

	Abbreviation	Teleosts SDMN brain nuclei	Putative mammalian correspondence	
Social behavior network	POA	Medial preoptic area	Medial preoptic area	
	vTn	Ventral tuberal nucleus	Anterior hypothalamus	
	aTn	Anterior tuberal nucleus	Ventromedial and ventrolateral hypothalamus	
	PAG	Periaqueductal gray	Periaqueductal gray and tegmentum	
	Vs	Supracommisural part of the ventral pallium	Medial extended amygdala (bed nucleus of the stria terminalis and medial amygdala)	Mesolimbic Reward System
	Vv/Vl	Ventral (Vv) and lateral (Vl) parts of ventral telencephalon	Lateral septum	
	Vc	Central part of the ventral telencephalon	Striatum	
	Vd	Dorsal part of the ventral telencephalon	Nucleus accumbens	
	Dm	Medial part of the dorsal telencephalon	Basolateral amygdala	
	Dl	Lateral part of the dorsal telencephalon	Hippocampus	
	TPp	Posterior tuberculum	Ventral tegmental area	

with the telencephalon and other hypothalamus regions (reviewed in O'Connell and Hofmann 2011). Several studies report its role in sexual, parental, and agonistic behaviors (Demski and Knigge 1971; Macey et al. 1974; Satou et al. 1984; Wong 2000).

- The vTn was proposed to be the teleost correspondence of the AH since it is localized between the POA and the ventral hypothalamus, it receives and sends projections to several hypothalamic regions and contains sex steroid receptors (O'Connell and Hofmann 2011 revised this information). Despite the fact that Goodson and Bass (2000) proposed the preoptic area–anterior hypothalamus region as a regulatory component of reproductive vocalizations in *Porichthys notatus*, other functional studies are yet not available.
- The homologue of the aTn is considered to be the VMH, however, only a subset of aTn cells are actually homologous (Goodson and Kingsbury 2013). It is localized in the ventrocaudal region of the hypothalamus, receiving and sending projections to several parts of the telencephalon, and contains sex steroid

hormone receptors. O’Connell and Hofmann (2011) provide further details. Functional studies are as clearly limited.

- The PAG is located near the torus semicircularis. It is reciprocally connected with several other nuclei and contains sex steroid hormone receptors (see O’Connell and Hofmann 2011, for more information). Functionally similar to mammals, it is as well associated with social communication, e.g., *P. notatus* (Kittelberger et al. 2006).
- The Vc seems homologous to the Str in mammals, essentially based on neurochemical studies (consider Wullimann and Mueller 2004 and O’Connell and Hofmann 2011, for more details).
- The Vd has been suggested to present homologies to the NAcc due to hodological evidence such as ascending dopaminergic projections or the presence of dopamine receptors and GABA immunoreactivity but at the neurochemical level shows similarities also to the Str (consider Wullimann and Mueller 2004 and O’Connell and Hofmann 2011, for more details). More studies are needed to fully comprehend the Vc and Vd nuclei.
- Unfortunately, a teleost homology for the mammalian VP node has not yet been identified.
- The Dm seems to match the blAMY based on hodology, neurochemistry, and lesions studies connecting this region to emotional learning, as in mammals, as reviewed in Portavella et al. (2002) and O’Connell and Hofmann (2011).
- The Hyp is the putative homologous of the Dl due to tract-tracing evidence and lesions studies in *C. auratus* showing its relevance in spatial learning; reviewed in Rodríguez et al. (2002) and O’Connell and Hofmann (2011).
- Lastly, the TPp homology is controversial. Amphibians and teleosts lack a midbrain dopaminergic population, however, TPp, located in the ventral diencephalon, seems homologous to mammalian VTA and/or substantia nigra because of its dopaminergic ascending projections to the striatum region and gene expression profiles (see O’Connell and Hofmann 2011 for details). On the other hand, a study in zebrafish revealed that posterior tuberculum cells seem homologous to A11 mammalian dopamine neurons, contrary to what happens in the VTA, constituted by A10 dopamine neurons (Tay et al. 2011). Based on transcription factor conservation and projection patterns they showed that ascending projections to telencephalon are scarce, while the most important dopaminergic connections between the subpallium and the ventral diencephalon are as a matter of fact descending. Consequently, the existence of a mesolimbic reward system in fish is questionable (Goodson and Kingsbury 2013) since the VTA is considered a primary component of the mesolimbic dopamine system (Spanagel and Weiss 1999; Bromberg-Martin et al. 2010).

3.2 The Cichlid Social Decision-Making Network

Endocrine modulation of the Social Decision-Making Network (SDMN), and subsequently of social behavior, in cichlid fishes, is supported by in situ hybridization studies in the mouthbrooder cichlid, *Astatotilapia burtoni*, which showed the expression of estrogen, progesterone, androgen, arginine vasotocin, and oxytocin receptors (Harbott et al. 2007; Munchrath and Hofmann 2010; Huffman et al. 2012; O'Connell et al. 2012; Loveland and Fernald 2017; Weitekamp et al. 2017), widely distributed along the areas of the SDMN.

So far, most of the published studies documenting the activation of the SDMN network, specifically in cichlids, used *A. burtoni* as a fish model. One example of this is the work undertaken by Maruska et al. (2013a, b). Since *A. burtoni* males can reversibly switch between dominant and subordinate status and rapidly show distinct phenotypes, the authors cleverly used a paradigm to manipulate social rank. Then they measured by qPCR brain immediate early genes (IEG), the first genomic response to a stimulus, as markers of neuronal activity, in several brain areas of males either ascending or descending in social status and compared with control individuals. For social ascending males, both *c-fos* and *egr-1* levels were higher in all the studied SDMN nuclei (Vs, Vv, POA, vTn, aTn, Dm, and Dl) (Maruska et al. 2013b). Surprisingly, descending males presented different activation patterns for *c-fos* and *egr-1* across the same areas, namely, increased *c-fos* expression levels in the Vs, POA, and aTn while *egr-1* mRNA levels were higher in the Vv, Vs, vTn, Dm, and Dl (Maruska et al. 2013a). Additionally, hormone levels are affected in minutes, which suggest that the SDMN is involved in integrating social information along with hormonal states, to favor social transitions (Maruska et al. 2013a, b).

On the other hand, Desjardins et al. (2010) studied how social information regarding potential mates affects females at the brain level. They induced different neural states in gravid females by exposing them to fights where their preferred males won or lost. Then they examined IEG, *c-fos*, and *egr-1* expression levels in the Vv (LS), POA, vTn (AH), aTn (VMH), PAG, Dm, and Dl, selected nodes of the SDMN. Their results demonstrated that reproductive nuclei, namely POA and VMH (see Sakuma and Pfaff 1979, for a supporting example on the VMH role in mammals' reproductive behavior), show the highest IEG expression when females see their preferred males winning. In contrast, the mammals LS homologue region, which is a nucleus associated with anxiety in mammals (Degroot et al. 2001) is highly activated when females see the male losing.

O'Connell et al. (2013) focused on how individuals process social cues, by presenting *A. burtoni* males with different sensory stimuli (visual and/or chemical) in distinct social contexts. They found that visual information (seeing a female or a male) is sufficient to elicit *c-fos* transcription in dopaminergic neurons of Vc, compared to the neutral (control) condition. Interestingly, in the case where males were exposed to an intruder male stimulus, the elicited genomic response is significantly correlated to aggression but not with motor activity. The authors suggest that the Vc can be involved in assessing stimulus visual valence.

Other researchers evaluated the influence of the nonapeptide isotocin in parental care by using the monogamous cichlid *Amatitlania nigrofasciata* (O'Connell et al. 2012). They quantified *c-fos* expression by in situ hybridization technique to compare biparental males housed with their mate (control males), single fathers with the mate removed or lone males with mate and offspring removed. They directed their interest to Vv, POA, and the central part of the dorsal telencephalon (Dc) and also in the co-localization of *c-fos* and isotocin in the POA. Single fathers increased paternal care immediately after mate removal and also showed significantly higher IEG activity levels in the Vv compared to lone males, as well as increased *c-fos* expression in the parvocellular preoptic isotocin neurons. In summary, these results show that isotocin is involved in paternal care by promoting parental behavior after mate removal and that Vv and POA are important underlying brain areas.

Finally, Roleira et al. (2017) analyzed, by qPCR, the patterns of brain activation of Mozambique tilapia (*O. mossambicus*) males subjected to territorial intrusions, in the presence or absence of a female audience and tested the SDMN hypothesis. Focused on studying the mechanisms underlying the audience effect phenomenon (see Sect. 3.1 for more details on this subject), they verified that, besides the increase of the territorial defense behaviors by focal males in the presence of females, contrasting social contexts originated different behavioral states represented by distinct patterns of functional connectivity across the SDMN nodes. In particular, no localized activity (i.e., immediate early genes expression *c-fos* and *egr-1*) of any of these nodes (Dm, Dl, Vv, Vs, POA, aTn, CG) was attributed to either of the treatments but instead different clusters of brain areas and corresponded densities of connections, supporting the SDMN model (Roleira et al. 2017). These cases and others, e.g., in the teleost fish *Danio rerio* (Teles et al. 2015), support the SDMN hypothesis and its involvement in the regulation of social behavior.

4 Cognitive Adaptations for Social Living

Social cognition is the process of acquiring information and also managing, storing, and applying it whenever is necessary, particularly in the context of social relationships (Dukas 2004). The term embodies a manifold of concepts such as perception, social learning, memory, attention, or decision-making (Dukas 2004), which allow an individual to apprehend social information and adopt proper behavioral responses.

The "Machiavellian intelligence hypothesis" (Byrne and Whiten 1988, 1997) was initially proposed to explain the evolution of cognitive abilities in primates as a result of social complexity. The main idea is that selective forces acted preferentially upon individuals with advantageous social tactics, such as manipulation and deception, which allow them to have more successful competitive interactions with others. Increased fitness is achieved when an individual benefits at the expense of others (manipulation); occasionally both parts gain (cooperation), while in other situations group members are unaware of the loss involved (deception). Clearly, the cognitive capacities of recognizing conspecifics and recalling relative status, affiliations, or even past events are essential for one to adopt the above-mentioned Machiavellian tactics (Byrne 1997). With this hypothesis, the authors also suggested that social cognitive abilities are related to size or structure of the brain, based on the fact that primates have larger brains and enhanced cognitive skills compared with other animals (Byrne and Whiten 1988, 1997). However, Dunbar (1992, 1995) was the first to test this hypothesis showing that primate group size correlates with relative neocortical volume. As a consequence, the "social brain hypothesis" (Dunbar 1998) as an alternative label was adopted, which posits that complex societies require more social cognitive competences and consequently larger brains, specifically neocortex tissue, to process the increasing degree of information involved. Interestingly, relative brain size is specifically associated with pair bonding, i.e., larger brains correlate with monogamy, suggesting that this was the main factor underlying brain evolution (Dunbar and Shultz 2007). Both the Machiavellian intelligence hypothesis and the Social brain hypothesis have been applied to other vertebrate taxa, namely fishes (Bshary 2006, 2011; Dunbar and Shultz 2007).

For instance, Pollen et al. (2007) compared closely related species of cichlids from the Ectodini clade of Lake Tanganyikan that differed in habitat preference and social organization. They obtained correlations between habitat features and brain size, cerebellar size, medulla, and olfactory bulb, while only telencephalon and hypothalamus correlated with sociality. The telencephalon is larger whereas the hypothalamus is decreased in monogamous species. These results endorse the "mosaic evolution model" of the brain because they suggest that selection acted differentially on distinct brain regions and that both environmental and social characteristics acted as selective pressures (Barton and Harvey 2000). Within this model, each brain region is functionally different, i.e., is responsible for a distinct set of behaviors and evolution acts only in the regions underlying the cognitive traits being selected (favoring its enlargement) since brain tissue is metabolic costly (Isler and van Schaik 2006). In contrast, the "developmental constraints model" argues that if selection acts on the brain, it would induce a change in whole brain structure (Finlay et al. 2001). Likewise, a more extensive study on 43 cichlid species of this lake corroborated the mosaic evolution model since brain structures showed variation in their patterns of evolution despite some contribution of concerted evolution (Gonzalez-Voyer et al. 2009a). Another study, focused on 39 species from Lake Tanganyika, showed that brain size is correlated with diet and female brain size correlates significantly with care type (Gonzalez-Voyer et al. 2009b). Specifically, in species where only the females care for the young, females had larger brains than females that are helped by males in the care of the young (biparental care) (Gonzalez-Voyer et al. 2009b). However, after controlling for brain size, only cerebellum and hypothalamus from males are actually negative-associated with female-only care (Gonzalez-Voyer and Kolm 2010). In the same study, cerebellum volume seems decreased with sexual selection, the hypothalamus is negatively associated with mating competition and telencephalon size shows sexual dimorphism and is negatively correlated with mating competition (Gonzalez-Voyer and Kolm 2010).

Having in mind the social brain hypothesis, Reddon et al. (2016) compared several related cooperative cichlid species from Lake Tanganyika and other noncooperative cichlids to test if cooperation is translated into larger brains. Typically, in cooperatively breeding species, fish live in groups with a dominant breeding pair and several conspecifics that act as helpers. Helpers defend the territory against predators and other conspecifics and participate in brood care. This apparent altruistic behavior has costs (e.g., slower growth rate) and benefits (e.g., lower mortality, higher parental reproductive success, and increased probability of acquiring territories) (Taborsky 1984b; Balshine-Earn et al. 1998). However, although cooperative behavior is complex requiring several cognitive competences, there were no differences in whole brain mass between cooperative and independently breeding species (Reddon et al. 2016).

Sylvester et al. (2010, 2013) centered their investigations of the mechanisms responsible for brain development comparing rock- and sand-dwelling cichlids from Lake Malawi (East Africa), fish that display differentiated brains and behaviors even though genetically similar (Loh et al. 2008). Rock-dwellers (“mbuna” species) are more territorial and aggressive, live in complex habitats, and eat algae; sand-dwellers (“non-mbuna” species) are seasonal-lek breeders and eat small prey utilizing acute vision. Interestingly, rock-dwelling cichlids have larger telencephalon and olfactory bulbs whereas sand-dwelling cichlids exhibit enlarged optic tecta, thalamus, and eyes (reviewed in Sylvester et al. 2011). By manipulating gene expression patterns of specific developmental genes (ventral Hedgehog—Hh and dorsal Wingless—Wnt), which integrate different signal transduction pathways (Sylvester et al. 2011), in cichlids and zebrafish, they were able to change telencephalon patterning (pallial/subpallial organization from mbuna to non-mbuna proportions, and vice versa, Fig. 3) and show that variations in early development are responsible for changing brain structures (Sylvester et al. 2010, 2013). Further studies that address not only variation in size but also the complexity and connectivity of different brain areas in cichlids are expected to highlight which brain features are responsible for such complex systems of social organization.

4.1 Social Skills in Cichlids

In fishes, a considerable body of literature has been published on social cognition and has distinguished the primary elements of social cognition (Bshary et al. 2002, 2014; Brown et al. 2011; Oliveira 2013; Bshary and Brown 2014). The following section presents a collection of these cognitive adaptations for social living in cichlids, including but not limited to individuals’ recognition, counting abilities, and transitive inference.

The ability of individuals to recognize others has been studied in some cichlids. In the cooperative breeder *N. pulcher,* by using playback videos, it was shown that these fish court their mates and fight against other conspecifics (Balshine-Earn and Lotem 1998). Other authors used manipulated digital images and showed that

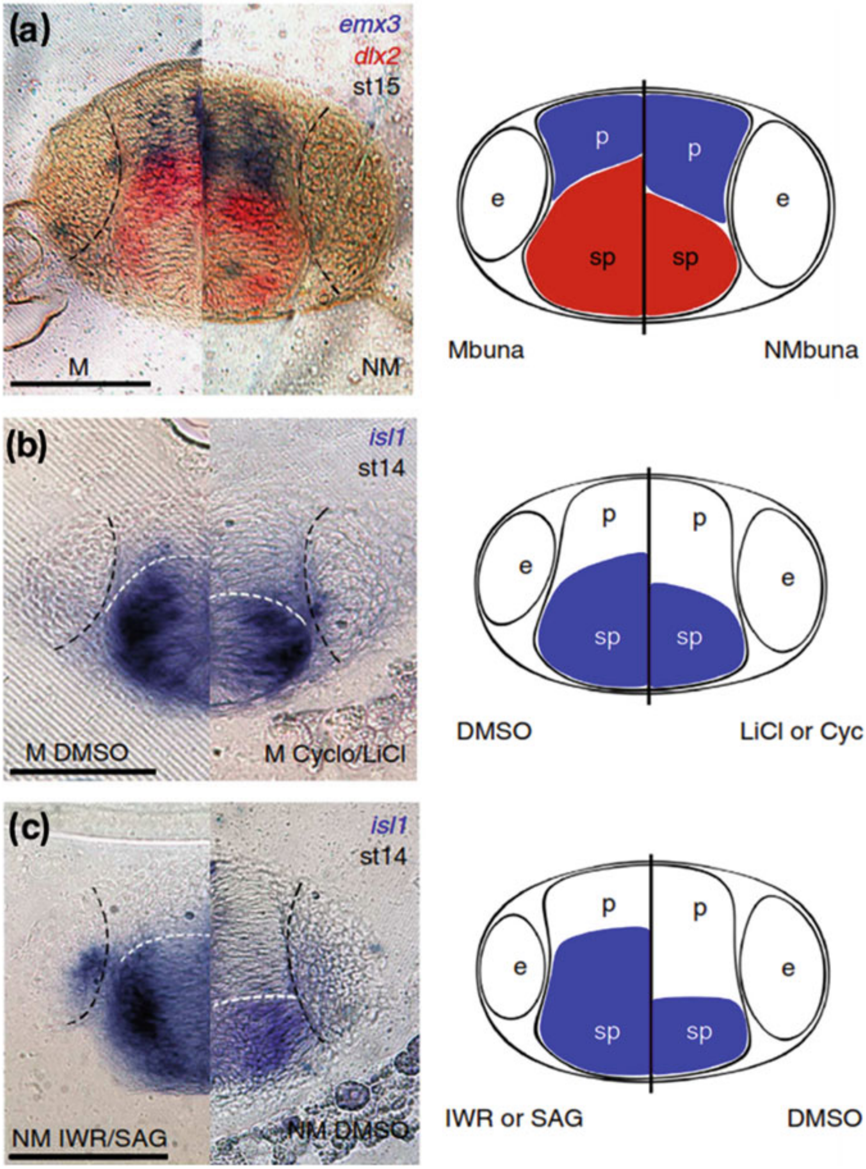

Fig. 3 Study of the mechanisms responsible for brain development in cichlid rock ("mbuna," M) versus sand ("non-mbuna," NM) dwellers (Sylvester et al. 2013). Left panels are transverse sections of the telencephalon, and right panels are schematics of the data represented on the left. Black dotted lines represent the position and size of the eyes in each section. Scale bar, 100 mm. (**a**) A "splitscreen" double ISH of *emx3* (blue) and *dlx2* (red) used to visualize the pallium and subpallium in mbuna (M), left, and non-mbuna (NM), right, showing the difference in pallial/subpallial proportions. (**b**) Expression of the subpallial marker *isl1* is depicted, and an expansion of the pallium (above dotted white line) in cyclopamine- or LiCl-treated mbuna (right side) versus DMSO control mbuna (left) is showed. LiCl is an activator of the Wnt pathway, whereas cyclopamine is an antagonist of the Hh pathway. (**c**) An expansion of the subpallium (below dotted white line) in SAG- or IWR-treated non-mbuna (left side) versus DMSO control non-mbuna (right) is shown.

N. pulcher can distinguish between familiar and unfamiliar conspecifics based on visual cues. Specifically, fish use facial features but not other body characteristics to discriminate among individuals (Kohda et al. 2015). Amazingly, this ability takes less than 0.5 sec (Kohda et al. 2015). Moreover, within this species, it was also shown that individuals can distinguish between kin and nonkin and preferably associate with kin (Hert 1985; Le Vin et al. 2010). This could be a way to improve (indirect) fitness by helping to raise kin and also to avoid inbreeding (Pusey and Wolf 1996). This species is also able to recognize predators only by using visual information (O'Connor et al. 2015b). In *Neolamprologus multifasciatus*, another cooperative species, territorial males are more aggressive to strange males than to strange females, while females exhibit the reverse (Schradin and Lamprecht 2000). Interestingly, the cave-breeding fish, *P. taeniatus*, recognizes its own odor (Thünken et al. 2009). This species can clearly distinguish between its own odor compared to an odor of an unfamiliar conspecific and additionally prefer the cave with its own scent over one with a familiar kin odor (Thünken et al. 2009). The authors suggest that this ability could probably confer them advantages in localizing their own cave territory and to avoid intrasexual competition (Thünken et al. 2009).

Another interesting phenomenon is the "dear enemy" effect, evidenced in territorial species, where dominant individuals show less aggressivity to familiar conspecifics than to unfamiliar ones (sensu Fisher 1954). The latter individuals induce an increased aggressive response as no previous interactions occurred between them and no previous information on their competitive abilities is available. These intruders are thus seen as potentially more threatening since they may try to control the territory if the resident does not counteract rapidly and efficiently (Temeles 1994). The dear enemy effect has been tested in several taxa, e.g., mammals, birds, reptiles, amphibians, and also in fishes (Ydenberg et al. 1988; Temeles 1994). In cichlids, it has been confirmed in *A. nigrofasciata* (Leiser and Itzkowitz 1999), *N. pulcher* (Frostman and Sherman 2004), and *O. mossambicus* (Aires et al. 2015) attesting to the capacity of cichlids to distinguish between familiar and unfamiliar conspecifics, as a way to adopt more optimized social responses. Interestingly, a study on *N. pulcher* has shown that low-ranking subordinates are more aggressive to a subordinate conspecific visitor than higher-ranking fish when compared with control groups (Ligocki et al. 2015b), showing that social behavior toward conspecifics is modulated according to the perception that an individual has of others. This can be seen as beneficial to the group by the dominants but perceived as a threat by subordinates.

Besides individual recognition, remembering past interactions could be advantageous to individuals, for instance as a mechanism to recall other males' physical condition. Thus, the duration of memory of dominance relationships was addressed in a study with *J. transcriptus* (Hotta et al. 2014). The authors staged fights with

◄

Fig. 3 (continued) SAG is an Hh agonist and IWR is a Wnt antagonist. Figure reproduced from Sylvester et al. (2013) with permission from Springer Nature paired-sized males and assessed winner and loser individuals and then loser males were able to interact with the winner male or with other males, 3, 5, or 7 days after the first trial. Results show that loser males only displayed subordinate behavior in the presence of the winner male and not to other rival males on day 3 and day 5 and that subordinate behavior disappeared on day 7 (Hotta et al. 2014). This study reports that subordinate males recall a fight up to 5 days maybe as a way to avoid confrontations with a "stronger" male.

Amazingly, cichlids can distinguish the social rank of conspecifics by direct experience but also make predictions about the relationship between individuals that were never compared by using the information available on known relationships (Grosenick et al. 2007). For instance, if A is more dominant than B ($A > B$), and B has a higher social rank than C ($B > C$), then A is hierarchically above C ($A > C$). This more complex social cognitive mechanism is named transitive inference. *A. burtoni* males were tested for the ability to infer hierarchy by watching pairwise fights of size-matched males. Only visual information was available. Bystanders were able to discriminate individuals and specifically the dominance hierarchy ($A > B > C > D > E$) by preferring to associate with the losers (Grosenick et al. 2007). Transitive inference was also supported in a highly social cichlid fish, *J. transcriptus* (Hotta et al. 2015a, b). This cognitive ability would able fish to avoid engaging in costly aggressive interactions with conspecifics that are "stronger" than them.

Another cognitive skill described in fish is their counting abilities. Freshwater tropical angelfish, *Pterophyllum scalare*, are able to discriminate between shoals ranging in size ratio 4:1, 3:1, and 2:1 (Gómez-Laplaza and Gerlai 2011). Interestingly, the relative size of the shoals instead of the absolute numerical difference between them was the main mechanism underlying this preference, since they were not able to distinguish more similar shoals (e.g., 1.7:1 ratio). This suggests that angelfish make relative comparisons between shoal sizes, always preferring to stay closer to the larger shoal (Gómez-Laplaza and Gerlai 2011). The competence to distinguish more from less seems conserved in cichlids and provides a means for species to benefit from shoaling (e.g., by acquiring increased protection against predators or efficacy in foraging).

Even though social learning has been reported in several teleost fishes as a way to gain information regarding antipredator, foraging, or migration behaviors among others (reviewed in Brown and Laland 2003), in cichlids, such studies are scarce. Barks and Godin (2013) tested if juvenile convict cichlid, *Amatitlania nigrofasciata*, could learn to distinguish novel visual cues as a threat or non-threat, by using social information from conspecifics, but without success. On the other hand, Alcazar et al. (2014) found that older males have more fighting abilities than younger ones, and in some cases, younger animals were larger. The authors consider age as a proxy of social experience (i.e., more social interactions) and suggest that social learning is a major advantage of agonistic competition.

Other social skills present in animals that live in communication networks are "eavesdropping" and "audience effects." When an individual directly communicates/signals to another, further animals may receive this information as well.

Hence, communication involves a signaler, a receiver, and also bystanders (McGregor 1993). These animals, which are not directly involved in the interaction, compose an audience, and their presence, influences the signaler behavior ("audience effects"). This means that signalers can strategically change the salience or intensity of their signals according to the presence of bystanders. This has been already tested in several teleosts (Doutrelant et al. 2001; Dzieweczynski et al. 2005, 2014; Plath et al. 2008; Plath and Schlupp 2008) and is a phenomenon that is also dependent on the composition of the audience (Doutrelant et al. 2001).

In the cichlid *A. burtoni*, Desjardins et al. (2012) showed that non-territorial males act more aggressively and court females when the territorial male is not watching them. They also tested for the effect of different audiences on the behavior of pairs of size-matched dominant males fighting each other and verified that when a larger male is in the audience, focal males decrease aggression, whereas a gravid female induces an increase in aggressive behavior, compared with controls. This confirms that *A. burtoni* males change their behavior if they are being observed but also that there is a fine-tune modulation of the behavior according to whom is watching, possibly to avoid unnecessary agonistic interactions and optimize reproductive opportunities (Desjardins et al. 2012). A study based on a similar paradigm focused on brain IEG *egr-1* activation pattern in several areas of the SDMN, Vs, Vv, POA, vTn, aTn, PAG, Dm, Dl, of both the signaler and the bystander, with different relative sizes (Desjardins et al. 2015). Results obtained with qPCR show that nuclei involved in reproduction and aggression, Dm, POA, and Vv, are differentially expressed in males that are fighting but surprisingly also in the males that are watching them, in comparison with control individuals. Furthermore, both when the audience was composed of larger males and when fighting males were larger, the Vv, a nucleus associated with anxiety was activated in the fighting males and observer males, respectively. Interestingly, the patterns of brain gene expression (namely in the POA and the Vv) between fighters and observers are more similar than controls, suggesting that the same circuit is activated whenever social behavior is expressed but also when social information is received and that the SBN plays a pivotal role in cichlids social cognition (Desjardins et al. 2015).

In the cooperative breeding cichlid *N. pulcher*, subordinates vary in their response to a predator according to the presence or absence of neighbors, specifically, they increase their aggressive behavior if another group of conspecifics is watching them, probably as a way to signal their ability for group survival (Hellmann and Hamilton 2014). On the other hand, bystanders that use the available social information are called eavesdroppers. Eavesdropping is the ability of individuals to indirectly collect information about others just by watching social interactions and use this information in their subsequent behaviors. This social skill is particularly advantageous as it is a way to acquire valid information, for instance on opponents' fighting abilities or potential mates, which involves no costs, since the animals do not engage in dangerous interactions. Eavesdropping has already been reported in several teleosts, proving the importance of this skill in social behavior (Oliveira et al. 1998; Doutrelant and McGregor 2000; Earley and Dugatkin 2002; Abril-de-Abreu et al. 2015) and also in the convict cichlid *A. nigrofasciata* (van Breukelen and Draud

2005). *A. nigrofasciatus* is a monogamous species where male and female establish a bond that sometimes is broken by one of the individuals to get access to another mate. Within this study, females were presented to other males (rival males), with the same size or larger than their mates and the divorce rate was evaluated. Then, rival males were allowed to interact with male mates in the presence of the female eavesdroppers. The authors found that there was an increased rate of divorce (50%) when rival males were larger than mates and females watched the interaction between the males, whereas the treatment with decreased divorce (0%) was the situation where males were similar in size and females did not eavesdrop (van Breukelen and Draud 2005). This study shows that these females tend to divorce when a higher quality male is available but they need to evaluate their relative condition by an eavesdropping tactic.

Besides the examples already mentioned, other very interesting social skills have been reported in teleost fishes such as cooperative hunting (Strübin et al. 2011; Vail et al. 2013), manipulation and deception (Bshary and Oliveira 2015) or collective cognition (Sumpter et al. 2008; Ward et al. 2011). In the future, we expect to understand further the neural circuits underlying these social cognitive processes in fish as more neurogenomic tools become available.

5 Neuroendocrine Regulation of Social Behavior

The relationship between hormones and behavior has been a matter of interest for several centuries. The initial paradigm established hormones as directly responsible for behaviors, grounded in classical experiences of castration and androgen replacement studies (see Oliveira 2004, for historical background). However, experiments showing that hormones rather increase the probability of the individuals to express behaviors instead of switching on and off behaviors altered this simplistic concept (e.g., Albert et al. 1993). Currently, it is clearly recognized that hormones act as modulators of the neural mechanisms underlying behavior (Oliveira 2009). On the other hand, intensive studies in recent decades have focused on the influence of social interactions on hormones. Actually, the social environment surprisingly feedbacks on neuroendocrine mechanisms, i.e., social interactions are responsible for changing hormone levels which, in turn, modulate perceptive, motivational, and cognitive mechanisms and ultimately subsequent social behavior (Oliveira 2004).

Mazur (1985) was the first to propose a reciprocal relationship between androgens and dominant behavior. Later, "The Challenge Hypothesis" (Wingfield et al. 1990) was presented to explain the adaptive nature of the androgen response to social interactions, and it has been characterized across all vertebrate taxa (Hirschenhauser and Oliveira 2006). The Challenge Hypothesis generates a number of predictions regarding the patterns of androgen social responsiveness according to mating system and parental care types, which have been extensively tested recently and in particular in cichlids (see Oliveira 2004, for a review of this topic)

Nevertheless, social modulation of neuroendocrine activity is not restricted to androgens (Goodson 2005; Summers et al. 2005; Godwin and Thompson 2012). The next sections will present examples of these interactions between hormones and social behavior, centering our discussion on sex steroids (11-ketotestosterone, KT; testosterone, T; estradiol, E2), cortisol (F), and the neuropeptides AVT and IT

5.1 Hormonal Actions on Behavior

As mentioned earlier, sex steroids receptors (AR, ER, PR) are distributed throughout the telencephalon and the diencephalon in specific areas related to social behavior, proving to be major actors in the regulation of these behaviors (*A. burtoni*, Munchrath and Hofmann 2010)

Reproductive behavior, for instance, seems to be intimately associated with sex steroids since castration studies in males abolishes spawning pit digging, nuptial coloration, and courtship *Pseudocrenilabrus multicolor* (Reinboth and Rixner 1970); *Sarotherodon melanotheron* (Levy and Aronson 1955); *Astatotilapia burtoni* (Francis et al. 1992; *O. mossambicus*, Almeida et al. 2014a). Exogenous administration of AR agonists also supports this association by promoting nest-building behavior or courtship *A. burtoni*, (O'Connell and Hofmann 2012); *A. nigrofasciata* (Sessa et al. 2013) while AR antagonists decrease courtship (O'Connell and Hofmann 2012); *A. nigrofasciata* (van Breukelen 2013). Estrogens also seem to play a complex role in nest-building behavior because either ER agonists or antagonists promote nest-building behavior (Sessa et al. 2013). Other researchers claim, however, that gonadectomized males maintain their reproductive behavior repertoire (*Hemichromis bimaculatus*, Noble and Kumpf 1936; *Andinoacara* (formerly *Aequidans*) *latifrons*, Aronson et al. 1960, *Sarotherodon melanotheron and Oreochromis upembae*, Heinrich 1967), which suggests that sex steroids influence on behavior is species specific. Furthermore, a more recent study on *A. burtoni* provided solid evidence that prostaglandin PGF2**α** is necessary and sufficient to induce reproductive behavior in *A. burtoni* females (Juntti et al. 2016). Since the injection of PGF2**α** in females induces spawning behavior, they generated mutants that had no expression of the putative PGF2**α** receptor (Ptgfr), by using CRISPR/Cas9 technology. Results show that female mutants are not able to express the final stages of reproductive behavior in as much as PGF2**α** acts presumably on the POA and the vagal lobe acting as a signaler of fertility into the brain where this receptor is expressed regulating sexual behavior (Juntti et al. 2016).

Aggression is also modulated by sex steroids since androgen-treated fish increase aggressive behavior (e.g., *A. burtoni,* Fernald 1976; *Andinoacara pulcher,* Munro and Pitcher 1985) whereas blocking androgen receptors lowers aggression levels (e.g., *A. nigrofasciata,* Sessa et al. 2013). However, apparently, there are independent neural circuits controlling reproductive and aggressive behaviors. For instance, in *A. nigrofasciata*, van Breukelen (2013) was studied, both in the laboratory and in the field, the effect of androgens on pre-spawning courtship and aggression by using flutamide as a blocker of androgen receptors. Results showed that flutamide was responsible for a significant decrease in the courtship behavior of males treated with flutamide Silastic implants compared to control or sham males. However, aggression toward conspecific males was not affected by this androgen receptor antagonist, supporting evidence for a decoupling between courtship and aggression in terms of neuroendocrine mechanisms. Castration experiments also corroborate this idea. Research with gonadectomized *O. mossambicus* males showed that these animals suffer a profound decrease in circulating androgens and stopped expressing reproductive behaviors, yet aggression was not affected (Almeida et al. 2014a). These observations and the possible enzymatic conversion of testosterone to estrogen, support the argument that androgens moderate aggressive behavior directly or via aromatization to estrogen. O'Connell and Hofmann (2012) concluded that in *A. burtoni* androgens are associated with reproductive behavior while estrogens moderate aggression by comparing the effects of agonists and antagonists for each sex steroid receptor. Studies focused on aromatase, the enzyme responsible for converting estradiol into testosterone, show a correlation between aromatase mRNA levels and aggression in *A. burtoni* (Huffman et al. 2013). Treating fish with fadrozole (aromatase inhibitor) decreases aggression and E2, increases T and increases brain aromatase expression in POA (Huffman et al. 2013). However, it has no effect on reproductive behavior (Huffman et al. 2013).

AVT and IT are also involved in social interactions, as it has been demonstrated in several investigations although with contrasting results. In the cooperative breeder, *N. pulcher*, IT regulates dominance interactions since IT treated fish increase submissive behavior (Reddon et al. 2012; Hellmann et al. 2015) but correlates negatively with affiliative behavior (Reddon et al. 2015). Moreover, IT may inhibit grouping behavior since injecting males with an oxytocin receptor antagonist increased grouping preference and an exogenous isotocin dose-dependent injection decreased this behavior (Reddon et al. 2014). Interestingly, IT treated males also increase responsiveness to social information, i.e., they are more aggressive to larger opponents (*N. pulcher*; (Reddon et al. 2012). O'Connor et al. (2016), however, reported a positive correlation between IT and both affiliative and submissive behaviors in the cooperative breeder. In *A. nigrofasciata*, blocking of IT inhibits parental care and removal of the mate induces overexpression of the immediate early gene *c-fos* on IT neurons localized in the POA (O'Connell et al. 2012). In the same study, IT does not seem to influence affiliative behavior toward the mate; however, blocking both AVT and IT receptors decreases this behavior while the pair bond is forming (Oldfield and Hofmann 2011). On the other hand, aggression seems to be related to higher expression levels of whole brain AVT in *N. pulcher* and *Telmatocromis temporalis* (O'Connor et al. 2016), whereas in *A. burtoni* dominant males, AVT injections elicit loss of status and reduce aggression which in turn are not changed when males are treated with an AVT antagonist (Huffman et al. 2015). Actually, AVT and IT (and its receptors) expressions in the whole brain seem species specific (O'Connor et al. 2015a) as well as the relation between IT and behaviors (O'Connor et al. 2016). Ramallo et al. (2012) provided a detailed characterization of the vasotocinergic system in *Cichlasoma dimerus*: AVT neuron projections are found mostly in the forebrain and the hindbrain while AVT stimulates the production of gonadotropins (LH and FSH) on pituitary extracts in vitro and androgens on testis culture. They also detected AVT mRNA and peptide in the testis thus showing the influence of AVT in the HPG axis as a neuromodulator in the central nervous system and playing a role as a neurohormone at a peripheral level.

The interaction between stress and glucocorticoids on fish survival, physiology, or reproductive capacity has been reported for several years (reviewed in Schreck 2010). However, cortisol produced by the HPI (Hypothalamus–Pituitary–Interrenal) axis also acts in the regulation of social interactions. Munro and Pitcher (1985) treated *A. pulcher* males with cortisol and fish seemed to increase submissive behavior. Another indirect evidence of corticosteroids modulating behavior is exemplified by a study in which *A. burtoni* males were presented with a video playback of a male displaying aggressively (Clement et al. 2005). In this case, non-territorial males with intermediate levels of F showed more direct aggression than subordinate individuals with high or low F, in turn, characterized by increased displaced aggression. The authors concluded that the behavioral response of subordinate males was moderated by cortisol levels and suggest the existence of an optimal cortisol value that would promote advantages in social challenges. Another study reports that corticosteroid receptors' gene expression is sex differentiated once males express higher levels of GR2 and MR in the liver, and the latter is correlated with submissive behavior in *N. pulcher* (O'Connor et al. 2013). Table 2 summarizes the effects of hormonal manipulations on the social behaviors described above.

5.2 Social Feedback on Neuroendocrine Mechanisms

In social species, individuals should be socially competent, i. e., they should optimize their behavior according to a constantly changing and challenging environment. To do so, individuals integrate information about the social environment they live with internal cues and respond in a more adaptive manner (Oliveira 2009). Steroid hormones play a central role in this adaptive and embodied mechanism since social interactions elicit quick plasma hormonal responses that modulate neural mechanisms through widely distributed steroid receptors (Oliveira and Oliveira 2014). For instance, male exposure to social stimuli, either a female or a conspecific male, induce a plasma androgen increase (*O. mossambicus,* Borges et al. 1998; *N. pulcher*, *Lamprologus callipterus*, *Tropheus moorii*, *Pseudosimochromis curvifrons*, *O. mossambicus*; Hirschenhauser et al. 2004, 2008; *A. nigrofasciata,* Sessa et al. 2013). A study on female mate choice revealed that *A. burtoni* males change their reproductive and aggressive behaviors, as well as androgen levels, according to female physiology (hormone release) and/or behavior and in turn females choose mates that release more androgens into the water (Kidd et al. 2013). Interestingly, visual information is per se sufficient to influence hormone systems since in *A. burtoni* seeing a dominant and larger male suppresses the dominant behavior of a smaller male and is responsible for a decrease in KT levels

Table 2 Effects of hormonal manipulations on social behavior

Species	Hormonal manipulation	Plasma hormones	Nest/ spawning pit building	Nuptial coloration	Courtship displays	Paternal care	Aggression	Mating/ Affiliative behavior	References
Astatotilapia burtoni	**Castration**	– T – KT	ND	ND	ND	ND	ND	ND	Francis et al. (1992)
Oreochromis mossambicus	**Castration**	– T – KT	–	–	–	ND	0	ND	Almeida et al. (2014a)
Aequidens pulcher	**Androgens added to water** T	ND	ND	ND	ND	ND	+	ND	Munro and Pitcher (1985)
	E2						–		
	F						–		
Astatotilapia burtoni	**Injections** T	ND	0	+	0	ND	+	ND	Fernald (1976)
Astatotilapia burtoni	**Injections**	ND	ND	ND	0 (DOM)	ND	+ (DOM/SUB)	ND	O'Connell and Hofmann (2012)
	E2								
	DHT				+ (DOM)		0 (DOM/SUB)		
	17α-20β-P				+ (DOM)		0 (DOM/SUB)		
	ER antagonist	–E2 and –T (SUB) 0 E2, T, P (DOM)			0 (DOM)		– (DOM) 0 (SUB)		
	AR antagonist	0 E2, T, P (DOM/SUB)			– (DOM)		0 (DOM/SUB)		
	PR antagonist	0 E2, T, P (DOM/SUB)			– (DOM)		0 (DOM/SUB)		

Astatotilapia burtoni	**Injections** Aromatase inhibitor	+T −E2	0	ND	0	ND	− (DOM)	ND	Huffman et al. (2013)
Amatitlania nigrofasciata	**Silastic implants** AR antagonist	ND	ND	ND	–	ND	0	ND	van Breukelen (2013)
Amatitlania nigrofasciata	**Injections** ITR antagonist	ND	ND	ND	ND	–	0	0	O’Connell et al. (2012)
Amatitlania nigrofasciata	**Injections** ITR + AVTR antagonist	ND	0	ND	ND	ND	–	–	Oldfield and Hofmann (2011)
Neolamprologus pulcher	**Injections** IT	ND	ND	ND	ND	ND	+ submission	0	Reddon et al. (2012)
Neolamprologus pulcher	**Injections** IT ITR antagonist	ND	ND	ND	ND	ND	ND	− (high/low dose) +	Reddon et al. (2014)

− decrease; + increase; 0 no effect; *ND* not described/not applicable and a gene expression increase of CRF, GnRH, and AVT (Chen and Fernald 2011). Agonistic interactions also elicit an androgen increase in *O. mossambicus* spectators (Oliveira et al. 2001). Unexpectedly in some situations, there are no hormonal responses; fish fighting with their image in the mirror display very aggressive behaviors, however, there are no changes in androgens (Oliveira et al. 2005). In this case, the evidence of a decoupling between agonistic behavior and androgens reveals that fish appraisal (interpreted by the fight outcome) seems to be necessary to induce an endocrine change. However, this result seems to be species specific (*A. burtoni*, Desjardins and Fernald 2010, and *Pundamilia* sp., Dijkstra et al. 2012), and raises the debate on the adaptive function of androgen changes. It seems that hormonal responses resulting from the perceived outcome of agonistic interactions would affect subsequent social interactions rather than affecting the current dispute between individuals. Probably, androgens fluctuations are a way to individuals take into account their potential to gain further interactions and maintain social status/dominance avoiding prejudicial defeats (Oliveira 2009). Indeed, animals winning social conflicts have a higher probability of winning subsequent interactions with other conspecifics while losing a fight has the opposite effect (Winner/Loser effect) (Hsu and Wolf 1999; *O. mossambicus*, Oliveira et al. 2009). Yet, the winner effect is blocked when individuals are treated with an androgen antagonist (Oliveira et al. 2009).

Another important evidence on social environment influencing hormones is that plasma androgen levels vary with social status. Dominant males typically have higher levels of androgens (KT and/or T) than subordinate males (*A. burtoni*, Parikh et al. 2006; *N. pulcher,* Desjardins et al. 2008; *O. niloticus*, Pfennig et al. 2012; *C. dimerus*, Morandini et al. 2014). In *N. pulcher*, non-territorial aggregation males have higher T and lower KT and helpers have higher F (Bender et al. 2008). Another study in the same species has shown that female breeders have higher levels of T than helper females or even males (Desjardins et al. 2008), suggesting that androgens may promote parental care. Looking at brain gene expression patterns dominant/breeder females are very similar to dominant males, evidence for a masculinization at the molecular and hormonal level of these females (Aubin-Horth et al. 2007). The keynote here is that steroid levels are a consequence of social status. Oliveira et al. (1996) demonstrated that urinary sex steroids levels after group formation are good predictors of social establishment; KT increased in territorial males and decreased in non-territorial males and no changes were reported in T levels when compared to levels prior to hierarchical establishment (see also Almeida et al. 2014b). On the other hand, social challenges raise differential hormonal responses according to individuals' social status. In *N. pulcher*, agonistic interactions elicit higher plasma levels of T and similar KT levels in dominant females than subordinate females, and in contrast higher levels of KT and equivalent levels of T in dominant males compared to subordinate males (Taves et al. 2009). Likewise, androgen levels of males socially isolated differ in their response according to their previous social status; dominant males decrease KT and subordinates show a tendency to increase KT whereas F varies depending on the prior social context (*O. mossambicus,* Galhardo and Oliveira 2014).

In turn, androgens modulated by social status determine for instance expression of secondary behavioral (e.g., nuptial coloration, spawning pit volume) and morphological traits (e.g., mandible width, dorsal fin height) specifically in territorial males (*O. mossambicus,* Oliveira and Almada 1998b). Dominant males typically have larger GSI (gonadosomatic index) than non-territorial males (*O. mossambicus,* Oliveira and Almada 1999; *O. niloticus*, Pfennig et al. 2012; *C. dimerus*, Alonso et al. 2012; *A. nigrofasciata*, Chee et al. 2013). However, subordinate males are still reproductively active despite differences in testis structure (Pfennig et al. 2012). Androgens likewise modulate color patterns in *A. burtoni* territorial males since KT levels (and aggression) are higher in yellow territorial males than in blue territorial males (Korzan et al. 2008). A flexible behavioral strategy seems to underlie this color-changing ability. Another very interesting illustration is what is observed in *A. burtoni* females. Sometimes they adopt a male-typical appearance and behavior, namely courtship behavior and aggressive territorial defense mostly toward other females (Renn et al. 2012). This intriguing behavior is associated with higher T levels and a nonsignificant trend to higher E2 comparatively to subordinate females (Renn et al. 2012). Data on the mentioned study cannot infer on the ultimate function of this apparently hormonal modulated behavior but one can speculate that this observed behavioral plasticity could confer them adaptive advantages in the competition for males.

Importantly, hormonal effects on behavior can occur not only by changes on plasma steroids but also through changes in the density of hormone receptors (Fuxjager et al. 2010). For instance, in *A. burtoni*, differences in mRNA expression levels of several hormone receptors have been found between males of different social ranks (Korzan et al. 2014). This is also evident in an interesting study with the teleost mangrove rivulus fish, *Kryptolebias marmoratus*, where the expression levels of androgen receptors change in response to fights, and this effect seems to be dependent on the fight outcome and baseline androgen levels (Li et al. 2014). Alternatively, androgens can also bind to hormone-binding proteins that regulate their bioavailability (Zeginiadou et al. 1997; Oliveira 2009) or produced in the brain de novo from cholesterol (Baulieu 1998; Schmidt et al. 2008; Pradhan et al. 2014), though studies confirming this in cichlids are still lacking. Finally, androgens can be even converted into other steroids by specific enzymes (e.g., aromatase) as already mentioned (Roselli et al. 2009; Cornil et al. 2012). In *A. burtoni*, for instance, subordinate males have more aromatase expression than dominant males, indicating a probable compensatory mechanism to low sex steroid levels in plasma (Huffman et al. 2013). A remarkable example on the reciprocity between hormones and behavior is the social regulation of reproductive plasticity in *A. burtoni*. A considerable number of studies in the last years provided a very detailed picture of how social environment impacts dramatically an individual. *A. burtoni* is an African maternal mouthbrooding species with a lek-breeding system. Males have two distinct phenotypes, which can rapidly reverse due to changes in the social environment. Dominant males are brightly colored (yellow or blue) with a black eye-bar, establish territories and attract females. In contrast, subordinate males show more faded coloration, school with females, fail to establish territories, and typically do not reproduce. Dominant males have an upregulated HPG axis comparatively to subordinate males (reviewed in Maruska and Fernald 2014) namely, higher levels of gonadotropins and expression of GnRH1 receptors at the pituitary; higher levels of plasma sex steroids (KT, T, and E2) and gonadotropins LH and FSH. Testes have larger GSI and increased expression of gonadotropins, androgens, estrogens, glucocorticoids, and mineralocorticoid receptors and steroidogenic acute regulatory protein. However, once a territory is available, subordinate males ascend in social rank and as expected circulating androgens rise but also profound changes occur at the level of behavior, brain, and reproductive system within different time frames (reviewed in Maruska and Fernald 2014).

In a more recent study, researchers have focused on the effect of social interactions on the AVT system. By assessing the levels of expression of the immediate-early gene *egr-1* by in situ hybridization technique, they showed that agonistic and courtship interactions induce differential patterns of activation of AVT neurons (Loveland and Fernald 2017).

Furthermore, AVT seems to be regulated by social status. In *O. mossambicus*, subordinate males have larger cell body areas of AVT neurons in magnocellular POA and gigantocellular POA and submissive behavior correlates with soma size of AVT cells in all three nuclei (parvo-, magno-, and gigantocellular) and AVT cell number in the magnocellular POA (Almeida and Oliveira 2015). Ramallo et al. (2012) compared dominant and subordinate males in *C. dimerus* soon after establishing hierarchy concluding that subordinates have larger AVT parvo-cellular neurons in the POA than dominant males, pointing to a putative role of these neurons in submissive behavior. AVT brain levels of *N. pulcher* detected by HPLC-FL are higher in subordinate than in dominant males and IT correlates negatively with affiliative behavior (Reddon et al. 2015).

In *O. mossambicus*, on the other hand, Almeida et al. (2012) used the same method to quantify the levels of both AVT and IT in several macro-dissected brain areas and the pituitary gland. Results show that the pituitary is the area with more concentration of the neuropeptides and the olfactory bulbs is the brain area with more abundance of AVT. Subordinate AVT pituitary levels are higher than those of dominants whereas dominant hindbrain IT levels are significantly higher compared to subordinates, suggesting a potential involvement of AVT in social stress in subordinate fish and of IT in the regulation of dominant behavior at the level of the hindbrain. A lack of correlation between AVT and IT levels suggests a decoupling between AVT and IT neuroendocrine systems at the CNS level. Moreover, the authors propose an independent control of hypophysial and CNS nonapeptide secretion. In another study, KT levels and V1a2 (AVT) receptor expression levels in the hypothalamus are more associated with territoriality and social dominance than with pair bonding (*Herichthys cyanoguttatus* and *Herichthys minckleyi*, Oldfield et al. 2013). Greenwood et al. (2008) studied AVT expression in *A. burtoni*. Results show that whole brain AVT expression is higher in territorial than in non-territorial males, however, in the posterior POA territorial males have higher levels of AVT expression but in the anterior POA AVT expression is lower than in non-territorial males. This last evidence may be related to AVT influencing the stress response in non-territorial males, which usually present higher F levels than dominant males (Fox et al. 1997). O'Connor et al. (2015a) studied IT and AVT and their receptors in several cichlids species and showed that there were differences in whole brain gene expression between social and nonsocial species, providing evidence for species-specific gene expression patterns relative to social behavior.

Another important component of social species is their social system and a more recent study conducted by Reddon et al. (2017) specifically addressed this matter. These authors characterized IT and AVT neurons, by immunohistochemistry, of several cooperative cichlid species with contrasting social systems. By comparing four highly social cooperatively breeding species with four other less social independent breeders, all of *Neolamprologus* genus, they verified that the first (higher social) group had fewer parvocellular isotocin neurons in the preoptic area than the other (less social), and that these two sets of fish could be distinguished just by the size and number of isotocin neurons (Reddon et al., 2017). They also report no distinction on vasotocin neurons. In summary, nonapeptides respond in a dynamic way to changes in social status and different social ranks parallel differences in nonapeptides. Although the differences seem to be species specific, researchers should be aware of the influence that each social living system can have on nonapeptides. Given the great diversity on the social organization of cichlids, it would be interesting to compare how nonapeptides affect or can be affected by other types of social system (e.g., type of mating or parental care systems).

Fishes can also perceive the social environment as a stressor and, as a consequence, a cascade of different physiological and behavioral responses occur, including HPI axis activation and subsequent production of corticosteroids (Barreto and Volpato 2006; Galhardo and Oliveira 2009). In social species, and in particular in cichlids, a negative correlation between cortisol and dominance has been reported for both sexes in *A. burtoni* (Fox et al. 1997) and *C. dimerus* (Alonso et al. 2012; Morandini et al. 2014) that can be related to chronic stress in subordinate males or social stability. However, in *N. pulcher*, dominant males have higher F levels and F correlates with social behavior only in subordinate males (Mileva et al. 2009). The authors explain these cortisol plasma levels arguing that dominant status in this species is difficult to achieve and maintain, or, in other words, dominant males are subjected to a higher allostatic load as proposed by Goymann and Wingfield (2004). Another possible interpretation pointed out is that a reproductively active fish could have higher cortisol levels since corticosteroids are associated with spawning or gametes production in other species. In the same species, subordinate female cortisol levels depend on the social context. When these females live in groups where the dominant breeding pair is aggressive to each other, they have higher cortisol levels whereas lower levels are detected in females engaging in more social and non-agonistic interactions with dominant females (Ligocki et al. 2015a). The necessity of looking into the whole social "picture" and not to only direct interactions to one focal individual is therefore highlighted. Additionally, in *A. burtoni*, besides androgen receptors, also glucocorticoid receptors mRNA are expressed in GnRH1 neurons in POA, responsible for regulating reproduction; territorial males have higher expression levels of ARα, MR, GR1a, and GR2 while non-territorial males have GR1b higher levels of mRNA (Korzan et al. 2014). Finally, Earley et al. (2006) studied agonistic interactions between *A. nigrofasciatus* males but no cortisol differences were detected between winners and losers. Corrêa et al. (2003) also reported no cortisol distinction between dominants and subordinates (*O. niloticus*).

6 Neurogenomics of Social Behavior

Neurogenomics is a recent and exciting avenue, which started to be pursued after the achievement of several genome-scale projects (Boguski and Jones 2004). Sequencing of several cichlids genomes and transcriptomes (Brawand et al. 2014), as well as the increasing advances in molecular biology and other genomic resources, plus their complex repertoire of social behavior, has launched cichlids as promising neurogenomic models for the study of social behavior. The aim is to understand what is the molecular basis of social behavior, i.e., to unravel the genes and pathways that regulate behavior as well as other development and physiological features underlying social interactions ("sociogenomics," Robinson et al. 2005). Again, the interaction between sociality and brain is reciprocal, so studies also seek to address how the social environment impacts genes (Robinson et al. 2005).

Social plasticity is a key characteristic of cichlids where the same genotype produces diverse behavioral phenotypes, which are distinguished by the expression of specific behavioral profiles. At the molecular level, each behavioral state corresponds to a different neurogenomic state, depicted by a distinct pattern of gene expression and consequently brain transcriptome (Cardoso et al. 2015). Differential gene expressions, specifically along the several nodes of the SDMN, allow multiple combinations of neural states, by changing the weight of each node and the strength of the connections between them (Cardoso et al. 2015). On the other hand, most of these nodes express receptors for neuromodulators and steroid hormones, responsible for the social regulation of the network (Munchrath and Hofmann 2010).

Thereafter, most neurogenomic research is based on transcriptomic studies in which brain gene expression is measured to see how it correlates with the behavior of interest. Several genes are then identified as candidate genes responsible for social behaviors. Afterward, it is especially necessary to perform "reverse genomic" studies where the putative genes are experimentally tested to ascertain their actual contribution to the behavioral phenotype (Harris and Hofmann 2014). This can be accomplished, for instance, by manipulating gene expression (e.g., pharmacology, transgenics, siRNA), performing brain mapping of gene expression, or identifying direct targets of novel transcription factors (Harris and Hofmann 2014).

6.1 Microarray Studies

Microarray hybridization analysis was the first technique to measure brain gene expression on a genome wide scale (Zhang et al. 2009; Wong and Hoffmann 2010; Qian et al. 2014). The underlying principle consisted of using nucleic acid probes, representing genes of interest fixed in a solid surface (microarray), and incubating them with fluorescently labeled cDNA that, in turn, hybridizes with the elements in the chip (Zhang et al. 2009). This means that the knowledge of the genes' sequence is required, limiting its production to a few (model) species (Zhang et al. 2009). Hence, heterologous microarrays were widely used to assess mRNA levels of closely related species (Renn et al. 2004). Next, we will describe several studies that applied microarrays to unveil social behavior at the molecular level.

The first transcriptomics study in a cichlid species was performed in *N. pulcher*. It used a heterologous microarray with ~4500 elements constructed from a cDNA *A. burtoni* library (Aubin-Horth et al. 2007) previously validated for other cichlid species (Renn et al. 2004). The authors compared dominant and subordinate individuals from both sexes at the behavior, hormonal, and molecular levels. Four genes were differentially expressed between dominant and subordinate brains, independently of sex: AVT, a myelin-basic protein, a CD-59 protein, and one unknown gene. AVT, for instance, had higher expression levels in dominant compared to subordinate individuals. Interestingly, dominant females had similar brain expression profiles to males, independently of status, and significantly higher levels of AVT expression than dominant males. Female dominant behavior and testosterone levels were also high and similar to dominant males while KT levels were markedly lower. Taken together, these findings indicate that dominant breeder females are very similar to males at the hormonal and molecular levels and that molecular and endocrine functions are separately (modular) organized and likely sex regulated (Aubin-Horth et al. 2007).

Renn et al. (2008) investigated whole brain gene expression in dominant and subordinate males as well as in females of *A. burtoni*. By comparing the different phenotypes with a homologous microarray array, they identified several gene candidates from neuroendocrine pathways associated with dominance or reproduction behavior. A number of genes already known to be involved in social dominance were confirmed along with the microarray analysis, namely GnRH1, galanin, AVT, or brain aromatase, all upregulated in dominant males. Transcription factors, cellular metabolism genes, cell cycle regulators, genes encoding structural proteins or neuropeptides were also detected and associated with the behavioral phenotypes. For instance, in dominants, higher expression levels of genes coding for structural proteins such as tubulin and actin, and genes involved in axonal growth, neuromodulin and neuroserpin, suggest increased brain structural reorganization within this phenotype. The authors also report increased expression of the neuropeptides somatotropin, prolactin, and somatolactin and proopiomelanocortin in dominant males, probably related to gonad maturation and growth. A significant finding to emerge from this study was the upregulation of GABA receptors in dominant males while kainite-type glutamate receptors are upregulated in subordinate males, suggesting different regulating mechanisms of dominance status and novel research targets to explore (Renn et al. 2008).

Machado et al. (2009) published a comparative study between two cichlid species with different mating strategies. Whole brain transcriptome from both males and females of *X. flavipinnis*, a monogamous species, and the polygynous *Xenotilapia melanogenys* were compared with the same array of *A. burtoni*. They also performed a meta-analysis combining their results with the two previously reported studies to compare sex-specific gene patterns. Data reveal that sex-specific gene profiles show great variation between species, supporting the idea that the mating system is responsible for major brain transcription changes. Comparative genomic studies across species are of extreme relevance because they can shed light on the ultimate causes (function and evolution) of behavior besides the proximate mechanisms usually approached (Wong and Hoffmann 2010).

Schumer et al. (2011) performed a comparative study between two closely related cichlid species, *Julidochromis marlieri* and *J. transcriptus*. While the latter species is characterized by a social system where males are dominant, territorial, and larger than females, the former species shows the opposite pattern. Thus, they investigated if the same pattern of gene expression was responsible for similarities on behavioral phenotypes, namely between *J. marlieri* females and *J. transcriptus* males. They used a heterologous microarray chip (*A. burtoni* array with ~20,000 features) to compare brain transcripts of both females and males of *J. marlieri* and *J. transcriptus* and obtained a set of genes related to aggression similarly expressed in both species. IT and parvalbumin are examples of potential regulators of this behavior since the corresponding genes were highly expressed on both *J. marlieri* females and *J. transcriptus* males. The results suggest that the mechanisms underlying aggressive behavior are conserved between species (Schumer et al. 2011).

O'Connell and Hoffman (2012) performed an investigation already described in the previous section. Since ER antagonist administration influenced aggression of *A. burtoni* males, independent of social status, they decided to analyze transcription patterns in POA, comparing individuals injected with ER antagonist or with vehicle. POA expresses 56% more genes in dominant males than in subordinate males. This is, however, not unexpected since subordinate males express lower levels of estrogen receptors (O'Connell and Hofmann 2012). Only four unknown genes were similarly regulated between these two phenotypes when ER antagonist was administered.

A study on *O. mossambicus* examined the effect of social odors in the transcriptomes of specific brain areas, namely, the olfactory bulb (OB) and the posterior part of the dorsal telencephalon (Dp, the homolog for the mammal olfactory cortex) (Simões et al. 2015). The authors used a microarray of *A. burtoni* to assess gene transcript patterns of dominant males subjected to urine from dominant and subordinate individuals, female conditioned water (either pre- or post-ovulated), or a blank control. They also recorded electro-olfactograms in dominant males subjected to the different stimuli to measure olfactory potency. One interesting finding is that hierarchical gene expression profiles are different between males and females in the olfactory bulb, meaning that this brain area seems to discriminate

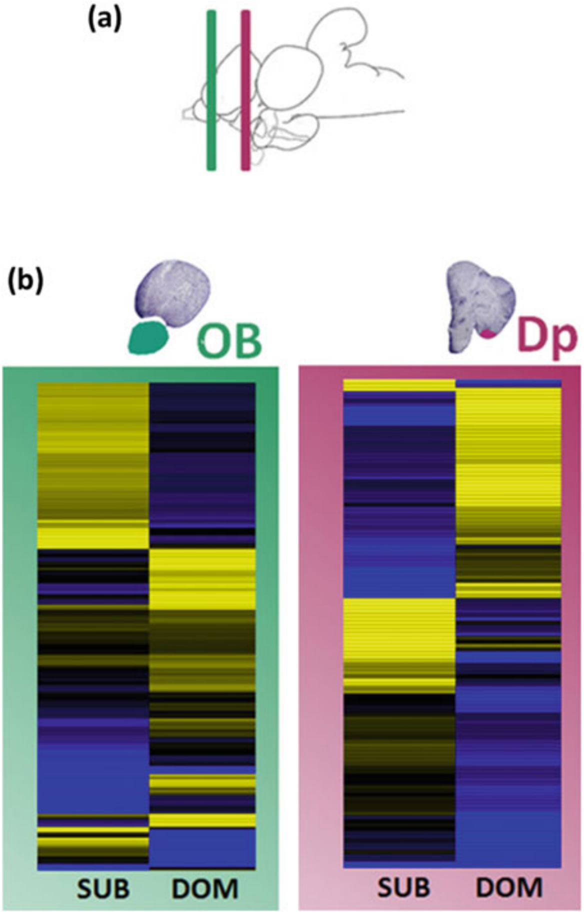

Fig. 4 Neurogenomics of social behavior in *O. mossambicus* (Simões et al. 2015). (**a**) A sagittal view of a tilapia's brain cut by two lines (green and violet) representing the location of the coronal cuts depicted illustrating the specific areas sampled olfactory bulb (OB) and posterior part of the dorsal telencephalon (Dp), respectively. (**b**) Hierarchical clustering of significantly differently expressed genes ($P < 0.01$) for the comparison of dominant and subordinate male olfactory cues in OB and Dp. The heatmaps (blue—downregulated, yellow—upregulated) show estimated gene expression levels

males from females while olfactory epithelium allows individual differentiation within each sex, evidenced by electro-olfactograms results (Simões et al. 2015). Likewise, transcriptomes of OB and Dp are considerably different for every social stimulus presented, indicating that olfactory system can discriminate social status and reproductive condition (Fig. 4; Simões et al. 2015). Several gene candidates were also uncovered, such as somatotropin, somatostatin, brain aromatase, GnRH1, pro-opiomelanocortin alpha 2, differentially expressed in olfactory bulb, or olfactory epithelium. Markers of neural activity, *egr-1* and cytochrome C oxidase were, in turn, downregulated in olfactory bulb area by fish subjected to male chemical cues when compared to fish stimulated with female odors. Hence, Simões et al. (2015) hypothesize a role of olfactory modulation on memory consolidation of social odors.

More recently, Renn et al. (2018) performed an interesting comparative transcriptomic study. The authors used a second-generation *A. burtoni* microarray to compare, at the molecular level, cichlids of the tribe Ectodini from Lake

Tanganyika, but with different mating systems (polygyny vs monogamy). They analyzed field samples of females and males of four closely related species, which evolved independently, and they obtained a set of genes that seem to be associated with monogamy, independent of species or sex. This comparative study seems to support the hypothesis that although these species went through independent evolutionary transitions from polygyny to monogamy, similar changes in brain gene expression patterns have occurred (Renn et al. 2018).

6.2 New Approaches to Neurogenomics

The microarray technique has, however, been replaced by more advanced technology. Recent progress has introduced the powerful next-generation mRNA sequencing, "RNAseq," which is based on deep-sequencing and quantitative analysis (see Qian et al. 2014, for a detailed description and several applications to fish transcriptomics). Besides being more sensitive, it produces a large quantity of sequence information obtained in an unbiased manner and not only gene expression information (Qian et al. 2014). It is possible to discover unknown transcribed regions, detect different gene isoforms, splicing sites, or UTRs (Qian et al. 2014). Currently, the costs of RNAseq are becoming increasingly accessible and are no longer a limiting factor. So far, there are a few published articles on cichlids with RNAseq analysis. Kasper et al. (2018) compared telencephalon transcriptomic patterns of alloparental egg care helpers (cleaners) and non-helpers (non-cleaners) of *N. pulcher*. In this species, the expression of these social phenotypes is not dependent on heritable genetic variation but is shaped during ontogeny and affected by social and ecological constraints (Kasper et al. 2018). Results showed that in the absence of the clutch, only the neural differentiation gene *irx2* is significantly different between cleaners and non-cleaners suggesting its involvement in the differentiation of these social phenotypes (Kasper et al. 2018). On the other hand, in the presence of the clutch, three genes, involved in neuroplasticity, hormonal signaling, and cell proliferation, were simultaneously upregulated in cleaners and non-cleaners, which seem to be commonly involved in the perception and integration of the clutch stimulus (Kasper et al. 2018). Two other studies focused on monogamy and bower building in cichlid fishes used RNA-seq to disentangle the associated evolutionary mechanisms (York et al. 2018; Young et al. 2019).

Finally, we would like to highlight epigenetics as an alternate neurogenomic mechanism of social plasticity. All the above-mentioned examples rely on transient changes in gene expression responsible for changing neurogenomic states of the brain. On the other hand, epigenetics is related to functional modifications of the genome in response to environmental information, without any change of DNA sequence (reviewed in Zhang and Meaney 2010; Roth 2012). These modifications are responsible for regulating gene expression and leading to changes in physiology, cognition, and behavior (Zhang and Meaney 2010; Roth 2012). There are several epigenetic processes, including DNA methylation, binding of non-coding RNA, or histone modifications that can influence gene expression and ultimately behavior, from early life to adulthood (Zhang and Meaney 2010; Cardoso et al. 2015). A study focused on DNA methylation of GnRH1 in *A. burtoni* showed differences in the methylation state of this gene throughout development and also after gestational crowding of the respective mouthbrooding mothers (Alvarado et al. 2015). Young from crowded mothers had a GnRH1 promoter hypomethylated and higher transcription levels of GnRH1 compared with control mothers, attesting social control of GnRH1 through epigenetic mechanisms (Alvarado et al. 2015). Lenkov et al. (2015) manipulated methylation state of subordinate individuals of the same species by injecting them with DNA methylating and demethylating chemicals. Fish with higher methylation states were found to be more likely to increase social status compared to individuals with lower methylation levels. Although associated with long-lasting and irreversible changes in behavior (Cardoso et al. 2015), epigenetics might be associated to more transient changes in social behavior such as reversible transitions between social ranks, promising to be a deep field to explore. In the near future, we hope to disentangle how and which genes, molecular pathways, and neural circuits regulate social behavior.

7 Conclusions

In summary, in this review we show that social behavior is amazingly diverse, complex, and dependent on several internal and external factors. Indeed, only an effective integration of these several building blocks that compose social behavior would allow the achievement of a thorough understanding. Using cichlids as study models of social behavior can give an important contribution to the field due to their extraordinary social diversification. Unfortunately, only a small number of cichlid species have been studied extensively but including a broader range of species in future research would be profitable. In addition, the increasing availability of highly developed molecular and genomic tools will certainly contribute to the rapidly expanding field.

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Respiratory Ecology of Cichlids

Lauren J. Chapman

Abstract For fishes, the availability of dissolved oxygen (DO) can affect performance and fitness traits and influence distribution patterns. Hypoxia occurs naturally in habitats characterized by low mixing and/or light limitation such as dense wetlands and profundal zones of deep lakes. In addition, human activities are increasing the frequency and extent of aquatic hypoxia through eutrophication and pollution. Thus, it has become increasingly important to understand consequences of hypoxia for fishes and mechanisms that facilitate persistence in low-DO habitats. With strong specialization in some cichlid species and high levels of intraspecific variation in others, cichlids have been a key group for exploring strategies for dealing with hypoxia. These include behavioral responses (e.g. aquatic surface respiration), evolution of mechanisms to maximize oxygen uptake and delivery, metabolic depression, use of anaerobic metabolism, and air breathing in a few species. Despite the diversity of strategies that have permitted some cichlids to persist under extreme hypoxia, low DO can incur potential costs such as smaller body size. Such costs may be offset by benefits of hypoxic habitats such as reduced predation risk. This review details the mechanisms used by cichlids for tolerating hypoxia and the costs and benefits of hypoxia tolerance.

Keywords Hypoxia · East Africa · Gills · Aquatic surface respiration · Metabolism · Wetland

1 Introduction

For fishes, the availability of dissolved oxygen (DO) can be a powerful limiting factor on performance (e.g., swimming, escape response) and fitness-related (e.g., growth, survival) traits and can strongly effect patterns of movement and

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L. J. Chapman (✉)
Department of Biology, McGill University, Montreal, QC, Canada
e-mail: Lauren.Chapman@McGill.ca

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distribution. While hypoxia occurs naturally in some aquatic habitats with low light and low mixing (e.g., swamps, flooded forests), environmental degradation is dramatically increasing the frequency and severity of hypoxia in inland and coastal areas through cultural eutrophication and pollution (Diaz 2001; Diaz and Rosenberg 2008, 2011). It is thus increasingly important that we understand the ecological consequences of hypoxic stress on fishes and mechanisms that permit persistence in hypoxic habitats.

Cichlid fishes have colonized a diversity of freshwater habitats (e.g., lakes, rivers, wetlands) and some estuarine and coastal habitats as well, representing a broad range of physicochemical conditions, including extreme hypoxia. With the strong specialization characteristic of some cichlid species and high levels of intraspecific variation in others, the cichlids have been a key group for exploring strategies for dealing with hypoxia and the ecological and evolutionary consequences of hypoxic stress. This chapter reviews key responses of cichlids to hypoxia and explores costs and benefits of hypoxia tolerance.

2 Measuring Hypoxic Environments

Units of dissolved oxygen vary among studies. Ecological investigations often report oxygen availability as the DO concentration, measured in mg O_2 l^{-1}, ml O_2 l^{-1} (1 mg $O_2 = 0.7$ ml O_2), or % saturation (1 mg O_2 l^{-1} at 25 °C at sea level = 12% saturation; 8.25 mg O_2 l^{-1} at 25 °C at sea level = 100% saturation). In water-breathing organisms, DO is taken up at a site of gas exchange, which is typically (though not always) the gills. Since the rate of oxygen diffusion from water to blood of the fish is a function of the partial pressure gradient between the two, physiological studies frequently report DO as the partial pressure of oxygen (PO_2) in the water in units of mmHg (torr) or kpascals (kPa, 1 kPa = 7.5 mm Hg; 1 mg O_2 l^{-1} at 25 °C at sea level = 2.49 kPa and 18.69 mmHg). The definition of hypoxia also varies among studies but can be very simply defined as a shortage of O_2. Regulators have applied the definition of hypoxia as waters with concentrations below 2–3 mg O_2 l^{-1} for marine and estuarine environments and below 5–6 mg O_2 l^{-1} for freshwaters (Diaz and Breitburg 2009). In their comparative analysis of experimentally derived oxygen thresholds (lethal and sublethal) of 206 species of benthic marine organisms, Vaqyer-Sunyer and Duarte (2008) reported a mean sublethal DO concentration (LC_{50}) of 2.61 ± 0.17 mg O_2 l^{-1} and a mean lethal concentration of 2.05 ± 0.09 mg O_2 l^{-1}, suggesting that 2–3 mg O_2 l^{-1} may be a broadly useful definition of hypoxia for marine systems. However, lethal and sublethal levels varied dramatically across taxa; and Vaquer and Duarte suggested that 4.6 mg O_2 l^{-1} would be a precautionary limit, protecting the 90th percentile of the distribution of mean lethal concentrations. It has also been argued that the definition of hypoxia should reflect its impact on organisms and include DO levels low enough to induce negative effects on the physiology and/or behavior of the target species (Pollock et al. 2007); and functional hypoxia, in the broadest sense, reflects any situation for a fish where the oxygen demands of the tissue exceed the circulatory supply (Farrell and Richards 2009). Thus, it is important to consider hypoxia in light of the species under investigation, since a DO level that induces a negative effect in one species may have no measurable effects in a hypoxia-tolerant species. Standardized measures such as critical oxygen tension (PO_2 at which there is a transition from an oxyregulator to an oxyconformer) are important traits in evaluating interspecific and interpopulational variation in low oxygen tolerance in fishes, because such metrics reflect the DO when physiological function is first compromised (Farrell and Richards 2009; Rogers et al. 2016).

In lowland tropical freshwaters, the home of most of the world's cichlids, hypoxia is characteristic of many systems with low mixing and high rates of organic decomposition, and/or inadequate light for photosynthetic production of oxygen, such as heavily vegetated swamps, flooded forests, floodplains, the deep waters of lakes and ponds, and some springheads (Chapman 2015). In tropical freshwaters, hypoxic conditions are often exacerbated by high temperatures that elevate rates of organic decomposition and reduce oxygen tension (Chapman et al. 2001). Chronic hypoxia and extensive anoxia are characteristic of some deepwater tropical meromictic lakes such as lakes Tanganyika and Malawi in Africa, driven by strong stratification, and decomposition of sinking organic matter (Spigel and Coulter 1996). In other tropical freshwater systems, strong seasonal variation in DO can occur associated with seasonal variation in precipitation, mixing, incident light, and water temperature. For example, in tropical intermittent streams, fast flowing, well-oxygenated waters in the wetter seasons can shift to isolated hypoxic pools during drier periods (Chapman and Kramer 1991). Nocturnal respiration in eutrophic lakes, tropical floodplains, or small exposed pools often drives diel variation in DO from hyperoxia at midday to hypoxia at night (Kramer et al. 1978; Junk et al. 1983; Chapman and Chapman 1993; Furch and Junk 1997), while pools characterized by little mixing under dense forest cover may be chronically hypoxic during periods of isolation (Chapman and Kramer 1991).

Although hypoxic (and anoxic) environments occur naturally, aquatic hypoxia is becoming more frequent and more widespread associated with anthopogenically induced nutrient enrichment and pollution of water bodies (Diaz 2001), including Lake Victoria, East Africa, the largest tropical lake in the world and home to an adaptive radiation of cichlids. In coastal and estuarine ecosystems, eutrophication driven primarily by nutrient enrichment has produced benthic hypoxia, which has led to population declines and mass mortality of benthic water-breathing taxa, and associated changes in community structure (Diaz 2001; Rabalais et al. 2001; Dybas 2005; Diaz and Rosenberg 2008, 2011). Climate change that leads to warmer waters is likely to exacerbate hypoxic conditions in aquatic systems because O_2 solubility decreases with rising water temperature while ectothermic (e.g., fish) metabolism increases (McBryan et al. 2013, 2016; Deutsch et al. 2015; McDonnell and Chapman 2015).

3 Cichlid Distribution in Hypoxic Habitats

From an evolutionary perspective, the cichlids are best known for the extraordinary adaptive radiations to form flocks of specialized species in large tropical lakes (e.g., Malawi, Tanganyika, Victoria). Within these systems, endemicity is high (99% or more), and many species have specific ecological requirements, as well as morphological, physiological, and biochemical adaptations that allow them to finely partition resources (Fryer and Iles 1972; Ribbink et al. 1983; Witte 1984; Eccles 1986; Ribbink 1991). In all three lakes, cichlids seem to have distributions defined, at least in part, by depth and the nature of the substrate (Ribbink 1991; Seehausen et al. 2008). These lake systems offer excellent venues in which to explore respiratory strategies and how they interact with lifestyle and environmental oxygen availability. In Lake Victoria, haplochromine cichlids range from stenotypic species that occupy specific geographical and depth zones to more eurytopic species that cross broad environmental gradients. Seehausen et al. (2008) explored replicate pairs of sympatric haplochromine populations and species and found that speciation occurred on all but the steepest environmental gradients where migration exceeds selection. Even those cichlids that share similar morphologies and diet may diverge in their oxygen window. For example, the molluscivorous endemic haplochromine *Haplochromis ishmaeli* is restricted to well-oxygenated habitats in Lake Victoria, while the widespread molluscivore *Astatoreochromis alluaudi* is found in both hypoxic and normoxic habitats (Rutjes 2006). It should be noted that the introduction of the predatory Nile perch (*Lates niloticus*) and effects of eutrophication (e.g., loss of water transparency and increasing extent and severity of hypoxia) coincided with the mass extinction of the Lake Victoria's endemic cichlids (Kaufman 1992; Seehausen et al. 1997; Balirwa et al. 2003). This has affected patterns of distribution, and there is increasing evidence that hypoxia has modulated the interaction between Nile perch and haplochromine cichlids, reviewed in Sect. 6. Even in small lake systems, cichlids show diversity in habitat use and ecology, as illustrated in Lake Massoko, a small maar lake near Lake Malawi where two ecomorphs of the haplochromine genus *Astatotilapia* persist: a planktonic morph in the deeper zone of the lake situated close to the anoxic boundary, characterized by an elongated head and blue males; and a shallow morph with a more littoral-based diet, characterized by a short head and yellow males (Malinsky et al. 2015).

The spectacular radiations in the Great Lakes are not observed in the riverine cichlids; though they are a diverse group in terms of morphology, behavior, and ecology (Lowe-McConnell 1991). In the large tropical river basins of South America, cichlids make up a small proportion of the species (6–10% of the freshwater fish fauna, Lowe-McConnell 1991). However, smaller riverine radiations have been documented, including the Lower Zaire rapids, where the endemism and abundance of cichlids is remarkably high (Roberts and Stewart 1976) and a river north of the Kalahari Desert where Joyce et al. (2005) discovered a riverine cichlid assemblage with functional diversity comparable to that of Lake Victoria. It was argued that the radiation was a remnant of a Pleistocene lake that dried up approximately 2000 year BP. In the larger river systems, where cichlids comprise a small component of the fish assemblages, one still finds a high degree of interspecific variation in habitat use from cichlid species that occupy fast-flowing well-oxygenated streams to species that occupy dense riverine swamps where hypoxia can be extreme or floodplain habitats such as the Amazon várzea where oxygen availability is temporarily and spatially heterogeneous. Some Amazonian cichlids show remarkable tolerance to hypoxia such as the oscars *Astronotus ocellatus* and *A. crassipinnis*, while other species such as blue discus (*Symphysodon aequifasciatus*) exhibit lower tolerance, which seems to reflect habitat associations in these taxa (Muusze et al. 1998; Chippari-Gomes et al. 2005).

Cichlids, in particular, tilapiines have also been widely introduced into many regions in the context of aquaculture. Part of the popularity of tilapias for culture is that they appear to tolerate a wide range of temperatures and water qualities and the fact that most tilapias feed low in the food web (Pullin and Lowe-McConnell 1982; Pullin 1991). The Nile tilapia has been an important for studies of hypoxia adaptation, yielding insights into the mechanistic underpinnings of tolerance to extreme hypoxia (Speers-roesch et al. 2010; Li et al. 2017). Invasive cichlids are increasingly common in the canal systems of Florida associated with escape or release from the pet trade industry or introductions for vegetation control or recreational fisheries. Schofield et al. (2007) reported 13 nonnative cichlids in Florida that have established breeding populations. In some cases, their success and negative impacts on the native faunas have been attributed to high tolerance to low DO. In the Rocky Glades region, a seasonally inundated wetland overlying karst substrate, dry season refuges often exhibit harsh conditions, particularly during the dry season when hypoxia is prevalent (Kobza et al. 2004). The invasive cichlid African jewelfish (*Hemichromis letourneuxi*) appears well adapted to the Rocky Glades conditions, which Schofield et al. (2007) attributed, at least in part, to its high tolerance to hypoxia.

The high degree of interspecific variation in habitat characteristics of cichlids, even among closely related species, likely reflects a complex suite of morphological, physiological, and biochemical traits that optimize persistence in a given context. In some cases, hypoxic tolerance is a key factor in limiting or permitting access to particular habitats. The next section explores more fully our current understanding of strategies used by cichlids for persisting under periodic or chronic extreme hypoxia. Two cichlid species are highlighted in this review, the Amazonian oscar (*Astronotus ocellatus* Cuvier, Fig. 1a) and the East African haplochromine cichlid (*Pseudocrenilabrus multicolor Schöller*, Fig. 1b) commonly referred to as the Egyptian mouth-brooder. These two cichlids are well known for their ability to persist under extreme hypoxia and have become model systems for exploring adaptations to hypoxia across multiple scales of biological organization (biochemistry, physiology, morphology, and behavior) and exposure times.

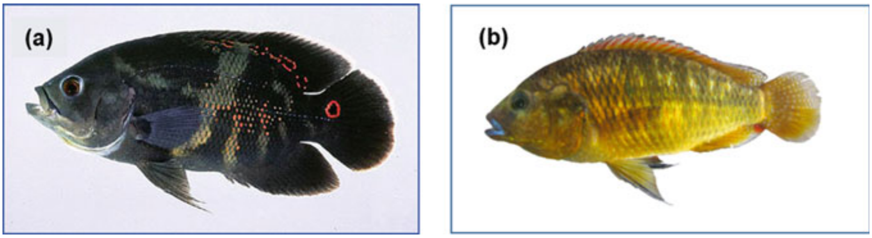

Fig. 1 Photograph of (**a**) the Amazonian oscar (*Astronotus ocellatus,* local name: acará-açu) reproduced from Florida Museum, photograph by Howard Jelks and Leo G. Nico, USGS (reproduced here with permission) and (**b**) the Egyptian mouthbrooder (*Pseudocrenilabrus multicolor*)

4 Strategies for Persisting Under Hypoxia

In general, aquatic hypoxia has led to one or more of the following strategies in fishes: (1) movement to habitats with higher DO; (2) evolution of mechanisms to maximize oxygen uptake or oxygen delivery to the tissues; (3) reduction of metabolic rate and/or activity to reduce oxygen requirements; (4) use of anaerobic metabolism, and (5) evolution of air-breathing organs. Evidence for air breathing exists for very few species of cichlids. Lowe-McConnell (1969) suggested that *Cichlasoma bimaculatum* may be able to breathe air based on the observation of its ability to survive out of water and its well-vascularized stomach. More recently, Johannsson et al. (2014) reported that the Magadi tilapia (*Alcolapia grahami*) breathes air not only under hypoxic conditions but also during normoxia and hyperoxia, which may be supported by its highly vascularized, physostomous swimbladder (Maina et al. 1995). Despite the limited occurrence of air breathing in the Cichlidae, the extraordinary diversity of the group and the ability of many species to persist in low-DO habitats has provided a rich literature on mechanisms underlying hypoxia tolerance in water breathers.

4.1 Behavioral Responses to Hypoxia

Behavioral responses to hypoxia provide flexibility to deal with variation in DO. In shallow water systems that experience hypoxia, a widespread behavioral response is use of aquatic surface respiration (ASR) whereby fish swim at surface and ventilate their gills with the microlayer of water in contact with air, which is richer in DO than underlying water (Lewis 1970; Kramer and Mehegan 1981; Kramer 1983a, b). Several different cichlid species have been reported to use ASR in response to progressive or acute hypoxia, including a diversity of species from lakes Victoria, Tanganyika, and Malawi (Verheyen et al. 1994; Chapman et al. 1995; Rosenberger and Chapman 2000; Reid et al. 2013a); Central American cichlids (Kramer 1983b);

and Amazonian species (Sloman et al. 2006; Soares et al. 2006). There is evidence to suggest that ASR is more common and/or more efficient among species from potentially hypoxic habitats (Kramer 1983b). In a study of 10 species of African cichlids, Verheyen et al. (1994) found that six cichlid species that inhabit well-oxygenated waters (four species from rocky littoral habitats in Lake Tanganyika, one from rocky littoral in Malawi, and one from Congo River rapids) did not use ASR when exposed to severe hypoxia. In contrast, three other lacustrine cichlids that inhabit less aerated waters over sand/mud between vegetation (two from Malawi and one from Tanganyika and river tributaries) and the eurytopic Nile tilapia did use ASR. Chapman et al. (1995) quantified ASR thresholds (the PO_2 at which fish spend 10%, 50%, or 90% of their time at the surface) and time to loss of equilibrium (LOE) under acute hypoxia exposure without surface access for nine cichlid species from Lake Victoria (eight indigenous, one introduced) and three from Lake Tanganyika. All 12 species used ASR in response to extreme hypoxia. However, in all haplochromine cichlids from Lake Victoria, except *Astatoreochromis alluaudi*, gill ventilation rates decreased with the onset of ASR behavior, suggesting the ASR increases DO availability to the gill surface of the fish; whereas in the three cichlids from Lake Tanganyika, gill ventilation rate did not show a consistent decline. In addition, tolerance, as indicated by time to low of equilibrium (LOE), was greater in the widely distributed swamp specialists than in the more stenotypic lacustrine forms; and lacustrine cichlids endemic to Lake Victoria were more tolerant to hypoxia than ecologically similar species from Lake Tanganyika. It is possible that having evolved in a shallow, swampy basin, haplochromine cichlids from the Lake Victoria region are, as a group, more hypoxia tolerant than cichlids from lakes Tanganyika and Malawi, where marginal wetlands, which tend to exhibit hypoxic conditions, are far less extensive. In their comparison of a swamp-dwelling population of the haplochromine cichlid *Pseudocrenilabrus multicolor* and two lake lake-dwelling haplochromine cichlids (*Astatotilapia velifer* and *Prognathochromis venator*) from minor lakes in the Lake Victoria basin Rosenberger and Chapman (2000) observed lower ASR thresholds in *P. multicolor*, which they attributed to its high tolerance to chronic hypoxia characteristic of its swamp habitat.

Some fishes, including several cichlids, increase the efficiency of oxygen extraction during ASR by swimming continuously across the surface, referred to as ram-assisted ASR, and/or through use of buccal bubble holding that may serve as a buoyancy compensation mechanism and/or to increase the oxygen content of the water passing over the bubble (Chapman et al. 1995; Rosenberger and Chapman 2000). Interestingly, cichlids tend to move both forwards and backwards at the surface film. Continuous forward motion is likely to enhance the efficiency of ASR by moving more well-oxygenated water over the gills than could be achieved by gill ventilation alone; however, backward swimming is less likely to do so but does expose the fish to more surface film. In their study of ASR behavior in 20 Amazonian floodplain lake species, Soares et al. (2006) found that two nonmigratory cichlid species increased their swimming speed associated with ASR, but migratory noncichlids showed overall higher surface swimming speeds.

Although ASR is more efficient than simply increasing ventilation under extreme hypoxia, time at the surface can incur costs in terms of energy and predator risk, which may account for very low DO levels at which ASR is initiated in many species (Kramer and Mehegan 1981; Kramer 1983a, b). In a recent study, Reid et al. (2013a) compared the ASR thresholds of the cichlid *P. multicolor* from a chronically hypoxic swamp surrounding Lake Nabugabo, Uganda, a satellite lake of the larger Lake Victoria, to ASR thresholds of introduced Nile perch (*Lates niloticus*), endemic haplochromines, and introduced Nile tilapia (*Oreochromis niloticus*) from Lake Nabugabo; and a literature review of ASR thresholds (81 values, Chapman and McKenzie 2009). *P. multicolor* was characterized by an average ASR_{10} threshold (PO_2 at which fish spend 10% of their time at the surface) in the lower 25th percentile of the distribution and exhibited the lowest ASR_{50} threshold of all fish examined, whereas lake-dwelling endemic haplochromine cichlids were characterized by higher thresholds (Reid et al. 2013a). The energetic costs of ASR may also account for changes in social behavior. For example, in their study of ASR in swamp-dwelling and open-water populations of the haplochromine cichlid *Astatotilapia* "wrought-iron," Melnychuk and Chapman (2002) found that the pre-ASR aggression rate was higher in swamp-dwelling "wrought-iron" than in the open-water populations, but the aggression rate dropped in both open-water and swamp-dwelling fish between the pre-ASR and post-ASR periods. The use of ASR may impose both time and energetic constraints that reduce aggression and may thus affect the development and maintenance of dominance hierarchies in cichlids.

4.2 Mechanisms to Increase Oxygen Uptake and Delivery

Water-breathing fishes that inhabit hypoxic habitats use many strategies to increase oxygen transfer from the environment to their tissues. One mechanism to meet routine metabolic requirements under hypoxia is to increase oxygen uptake through an enlarged gill surface area. The Family Cichlidae has fueled a rich body of research on relationships between gill morphology and hypoxia using both interspecific and intraspecific studies, with the latter comparing populations from hypoxic and normoxic habitats. Interspecific patterns suggest that a large gill surface area may contribute to persistence under hypoxia; however, highly active fish also require a large gill surface, adding to the complexity of habitat—gill surface area relationships.

Galis and Barel (1980) studied the functional morphology of the gills of African lacustrine cichlids from a sample of more than 80 species. They found cichlids frequenting oxygen-poor waters tended to possess gills with closely spaced secondary lamellae, with the exception of *Limnochromis permaxillaris* for which they evoked a potential trade-off between trophic and respiratory morphology (see below). However, Galis and Barel (1980) also observed a high frequency of secondary lamellae in cichlids with an active pelagic life, reinforcing the significance of both DO and metabolic requirements in driving variation in gill size (Palzenberger and Pohla 1992). In comparing two closely related cichlid species *Haplochromis angustifrons* and *H. elegans*, Galis and Barel (1980) noted that the larger gill surface area in *H. angustifrons* likely reflected its tendency to forage in oxygen-poor mud, in contrast to the oxygen-rich deposits that were targeted by feeding *H. elegans* (Galis and Smit 1979). Bouton et al. (2002) quantified ecological correlates of head shape for six species (one to three populations) of rock-dwelling haplochromine cichlids from Lake Victoria. They estimated the volumes of three head compartments (oral, suspensorial, and opercular) and found that DO explained most of the variation in the volume of the head compartments, in particular the opercular compartment containing the gills. Although their analysis combined both interdemic and interspecific effects, the patterns suggest that that gill volume varies negatively with DO and can influence head shape.

4.2.1 Gill Plasticity

Interpopulational studies in species that cross strong oxygen gradients in the field can be very useful for detecting phenotypic changes in response to hypoxia by reducing phylogenetic effects. In a study of *Pseudocrenlabrus multicolor* in the Mpanga River drainage of western Uganda, total gill filament length was calculated from specimens collected from two low-oxygen swamp sites, five open-water river sites, and a river site receiving swamp effluent (Fig. 2a). Total gill filament length of *P. multicolor* was greater in populations from hypoxic swamp sites compared to populations from well-oxygenated lake and river sites; and intermediate in the river site with swamp inflow characterized by fluctuating DO (Chapman et al. 2000, 2002, 2008a; Wiens et al. 2014, Fig. 2b). For one high- and one low-DO population, total gill surface area was estimated by quantifying the density and area of the gill lamellae; *P. multicolor* from the hypoxic field population exhibited a larger gill surface area than fish from the a well-oxygenated lake site (Chapman et al. 2000). Phenotypic variation across DO gradients may reflect genetic and/or phenotypically plastic adaptation to local selective pressures. Lab-rearing experiments with *P. multicolor* have demonstrated a high degree of developmental plasticity in gill size, brain size, and body shape in response to the DO of the rearing environment. Crispo and Chapman (2010a) reared full sibs from multiple populations of *P. multicolor* from the Mpanga River under either low DO (1.3 mg O_2 l^{-1}) or high DO $\geq$7.5 mg O_2 l^{-1}, ambient temperature of 25.5 °C). Overall, gill size was greater in full sibs reared under hypoxia, presumably a strategy for increasing oxygen uptake capacity and brain size was smaller, presumably do to the high aerobic cost of brain function (Fig. 3a, b). Fish reared under hypoxia exhibited gills that were on average 35% larger in total gill filament length and 56% larger in the area of the hemibranchs, while brain size was on average 10% smaller. Population level differences were also detected in some traits (e.g., brain mass), suggesting genetic components to trait divergence, but most variation among treatments in gill size was due to plastic effects (Chapman et al. 2008a; Crispo and Chapman 2010a). Mitochondrial DNA and microsatellite studies provided evidence for high gene flow

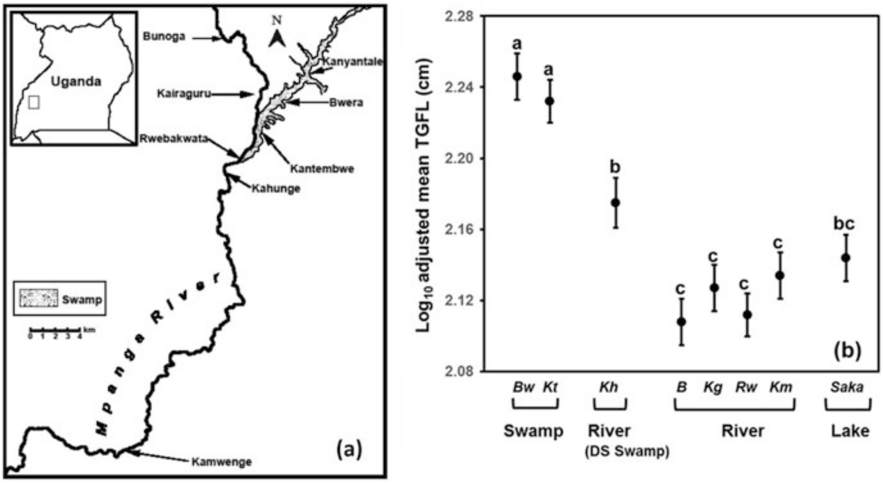

Fig. 2 (**a**) Map of the Mpanga River drainage, western Uganda, showing location of sampling sites (Lake Saka location not included). (**b**) Mean mass-adjusted $\log_{10}$-transformed total gill filament length (±standard error) for *Pseudocrenilabrus multicolor* from seven sites in the Mpanga River and nearby crater lake Saka. Data were adjusted to a common body mass of 4.3 g using ANCOVA. Fish were collected from two hypoxic swamp sites (Bwera [Bw], Kantembwe [Kt]), four open-water river sites characterized by relatively high DO (Bunoga [B], Kiaragura [Kg], Rwebwekata [Rw], Kamwenge [Km]), one swamp effluent river site where DO fluctuates annually associated with swamp input in the river (Kahunge [Kh], labeled as River—DS (downstream) of Swamp), and one well-oxygenated lake site (Saka). Sites that share the same letter are not significantly different

among *P. multicolor* populations from divergent DO environments in the Mpanga drainage (Crispo and Chapman 2008, 2010b). Thus, in this system, plasticity in respiratory traits may be selected for on the meta-population scale.

High levels of developmental plasticity in gill size and shape has also been reported for other haplochromine cichlids including the Lake Victoria endemic *Haplochromis (Yssichromis) pyrrhocephalus*, which showed an increase of 80% in gill surface area in the full sibs raised at 10% saturation versus full sibs reared at 80–90% saturation at 25.5 °C (Rutjes 2006). In the widespread haplochromine cichlid *Astatoreochromis alluaudi*, Chapman et al. (2007) reported an increase of 27% in the total gill filament length and 35% in the total hemibranch area of full sibs reared at ~1 mg $O_2\ l^{-1}$ versus full sibs reared in normoxic water (~7.5 mg $O_2\ l^{-1}$). In addition to plastic variation in gill surface area driven by changes in the size of the gill filaments and the size of the gill lamellae, some fishes can alter their gill surface area by what is referred to as remodeling. Gill remodeling was first observed in crucian carp and goldfish (Nilsson et al. 2012) and involves either the expansion of the cell mass between the lamellae on the gill filaments referred to as the interlamellar cell mass (ILCM) that decreases the effective gill surface area or a reduction of the ILCM through apoptosis that exposes the gill epithelium and increases oxygen uptake capacity (Sollid and Nilsson 2006; Nilsson 2007; Tzaneva

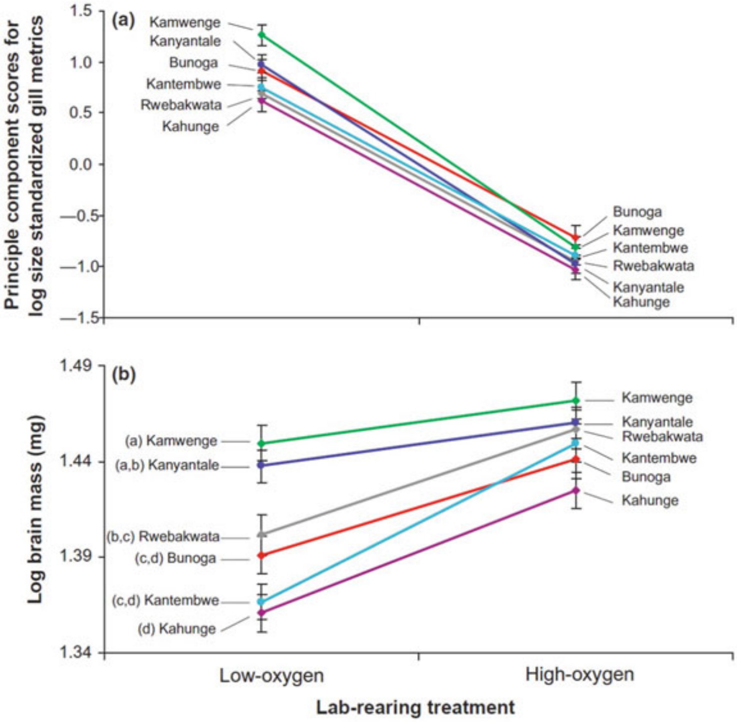

Fig. 3 Interpopulational variation in the gill size of *Pseudocrenilabrus multicolor*. (**a**) Adjusted mean values (±standard error) of principle component 1 scores for the $\log_{10}$-transformed body mass-standardized gill metrics from the mixed-model ANOVA for F_1 *P. multicolor* whose parents were collected from six sites in the Mpanga River drainage of western Uganda. F1s were raised under high- or low-oxygen conditions in a laboratory-rearing experiment. Measurements of five gill metrics were made including total gill filament length, average gill filament length, total number of gill filaments, total hemibranch area, and total perimeter of the hemibranchs (see Crispo and Chapman 2010 for details of measures). Gill metrics were standardized to a common body mass, and PCA scores were used as the response variable (see Crispo and Chapman for details). PCA extracted one component (reflecting gill size) with an eigenvalue greater than one. (**b**) Adjusted mean $\log_{10}$-transformed brain mass. Location of populations of origin are indicated on Fig. 2a. Letters in panel b indicated homogeneous subsets from Tukey post hoc tests. Figure modified from Figs. 1 and 2 in Crispo and Chapman (2010) with permission from the Journal of Evolutionary Biology

et al. 2011; Nilsson et al. 2012). Gill remodeling has been reported from one species of cichlid, the Magadi tilapia (*Alcolapia grahami*), a species that persists in hot and alkaline lagoons of Lake Magadi, East Africa. Johannsson et al. (2014) reported interlamellar cell masses that completely filled interlamellar spaces in fish collected from a lagoon with high reactive oxidative species (ROS), but little or no ILCM in fish from a lagoon with lower ROS levels. Of the many components of ROS, hydrogen peroxide can pass through cell membranes to increase ROS levels in the body and thus may induce the formation of the ILCM.

Costs of Enhanced Gill Apparatus Larger gills should be advantageous under hypoxic conditions by increasing oxygen uptake capacity; however, there may be costs associated with gill proliferation that negatively affect other aspects of fish performance (e.g., passive ion loss from the gills) or lead to fitness trade-offs, whereby adaption to the home environment comes at a cost of adaptation to the alternative environment (Schluter 2000; Kawecki and Ebert 2004). For example, because of the compact, laterally compressed head morphology characteristic of most teleosts, the production of large gills may affect surrounding morphological structures that are involved in feeding or swimming (e.g., body shape). The consequences of such functional-morphological trade-offs may limit feeding performance, swimming efficiency, or other fitness-related traits, and therefore contribute to the maintenance of phenotypic divergence among populations from different DO environments. The widespread East African cichlid *Astatoreochromis alluaudi* shows strong patterns of interpopulational variation in the size of its pharyngeal jaws and gills (Chapman et al. 2007; Binning et al. 2010). In addition, changes in these two structures can be induced by variation in diet and DO, respectively. When fed on hard prey (e.g., molluscs), *A. alluaudi* will develop large pharyngeal jaws with hypertrophied muscles; while a softer diet leads to reduction in pharyngeal jaw size and associated musculature (Greenwood 1965; Huysseune et al. 1994). And when reared under hypoxic conditions, the total gill surface area and total gill filament length of *A. alluaudi* is greater than in normoxia reared sibs (Chapman et al. 2007; Chapman unpubl. data). Across six populations of *A. alluaudi* from sites in Uganda, Binning et al. (2010) found a negative correlation between composite morphological variables related to the size and shape of the gill apparatus and pharyngeal jaw size. Their results suggested that jaw size can be indirectly altered by the physicochemical environment (conductivity and DO) due to correlated effects on gill size, thus providing evidence for spatial constraints and morphological trade-offs between gills and pharyngeal jaws. Smits et al. (1996) reported that the total head volume in snail-eating *A. alluaudi* was 31% larger than in fish from an insect-eating population and observed reallocations of the respiratory apparatus without associated change in gill size. In this case, a trade-off between pharyngeal crushing (jaw size) and respiration was not supported; however, the changes in trophic morphology did result in a change in gill shape. A correlation between gill size and body shape has been documented in the cichlid *P. multicolor* when F1s were reared from multiple populations under either low- or high-oxygen conditions. Full sibs reared under hypoxia were characterized by larger gills (as described above, Fig. 3), larger heads, and deeper bodies, likely a response to gill proliferation (Crispo and Chapman 2010a, 2011; Wiens et al. 2014).

Another potential cost of maintaining large gills might be suboptimal swim performance if the changes in body shape associated with hypoxia (larger heads, deeper bodies) affect streamline (Rouleau et al. 2010). Gotanda et al. (2012) compared the critical swim speed and fast-start performance of F1-generation *P. multicolor* reared under low- or high-DO conditions and tested under their home condition. They found no difference in critical swim speed between rearing treatments. In fast-start trials, hypoxia-reared fish reacted faster and used double bends more often than normoxia-reared conspecifics, but they achieved similar performance. These findings suggest that *P. multicolor* are capable of achieving the same level of swim performance under their home DO condition; however, there may be a cost to performance if fish move into the alternative habitat or a home advantage (normoxia-reared fish may show lower performance if they moved to a hypoxic environment). This is an area for future study, but would be an important signature of local adaptation in *P. multicolor* populations.

In their study of the functional morphology of the gills of African lacustrine cichlids, Galis and Barel (1980) reported a high density of gill lamellae in some less active, algal scraping species that do not normally encounter hypoxia. They suggested that space available for gills may be relatively small in cichlids of this trophic guild; however, fish might compensate with a high lamellar frequency and high waterflow over the gills. Thus, studies exploiting both interspecific and intra-specific comparisons suggest that nonrespiratory factors may influence the extent of divergence in respiratory characters, and vice versa.

4.2.2 Increasing Blood Oxygen Transport

There is great diversity in blood oxygen transport traits of fishes that appear to have evolved in response to both functional hypoxia driven by metabolic demands and environmental hypoxia, and this have been studied in several African and South American cichlids. Blood oxygen transport in most teleost fishes is dependent upon the protein hemoglobin, and transport can be increased by adjusting the affinity of hemoglobin for oxygen, increasing the number of erythrocytes in circulation, and/or increasing hemoglobin concentration [Hb] (Hughes 1973; Johansen et al. 1978; Jensen 1991; Brauner and Val 2006; Wells 2009). Short-term increases in Hct (volume percentage of red blood cells in blood) and hemoglobin [Hb] in response to seasonal or acclimation-induced hypoxia have been reported in some species of cichlids that inhabit hypoxic environments. In their study of the endemic cichlid fauna of the crater lake Barombi Mbo in Cameroon, Green et al. (1973) found much higher blood hemoglobin concentration (16.55 g dl^{-1}) in a cichlid species that periodically fed in the deoxygenated hypolimnion than in 10 other endemic cichlids ([Hb] range = 5.55–8.70 g dl^{-1}), which were restricted in their distribution to the upper lake stratum. And, in their study of hypoxic swamps surrounding Lake Nabugabo in Uganda, Chapman et al. (2002) found that swamp-dwelling *Pseudocrenilabrus multicolor* was characterized by higher Hct and [Hb] than lake-dwelling haplochromine cichlids from the same system.

Oxygen-binding properties of hemoglobin in fishes are also important traits in dealing with environmental hypoxia. These properties can be described by the relationship between the partial pressure of oxygen and the fraction of the oxygen-bound Hb, which is referred to as an oxygen equilibrium curve. The shape of the curve is quantified by Hill's coefficient that ranges from 1 when it is hyperbolic to ~3 when it is sigmoidal (Wells 2009). The P_{50} represents the PO_2 at which 50% of the hemoglobin and is used to describe blood oxygen affinity. Increases in P_{50} have been reported in several studies exploring fish response to hypoxia, associated with increased pH (Bohr effect), decreased erythrocytic concentration of organic phosphates (adenosine and guanosine triphosphates, ATP and GTP, respectively), or variation in the organic phosphate ratio (e.g., Bartlett 1978; Monteiro et al. 1986; Val et al. 1992; Rutjes et al. 2007). Teleosts also often have complex hemoglobin systems (multiple hemoglobins and hemoglobin polymorphisms, Fyhn et al. 1979; Riggs et al. 1979; Perry and McDonald 1993; Perez et al. 1995), and an alternative strategy for increasing P_{50} under hypoxia is a change in the iso-Hb composition.

Rutjes et al. (2007) explored the effects of life-long exposure to hypoxia in three Lake Victoria cichlid species by rearing young *Astatooreochromis alluaudi, Haplochromis ishmaeli*, and a tilapia hybrid (*Oreochromis*) in a split-brood experiment under normoxia or hypoxia (10% air saturation). They found that hypoxia-reared fish of all three species exhibited an increase in hemoglobin concentration [Hb] and hematocrit (Hct) contributing to their ability to maintain oxygen transport capacity under hypoxia. In the hypoxia-reared tilapia, intraerythrocytic GTP levels decreased, a response consistent with adaptive increase in blood oxygen affinity. However, in *H. ishmaeli*, hypoxia-reared fish showed a different iso-Hb pattern compared to normoxia-reared sibs, which correlated with a higher Hb-O_2 blood oxygen affinity. Baptista et al. (2016) explored blood response to acute hypoxia in the Amazonian oscars (*Astronotus ocellatus*) exposed to 0.5 mg O_2 l^{-1} at 27 °C for 3 h followed by 3 h of post-hypoxia recovery. Hypoxia and recovery groups were compared to a normoxia control group. They observed increased hematocrit, hemoglobin concentration ([Hb] mg/dl), red blood count (RBC), and mean corpuscular hemoglobin concentration (MCHC) in response to acute hypoxia, in addition to signals of widespread metabolic depression (see Sect. 4.3 below). After 3 h recovery, [Hb], RBC, and MCHC returned to normoxia levels, while Hct remained slightly elevated. Baptista et al. (2016) also reported increases in the expression of Oscar HIF-1∞ and VEGF mRNA in the hypoxia treatment suggesting that these may be useful molecular indicators of exposure to acute hypoxia.

The cardiovascular system of fishes has a central role in delivering oxygen taken up through the respiratory surface to the tissues, and some aspects of cardiovascular responses to low PO_2 (heart rate reaction to acute hypoxia exposure) have been well studied in fishes (see Gamperl and Driedzic 2009 for review); however, studies focusing on cichlid cardiovascular response to hypoxia are few. One exception is the study by Marques et al. (2008) that exposed the African cichlid *Haplochromis piceatus* to chronic hypoxia ($PO_2 = \sim 15$ mm Hg for 3 weeks). The authors observed an increase in cardiac myocyte density that resulted in a smaller ventricular outflow track and reduced size of the central ventricular cavity. Their results suggest that cardiac remodeling in response to hypoxia acclimation reduces the wall tension required to eject ventricular blood.

4.3 Mechanisms to Reduce Aerobic Demands

Another strategy used by fish to persist under extreme hypoxia is to reduce metabolic demands. A lower metabolic rate under hypoxia may limit the extent of activation of O_2-independent pathways of ATP production (Richards 2009) but has the disadvantage of reducing aerobic metabolism and the amount of energy available for many biochemical processes. Nonetheless, a relatively low routine rate of oxygen consumption (measured under normoxia) seems to be characteristic of some cichlid species that inhabit chronically hypoxic waters such as *Pseudocrenilabrus multicolor* (Rosenberger and Chapman 2000; Chapman et al. 2002) and *Astronotus ocellatus* (Scott et al. 2008).

Many fish species can be described as metabolic oxygen regulators, keeping their oxygen consumption more or less constant over a wide range of oxygen availability in the water; however, when the PO_2 becomes too low to meet oxygen demands, the metabolic rate of the fish will shift from oxyregulation to oxyconformation and shift to anaerobic metabolism, a level referred to as the critical oxygen tension (P_{crit}) (Ultsch et al. 1978; Yeager and Ultsch 1989). A very low critical oxygen tension is characteristic of many hypoxia-tolerant fishes. In their study on interior swamps in the Lake Victoria basin, Chapman et al. (2002) found that a swamp-dwelling population of the cichlid *Pseudocrenilabrus multicolor* was characterized by a lower average P_{crit} (8.5 mmHg) than lake-dwelling *P. multicolor* from the same basin (13.6 mmHg) indicating greater tolerance to hypoxia in the swamp-dwelling population. In a related study, Rosenberger and Chapman (2000) reported a lower critical oxygen in swamp-dwelling *P. multicolor* from the Lwamunda Swamp surrounding Lake Nabugabo Uganda than in two lake-dwelling haplochromines (*Prognathochromis venator* from nearby Lake Kayanja and *Astatotilapia velifer* from Lake Nabugabo), indicating interspecific variation in hypoxia tolerance that correlates with environmental oxygen availability, though clearly other factors that differ among systems may also come into play. In their review of critical oxygen tensions for East African cichlids, Melynchuk and Chapman (2002) found that the two groups (of 16 species/populations) that exhibited the lowest critical tensions were swamp-dwelling populations of two widely distributed species (*A. alluaudi* and *P. multicolor*).

Critical oxygen tension can vary in fishes in response to both short-term acclimation and long-term hypoxia exposure. In their study of the effect of life-long exposure to hypoxia in *P. multicolor*, Reardon and Chapman (2010a) reared F1 offspring from three populations of *P. multicolor* collected from sites of varying DO levels: a hypoxic swamp site, a normoxic lake site, and a fluctuating DO river site. F1 offspring from all sites were reared to maturity under low DO (1.3 mg O_2 l^{-1}) and normoxia (7.6 mg O_2 l^{-1}) at 25 °C. Fish from all three populations showed a significantly lower P_{crit} when reared under hypoxia, and there was no effect of population of origin on P_{crit}. Thus, differences in P_{crit} observed among field populations may reflect, at least to some degree, a phenotypically plastic response.

Another strategy to deal with acute or chronic exposure to hypoxia is the use of anaerobic metabolism. Studies of many hypoxia-tolerant fishes show increased oxygen-independent ATP production (Land et al. 1993; Jibb and Richards 2008) with increased reliance on the contribution of glycolysis to produce ATP (Hochachka et al. 1996; DeKoning et al. 2004; Pollock et al. 2007). However, the yield of ATP is very low during anaerobic glycolysis (15- to 30-fold lower) than if mitochondrial respiration occurs (Hochachka and Somero 2002; Richards 2009). Thus, use of anaerobic metabolic pathways for anything beyond small bursts of activity in fishes requires large reserves, results in accumulation of deleterious end products, and presents a problem for maintenance of cellular energy balance (Richards 2009; Seibel 2011). Fishes living under hypoxia exhibit a suite of adaptations (as discussed above) to facilitate aerobic survival, and evidence from fishes living in some stable hypoxic habitats suggests that anaerobic metabolism is used at most to supplement aerobic metabolism. However, some Amazonian cichlids with remarkable tolerance to hypoxia exhibit a suite of biochemical adaptations, a combination of metabolic depression and activation of anaerobic metabolism in response variation in DO. The Amazonian oscar (*Astronotus ocellatus*), locally known as acará-açu, is a hypoxia-tolerant cichlid that inhabits floodplains and flooded forest in Brazil where it can experience dramatic diel fluctuations in DO. This cichlid exhibits extreme tolerance to low DO surviving at ≤ 0.4 mg O_2 l^{-1} at least 20 h and complete anoxia for up to 6 h at 28 °C (Muusze et al. 1998; Almeida-Val et al. 2000; Richards et al. 2007) and has become a model species for exploring metabolic responses to hypoxia and anoxia.

Muusze et al. (1998) exposed *A. ocellatus* to stepwise declining oxygen levels and reported a significant decrease in standard metabolic rate starting at 30% air saturation (at 28 °C); however, there was no change in blood lactate levels until 6% air saturation, suggesting that *A. ocellatus* suppresses its metabolic rate decreasing the rate of ATP turnover without shifting to anaerobic metabolism until reaching severe hypoxia or anoxia. In a later study by Scott et al. (2008), *A. ocellatus* specimens were exposed to progressive decline in O_2 concentration from ~140 to 10 mmHg at 28 °C over 1.5–2 h. Depression in oxygen consumption rate began at an average critical oxygen tension of 46 mm Hg and strong metabolic depression was evident with an O_2 consumption of only 14% of the normoxic rate at 10 mm Hg. The authors also observed a significant contribution of anaerobic metabolism to ATP supply with plasma lactate concentrations increasing threefold during severe hypoxia. An increase in H+ and lactate production suggest that this species tolerates anaerobic by-products; however, the acid–base imbalance and lactate accumulation was not observed until the environmental oxygen was less than the P_{crit}. Studies exploring ATP-consuming processes in the oscar under hypoxia have demonstrated a reduction in Na+, K+-ATPase in gill and kidney during hypoxia (Richards et al. 2007) that is accompanied by a decrease in ion exchange at the gills and a reduction in nitrogenous waste production (urea and ammonia, Wood et al. 2007). Richards et al. (2007) demonstrated that the decrease in these ATP consuming processes was not accompanied by a significant change in ATP concentration, suggesting that a reduction in ATP-consuming processes contributes to persistence to extended hypoxia exposure in this species. Thus, the extraordinary hypoxia and anoxia tolerance in this species seems to be facilitated by metabolic depression and a sacrifice of O_2 extraction under severe hypoxia, likely to reduce passive leakage of ions across the gills, and a recruitment of anaerobic metabolism. The critical oxygen tension of the Amazonian oscar is surprisingly higher than some other Amazonian fishes, as well as some other hypoxia-tolerant cichlids such as swamp-dwelling *P. multicolor* (8.51 mm Hg), *A. alluaudi* (9.5 mm Hg), and the juvenile tilapias *Oreochromis leucostictus* (13.9 mm Hg) and *Tilapia rendalli* (15.5 mm Hg) collected from swamps surrounding Lake Nabugabo, Uganda (Chapman et al. 2002). However, the hypoxia/anoxia tolerance of the oscar is exceptional, which seems to reflect is ability to recruit anaerobic metabolism. Scott et al. (2008) point out that this anomaly of a relatively high P_{crit} and exceptional tolerance to hypoxia/anoxia suggests that P_{crit} is not always a reliable index of hypoxia tolerance in fishes. The oscar also shows a remarkable ability to match cellular oxygen supply to demand as they grow. Sloman et al. (2006) demonstrated that large oscars have a lower critical oxygen tension (55 mmHg) than small oscars (70 mmHg), supporting earlier studies demonstrating a longer survival time in large oscars exposed to extreme hypoxia and a greater anaerobic enzymatic capability (Almeida-Val et al. 2000). Sloman et al. (2006) also observed that smaller oscars initiated aquatic surface respiration at a lower threshold than larger fish, a counterintuitive response given their lower tolerance to hypoxia. Sloman et al. (2006) argued that juveniles may accept a greater physiological compromise under hypoxia to minimize predator risk associated with ASR and of movement out of shelter.

5 Hypoxia and Reproductive Traits in Cichlids

The family Cichlidae is characterized by a long period of parental care, with one or both parents protecting the young between spawning and independence (when they begin free-swimming). This high level of parental care can contribute to the survival of offspring in hypoxic environments but may also impose costs such as increased energy expenditure and greater predator risk. The diversity of parental strategies in the Cichlidae has been described in detail by Keenleyside in his 1991 review, where parental care is classified based on the physical relationship between the offspring and their parents. Substrate brooders are cichlids in which the parents maintain and protect their brood on or close to the substrate from the time of spawning to independence, whereas mouthbrooders are cichlids in which the parents carry their offspring in their mouth until independence (Keenleyside 1991). The second major criterion for classifying patterns of parental care in cichlids is the gender of the care giver, which can be one (either gender) or both parents, depending on the species (see Balshine and Abate 2021).

The energetic cost of reproduction increases as more energy is invested into parental care (Fryer and Iles 1972; Jones and Reynolds 1999), and one would predict that alternative oxygen environments would affect the costs and benefits of parental care (Hale et al. 2003). Some substrate brooders promote growth and survival of their eggs by guarding the eggs, fanning to aerate eggs, and mouthing to clean and remove dead and diseased eggs (Baylis 1974; Wootton 1990; Keenleyside 1991). Once the eggs hatch into "wrigglers," they are carried in the mouth of the parent to an excavated pit or vegetation, the choice of which may depend on DO availability as described for the Central American cichlid (*Archocentrus* [formerly *Herotilapia*] *multispinosa* by Courtenay and Keenleyside (1983)). In *A. multispinosa*, parents spit the eggs onto vegetation when DO is low, which places them in a better-oxygenated habitat near the surface. In mouthbrooders, ventilation and cleaning of the eggs take place inside the mouth of the parent via a behavior referred to a churning, which moves the brood around in the mouth (Oppenheimer and Barlow 1968; Fryer and Iles 1972). It has been suggested that the primary function of churning is to meet the brood's respiratory requirements. As the young develop in the mouth, the churning rate declines, which may reflect the increasing ability of the young to meet their own respiratory needs (Oppenheimer and Barlow 1968).

Costs of parental care in cichlids may be particularly severe under hypoxia due to the challenge of providing oxygen to the eggs while meeting the increasing oxygen demands of the parents of doing so. Wen-Chi Corrie et al. (2008) quantified the behavioral response to progressive hypoxia in the maternal mouthbrooder *P. multicolor*. This species responded to progressive hypoxia by performing aquatic surface respiration; however, brooding females showed higher ASR thresholds than males, but nonbrooding females did not differ from males. A high ASR threshold in brooding females may reflect various aerobic costs such as churning or provide increased oxygen to the young by bringing them to the surface. Reardon and Chapman (2010b) further explored the cost of mouth brooding under hypoxia in *P. multicolor*. They acclimated fish of swamp origin to hypoxia (1.4 mg O_2 l^{-1}) or normoxia (8 mg O_2 l^{-1}) for a minimum of 6 months. Standard metabolic rates of hypoxia-acclimated (measured at 2.7 mg O_2 l^{-1}) and normoxia-acclimated females (measured at 7.6 mg O_2 l^{-1}) were lower in both brooders and nonbrooders. However, SMR rates were 48% higher in brooding females compared to postbrooding females for both hypoxia- and normoxia-acclimated fish. No differences in brood maintenance metabolism, female relative condition, embryo size, and embryo number were observed between treatments, but the length of the brooding period (from spawning to release of fry from the mouth) was 27% shorter in hypoxia-acclimated females suggesting accelerated development of offspring under hypoxia, which may reduce the overall costs to female brood maintenance under hypoxia.

5.1 Effects on Growth, Fecundity, and Secondary Sex Characteristics

In addition to the costs of parental care, hypoxia should, theoretically, trigger an overall reduction in energy available for both somatic growth and reproduction.

Hypoxia can affect growth by influencing metabolic pathways, metabolic rate, and allocation of energy resources; and growth depression is a widespread response to hypoxic stress (Wang et al. 2009). Hypoxia has also been observed to affect reproduction in fishes by altering the concentration and ratio of sex hormones, disrupting gonad formation and development, altering fertilization and spawning behavior, and impairing embryo development (e.g., Wu et al. 2003; Landry et al. 2007; Thomas et al. 2007; Hassell et al. 2008; reviewed in Wu 2009).

Interpopulational studies on the reproductive biology of *P. multicolor* in the field have yielded insights into the long-term response of fish populations to divergent oxygen environments. *P. multicolor* populations from hypoxic environments are characterized by a smaller female size at maturity, smaller egg size, and smaller juvenile size, but a larger number of eggs than conspecific females from normoxic sites, thus demonstrating a trade-off between egg size and number among high- and low-DO sites, with no difference in batch reproductive effort (Reardon and Chapman 2009, 2012). Kolding et al. (2008) quantified the effect of ambient oxygen on growth and reproduction in Nile tilapia (*Oreochromis niloticus*) and reported a decrease in both size at maturity and estimated asymptotic size with decreasing O_2 concentration. They did not observe a trade-off in egg size and number, with fish reared under hypoxia producing smaller eggs with similar relative fecundity and lower gonadosomatic index than larger normoxia-reared fish. It has been argued that small size of eggs, embryos, and/or juvenile fish under hypoxic conditions may afford higher fitness than larger individuals at the same stage of development (e.g., Sargent et al. 1987; Hendry et al. 2001; Reardon and Chapman 2012), because a higher surface area to volume ratio theoretically provides a larger surface area to meet metabolic demands. However, there is still speculation as to whether the hole egg is metabolically active, which could alter the prediction (e.g., Einum et al. 2002; Kolm and Ahnesjo 2005; Rombough 2007). In addition, some studies report slower growth and/or smaller size under hypoxia as evidence of negative fitness effects, that is, small size is a limitation of the growth environment (Wu 2009; Mueller et al. 2011).

The endocrine system acts as the primary regulator of fish reproduction in teleost fishes, and recent studies suggest that hypoxia may disrupt aromatase activity necessary for the conversion of testosterone to estradiol (Shang et al. 2006; Landry et al. 2007), which has the potential to negatively affect reproduction by modifying both behavior and gonad maturation. In their study of the effects of hypoxia on sex hormones (estradiol and testosterone) of female *P. multicolor*, Friesen et al. (2012) compared females from one low- and one high-DO population in each of two regions of Uganda. In both regions, hypoxic populations were characterized by higher levels of testosterone than high-DO populations, a higher testosterone/estradiol ratio, and a lower proportion of brooding females, providing evidence consistent with hypoxia-mediated endocrine disruption in populations of *P. multicolor* experiencing life-long hypoxia.

Another potential cost under hypoxia for reproducing cichlids is the energetic cost of male nuptial color expression and courtship displays. McNeil et al. (2016) examined the role hypoxia in driving divergence in two sexually selected traits, male color, and reproductive behavior in *Pseudocrenilabrus multicolor*. They used a field survey to describe natural variation in male nuptial color patterns across habitats divergent in DO and lab studies on wild-caught fish from a low-DO and high-DO habitat to test for differences in reproductive behavior under low- and high-DO conditions, respectively. In energetically challenging low-DO environments. male *P. multicolor* were more red, and in high-DO environments fish were typically brighter and more yellow. The frequency of reproductive displays in fish of low-DO origin was 75% lower when tested under hypoxia. In a complimentary study of male *P. multicolor* acclimated to hypoxia or normoxia for 5 months, males acclimated to low DO reduced their total number of displays (courtship + aggression) compared to high DO-acclimated males (Gotanda et al. 2011). McNeil and colleagues suggested that lower reproductive display frequency in males from hypoxic habitats in combination with the observed male color variation may reflect a tradeoff whereby male *P. multicolor* from low-DO populations maintain mate attraction by increasing levels of (potentially) more costly nuptial colors (i.e., red) and reducing energetically expensive courtship displays.

6 Hypoxic Refugia from Piscine Predators

Despite potential costs for fish that persist in hypoxia habitats, there may be benefits of these extreme habitats that offset physiological and/or biochemical costs such as reduced competition, predation, and/or disease. In particular, several recent studies provide evidence for reduced predation pressure for fishes in hypoxic habitats, that is, prey may benefit if high tolerance to hypoxia permits access to refugia from less tolerant predators (Anjos et al. 2008; Chapman et al. 2002; Robb and Abrahams 2003; Reid et al. 2013b). For example, for some potential prey in the Lake Victoria basin of East Africa, including several haplochromine cichlids, hypoxic refugia have mitigated impacts of a large introduced piscivore the Nile perch (*Lates niloticus*). Nile perch were introduced to Lake Victoria and other lakes in the region (Nabugabo, Kyoga) in 1950s and 1960s to compensate for depleting commercial fisheries and, in the case of Lake Victoria, also to promote sport fishing (Balirwa et al. 2003; Pringle 2005). Although many fish stocks in Lake Victoria had declined before the dramatic increase in the Nile perch population in the 1980s (including haplochromine cichlids in some areas of the lake), the rapid increase of the Nile perch coincided with the further decline or disappearance of many fish species, most notably the disappearance of over 40% of the endemic haplochromine cichlids (Kaufman 1992; Witte et al. 1992; Kaufman and Ochumba 1993; Balirwa et al. 2003; Chapman et al. 2008b; Goudswaard et al. 2008). Eutrophication and fishing pressure on haplochromine cichlids in some areas of the lake have also been implicated in decline of native fishes; however, the Nile perch seems to have been an important driver (Balirwa et al. 2003; Chapman et al. 2008b; Goudswaard et al. 2008; Taabu-Munyaho 2014). Similar changes in fish assemblages have occurred with Nile perch introduction into other lakes in the basin, including Lake Nabugabo, a lake where eutrophication has been minimized by the Lwamunda Swamp that surrounds much of the lake margin, as well as limited shoreline development (Ogutu-Ohwayo 1993; Chapman et al. 2003, 2008b), thus highlighting the significance of the Nile perch in influencing fish assemblage dynamics in this system. Although many species have disappeared or undergone a dramatic population decline in lakes with Nile perch, some indigenous species have persisted with Nile perch and have been resilient to increasing eutrophication and other stressors (see Natugonza et al. 2021). Over the years, interest in conservation of the residual fauna in lakes Victoria, Kyoga, and Nabugabo has triggered studies to identify fish faunal refugia, that is, habitats where native fishes are protected from Nile perch predation. A growing body of evidence suggests that wetlands in the Lake Victoria basin serve as both structural and low-oxygen refugia for fishes that can tolerate wetland conditions and function as barriers to dispersal of Nile perch (Chapman et al. 1996, 2002; Schofield and Chapman 1999; Mnaya et al. 2006; Chretien and Chapman 2016). Ecophysiological and ecological studies on the fishes of the Lake Nabugabo system have demonstrated that some cichlids and some native noncichlids that are relatively tolerant of hypoxia are able to persist in the dense interior of hypoxic swamps (Chapman et al. 1995, 2002; Chapman and Chapman 1998; Rosenberger and Chapman 2000; Rutjes 2006) where Nile perch is absent or in the wetland ecotones where Nile perch are rare. Relatively to swamp-dwelling fishes in the basin, Nile perch has a low tolerance to hypoxia as indicated by its high threshold for ASR, its high critical oxygen tension, and its distribution and selection for waters of high DO (Schofield and Chapman 2000; Chapman et al. 2002, Nyboer and Chapman 2013). The ecotone of the wetland/open water is a particularly important refugium because interaction with the main lake waters elevates DO to more moderate levels, but structural complexity is still high. Reid et al. (2013b) characterized the fine-scale patterns of distribution and abundance in wetlands of Lake Nabugabo, Uganda to determine peaks in native fish abundance and richness ("peak refugia," Fig. 4a). They hypothesized that if native fishes are more tolerant of wetland conditions that Nile perch (the invader), there may be some particular distance from the wetland edge where predator-prey encounters are minimized, but beyond which conditions become less hospitable (due to extremes of the physicochemical environment), limiting prey abundance and fitness (Fig. 4a). Reid et al. (2013a, b) tested this idea using a series of wetland transects extending across the lake-wetland edge in Lake Nabugabo. They observed strong clines in water temperature, pH, DO, depth, and vegetation density over the 110-m transects that extended from 10 m offshore to 100 m into the wetland, and narrow peak refugia precisely at the lake-wetland edge where both fish richness and abundance were the greatest. Endemic haplochromines were most abundant at the swamp edge, and none were found in the swamp interior; whereas the hypoxia tolerant *P. multicolor* was most abundant in the swamp interior (Reid et al. 2013a, b, Fig. 4b). Nile perch were rare in the ecotone and absent in the swamp interior (Reid et al. 2013a, Fig. 4b). The harsh physicochemical conditions that characterize the dense wetland interior force lacustrine species, including the endemic haplochromines in this system into narrow, edgy habitats where conditions are most lake-like, but still afford some protection

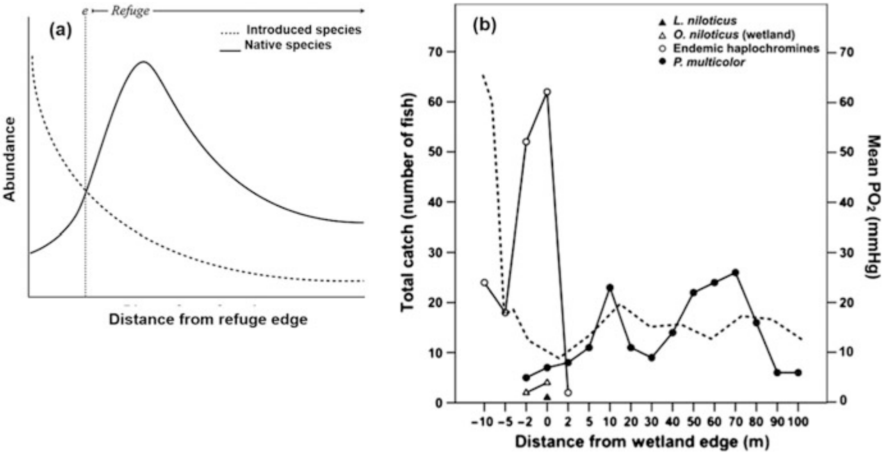

Fig. 4 (**a**) Theoretical relationship between the abundance of native species and distance from the refuge edge. Peaks in native species abundance are predicted to occur some distance from the refuge edge (indicated by the dotted reference line and the symbol e) where the abundance of introduced species is minimized. Reproduced from Reid et al. (2013b) with permission from Aquatic Conservation. (**b**) The distribution and abundance of four fish taxa along a negative dissolved oxygen gradient (dotted line) in the Lwamunda Swamp of Lake Nabugabo, Uganda. Positive distances are indicated from the wetland-lake interface into the wetland, negative distances are from the interface toward the open water of the lake. Reproduced from Reid et al. (2013a) with permission from Ecology of Freshwater Fish

from Nile perch (Reid et al. 2013b). The dense interior of the wetland harbored an assemblage of swamp specialists that likely inhabited these wetlands before the introduction of the Nile perch (Reid et al. 2013b).

In Lake Victoria, intense fishing pressure on the Nile perch has coincided with resurgence of some native fishes, most notably, an increase in the biomass haplochromine cichlids, representing a few species and only a few trophic groups (Witte et al. 2000, 2007; Chapman et al. 2003; Matsuishi et al. 2006). In Lake Nabugabo, intense fishing of Nile perch has also coincided with the resurgence of some native species, particularly haplochromine cichlids, as well as shift in the distribution of Nile perch and a decrease in its average size (Chapman et al. 2003; Paterson and Chapman 2009; Chretien and Chapman 2016).

Chretien and Chapman (2016) analyzed one year of fish distribution data in Lake Nabugabo to describe the fish community 50 years after the introduction of the Nile perch. Of the environmental parameters measured, they found that water depth and DO concentration were the main environmental factors shaping the fish community distribution and that Nile perch and its major prey, haplochromine cichlids, showed contrasting ecological requirements. Comparison with previous studies over the past 15 years showed a decline in the catch per unit effort of Nile perch and a resurgence of haplochromine cichlids in certain habitats. Chretien and Chapman (2016) suggested that differences in the abiotic requirements of Nile perch and haplochromine cichlids combined with heavy fishing pressure on Nile perch have promoted resurgence of the native fish fauna.

In the Lake Victoria basin, haplochromine cichlids have faced increasing exposure to hypoxia in wetland ecotones where some species have persisted in the face of Nile perch predation but also in response to cultural eutrophication and climatic variability, which may have contributed to eutrophication and associated declines in dissolved oxygen availability. For such species, selection for tolerance to hypoxia may have resulted in phenotypic change to increase oxygen uptake capacity and/or oxygen delivery. Van Rijssel et al. (2016) provide a compelling set of data that explores the relationship between climate variability, environmental variables (water temperature, DO, and water transparency), and gill surface area of four haplochromine cichlids species over the past five decades in Lake Victoria. They found that during a period of severe eutrophication and reduction in DO levels, gill surface area in three of the four haplochromine cichlid species increased, consistent with adaptive response to hypoxia; while during the 2000 when wind speed, DO, water transparency, and water temperature increased, cichlid gill surface area decreased (see Fig. 3 in van Rijssel et al. (2016)). These results suggest rapid phenotypic change in Lake Victoria cichlids. The source of the phenotypic change in gill size in these field populations may be plastic and/or genetic; however, a high degree of developmental plasticity in gill size in response to hypoxia has been reported in lab-rearing studies of *A. alluaudi* (Chapman et al. 2007) and *H. pyrrhocephalus* (Rutjes 2006). For such species, selection for tolerance to hypoxia may have resulted in phenotypic change to increase oxygen uptake capacity and/or oxygen delivery. In other related studies, morphological changes (body shape, photic traits) have been reported in recovering haplochromine cichlids in Lake Victoria that correlate with environmental change (Witte et al. 2008; Van der Meer et al. 2012; van Rijssel and Witte 2013; van Rijssel et al. 2014). Although many species of haplochromine cichlids in Lake Victoria are presumed extinct, the ability for some species to persist in the face of eutrophication and Nile perch predation, among other environmental changes, may reflect rapid adaptive phenotypic trait change.

7 Summary

Cichlid fishes have provided valuable insights into strategies for dealing with hypoxia and the ecological and evolutionary consequences of hypoxic stress. In particular, studies of the Amazonian Oscar *Astronotus ocellatus* and the Dwarf Victorian Mouthbrooder *Pseudocrenilabrus multicolor* have highlighted the complexity of response to hypoxia from the molecular to the whole-organism level. *Astronotus ocellatus* shows a remarkable ability to withstand extreme hypoxia and normoxia despite its anomalously high critical oxygen tension and the unexpected higher tolerance to hypoxia in adult versus juveniles. Unraveling these physiological conundrums has yielded exciting insights into anaerobic strategies in this species and predator risk-hypoxic trade-offs. Studies of the eurytopic haplochromine cichlid *Pseudocrenilabrus multicolor* have contributed to our understanding of the role of DO as a divergent selective agent. This widespread cichlid shows dramatic interpopulational variation in respiratory traits between low- and high-DO environments and potential trade-offs between respiratory and nonrespiratory traits that may be important in the maintenance of distinct respiratory phenotypes. Rearing studies of *P. multicolor* and other haplochromine cichlids have demonstrated a strong role of developmental plasticity in providing flexibility to respond divergent oxygen environments. By expanding the environmental conditions under which organisms can survive, developmental plasticity may be important for persistence in changing and/or novel DO environments. Whether this facilitates or constrains evolutionary change may depend on such factors as the quality and costs of the plastic and evolutionary response, the stability of the environment, and the amount of gene flow among populations.

Despite the diversity of strategies that have permitted some cichlid species to persist under extreme hypoxia, life in low-oxygen habitats may incur a number of costs including growth depression, reduced allocation to reproduction, and costs associated with parental care. Such costs may be offset by the benefits of hypoxic habitats such as reduced competition and predation. For example, several recent studies of African cichlids provide compelling evidence for reduced predation pressure in hypoxic habitats and highlight the significance of hypoxic refugia for hypoxia-tolerant cichlids in the face of invasive piscivores. The recovery of some species of haplochromine cichlids in the Lake Victoria basin and their ability for rapid phenotypic change in response to the ecological turmoil and environmental change in the lake basin provide evidence for resilience in at least a small component of this once diverse cichlid fauna.

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Feeding Ecology of Lake Tanganyika Cichlids

Tomohiro Takeyama

Abstract Among the ancient Great Lakes of East Africa, Lake Tanganyika is the oldest and possesses about 250 species of cichlid fishes. Most are endemic species and have rapidly evolved with high diversification in morphology, behavior, and ecology through adaptive radiation into novel habitats. Cichlids are distributed from the shallow margins to the deep area in the lake, while the assemblages of the cichlid community indicate higher density and diversity in the shallow rocky regions in which some cichlid species that utilize similar diet niches coexist. In this chapter, I summarize research about feeding ecology, morphological traits in relation to foraging behavior and diet utilization, and food web structure in the cichlid community of Lake Tanganyika. Furthermore, I point out future directions in terms of current novel approaches that would contribute to understanding sympatric speciation with expanding novel diet/feeding niches, the diversification of species, food web constructions, and mechanisms for coexistance; including evo-devo, symbiosis with microorganisms in guts, stable isotope analysis, and behavioral syndrome/personality studies for the Lake Tanganyika cichlids. The integration of these studies will help us understand the ecological and evolutionary insights of feeding ecology and provide new aspects of adaptive radiation and sympatric speciation in Lake Tanganyika cichlids.

Keywords Adaptive radiation · Trophic niche and trophic guild · Cichlid community · Foraging habitat · Feeding behavior and ecomorph · Coexistent mechanism

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T. Takeyama (✉)
Department of Biosphere-Geosphere Science, Okayama University of Science, Okayama, Japan
e-mail: takeyama@big.ous.ac.jp

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1 Introduction

Lake Tanganyika is one of the ancient lakes located along the Great Rift Valley of Eastern Africa (Fig. 1). It is the second-deepest, -oldest, and -largest by volume freshwater lake in the world (Cohen et al. 1993). *The Cichlid Fishes of the Great Lakes of Africa* by Fryer and Iles (1972) is one of the landmark publications of

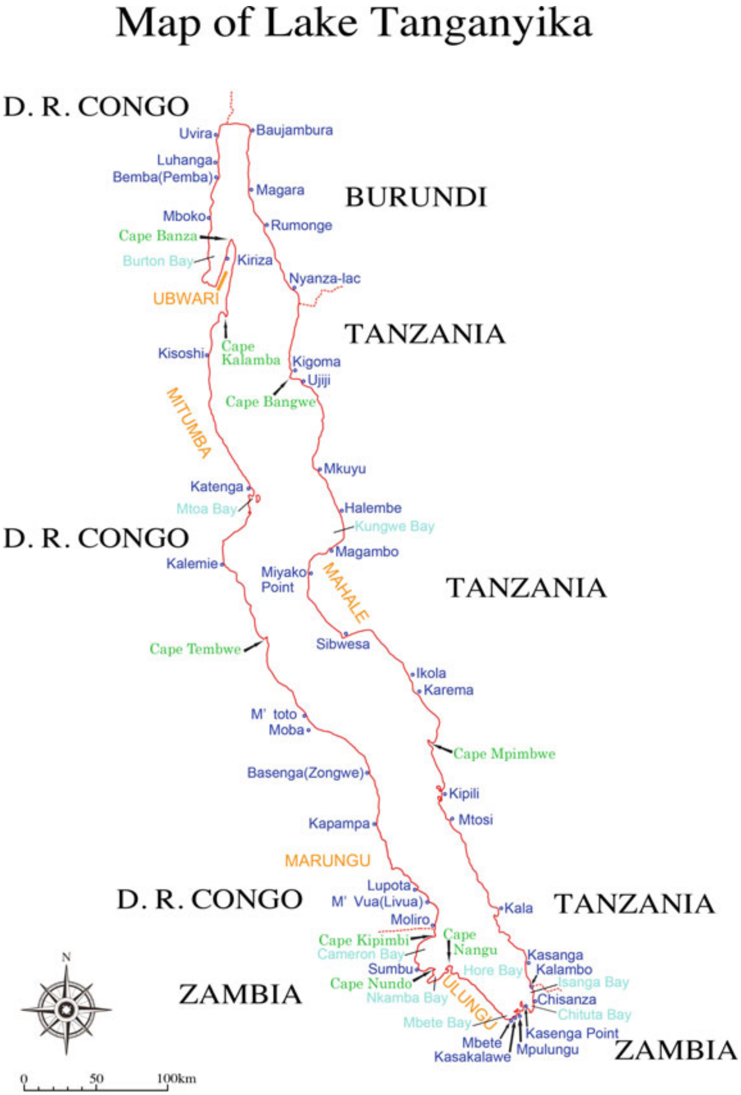

Fig. 1 Map of Lake Tanganyika. The locations on the map are from Kawanabe et al. (1997) and Konings (2019)

cichlid research in African Great Lakes. They synthesized comprehensive information about the biology and evolution of the cichlids in Lakes Victoria, Tanganyika, Malawi, and some small lakes of East Africa. After that Lowe-McConnell published a remarkable book entitled *Fish Communities in Tropical Freshwaters*, where she summarized not only the fish fauna in African Great Lakes but also referred to the fish ecology and diversity in several regions including river ecosystems (Lowe-McConnell 1975).

For the last four decades, cichlid flocks in Lake Tanganyika have attracted many field scientists with phylogenetical, ethological, behavioral ecological, genetical, ecological, and morphological perspectives (Paugy 2010). Lake Tanganyika cichlids have been recognized as the ideal models of vertebrate evolution, speciation (adaptive radiation), and diversification in the wild (Kornfield and Smith 2000; Kocher 2004; Seehausen 2006; Burress 2014). Since 1979, a Japanese-African cooperative research team, led by Hiroya Kawanabe, has been studying the biology of fishes in the littoral zone of Lake Tanganyika. They have examined behavior, ecology, genetics, and evolution of cichlids, with a view to clarifying the factors for why so many species coexist. To figure out the mechanism of coexistence in cichlid communities, the team introduced an innovative method, SCUBA diving, with direct observations of cichlid behavior in their underwater natural habitat, focusing on their complex social relationships within inter- and intra-specific interaction, based on individual identification techniques. Some of the outputs from their field work is compiled in a book entitled *Fish Communities in Lake Tanganyika*, edited by H. Kawanabe, Michio Hori, and Makoto Nagoshi (Kawanabe et al. 1997).

In Lake Tanganyika, cichlid fishes show explosive expansive speciation via adaptive radiation, where the number of species is over 250 including many endemic species (Poll 1953, 1956). The cichlids are distributed throughout the lake, in both littoral and pelagic zones, especially the rich cichlid fauna in the littoral rocky habitat (Lowe-McConnell 1975). On the other hand, the fish community is relatively simple in the pelagic zone, where the large cichlid, *Boulengerochromis microlepis* (c.a. 800 mm, Fig. 2), predatory centropomid genus *Lates* (*L. angustifrons*, *L. mariae*, *L. microlepis*, *L. stappersi*), and clupeids, *Stolotrissa tanganicae* and *Limnothrissa miodon,* range widely (Coulter 1991). In the deep area, predatory cichlids of the genus *Bathibatini* and catfishes of the genus *Chrisichthys* occur (Coulter 1991). The diversification of the cichlid community caused by their adaptive radiation has resulted in the expansion of their distribution throughout the heterogenous habitats of the Lake. For the adaptive radiations of the cichlids, some significant factors, including their morphology, behavior, and feeding habitat (diet), have played innovative roles (Burress 2016).

For adaptive radiation of Lake Tanganyika cichlids, two conditions in relation to natural selection would be required: the formation of a novel habitat and possession of “key innovations” such as morphological and/or behavioral traits that allow adaptation to a new niche (Sturmbauer et al. 2006). The former factors include an ecological opportunity in relation to habitat heterogeneity (e.g., rocky or sandy bottom, littoral, open, and deep waters) in the lake in which might be sometimes created by historical fluctuations in water level Rossiter (1995). Such fragmentation

Fig. 2 Pair of *Boulengerochromis microlepis* with their free-swimming young (Depth: 10 m). Photo by Tomohiro Takeyama

among habitats could act as barriers for gene flow among the populations, and thus consequently promoted speciation (Kawanabe et al. 1997). The latter factors include the morphological features such as jaws with teeth and pharyngeal jaws (Fig. 3) together with a gape that allow them to utilize variable diets and behavioral traits such as parental care for broods (eggs, embryos, and juveniles; Kuwamura 1986, 1997; Sefc 2011). For the process of adaptive radiation, sexual selection could also play a fundamental role to establish genetic isolation (Seehausen 2006; Wagner et al. 2012). Contrary to the predictions, recent research suggests that hybridization between species could facilitate the speciation in Lake Tanganyika cichlid flocks (Weiss et al. 2015). Hybridization may generate new species and promote sympatric speciation between species, including functional novelty (e.g., allelic mutations in the opsin gene) and niche widening (Seehausen 2004; Abbott et al. 2013; Hedrick 2013; Harrison and Larson 2014; Pfennig et al. 2016; Meier et al. 2017; Selz and Seehausen 2019). In the process of sympatric speciation and adaptive radiation of the cichlids in Lake Tanganyika, each species has established a specific food niche with unique morphological and behavioral adaptations related to foraging. As a result, the current food web of cichlids consists of complex relationships not only between cichlids and their prey species but also among species.

2 Food Web Structure of the Cichlid Community

A food web is a description of interspecific relationships among predator and prey in a given community. In general, a food web is constructed by direct observations of a predator and its prey and/or stomach (gut) contents analysis (Michener and Kaufman 2007). The early description of a food web of a cichlid community was by Fryer (1959) at rocky and sandy shores in Lake Nyasa (Lake Malawi). Cichlid species are abundant along rocky shores where the primary production is from the algal film

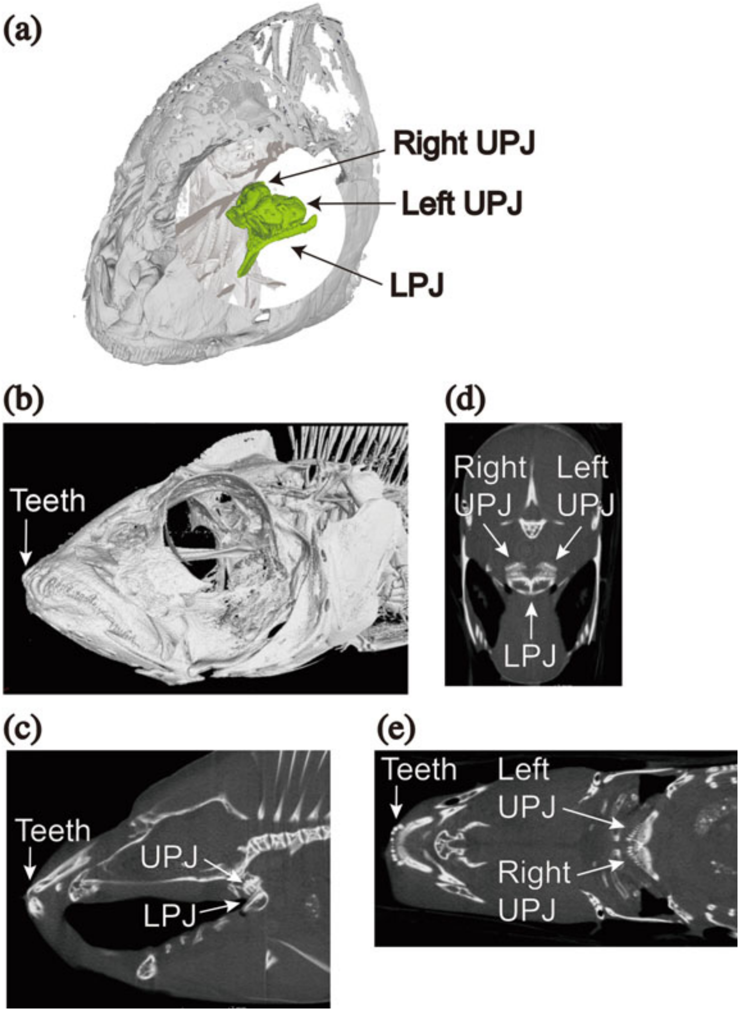

Fig. 3 Teeth and pharyngeal jaws of Tanganyika cichlids. Upper and lower pharyngeal jaws of *Petrochromis* sp. (**a**). Head of *Neolamprologus savoryi* (**b**). Lateral (**c**), frontal (**d**), and ventral (**e**) views of X-ray photographs of *N. savoryi*. LPJ and UPJ: lower and upper pharyngeal jaws, LT and UT: lower and upper jaws. Created by Tomohiro Takeyama

(aufwuchs) and at least 10 species of cichlids utilize that as food resources. Insect larvae (Hydropsychid larvae and *Neopterla spio* nymphs) are consumed by several cichlid species. This utilization of similar food resources by multiple species suggests that niche (diet) partitioning and coexistence mechanisms will underlie the cichlid community.

3 Community Structure and Trophic Guilds of Cichlids in Lake Shore Areas

In Lake Tanganyika, Hori et al. (1983) conducted a field survey at the Luhanga shore in the northwestern part of Lake Tanganyika. In 1980, they carried out a census to count every species of rock-dwelling cichlid fish with SCUBA diving in a 20 m × 20 m quadrat set on predominantly rock and stone bottom, from the shore line to the depth of about 11 m. In this area, ca. 7000 fish inhabited the quadrate (400 m^2), represented ca. 41 species, and most of them cichlids, representing ca. 18 individuals per m^2. Dominant substrate types (e.g., rock, stone, gravel, sand, or mud) and water depths differ in the abundance of each species, in relation to trophic guilds (feeding groups): epilithic algal (aufwuchs) feeders, plankton feeders, detritus feeders, shrimp eaters, zoobenthos feeders, piscivores (including predators on juvenile cichlids), and scale-eaters (Hori 1987; trophic guilds category following Hori 1991, 1997; and Takeuchi et al. 2010). The plankton feeders, *Neolamprologus brichardi* and *N. savoryi,* are the most numerous group (56% of fish found, 10.2 fish/m^2), since these species sometimes form large colonies on the boulder substrate with cooperative breeding groups consisting of a dominant breeding pair, helpers and juveniles (Taborsky and Limberger 1981). The second most abundant groups are omnivorous cichlids (e.g., *Telmatochromis bifrenatus* and *Julidochromis regani*; 21% of fish found, 3.8 fish/m^2) and aufwuchs feeders (e.g., *Tropheus moorii*, *Petrochromis polyodon*, and *Telmatochromis temporalis*; 18% of fish found, 3.3 fish/m^2). On the other hand, zoobenthos feeders (e.g., *Lamprologus modestus, L. modestus, L. leleupi*, and *L. tretocephalus*) and piscivores (e.g., *Lamprologus elongatus* and *L. lemairii*), and scale eaters comprised only about 2% of all the fish found (0.4 fish/m^2).

Species assemblages of the cichlid community in a littoral zone differed among sites within the lake. Hori et al. (1993) compared the fish communities from three littoral rocky habitats, at Luhanga shore (the northwestern part), Mahale (the middle-eastern part) and Mpulungu (the southern end), within a quadrat of the same size area (400 m^2). In each site, ca. 40 species occurred, most of which were cichlids. The number of species at Mpulungu is greater than the other two sites. However, the fish density present at Mpulungu is lower than that at Luhanga and Mahale. The species assemblages at Luhanga and Mahale are similar, though the species composition and community structure at Mpulungu is very different from the other two sites. The species and feeding guilds in Muplungu are different from those in Luhanga, but the trophic groups are like each other. According to Hori (1991, 1997) and Takeuchi et al. (2010), species are categorized into seven major trophic groups: (1) aufwuchs feeders, (2) plankton feeders, (3) detritus feeders, (4) shrimp feeders, (5) zoobenthos feeders (other than shrimp eaters), (6) piscivores (including juvenile eaters), and (7) scale eaters. In Mpulungu, aufwuchs feeders include 16 species including the following genera: five species of *Petrochromis*, two species of *Telmatochromis*, one species of each *Interochromis*, *Limnotilapia*, *Tropheus*, *Simochromis*, *Psudosimochromis*, *Xenotilapia*, *Eretmodus*, *Julidochromis*, and *Neolamprologus*

Fig. 4 *Variabilichromis moorii* with free-swimming young (Depth: 10 m). Photo by Tomohiro Takeyama

(= *Variabilichromis*). Plankton feeders consisted of 10 species belonging to five genera: four species of *Neolamprologus*, three species of *Cyprichromis*, one species of *Paracyprichromis*, *Xenotilapia*, and *Lamprichthys* (noncichlid), respectively. Four detritus feeders are assigned to different genera: *Ophthalmotilapia*, *Cunningtonia*, *Cyathopharynx*, and *Aulonocromis*. Seventeen species utilized benthic animals. Six species of four genera (three species of *Neolamprologus*, one species of each *Lamprologus*, *Altolamprologus*, and *Gnathochromis*) are shrimp eaters and 11 species belonging to six genera (five species of *Neolamprologus,* two species of *Lepidiolamprologus*, one species of each *Xenotilapia*, *Lobochilotes*, *Ctenochromis*, and noncichlid *Hippopotamyrus*) are zoobenthos feeders. Piscivores involved nine species, mainly genus *Lepidiolamprologus* (five species) and one species each of *Neolamprologus*, *Haplotaxodon*, and one species of a perch, genus *Lates*, and one species of a spiny eel (genus *Mastacembelus*). Both the species of scale eaters are within the genus *Perissodus*.

The most abundant species in Mpulungu are aufwuchs feeders (*Telmatochromis vittatus*: 14.2% of fish found, *Variabilichromis moorii* (Fig. 4): 13.6% of fish found). The second largest guilds are zooplankton feeder *Cyprichromis leptosoma* (9.1%) and detritus feeder *Ophtalmotilapia ventralis* (6.4% of fish found). By trophic groups, aufwuchs feeders are the majority in both number of species and individuals (49% of fish found). The second most abundant group is the plankton feeders that accounted for 26% of the total number of fishes. The third most abundant trophic groups are the detritus feeders (10%) and the piscivores (8% of all individuals). The shrimp feeders and zoobenthos feeders are rich in species numbers, but their abundances are only 3% and 2% of the total number of fishes, respectively. Two

Fig. 5 Rocky and sandy bottom at Kasakalawe Point (Depth: 5 m). Photo by Tomohiro Takeyama

scale eaters are also in the minority group that accounted for 2% of the total number of fishes.

At two other rocky shores in the southern end region of Lake Tanganyika, Kalambo and Kasakalawe (Fig. 5) cichlid communities have been investigated (Sturmbauer et al. 2008). In Kalambo and Kasakalawe, ca. 41 and 46 sympatric cichlid species were recorded, respectively, in each 400 m^2 (20 m × 20 m square) study areas on rock-cobble substrates. Fish abundance in each study transect seemed similar (881.0 and 915.1 individuals, respectively); however, relative densities of dominant species were different between the two sites. Similar to the results in Mupulungu, in Kalambo, aufwuchs feeders were the most abundant and three species, *V. moori*, *Tropheus moorii*, and *Eretmodus cyanostictus* (Fig. 6) are found with 28.9%, 12.3%, and 5.7% of the total cichlids, respectively. The detritus feeders, *Aulonochronus dewindti* and *Ophtalmotilapia ventralis* are the secondary abundant trophic groups found with 18.9% and 9.9% of the total number of cichlid fishes, respectively. In Kasakalawe, although aufwuchs feeder was also recorded as the most abundant group, *V. moorii* show the highest abundance with 60.4% of all cichlid individuals. On the other hand, the aufwuchs feeder, *E. cyanostictus*, the detritus feeders *O. ventralis* and *A. dwendti* and a plankton feeder *Neolamprologus cuadopunctatus* accounted for 11.0, 4.1, 2.8, and 2.7% of the total number of fishes, respectively.

In each research site, several species, especially cichlids, belonging to the same trophic group coexisted in relatively small areas (400 m^2) at high densities. The species-specific differences in morphologies, feeding behaviors, and ecological factors (feeding habitat) should have played important roles to allow the coexistence of the sympatric cichlids that utilize similar diets. Hori (1987) investigated the fine

Fig. 6 *Eretomodus cyanostictus* (Depth: 6 m). Photo by Tomohiro Takeyama

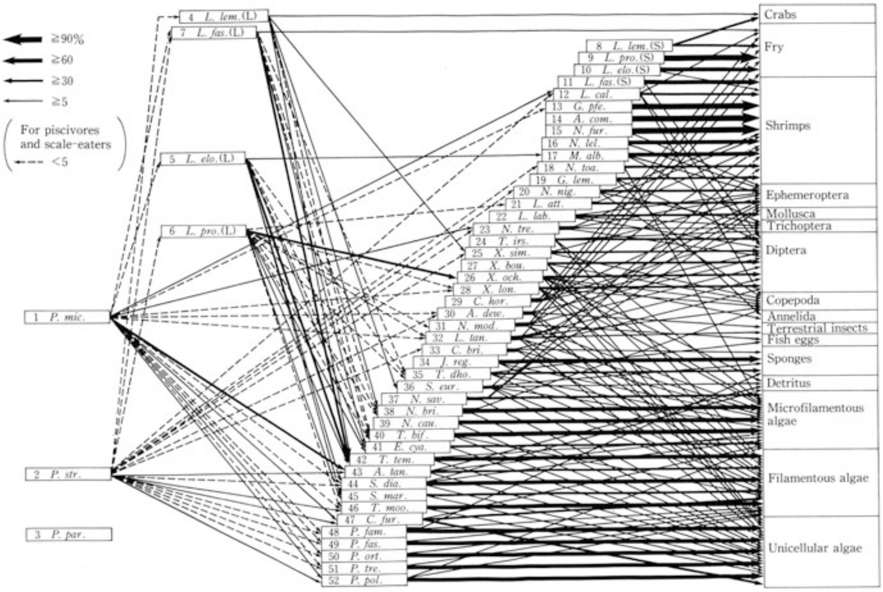

Fig. 7 Food web of cichlid community at Mahale from stomach contents analysis (from Hori 1987). Arrows show the diet for each species. Thickness of arrow indicates the degree of utilization of each food items. Prey species for piscivores and scale eaters include underwater observations. (L): large (adult) fish, and (s): subadult fish

stomach contents from wild caught specimens on the rocky shore in Mahale and showed a food web from the 48 species (Fig. 7). Of 48 species, 14 species are herbivores and most of the others utilized zoobenthos that include specialized shrimp eaters. Generally, in the aquatic food webs, piscivores are the top predator; however, two species of scale eaters show the highest trophic position since they fed on the scales of piscivorous cichlids in the littoral fish community of Lake Tanganyika. Hori et al. (1993) conducted the same research at the study site in Luhanga and the food web was similar to that in Mahale.

3.1 Trophic Niches

As mentioned above, the feeding guilds (trophic groups) of the cichlid community consisted of seven groups: aufwuchs feeders, plankton feeders, detritus feeders, shrimp eaters, zoobenthos feeders, piscivores, and scale eaters. Furthermore, from the stomach contents analysis, the aufwuchs feeders are divided into three groups: unicellular algal feeder, filamentous algal feeder, and microfilamentous algal feeder. Here I describe various feeder characteristics (e.g., jaws; teeth; behavior) and the habitats (substrate; depth) where the guilds occur.

3.2 Aufwuchs (Algae) Feeders

Within algae feeders, species-specific differences in morphology of oral jaws, teeth, and feeding behavior play important roles for diet divergent and coexistence (Yamaoka 1983a; Yamaoka et al. 1986). Each aufwuchs feeder has unique foraging methods in relation to the morphological features in teeth shapes (Mbomba 1983; Yamaoka 1987; Figs. 8 and 9). Grazers basically have fork-like teeth with tricuspid crowns and comb unicellular algae from epilithic assemblages on the surface of rocks, except *Interochromis loocki* has bicuspid jaw teeth. Browsers have bicuspid crown teeth on the outermost edges of both jaws, and nip and nibble filamentous algae on substrates. Scoopers protrude and plunge their jaws into the surface on the sandy bottom to intake small amount of sand (usually fine sand) and filter prey while discharging sand through the opercular openings. Scrapers rub epiphyton from the rock surface with similar sized chisel-like teeth.

In general, aufwuchs feeders establish and defend a foraging territory against other aufwuchs feeders including conspecifics and heterospecific individuals (Yamaoka 1982; Yamaoka 1983b; Takamura 1984; Kohda and Yanagisawa 1992; Kohda 1995; Karino 1998; Morley and Balshine 2003; Ochi et al. 2009). On the other hand, herbivorous cichlids sometimes construct overlapping territories among species (Kohda 1991; Kuwamura 1992; Kohda 1998). The territory owners of these herbivores defend their territory against intruders, especially conspecific and heterospecific herbivores (Fig. 10). For example, each individual of three herbivores, *T. moorii, Petrochromis trewavasae* (Fig. 11a), and *P. orthognathus* (Fig. 11b), maintains discrete intra- and interspecific territories (Kohda 1991). The dominance hierarchies exist irrespective of species, depending on body size differences in territory owners. Thus, in the areas where heterospecific aufwuchs feeders coexist,

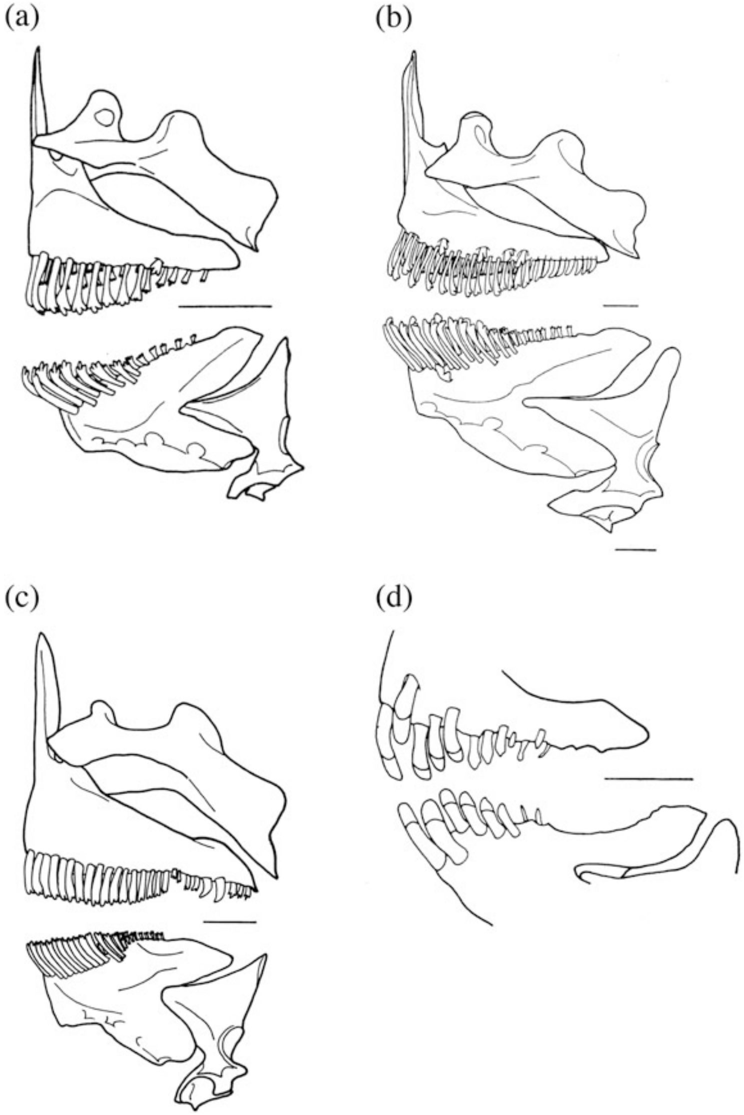

Fig. 8 Jaws of aufwuchs feeders (from Yamaoka 1987). *Petrochromis orthognatus* (grazer, (**a**)), *Interochromis loocki* (grazer, (**b**)), *Tropheus moorii* (browser, (**c**)), and *Eretomodus cyanostictus* (scraper, (**d**))

the neighbors of different species seem to act like an individual of the same species. Moreover, removal experiments in the field suggest that *P. trewavasae* allows smaller *T. moorii* to maintain territories against larger *P. orthognathus*.

Aufwuchs feeders show preferences for the depth and substrates of their foraging territories. The distribution (density) of aufwuch feeders along the depth and

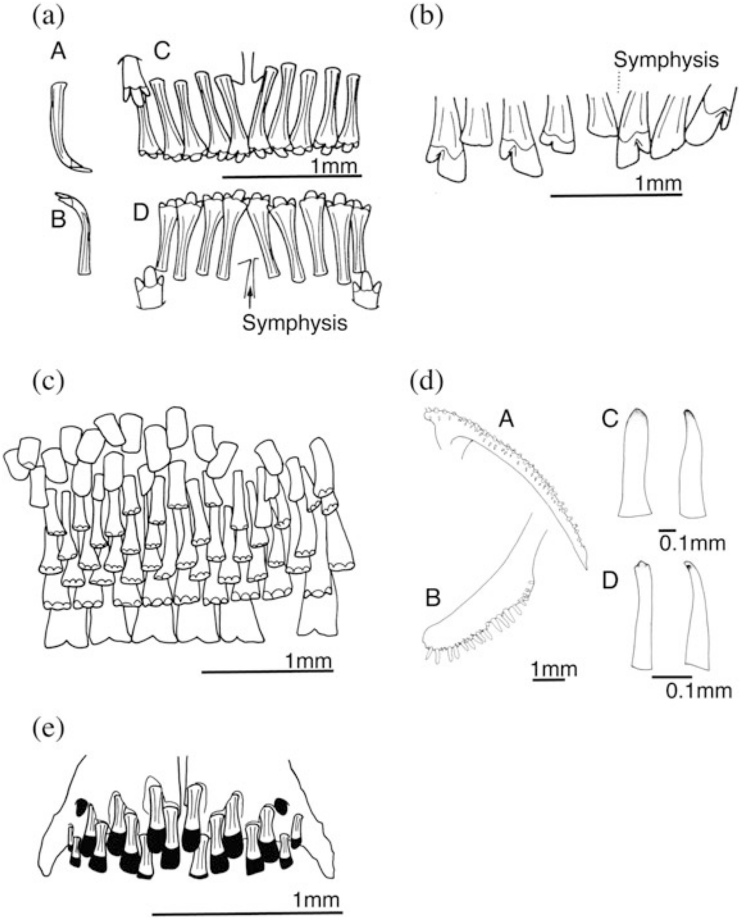

Fig. 9 Teeth of aufwuchs feeders; from Yamaoka 1987: (**a**)–(**c**) and (**e**); from Takahashi and Nakaya 1997: (**d**). Teeth of *Petrochromis orthognatus* (**a**): teeth of (A) upper and (B) lower jaw; (C) upper and (D) lower jaw. Teeth of upper jaw of *Interochromis loocki* (**b**) and *Tropheus moorii* (**c**). Jaws and teeth of *Xenotilapia sima* (scooper), (**d**): (A) ventral and (B) dorsal view of upper jaw. Teeth of upper jaw of *Eretomodus cyanostictus* (**e**) and (C) and (D): labial view (left drawings) and lateral view (right drawings) of teeth in outer series of jaws of two different individuals

substrate types are analyzed based on the 20-year census data on the permanent quadrats in a rocky shore at Kasenga Point (Fig. 12) located at the south end of Lake Tanganyika (Takeuchi et al. 2010). Overall, fish density did not differ widely at each water depth (Fig. 13). However, at the trophic group level, grazers and browsers showed species-specific preferences for using the depth ranges (Hata and Ochi 2016). Among grazers, two territorial species, *P. polyodon* and *P. famula*, and a non-territorial species, *P. fasciolatus,* sometimes forage with large schools within *Variabilichromis moorii* territories, which include large amounts of algae (Takamura 1984; Kohda and Takemon 1996; Kohda 1998; Ochi et al. 2009). On the other hand,

Fig. 10 Territory defense of *Tropheus moorii.* Photo by Tomohiro Takeyama

three species of grazers, *P. trewavasae*, *P. horii,* and *Interochromis loocki,* occupy overlapping wide depth ranges at deeper areas (Takamura 1984; Takahashi and Koblmüller 2014). Territorial browsers *V. moorii* and *T. moorii* inhabit the shallow zone, but the latter species is distributed over relatively deeper and wider depth ranges, where the density of competitors for diet resources are lower and are also the lower competitive area for the territorial defense, despite lower algal productivity (Karino 1998; Sturmbauer et al. 2008). Two species of browsers, *Pseudosimochromis curvifrons* and *Simochromis diagramma*, that have no feeding territory utilize similar depth zones to that of *V. moorii.* Relative deeper area, non-territorial browsers, *Limnotilapia dardennii* and *Telmatochromis temporalis,* overlap in their depth with one another (Hata and Ochi 2016). The scraper, *Eretmodus cyanostictus*, occupies the shallowest zone, and the scooper *Xenotilapia papilio* inhabits the deepest zone among herbivorous cichlids.

Herbivorous species inhabiting similar depth ranges and substratum type including inclination are separated between ecomorphs (Hata and Ochi 2016; Figs. 14 and 15). For example, three grazers, *P. fasciolatus*, *P. polyodon,* and *P. famula,* occurred at the same shallow depth zone, but *P. fasciolatus* show a significant preference for a lower inclination of substrate (flat stones) compared to the latter two species. Those differences in distribution along depth and preference for substrate among aufwuchs feeders would reflect the abundance and distribution of algae. Karino (1998) suggests that the relationships between costs and benefits of the territory defense would affect the territory site along the depth. In *T. moorii*, territory size changes with depth: as the water depth increases, the territory sizes are bigger, where density (quality) of algae is poor. The interspecific competition is higher in shallow rocky area, resulting in the smaller territory size. These results suggest that the territory size (quality of algae) and the defensive costs are a trade-off.

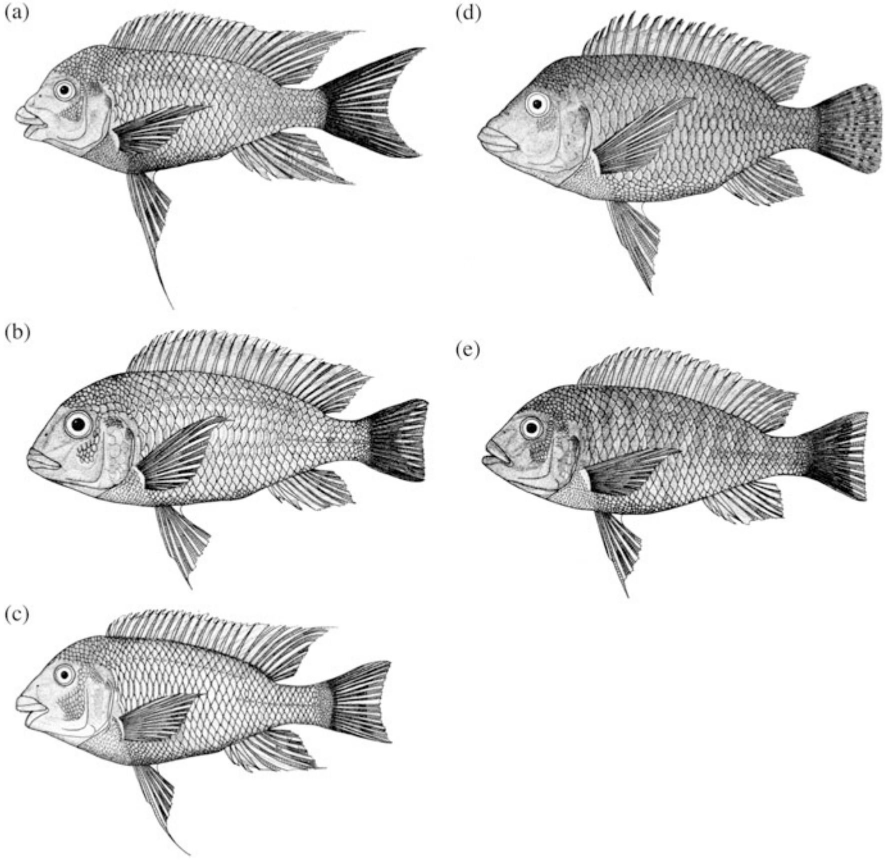

Fig. 11 Herbivorous cichlids genus *Petrochromis* inhabiting at shallow rocky shore (from Yamaoka 1983). *Petrochromis trewavasae* (male, (**a**)), *P. orthognatus* (female (**b**)), *P. polyodont* (male (**c**)), *P. famula* (female (**d**)), and *P. fasciolatus* (male (**e**))

3.3 Shrimp Eaters and Zoobenthos Feeders

Zoobenthos feeders, including shrimp eaters, utilize similar but slightly different prey sizes, proportions of prey items, and microhabitats (on, between, or under stones), via different capturing techniques among 14 sympatric species (Hori et al. 1993, Fig. 16): *Altolamprologus compressiceps*, *Gnathochromis pfefferi*, *Lamprologus callipterus*, *L. lemairii*, *Lepidiolamprologus elongatus* (Fig. 17), *Lep. profundicola*, *Lobochilotes labiatus* (Fig. 18), *Neolamprologus fasciatus*, *N. furcifer*, *N. leleupi*, *N.mondabu*, *N. savoryi*, *N. toae,* and *N. tretocephalus*. Stomach contents analysis revealed that volumetric proportions of shrimps of total stomach contents are different among the 14 species (Yuma et al. 1998). Six species (*A. compressiceps*, *G. pfefferi*, *L. callipterus*, *N. leleupi*, *N. toae,* and small size *N. fasciatus*) specialized on shrimp (more than 80% of whole stomach contents). For

Fig. 12 Rocky shore at Kasenga Point (depth: 5 m). Photo by Tomohiro Takeyama

small *L. lemairii* (27–66 mm in standard length), shrimp are important prey (more than 50% of whole stomach contents), but they also feed on small fishes. For the other species, the abundance of shrimp is less than 50% of total stomach contents, and the relative importance of another benthic prey (e.g., Diptera larvae and Ephemeroptera nymphs) increases. Two species of the genus *Lepidiolamprologus* (small *Lep. elongatus* and small *Lep. profundicola*: 66–69 mm in standard length), three species of the genus *Neolamprologus* (*N. savoryi*, *N. furcifer*, *N. mondabu*) and *Lob. labiatus* depend on shrimps, but other food items are contained in their stomachs. The preferences for shrimp size and hunting habitats are also different among shrimp eaters. *N. toae* prefers large size shrimps. The three cichlids, *G. pfefferi*, *L. callipterus,* and *N. leleupi*, capture small shrimps on the rock surface. The former two species frequently tend to forage with other shrimp eaters. Middle-sized shrimps are preferred by *Lob. labiatus*, *A. compressiceps*, small *L. lemairii,* and *Lep. elongatus*. Except *Lob. labiatus*, these species frequently follow other foraging cichlids and capture shrimps and escape from them (Takamura 1984). Among zoobenthos feeders, *Lob. labiatus* has a unique feeding method with peculiar mouth morphology. This species is specialized in sucking up small invertebrates (e.g. mayfly larvae, midge larvae and shrimps) from rock crevices and/or cracks in rocks with fleshy lips, and sorting them through their gill rakers (Kohda and Tanida 1996; Kohda et al. 2008). This cichlid also uses other shrimp eaters and chooses a foraging site nearby where the shrimp might avoid predation by other foraging fishes. Each individual *Lob. labiatus* has a foraging territory, the area of which depends on body size and it defends that against conspecifics of similar size, but not against fish of different sizes. Prey items were similar among individuals, but larger fishes tended to capture larger prey at larger crevices. This means that their diet niches show strong similarity, but they vary in their utilization of microhabitat to prey upon the zoobenthos. Therefore, in this species, although the territories do not overlap among similar sized fish, the territories defended by different size-classed individuals were overlapping (maximum seven; Kohda et al. 2008). Such

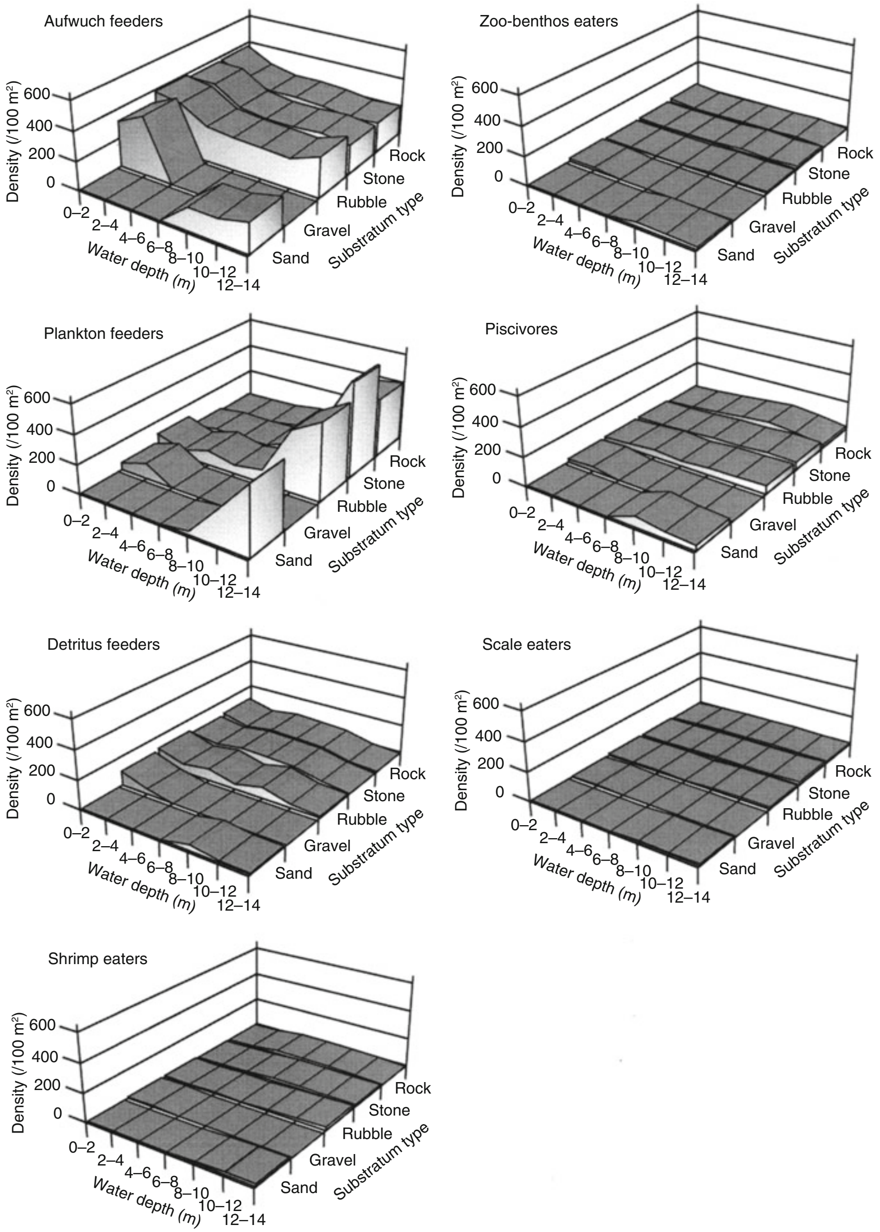

Fig. 13 Distribution (density/100 m^2) of cichlids for each trophic group in relation to water depth (m) and substratum type at Kasenga Point from census data during 20 years from Takeuchi et al. (2010)

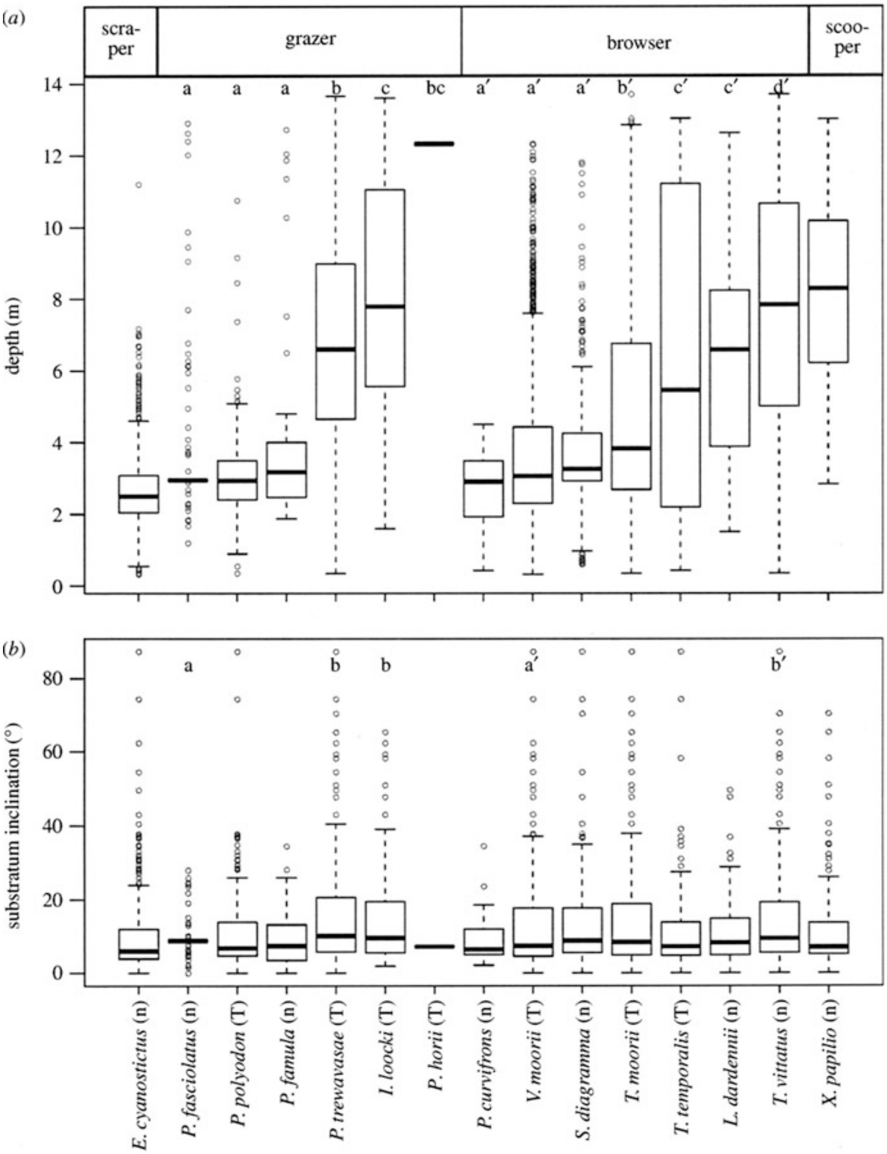

Fig. 14 Habitat preferences for water depth (**a**) and substratum inclination (**b**) in herbivorous cichlids at Kasenga Point observed from 1995 to 2008 (from Hata and Ochi 2016). Species with feeding territory (T) and without any feeding territory (n) are indicated in parenthesis following species name. Different letters (a–d, or a′–d′) above bars show significant differences among species within grazer and browser, respectively

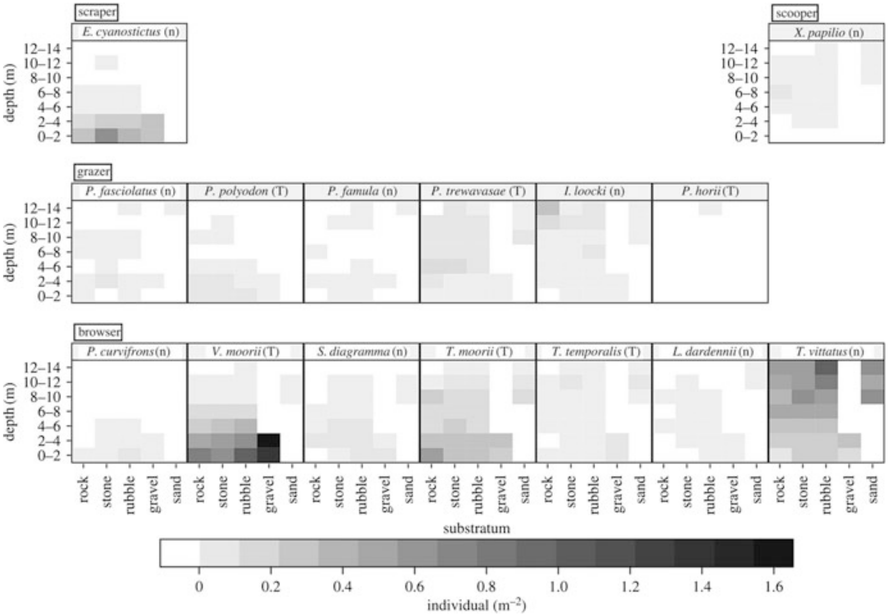

Fig. 15 Distribution of herbivorous cichlids in each depth and substratum type at Kasenga Point observed from 1995 to 2008 (from Hata and Ochi 2016). Letters in parenthesis following species names are as same as those in Fig. 14

overlapping territories allow sympatric coexistence among conspecific individuals in *Lob. labiatus*.

Large sized males of *L. callipterus* collect empty shells (e.g., *Neothauma* spp.) for spawning sites, and small sized females (“dwarf” females) hide inside the shells and provide parental care after spawning. On the other hand, young smaller males sometimes join a foraging group of two to seven conspecifics and cruise along the substrate and take small invertebrates in a huge area (Yuma 1994). This species also forms a foraging school with individuals of *G. pfefferi* (Hori et al. 1983). Solitary individuals or a pair of *N. furcifer* defend a small area on the overhanging rock surface and forage on benthic animals from on or near the rock surface. *N. leleupi* move individually along a rock surface and catch prey on the rock surface and from crevices. *N. mondabu* appear to exclusively use foraging behavior to capture benthic animal prey. This fish stirs up gravels or turns rubble over to find prey.

3.4 Piscivores

Field observations of hunting behavior by piscivorous cichlids show similarity of prey species and differentiation in hunting techniques resulting in hunting success on a rocky shore of Luhanga, northwestern end of Lake Tanganyika (Hori et al. 1983;

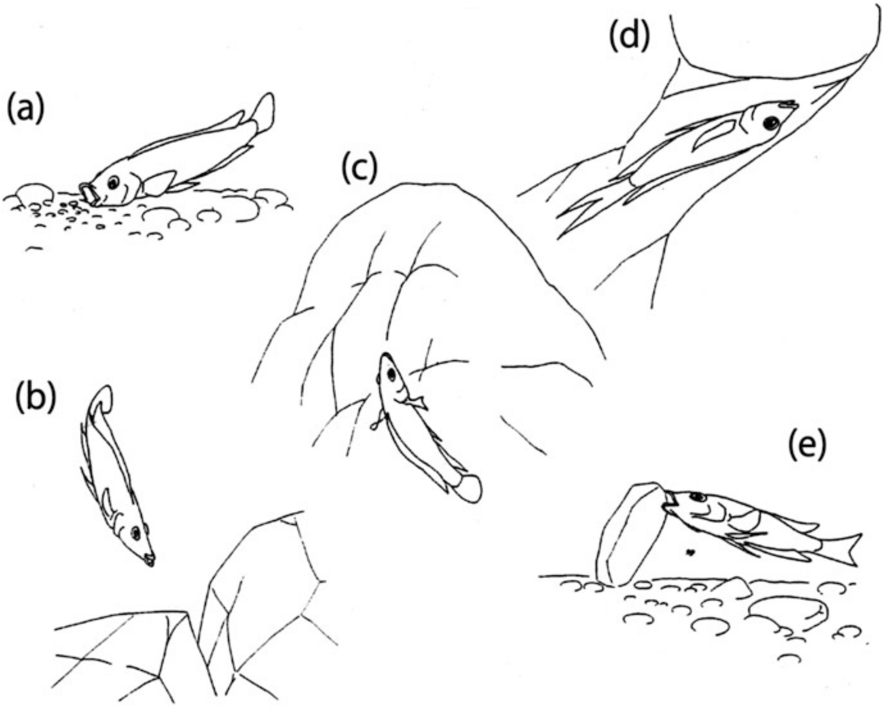

Fig. 16 Typical feeding behaviors of sympatric benthos and shrimp eaters of tribe Lamprologini (from Hori et al. 1983). *Lamprologus callipterus* forages a prey near the sandy bottom (**a**). *Altolamprologus compressiceps* snatches a prey on a rock surface or a slit between stones (**b**). *Neolamprologus leleupi* snatches a prey on a crevice of a rock surface (**c**). *N. furcifer* picks up a prey from a rock surface of and overlapping rock (**d**). *N. modestus* has a unique hunting technique: turning over a flat rubble and picking up exposed prey on a gravel bottom (**e**)

Hori 1987). Four piscivorous species of the tribe Lamprologini, *Lamprologus lemairii*, *Lep. elongatus*, *Lep. Profundicola,* and *N. fasciatus* attack mutual prey species that are juveniles of *Neolamprologus brichardi*, young of *Telmatochromis bifrenatus,* young of *T. temporalis*, juveniles of *Lep. elongatus*, *Haplotaxodon microlepis*, *Perissodus microlepis*, young of *Tropheus moorii,* and *Limnotilapia dardenei*. The three predatory cichlids, *Lepidiolamprologus elongatus*, *Lepidiolamprologus profundicola,* and *Neolamprologus fasciatus*, often follow at a distance behind large sized fish (e.g., herbivorous cichlids) and achieve higher hunting success compared to solitary hunting (Hori 1993). Of the three piscivores, two cichlids, *Lep. elongatus* and *Lep. profundicola*, follow large fish (e.g., a mastacembelid eel) for the former species and herbivores (e.g., *Petrochromis polyodon* and *Varicorhinus tanganicae*) for the latter species (Fig. 19a, c). However, *N. fasciatus* rarely utilizes the following hunting method (Fig. 19b). For the piscivores, the presence of other piscivorous individuals both conspecific and heterospecific nearby promotes successful results of predation. Those piscivores

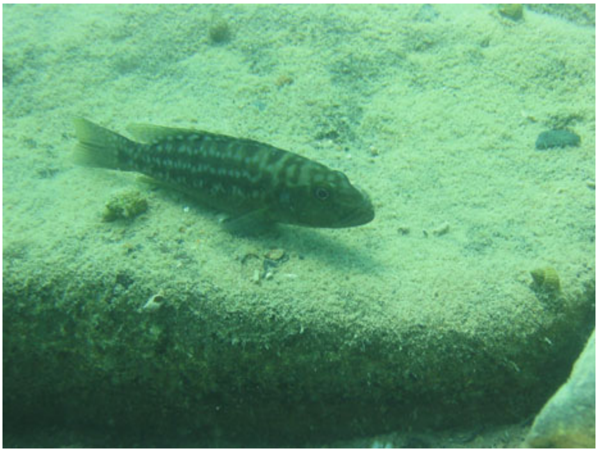

Fig. 17 *Lepidiolamprologus elongatus* (depth: 10 m). Photo by Tomohiro Takeyama

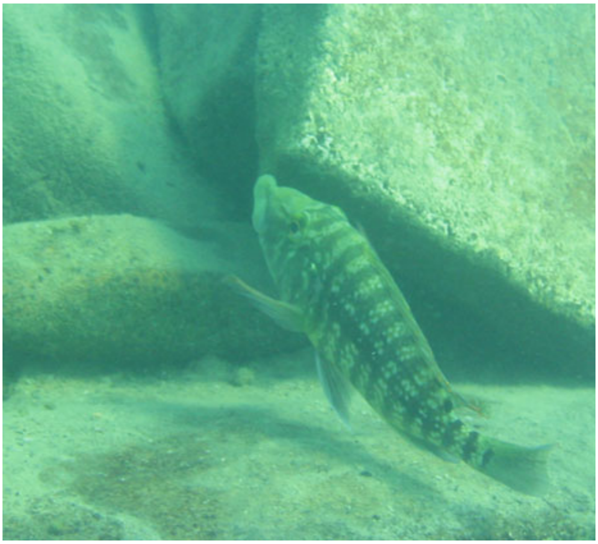

Fig. 18 *Lobochilotes labiatus* (depth: 5 m). Photo by Tomohiro Takeyama

are potentially competitors for the similar diet resources, but mutual existence can improve their hunting success. Such latent facilitative interactions may be the coexistence mechanism for the sympatric piscivorous cichlids (Bruno et al. 2003).

3.5 Scale Eaters

Piscivore fishes are lethal predators, whereas a scale-eating fish that scrapes the scales from the body side of the prey fish is a nonlethal predator. Scale eating is a unique feeding behavior that has evolved in diverse fish taxa. Sazima (1983) summarized scale-eating fishes distributed in at least five families in freshwater and seven families in marine habitats (Characid: Sazima 1983; Peterson and Winemiller 1997; Ambassidae: Grubh and Winemiller 2004; Pironia: Janovetz 2005). In Lake Tanganyika cichlids, seven species in the genus *Perissodus* (*P. microlepis* Fig. 20, *P.* (*=Plecodus*) *straeleni, P.* (*=Plecodus*) *paradoxus, P. eccentricus, P.* (*=Plecodus*) *elaviae, P.* (*=Plecodus*) *multidentatus, and P.* (*=Xenochromis*) *hecqui*) out of nine species of the endemic tribe Perrisodini are scale eaters; two other species (*Haplotaxodon microlepis* and *H. trifasciatus*) are a general carnivore and a plankton feeder (Koblmüller et al. 2007; Takahashi et al. 2007a, b, Fig. 21). Within the genus *Perissodus*, Takahashi et al. (2007a, b) analyzed stomach contents from wild caught fish. *X. hecqui* captured mainly copepods (c.a. 54% of items in contents of stomach) and also preyed upon young fish; thus, this species emerged as a plankton feeder. On the other hand, the other six *Perissodus* species show higher dependence on scales, but the degree of reliance on scale-eating differs among species. Three species (*P. microlepis, Ple. paradoxus,*

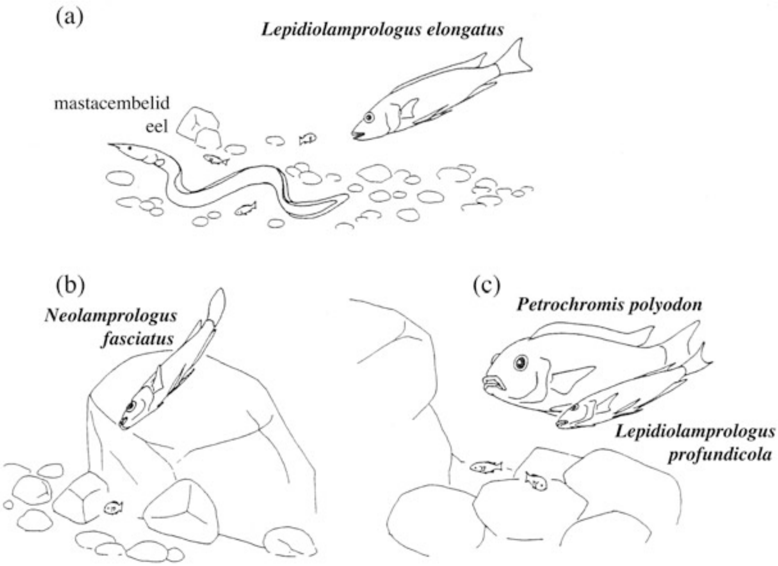

Fig. 19 Hunting behaviors of sympatric piscivorous cichlids (from Hori et al. 1983). *Lepidiolamprologus elongatus* follows a mastacembelid eel and preys an exposed fish (**a**). *Neolamprologus fasciatus* stalks from behind a small rock and darts at the prey from the top of the stone (**b**). *Lep. elongatus* swims close beside a large herbivorous fish and darts out to catch the prey (**c**)

Fig. 20 *Perissodus microlepis* with its young (depth: 5 m). Photo by Tomohiro Takeyama

P. eccentricus, and *Ple. elaviae*) intake scales at 90% or more higher ratios of total diet composition, suggesting they specialize in the scale-eating habit. Percentages of scales in the stomach contents of *Ple. straeleni* and *Ple. multidentatus* are c.a. 65% and 45%, respectively, but these two species also use fish skin (c.a. 16% and 45%, in each fish), suggesting they remove scales with the skin of prey fish. In *P. microlepis*, the diet shifts ontogenically from plankton (e.g., copepods) to exclusively scales (Nshombo et al. 1985; Takeuchi et al. 2016).

The depth distributions of the scale-eating cichlids in Lake Tanganyika were examined by Takahashi et al. (2007a, b). Two species of genus *Haplotaxodon* inhabit shallow waters less than 20 m in depth. In seven species of the genus *Perissodus*, the distribution of depth ranges is divided into three groups. *P. microlepis* and *Ple. straeleni* inhabit shallow rocky regions. Four species, *P. eccentricus*, *Ple. elaviae, Ple. multidentatus,* and *X. hecqui* are distributed in deeper regions (deeper than 40 m). *P. paradoxus* have relatively a wide range from deep water (more than 100 m) to shallow (less than 20 m) rocky regions.

Phylogenetic relationships of nine species in tribe Perrisodini based on AFLP suggest that scale eating evolved from general carnivores to the highly specializations of scale-eating species in relation to teeth morphology (Takahashi et al. 2007a, b, Fig. 21a). In addition, the origin of the scale-eating habit is suggested to have evolved in deepwater regions of the lake. Koblmüller et al. (2007) conducted a phylogenetic analysis by mitochondrial DNA and AFLP makers; and they concluded that most scale eaters of Perrisodini evolved in deepwater habitats and then two species of highly specialized scale-eaters *P. microlepis* and *Ple. straeleni*

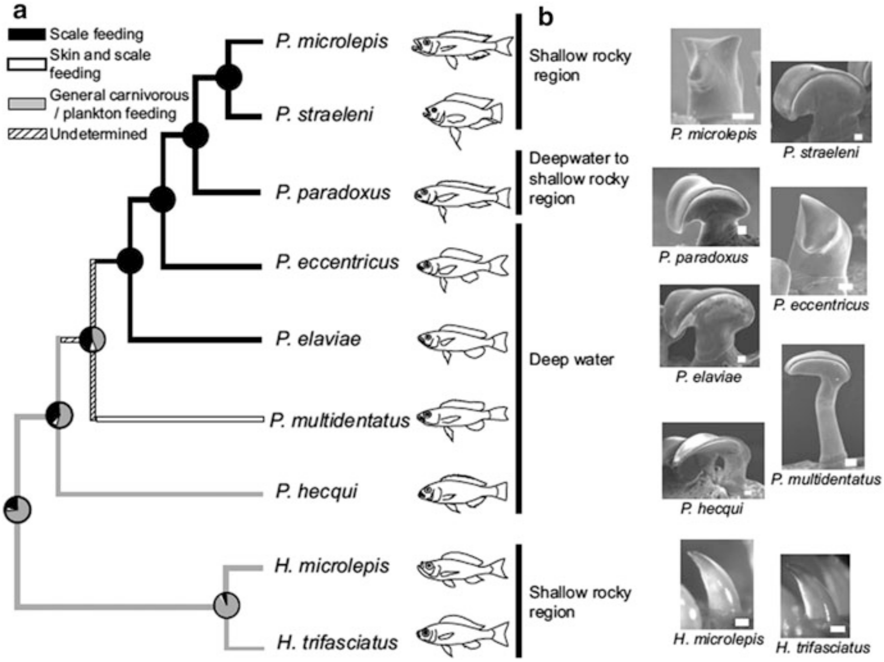

Fig. 21 Ancestral state for feeding habits (**a**), habitat region (depth) and oral teeth morphology (**b**) of nine species of tribe Perrisodini (from Takahashi et al. 2007a, b). (**a**): Different bar patterns show the ancestral state of the diet estimated using the maximum parsimony method. The diagram of each circle on the branch indicates the calculated probability of the respective feeding habit by the maximum likelihood method. (**b**): The depth of habitat and teeth shape of each species. Scale bars in the photographs show 0.1 mm

subsequently differentiated. In all Perrisodini species, teeth on both upper and lower jaws are arranged in a single row (Liem and Stewart 1976; Takahashi et al. 2007a, b, Fig. 21b). Tooth morphology of two *Haplotaxodon* species is different from other *Perrisodini.* They have relatively small and slightly backward curved conical-shaped teeth. Among the genus *Perrisodus*, morphological features of teeth are divided into two groups: the teeth of *P. microlepis* and *P. eccentricus* are strongly curved, with a stout stem base with spine-like point(s), whereas the teeth of *Ple. straeleni, Ple. paradoxus, Ple. elaviae, Ple. multidentatus,* and *X. hecqui* are relatively large, held on stalked stems, of which the crown is widely shaped with a fine edge and strongly curved backward.

Liem and Stewart (1976) described asymmetrical jaws in *P. eccestricus* that may allow approaching its prey much more stealthily. The ratio of right- and left-opened individuals appears to be equal numbers (but without quantitative data). The “righty” morph that has a left-opened mouth attacks the right side of the belly of the prey fish and the “lefty” morph that has a right-opened mouth attacks the left side of the prey. Thus, the asymmetrical mouth opening of scale eaters has been recognized as an adaptive morphology for removing scales. Hori et al. (1993) conducted field observations of the frequency of the asymmetrical morphs (left- or right-opening mouth) of *P. microlepis* in two wild populations over 10 years. He points out the following issues: (1) the frequency of the two morphs has not remained equal (1:1) in a given population in a single year; (2) the ratio of two morphs shows yearly oscillation around unity; (3) the minor morph has higher foraging success than the major morph; and (4) the heredity mechanism of the two morphs according to the relationships of the handedness between parents and their broods because *P. microlepis* provide biparental care. This suggests that frequency-dependent (natural) selection maintains the two morphs in the population (higher advantage in the minor morph); and the two morphs are genetically determined by a single locus-two alleles system (a simple Mendelian inheritance). The advantage of the minor phenotype is caused by the interspecific interaction between scale eaters and prey species, since the target fishes tend to pay attention to the one body side, which is exposed frequently to attack by the scale eaters of the predominant morph. Therefore, the vigilance of prey fishes against the opposite side of the prey's body would become reduced, and minor phenotypes of the scale eaters could attack and scrape scales with ease. Theoretical models also support this hypothesis that the frequency dependent selection with higher fitness for the minor phenotype acts as the mechanism to retain both of two morphological types in a population (Takahashi and Hori 1994). Stomach contents analysis from wild populations shows that each morph collects more scales from the body side of the prey species that associated with each asymmetric mouth (Takeuchi et al. 2016). In field experiments, the coexistence of both morphs facilitates the hunting success for both handedness individuals within a population (Indermaur et al. 2018).

After the milestone article on *P. microlepis* by Hori et al. (1993), this textbook example of evolutionary biology had many supportive, inconclusive, and negative studies thereafter. Subsequent discussions focused on evidence of frequency-dependent selection, bimodal distribution of mouth opening, the genetic mechanism of asymmetry, the proportion of the two forms in the wild population, disassortative mating between the two morphs, and effects of genetics and environments on asymmetric ontogenetic formation (reviewed by Raffini et al. 2019). Hori and his colleagues have continued the long-term (over 31 years) field surveys of *P. microlepis* and *Ple. straeleni* to investigate temporal dynamics of the ratio of laterality of each species in a single population at Kasenga Point in Zambia (Hori et al. 2019). Their results show that the ratio of the two morphs of each species shows oscillations with a term of about 4 years in a semisynchronized pattern, suggesting that frequency-dependent selection not only maintains the asymmetrical morphology in both species but also operates across the two species.

Scale-Eating Strategies

The scale-eating behaviors of *P. microlepis* and *Ple. straeleni* have been studied in both field and laboratory conditions. According to the high-speed recordings in the laboratory, behavioral differences in tearing scales off the flank of prey fish correspond to the differences in the dental morphology between the two species

(Takahashi et al. 2007a, b; Takeuchi et al. 2012). *P. microlepis* presses the mouth on the belly of the prey tightly and quickly spins its body to scrape scales away with the tip edges on the teeth. On the contrary, *Ple. straeleni* presses the mouth against the prey's body side-on and keeps the mouth tightly on the flank as the prey attempts to break away. Then, during the attack, the mouth of *Ple. straeleni* shifts backward along the belly of the prey and scrapes scales from the flank of the prey with the edges of their curved teeth. According to the field observations of the two species in shallow rocky areas, scale-eating methods include several similar techniques: aiming, mingling, and stealthy approach are observed for both species (Nshombo 1994a, b). Pursing and waiting are found in *Ple. straeleni*. In *P. microlepis*, stooping, following, and ambushing are exclusive foraging methods. *P. microlepis* also expresses polychromatism (four body color morphs: beige, dark, gray, and stripe types, Nshombo 1994a), and each morph tends to use a specialized hunting technique. This species seems to select the hunting method corresponding to prey fish. For example, *Neolamprologus brichardi* are frequently attacked by mingling, and *Cyathopharynx furcifer* have their scales removed by waiting (Nshombo 1994a). *Ple. straeleni* show sexual dichromatism (Yanagisawa et al. 1990) and more complex polychromatism, and aggressive mimicry (Boileau et al. 2015). Model species of mimics for *Ple. straeleni* are *N. sexfasciatus* and *Cyphotilapa gibberosa*, and all of them have white and black stripes with blue fins. Contrary to the predictions, *P. straeleni* do not use the mimic colorations to parasitize (hunt the target of scale-eating) the model species, suggesting the opportunity of camouflaging effect that may allow them to easily approach the target species which are mainly herbivorous cichlids (Yanagisawa et al. 1990; Nshombo 1994b).

The target species for *P. microlepis* are variable, though they mainly remove the scales from aufwuchs feeders that have larger and flat bodies: for example, genus *Petrochromis*, *Tropheus,* and *Simochromis* (Nshombo et al. 1985; Kovac et al. 2019). On the other hand, *Ple. straeleni* seems to utilize not only herbivorous cichlids but also abundant species of the tribe Lamprologini (e.g., *Neolamprologus brichardi*, Nshombo 1994a; Boileau et al. 2015). The two scale eaters attack the prey species in different situations: feeding, territorial attacking, courtship display, passing, motionless, moving, and stationary (Nshombo 1994a, b). In both species, the hunting success is higher when the prey species are in territorial disputes, courtship displays, and are motionless (M. Hori, unpublished data). Among the cichlid communities in the shallow rocky areas, the abundances of *P. microlepis* and *Ple. straeleni* are relatively low. The ratios compared to the total observed fish are 1.07% and 0.05% at Luhanga (Hori et al. 1983), and 1.04–6.64% and 0.01–1.88% at Kasenga (Takeuchi et al. 2010), for *P. microlepis* and *Ple. straeleni*, respectively. Therefore, potential prey fishes are in huge numbers for the scale eaters. But the hunting success rates are not very high (less than 20% for *P. microlepis*; less than 30% for *Ple. straeleni*, Hori 1987). However, the hunting success increases for both species when an individual of the other species is by chance nearby (circa 50 cm) but not so when only conspecific individuals are present, suggesting that two scale-eater species benefit by coexistence (Hori 1987).

4 Future Directions

This last section describes recent cichlid studies and suggests some directions for future studies not only on Tanganyika but also on other cichlid groups in the Great Lakes of East Africa. Topics on food web structure including food resources of the cichlid community are considered. Furthermore, the application of the current field of developing approaches in four aspects of cichlid research: (1) an evolutionary development (evo-devo) approach for the ontogenetic construction of forms related to feeding behavior, (2) in relation to the possibility of microbial coevolution in the guts of herbivorous cichlids, (3) perhaps preserved fish collections preserve the history of past food web records and the evolutionary history of morphological changes, and (4) individual differences in foraging behavior may be key to elucidating the mechanism of coexistence in cichlid communities and the evolutionary process of adaptive radiation and sympatric speciation.

4.1 Food Web Structure and Topology of Food Webs

The biological diversity in a given community has been evaluated by indices such as Simpson (1949), Shannon (1948), and Clarke and Warwick (2001). Another view of the evaluation of biodiversity is through the topology of food webs and food web structures. Food web topology focuses on the complexity of the number of nodes (each species) and links (connection between predator and prey), and food webs are the summary of predator-prey relationships in a given community (Cohen 1978; Thompson and Townsend 2005). Food web topology is constructed by a summary of direct relationships between a single prey or diet and a single predator from field observations and/or analysis of stomach contents. Although food web structure is also derived from the predator-prey connections based on gut contents, the approach using stable isotope analysis shows indirectly the relationships among potential diet items for each consumer as transfers of isotopes (e.g., carbon and nitrogen) on C and N dimensions within an isotopic bi-plot (DeNiro and Epstein 1978, 1981; Fry 1991; see Box 2 in Nyingi et al. 2021).

With respect to research studies of the Lake Tanganyika cichlid community, Hori et al. (1993) applied the biodiversity index to compare communities at different locations. However, studies of food web structure and food web topology in Lake Tanganyika cichlid flocks have been limited. The complexity of food web topology may reflect the differences in the diversity of species (species richness) among the habitats (e.g., coastal rocky and sandy area, open and deep waters) in the lake. In a given food web, differences in δ^{15}N values between primary producer(s) and top consumers (top predators) usually show the lowest and the highest, respectively (Vander Zanden et al. 1999). Food chain length is a measure of the number of trophic levels in an ecosystem. There can be differences in length and species diversity, if the ecosystem with longer food chain length contains higher species richness (Doi et al.

2012). Since Lake Tanganyika cichlid flocks consist of more sympatric species, the evaluation of the correlation between food-chain length and species diversity can provide an answer to an attribution of the theory.

Interspecific overlapping of ecological niches is one of the fundamental concepts that predicts competition and coexistence among species (Pianka 1974). To understand the mechanism of coexistence in the cichlid community, recognition of niche range occupied by each species could be the effective point. Measurement of species-specific niche width will provide the perspective on resource partitioning among species that are potentially competitors for similar diets in the cichlid community. Evaluation of interspecific differences in values of carbon and nitrogen isotopes is a powerful tool to compare niche partitioning. For Malawi cichlids, this approach was applied to five sympatric species that utilize similar food resources (Genner et al. 1999). The results showed that the five species including algae feeders and a planktivore do not exhibit remarkable differences in their isotopic values. Hata et al. (2015) applied this isotopic analysis to compare the ratios of carbon and nitrogen isotopes among 14 species of sympatric aufwuchs-eaters including five feeding ecomorphs (e.g., grazer, browser, scooper, scraper, and biter) inhabiting the shallow rocky shore in Lake Tanganyika. The δ^{15}N of grazers was lower than those of browsers and scoopers, suggesting that grazers consume periphyton primarily, and the others utilize not only periphyton but also benthic animals (e.g., Chironomid larvae). On the other hand, the δ^{13}C values were overlapping among species, suggesting that these herbivorous cichlids rely on primary production of periphyton. The application of this isotopic approach to the coexistence of species in the cichlid community in various habitats in Lake Tanganyika will undoubtedly contribute to our understanding of the segregation of diet and degree of the niche overlapping, and moreover food web structure.

4.2 Symbiosis with Microorganisms

In general, herbivorous animals have a symbiotic partnership with in vivo microorganisms in their digestive organs. Well-known examples of such interspecific relationships are known in the guts of termites and cockroaches for symbiotic digestion of cellulose and lignocellulose (Bandi et al. 1995; Brune 2014). Aufwuchs feeders require specialization of digestive enzymes and relatively longer intestines in which to digest algae that contain celluloses (Yamaoka 1985; Wagner et al. 2009; Tada et al. 2017). Sturmbauer et al. (1992) compared the activity of digestive enzymes (trypsin, amylase, and laminarinase) among four aufwuchs eating cichlids in Lake Tanganyika and showed that the activities of trypsin and amylase do not differ among species but that of laminarinase is more active in a detriticorous-microalgivorous cichlid (*Petrochromis orthognathus*).

Hata et al. (2014) focused on the relationships among algal, cyanobacterial composition in algal farms (some herbivorous cichlids defend feeding territories and keep algae for territorial foraging there), and stomach contents including microorganisms for 16 species of aufwuchs cichlids in Lake Tanganyika. Metagenomic amplicon sequencing analysis (454-pyrosequencing of SSU rRNA) showed that the cyanobacteria community structures in their stomachs are highly diverse among species, suggesting that the microorganism community is species-specific for the cichlids. Baldo et al. (2017) expanded the target species involving not only algae-feeders but also carnivores and scale eaters in Lake Tanganyika cichlids and analyzed the gut microbiota by 16 s rRNA amplicon sequencing. They showed that the bacterial taxonomic functional diversities differed between carnivores and herbivores. Herbivorous cichlids have similar compositions that contain more bacterial taxa (higher diversity), and this suggests convergent characteristics of the gut microbiota across species.

For aufwuchs feeders, the length and coiling pattern of their intestines change ontogenetically (Yamaoka 1985), but the relationships among composition and activity of digestive enzymes and ontogenetic shifts of diet are still unclear. Moreover, future studies on digestive enzymes, functions of symbiotic microorganisms, and phylogenetic comparisons of gut microbiota among species (parallelism) will contribute to our understanding of the wide utilization of diet niches through adaptive radiation of Lake Tanganyika cichlid flocks. Insights into the symbiosis between host and microbiota in the guts will be the basis for understanding not only nutrient digestion and metabolism of cichlids but also coevolution and symbiosis between host species and microorganisms in digestive organs associated with the expansion of the diet niche width of cichlids (Sullam et al. 2012; Wong and Rawls 2012; Butt and Volkoff 2019).

4.3 Evo-Devo in Morphology in Relation to Foraging

A recent broad approach of evolutionary developmental biology, “evo-devo,” investigates correlations between developmental process of individuals and evolutionary changes via phenotypes (Müller 2007; Irschick et al. 2013; Gilbert et al. 2015). Genetics of development of morphology from an evolutionary aspect, especially of jaws and skulls, has been applied to Malawi cichlids by Albertson and his colleagues (Albertson et al. 2003, 2005; Cooper et al. 2011; Conith et al. 2018). They combined traditional morphological approaches (e.g., morphometrics) and evolutionary genomics approaches (e.g., QTL mappings for evo-devo traits) to elucidate the process of adaptive radiations of cichlid flocks in East African Great Lakes (see Hu and Albertson 2021). Since Lake Tanganyika cichlids also have broad food habits that are dependent on jaws, teeth, and skull morphology, an evo-devo approach is one of the research frontiers to understand how morphological key innovations play a role in adaptive radiation in Lake Tanganyika cichlids (e.g., diversification of teeth shapes of herbivores and scale eaters).

From different perspectives, the evo-devo approach can clarify sex differences in the morphology, “ecological sex traits.” Ecological sex traits are differences between males and females as a result of the initial divergence of ecological niches between the sexes (Shine 1989; Temeles et al. 2000, 2010). Ronco et al. (2019) indicate that there is a sexual difference between gill size, which determines diet size by filtering food resources, and the oral cavity associated with parental care strategies (i.e., biparental mouthbrooding, maternal mouthbrooding, and nest guarding without mouthbrooding) in Lake Tanganyika cichlids. Female cichlids of maternal mouthbrooding have shorter gill rakers and smaller buccal cavities as a consequence of sexual differences in trade-off between trophic and reproductive functions. These results suggest that the ontogenetic development (e.g., gene expression) of gill rakers is different between males and females. Thus, the evo-devo approach has the potential to understand the processes and mechanisms of morphological adaptation influencing the coevolution of trophic web structures and parental care strategies in the adaptive radiation of cichlid flocks.

4.4 Reconstruction of Ancient Food Web and Morphological Evolution from Preserved Collections

van Rijssel and colleagues analyzed preserved cichlid specimens from Lake Victoria and revealed historical changes of the environment (van Rijssel et al. 2017) and morphological changes of cichlids under variable pressures of natural selection (van Rijssel et al. 2015). Quantitative analysis of morphology in four haplochromine cichlids showed their rapid adaptive changes (microevolution) in premaxilla shapes, reflect the diet shifts during the past 30 years (1978–2006). Based on the carbon and nitrogen stable isotope analyses of preserved fish collections, they evaluated the effects of eutrophication on dietary change and habitat differences in four haplochromine cichlids with different diet use (e.g., two zooplanktivores, one molluscivore/detritivore, and one zooplanktivore/insectivore). Their results suggest that especially the changes of δ^{13}C values might reflect the increase of primary production due to eutrophication in the lake. Thus, this research claimed that preserved samples could not only be used as an indicator of environmental changes but also for reconstructing the past environments in the lake. Reconstructions of the past environments and evaluating the responses of adaptive morphological changes from fish collections should be also quite challenging for Lake Tanganyika cichlids.

4.5 Personality/Behavioral Syndromes in Foraging Behaviors

Studies of inter-individual differences in behavior (“personality” or “behavioral syndrome”) have been developed in the field of behavioral ecology during recent decades (reviewed in Sih et al. 2004; Dingemanse et al. 2010; Bengston and Jandt 2014). These behavioral syndrome studies focus on the relationship between behavioral differences and fitness consequences. For example, some individuals tend to be generally aggressive or bold, while others are generally less so. This phenomenon could be expressed either within the relationship of the same individual between the different contexts (e.g., correlations between hunting behaviors for different prey) or the relationships across different behaviors (e.g., correlations among foraging, aggressive, and mating behaviors). In Lake Tanganyika cichlids, a piscivorous fish *Lepidiolamprologus profundicola* shows individual specializations in foraging behavior (Kohda 1994). Hunting behavior of this fish consists of nine techniques, including an associated feeding (e.g., dashing from an assemble or beside the other cichlid species, Fig. 22). Each individual (total 18 fish observed) showed a consistent hunting specialization for up to 4 months among several hunting techniques that are employed in relation to microhabitat (hunting sites). In other Lake Tanganyika cichlids, a given individual may use several (alternative) foraging responses and can use different feeding methods according to the situation, habitat, or prey species. Ecological niche theory predicts that there will be little or no overlap in niche width between sympatric species because competition between species prevents coexistence. The theory also predicts that each species occupies a particular niche range of food resources, including intraspecific variation among individuals (Sih et al. 2004). In such circumstances, individual differences and/or specializations in foraging behavior may promote the coexistence of species sharing similar diet niches as a result of moderating intraspecific competition for resource use, as well as interspecific competition (Schliewen et al. 1994; Schluter 2000). In addition, diversification in personality dimensions in behavioral trends (e.g., shy-bold continuum) that correlate with foraging tactics and promote resource partitioning may contribute to the advance into new habitats and the potential development of new species (Wolf and Weissing 2012). Further studies of the relationships among inter-individual differences in foraging behavior and their fitness consequences for individual fish will contribute to our understanding of the diversification and underlying mechanisms of coexistence in species in the cichlid community that use similar diets in Lake Tanganyika.

5 Conclusion

In the past half century, researchers of feeding ecology in Lake Tanganyika cichlids have been providing insights into adaptive radiation for specific diet niches, species composition, and mechanisms for coexistance within cichlid communities. The next step in research on the feeding ecology of cichlids will be to integrate traditional research techniques (e.g., behavioral observation, stomach content analysis, morphological comparison) with advanced approaches. The latter include the analysis of food webs with stable isotopes, genetic and functional studies of endosymbiotic microorganisms, evo-devo in morphology, and personality of feeding behavior. I also emphasized that an integrated understanding of the feeding ecology at the individual level up to the food web level will be a significant point for future studies

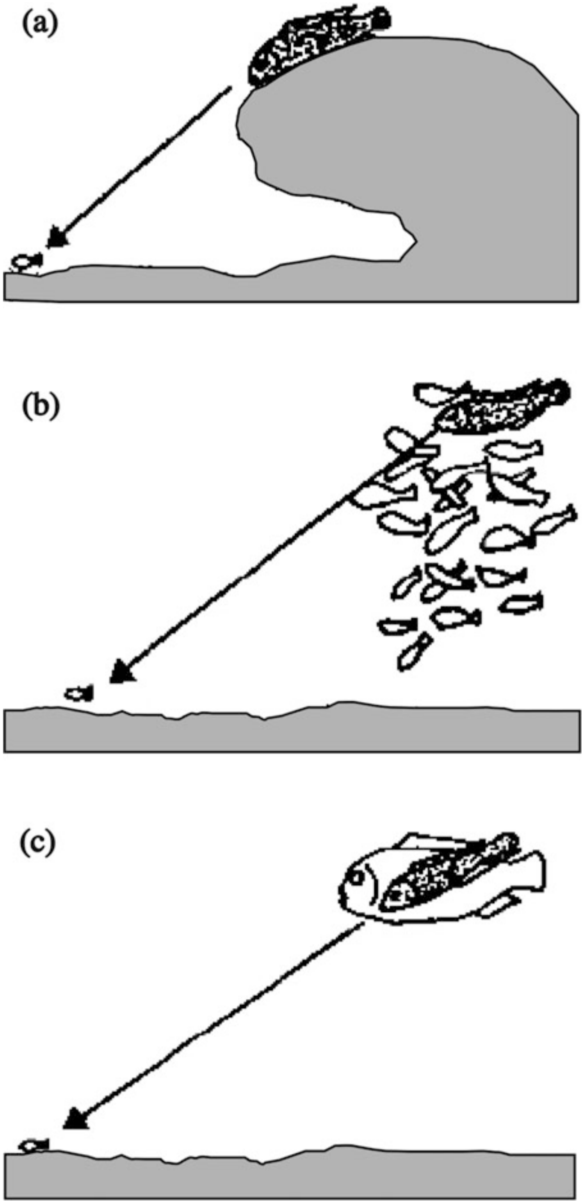

Fig. 22 Diagrams of three of nine hunting techniques in *Lepidiolamprologus profundicola* (from Kohda 1994). Dashing alone from an assemble (**a**), dashing from a group of heterospecies (**b**), and dashing from beside another species (**c**)

of cichlids. The decision-making behind a feeding behavior affects an individual's fitness and hence the dynamics of population size. The species population dynamics can then alter the composition of the communities to which they belong, thereby altering the dynamics of the food web structure in a given ecosystem.

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Patterns of Trophic Evolution: Integration and Modularity of the Cichlid Skull

Yinan Hu and R. Craig Albertson

Abstract A key axis of diversification among cichlid species is trophic specialization, and much effort has been dedicated to revealing the factors that have contributed to the vast array of feeding morphologies that have evolved in this group. While the physical environment, especially within the large East African lakes, has undoubtedly facilitated their evolutionary success, there must also be intrinsic attributes of cichlids that have increased their evolutionary potential. The modular design of organisms has been credited for promoting diversity across metazoans. This is because the mixing and matching of preexisting anatomical "units" is a more efficient way to expand ecological diversity than the independent evolution of each component part. We suggest that modularity may also play an important role in cichlid craniofacial diversification. We review work focused on describing modularity in cichlids at multiple levels of biological organization—e.g., genetic, anatomical, and functional—and how each can explain the pattern and pace of morphological evolution in this group. We show further how changes in the action of a single molecular pathway—the Hedgehog signal transduction pathway—can promote integration at multiple levels. We consider this pathway to be a molecular "hotspot" for early and ongoing diversification in this group. Understanding the factors that promote and constrain biological diversity is an important topic in evolutionary biology. As cichlid researchers, we are in a unique position to contribute key insights into this question.

Keywords Craniofacial · Evolvability · Hedgehog signaling · Integration · Modularity · Phenotypic plasticity

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Y. Hu
Biology Department, Boston College, Chestnut Hill, MA, USA
e-mail: hucy@bc.edu

R. C. Albertson (✉)
Department of Biology, University of Massachusetts, Amherst, MA, USA
e-mail: albertson@bio.umass.edu

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1 Key Innovations in the Evolutionary Success of Cichlid Diversification

The family Cichlidae exhibits unparalleled diversity among vertebrates, with many thousands of species estimated (Kocher 2004), of which 1700+ have been scientifically described (Froese and Pauly 2020). These fishes are renowned for both the extent and the speed in which they diversify. East African cichlids, in particular, have demonstrated a remarkable capacity for "explosive" adaptive radiations (Kocher 2004). The resulting diversity is tremendous, as these cichlids differ in multiple phenotypic dimensions including diet, habitat, body shape, coloration, and behavior. Consequently, the study of cichlid evolution demands input from multiple biological disciplines including (but not limited to) ecology, physiology, neurobiology, anatomy, development, genetics, and genomics. Despite many decades of research, an ongoing challenge for cichlid biologists is to identify the factors that have contributed to their unmatched evolutionary success. To put it another way, why are cichlids more *evolvable* than other lineages?

This question has led to the search for "key innovations" that underlie the evolutionary success of this system. Many such innovations have been proposed including the evolution of egg-dummies and maternal mouthbrooding (Salzburger et al. 2005), as well as a modified pharyngeal jaw apparatus (Liem 1978). These represent some of the more obvious phenotypic novelties specific to this group. Here we explore more cryptic aspects of the cichlid body plan. Specifically, we review, or rather revisit, the concept of *modularity* in the cichlid feeding apparatus, and its potential role in promoting the origins and maintenance of eco-morphological diversity in this group. This is an idea that originated with the seminal work of Karel Liem, who posited that the modular nature of cichlid feeding kinematics enables rapid niche shifts without appreciable changes in anatomy (see McConnell 2021). Termed "modulatory multiplicity," this concept was used to explain, operationally, how cichlids diverge in niche-space (Liem 1978, 1979). We extend this foundational idea to include a consideration for modularity at the genetic, anatomical, functional, and evolutionary levels. We discuss how modularity at each level may arise and how each influences evolutionary potential in general, and may have shaped cichlid *craniofacial* diversity in particular. We provide a review of recent molecular insights into the *integration* of the cichlid skull. Finally, we put forward a model that combines all of these concepts under a common experimental framework, and explain how this paradigm may be used to explain the evolutionary potential in this group.

2 Modularity as a Driving and Constraining Force in Morphological Evolution

Modularity is the relative degree of connectivity in a system. In anatomical structures, a module refers to a tightly correlated set of traits that is relatively independent from other such trait sets. Conceptually, modularity is often presented as the opposite of integration. For example, when a high degree of covariation is observed across a set of traits (e.g., x, y landmarks placed on the body of a fish, Fig. 1a), then the entire anatomical unit described by these traits (the entire body of the fish in this example) is interpreted as being "integrated," representing a single module. On the other hand, if two different regions of an anatomical structure vary independently from one another (e.g., the head and body, Fig. 1b), then each may be considered a separate module. In practice, of course, the degree of connectivity between traits exists along a continuum between fully integrated and completely modular, with most exhibiting intermediate levels. Thus, integration is a matter of degrees. It is also a matter of context and scale. Since the degree of covariation between traits is a statistical construct, one's ability to detect modularity largely depends on the resolution of the analysis (e.g., the number of landmarks included). For instance, one could further investigate shape variation in the cichlid head by adding additional landmarks, and this would likely lead to the discovery of additional layers of modularity (e.g., the neurocranium and oral jaws might represent separate modules, Fig. 1c). Similarly, there might be distinct modules within the mandible if examined in finer detail (e.g., Fig. 1d).

There are a number of analytical methods that have been developed to quantitatively assess integration/modularity in a system (Wagner 1984; Cheverud 1982; Goswami and Polly 2010; Klingenberg 2008; Adams 2016). A thorough review is outside of the scope of this chapter, but it is worth noting that the most widely used methods rely on defining anatomical modules a priori and then assessing the degree of covariation within and between these putative modules (e.g., modularity is supported if covariation is significantly higher within than between putative modules). In other words, the study of integration and modularity can be biased.

Despite these caveats, modularity/integration are considered important concepts in evolutionary biology, and are often discussed within the context of trait Evolvability (Klingenberg 2008; Pigliucci 2007, 2008; Laland et al. 2015). For example, a modular pattern of variation is generally considered favorable in promoting diversification, as it allows different parts of the organism to respond independently to selection. A modular organization of traits provides a solution to inconsistent, or even antagonistic, selective pressures for different functional requirements. It could allow, for example, one trait to respond to divergent selection in a new environment, while maintaining the core functional role of an adjacent trait by allowing it to remain invariant under stabilizing selection. Alternatively, a global pattern of trait integration is generally considered to be a constraint on morphological evolution. This is because a mutation that might be advantageous for one trait would cause corresponding changes across multiple traits, thereby increasing the

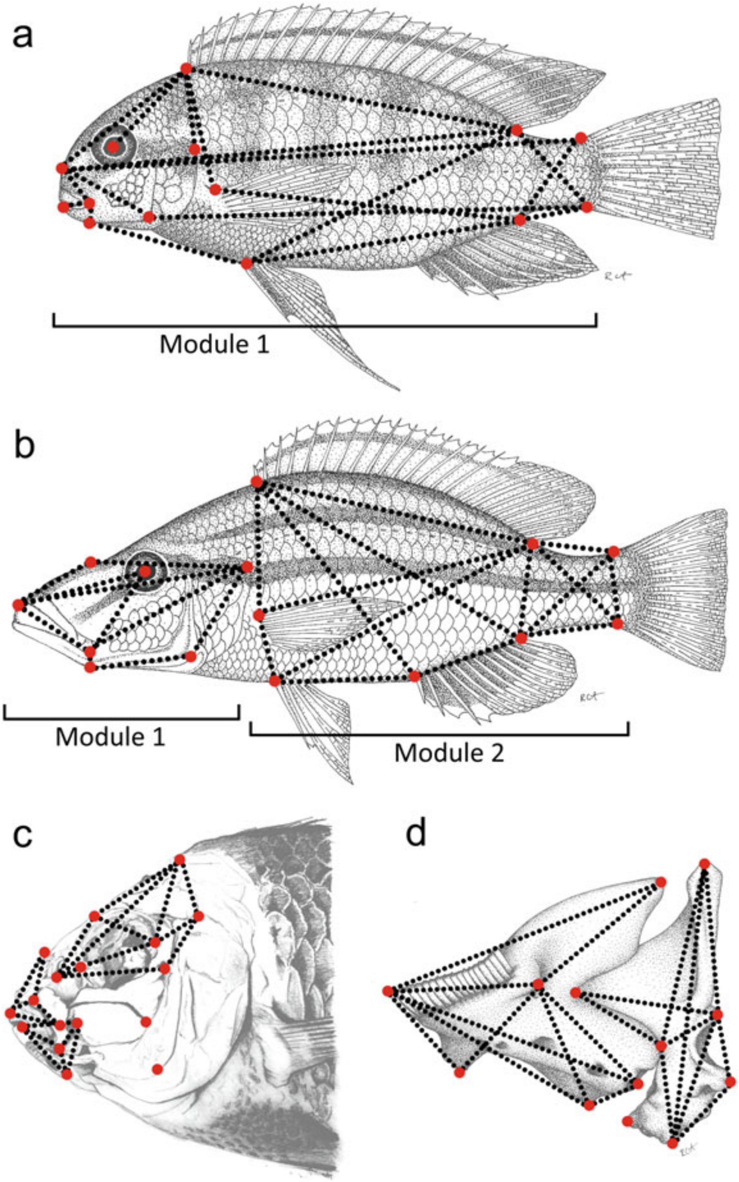

Fig. 1 Integration and modularity of the cichlid body plan. Integration refers to the relative degree of covariation within and between anatomical regions. Dotted lines indicate landmarks that exhibit a significant degree of covariation within a population. (**a**) indicates an integrated pattern of variation, whereas (**b**) indicates a more modular patter. (**b–d**) illustrate modularity at different scales—i.e., full body, head, and within the mandible

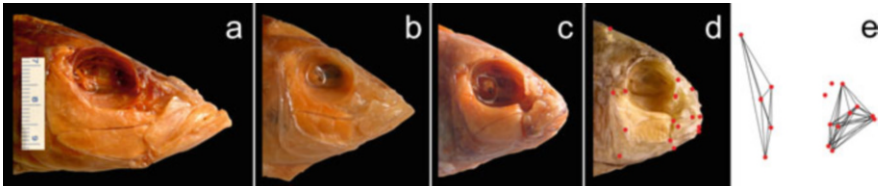

Fig. 2 Morphological divergence and modularity among Lake Malawi cichlids. The primary axis of divergence among Lake Malawi species involves variation in oral length (Cooper et al. 2010), which is illustrated with the representative species: *Pallidochromis tokolosh* (**a**), *Alticorpus macrocleithrum* (**b**), *Gephyrochromis lawsi* (**c**), and *Tropheops sp.* "red cheek" (**d**). Notably, a pattern of divergence that involves variation in the oral jaws matches the best-fit model of modularity among Lake Malawi cichlids, which involves a pattern wherein the oral jaws represent a distinct variational module (**e**, after Parsons et al. 2011)

probability of an overall deleterious outcome. However, if the axis of selection happens to favor a correlated response across multiple traits (e.g., an overall wider head), then a more integrated body plan could facilitate a rapid evolutionary response. Thus, a balance between modularity and integration is necessary to promote both efficient (i.e., fast) and extensive (i.e., disparate) morphological evolution. It is for this reason that intermediate levels of integration are generally considered optimal for promoting morphological evolution (Hansen 2003).

Given these considerations, a number of predictions can be made with respect to the putative role of integration and modularity in shaping cichlid radiations. For example, the anterior skull, including the oral jaws, is widely considered to be one of the more morphologically disparate regions of the cichlid body (Fryer and Iles 1972; Cooper et al. 2010). The ability of the oral jaws to respond quickly and extensively to divergent selection suggests that this region constitutes a distinct module. This hypothesis is supported by empirical data for cichlids from lakes Victoria, Malawi, and Tanganyika (Parsons et al. 2011, Fig. 2e), all of which exhibit a high degree of covariation among oral jaw traits, and less covariation between the oral jaws and the rest of the skull. Modularity between the anterior and posterior skull has also been observed in other vertebrates, especially those undergoing rapid diversification such as a dog (Drake and Klingenberg 2010), damselfish (Cooper and Westneat 2009), and Phyllostomid bats (López-Aguirre et al. 2015). Alternatively, integration between facial and calvarial shapes has also been noted and seems to be common in other systems (e.g., primates, Pérez-Claros et al. 2015; laboratory mice, Parsons et al. 2015). The basis for the integration between the skull and the facial skeleton appears to be due to direct physical interactions between them during early development and growth (reviewed in Parsons et al. 2015). These observations raise the interesting hypothesis that adaptive radiations in skull morphology involve "breaking" this putatively ancestral pattern of integration, such that the facial skeleton can vary independently from the posterior skull. Nested within this hypothesis is the more specific prediction that the *magnitude* of modularity in the cichlid head is different from that in other lineages of fish that have not evolved as extensively. For instance, if modularity promotes morphological diversification, then one would expect the cichlid head to be more modular (i.e., less integrated) than that in a lineage that does not exhibit the same degree of morphological disparity (e.g., centrarchids, catfish).

In addition, the predictable nature of cichlid radiations suggests a degree (and/or pattern) of integration among regions of the body that results in predictable phenotypic response across an array of traits as lineages exploit new environments. For instance, the cichlid radiations in lakes Victoria, Malawi, and Tanganyika are associated with qualitatively (e.g., Fryer and Iles 1972) and quantitatively (i.e., Young et al. 2009; Cooper et al. 2010) similar shifts in distinct craniofacial traits. These include shifts in the profile of the skull (steep vs. shallow) and the relative length of the mandible. In spite of age differences that constitute several orders of magnitude (~0.2 MY for Victoria, ~2 MY for Malawi ~20 MY for Tanganyika), the primary axis of variation in each radiation captures correlated shifts in these two traits. On one end of the spectrum are species with short jaws and steep craniofacial profiles, whereas the opposite extreme is defined by species with long jaws and shallow profiles (Fig. 2). All else being equal, the former shape configuration should be optimal for generating and resisting forces associated with a biting/crushing mode of feeding, whereas the latter configuration should facilitate a sucking/ram-mode of foraging. The similarity of this ecomorphological shape axis across cichlid lineages suggests a fundamental integration among component parts of the cichlid skull. Alternatively, a common selection axis might be acting independently upon each aspect of the cichlid head resulting in a correlated evolutionary response. This is a valid alternative hypothesis, but for the reasons presented below, we find this scenario to be less likely to fully explain these patterns. Notably, while the primary axis is shared between cichlid radiations, more disparity was noted in the older lineages. This suggests that over time, integrated modules can be broken down into finer units allowing for the evolution of greater morphological diversity. Thus, integration and modularity may themselves evolve. While some empirical and circumstantial evidence for these ideas are presented in the literature, there is much work to be done along these lines. Some critical outstanding questions that remain include: How does modularity arise over development? Does it change at different life history stages? To what extent does modularity at one biological level influence the modular organization at another level? How readily does modularity evolve? We explore these questions in greater detail below.

3 Modularity at Multiple Levels

Modules can be observed and studied at multiple levels in biological systems. With respect to morphological evolution, phenotypic modularity is the most common level of focus, but as we discuss below it is important to consider other levels of modularity and how they may impact one another.

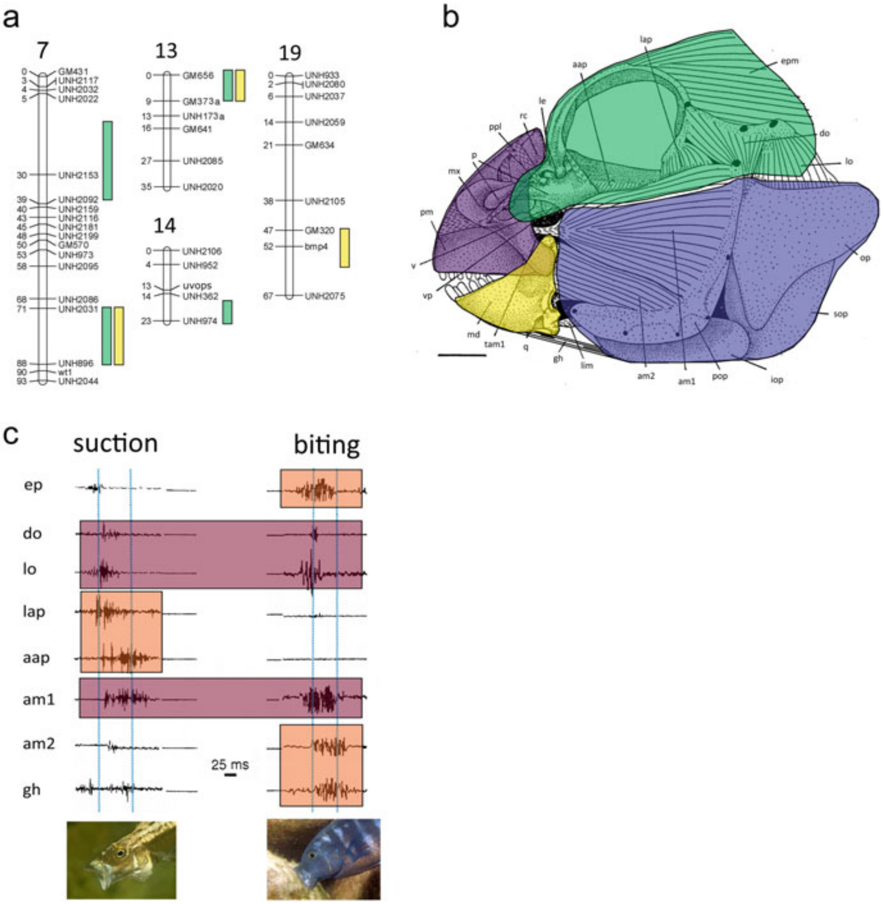

Fig. 3 Modularity at multiple levels. While integration and modularity are often considered at the phenotypic level, the manifestation of covariation is due to many factors including the genetic architecture of traits under consideration as well as the functional modalities employed by the organism over it life. Thus, modularity can be observed and studies at these other levels. (**a**) Considers modularity in the G–P map, where variation in two distinct traits map to overlapping regions of the genome, depicted here as green and yellow bars. In this example, loci that overlap are on linkage groups 7 and 13 (modified from Cooper et al. 2011). (**b**) depicts modularity in the cichlid skull (illustration modified from Fig. 5 in Liem 1979), where different shaded regions represent areas of the skull exhibit high levels of covariation relative to other regions (i.e., phenotypic modules). (**c**) illustrates modularity in feeding mechanics (electromyograms are modified from Figs. 6.3 and 6.5 in Liem 1991). Here we consider distinct sets of muscles that are active in distinct foraging behaviors as being modular (orange boxes), and muscles that are active across foraging behaviors as integrated. Images courtesy of Ad Konings and Cichlid Press

3.1 *Phenotypic Modularity*

At the phenotypic level, a module is generally defined as a group of traits that are highly integrated/correlated to each other, but are independent of traits in different modules (e.g., Figs. 1, 2e, and 3b). As mentioned above, the study of phenotypic modules usually involves grouping traits (e.g., landmarks in the figure above) based on a priori hypotheses about their putative embryological or functional relationships, and then statistically comparing levels of covariation within and between these putative modules. Several attempts have been made toward the development of more exploratory analyses that do not require a priori hypotheses, such as systematically evaluating all modular combinations (Márquez 2008; Parsons et al. 2012) and cluster analysis (Goswami 2006), but these have yet to be embraced by the field, owing perhaps to the very large numbers of animals needed to discern meaningful trends. More work is clearly necessary to develop unbiased methods to search for modular patterns of variation, as this will be important to discern the actual patterns of integration that exist within and among anatomical units.

In cichlids, both biased and non-biased approaches have been taken to examine phenotypic integration and modularity. An unbiased approach based on Márquez (2008) was used to explore patterns of modularity in the head of cichlids from lakes Tanganyika, Malawi, and Victoria, and while some differences were noted in each lineage, the oral jaws consistently constituted a module that was distinct from the posterior region of the skull (Parsons et al. 2011; e.g., Fig. 2e). In a similar study, modularity was explored in the mandibles of two Lake Malawi cichlid genera, which revealed discrete differences in patterns of covariation (Parsons et al. 2012). This latter finding in particular suggests that modularity can evolve between closely related lineages. More subjective methods have revealed both modular and integrated patterns of variation. For instance, Webb and colleagues (Bird and Webb 2014; Webb 2013) examined the morphology and development of cranial lateral line canals in two cichlid species, and noted integration between canals on different bones (Bird and Webb 2014) but modularity between the canals and their underlying dermal bones (Webb 2013). Modularity was observed in functionally distinct regions of the cichlid mandible (Albertson et al. 2005), while integration was noted for cichlid brain size and certain aspects of head shape (Tsuboi et al. 2014). While outside the scope of this chapter, it is worth noting that integration and modularity of cichlid color patterning have also been studied using similar methods (Brzozowski et al. 2012; Albertson et al. 2014). This general balance between integration and modularity of the cichlid skull is consistent with the observation of both extensive but often stereotypical craniofacial diversification in this group.

The study of phenotypic integration in cichlid hybrids has led to insights into the evolution of this group. For example, hybridization is thought to be a mechanism through which extensive phenotypic diversity is achieved in young evolutionary lineages. Termed the hybrid swarm theory of adaptive radiation (Seehausen 2004), it suggests that periodic mass hybridizations precipitated by dramatic ecological shifts can seed bursts of diversification through the reshuffling of genetic variation, leading to new combinations of alleles that produce new phenotypes. A study by Parsons et al. (2011) showed that compared to either parental species, F_2 hybrids showed a significant reduction in phenotypic integration. If integration acts as a constraint on morphological evolution, then hybridization could provide a means of overcoming this constraint and a mechanism through which greater phenotypic diversity may be achieved.

An important outstanding question in the field is how integration arises during development. Two important factors are thought to contribute, genetics and kinematics. As we describe below, each can have a pronounced impact on patterns of covariation that are measured in the phenotype.

3.2 Genetic Modularity

At the genetic level, modularity describes shared vs. distinct genetic underpinnings. This is often put in the context of the genotype–phenotype (G–P) map (Albertson et al. 2005), and quite simply refers to whether genetic variation at one locus in the genome affects variation in more than one trait (Fig. 3a). Either genetic pleiotropy or tight genetic linkage between adjacent genes can underlie modularity at this level.

One approach to the study of genetic modularity is through the use of genetic mutations in model organisms. In the simplest terms, when genetic knockout leads to the disruption of more than one trait (i.e., pleiotropy), these two traits may be considered integrated. Of course, gross perturbation of genetic systems may lead to patterns of covariation that could never exist in nature, and thus one should take care not to over interpret such results. Nevertheless, pleiotropy revealed through such loss of function experiments can offer interesting hypotheses with respect to where one might look for covariation in wild populations. For instance, a genetic mutation that influences neural crest cell (NCC) development will perturb many structures in the head, some of which might exhibit high levels of covariation in natural populations. In this way, genetic mutation acts as a means to reveal the developmental architecture and relatedness of seemingly distinct anatomical structures.

Model organisms can also be used to more directly assess the role for genetic mutation in shifting patterns or magnitudes of phenotypic integration. In one such study Hallgrimsson and colleagues (2006) compared patterns of variation in wild-type and brachymorph (bm) mice. The bm mutation affects the composition of cartilage extracellular matrix and growth of the chondrocranium. Since the chondrocranium and dermatocranium physically interact during skull growth, it was hypothesized that the bm mutation should affect variation across the entire skull (i.e., not just the chondrocranium). This was shown to be the case, as the bm mutation led to differences in both patterns and levels of integration across the mouse skull. This study illustrates how a single mutation can alter covariance structure in a way that could potentially influence the evolutionary potential of a trait. In a similar study, investigators examined patterns of modularity in wild-caught, “wild-type,” and mutant lines of zebrafish (Parsons et al. 2018), and showed that domestication, genetic background, and point mutations all have a significant effect on craniofacial modularity. Notably this work showed that a single mutation is capable of shifting patterns of modularity between alternate, “preset” patterns among wild types with minimal impact on mean shape. In other words, genetic changes may influence evolutionary potential by changing underlying patterns of variation without directly changing the traits that are exposed to selection (Parsons et al. 2018).

Cichlids are still developing as a laboratory model system. While gene manipulations are less common (but see, Fujimura and Kocher 2011; Juntti et al. 2016), forward genetic mapping can be applied as an alternative. Instead of beginning with a known mutation (as above), researchers can begin with the phenotype and work their way to the genotype via hybrid pedigree mapping. Also known as quantitative trait loci (QTL) mapping, this method can reveal the number and genomic location of loci that influence phenotypic variation (e.g., Albertson et al. 2003). With respect to genetic modularity, one can identify traits that are regulated by common or distinct genetic loci. For instance, Albertson and colleagues (Albertson et al. 2005; Albertson and Kocher 2006) showed that variation in certain dimensions of the cichlid mandible was correlated, but variation in other dimensions was not. They showed further that patterns of covariation in the mandible matched the number of shared loci for each trait. Specifically, the height of the articular process of the jaw was shown to be tightly correlated with the overall length of the jaw, and these two traits shared 2/3 quantitative trait loci (QTL). This pattern of integration is consistent with the common roles these traits play during feeding—i.e., mechanically, the articular process acts as the in-lever whereas the length of the jaw acts as the out-lever during jaw adduction/closing. Alternatively, the articular and retroarticular processes of the lower jaw are functionally decoupled, with the latter acting as the in-lever during jaw abduction/opening. These two elements did not covary in cichlid populations, and exhibited no overlap in QTL (0/8) for shape variation. This study was extended to show overlapping genetic bases for skull and mandible shape, which corresponded to the covariation of these shapes across cichlid species and was consistent with a common functional role for these traits in generating and resisting forces generated during the action of biting (Cooper et al. 2010, 2011). It is notable that in the studies above there was concordance in integration at the anatomical, genetic, functional, and evolutionary levels. This corresponds to theory, which suggests that genetic correlations might evolve to match common functional demands, and that this should facilitate evolutionary divergence (e.g., Wagner et al. 2007, and references therein). The underlying notion is that, if a combination of traits function in a coordinated fashion, a common genetic underpinning for those traits (i.e., a group of traits controlled by the same gene or genetic locus) would enable selection to act more efficiently to alter function in a changing environment. That is, instead of multiple independent mutation events, a single mutational event could cause widespread change among the necessary traits. In other words, genetic modularity can amplify the effect size of mutations, thus enhancing variability and providing more material for selection to work on, which may ultimately lead to enhanced Evolvability.

While pleiotropy is widely assumed to underlie phenotypic integration at the genetic level (e.g., Ehrich et al. 2003; Cheverud et al. 2004), the genetic basis of integration may be far more complicated. Recently, a method for deriving an individual-level metric for integration (Hu et al. 2014) and modularity (Parsons et al. 2012) was developed (also see Parsons et al. 2021). This represents an important innovation as it allows integration and modularity, which are by definition a population-level metric, to be examined at the individual level. An outcome of this innovation is that integration or modularity can be considered a quantitative trait, and their genetic basis can be mapped. If these phenomena arise as a secondary consequence of shape variation then we would expect loci that underlie integration and modularity to be the same as those that underlie shape. Alternatively, if the genetic factors that mediate *covariation* in shape are distinct from those that underlie *variation*, then QTL for integration and modularity should be distinct from those that underlie shape variation. At the moment, empirical data appear to favor the latter hypothesis that morphological variation and covariation have distinct genetic bases. When the genetic underpinning of Modularity and integration in the cichlid mandible were mapped (Cooper et al. 2011; Parsons et al. 2012; Hu et al. 2014), both were found to be largely (but not completely) distinct from previously identified QTLs for mandibular shape (Albertson et al. 2005; Cooper et al. 2011).

Whether via genetic pleiotropy or another mechanism, the next step in this process will be to identify the specific genetic loci that underlie variation in integration and modularity between cichlid species. Such insights will provide a foundation for investigations into how these phenomena manifest themselves over ontogeny, and how they influence phenotypic evolution.

Another benefit of the individual metric is the ability to perform phylogenetic comparisons across many species. Traditionally, in order to document differences in integration between species, data must be collected on a population of each species, which makes multispecies comparisons difficult due to the huge sample size required. Even for a relatively small phylogeny of 20 species and a modest sample size of 25 animals, 500 animals would need to be phenotyped. The new individual metric allows researchers to compare integration across a large number of taxa, as it only requires a handful of specimens for each species. This, in turn, enables the application of phylogenetic methods to investigate the evolution of phenotypic integration in detail. The utility of this approach has been demonstrated for centrarchids (Smith et al. 2015) and Antarctic notothenioids (Hu et al. 2016), and as high quality cichlid phylogenies emerge, we anticipate this to be a fruitful direction of future studies.

3.3 Functional Modularity

The studies above illustrate how modularity at the genetic level can influence modularity in the phenotype. Another mechanism that can influence the manifestation of integration is the kinematic modalities of the skull. Such functional integration generally describes parts of an organism that are thought to be involved in performing a certain task/function as a coordinated unit. Thus, functional modularity refers to distinct anatomical units that are involved in distinct tasks, whereas functional integration refers to distinct anatomical units that participate in a similar task. A classic example of functional modularity is the oral and pharyngeal jaws of cichlids. The former is involved in the action of prey capture, whereas the latter is involved in the processing of prey. The functional decoupling of these two anatomical units is credited for the evolutionary success, at least in terms of eco-morphological diversification, of cichlids (Liem 1973; Hulsey et al. 2006). Examples of functional integration might include the separate bony elements/processes within the skull whose coordinated movements are necessary for producing a functional output. For instance, as noted above the mandible can be described as two opposing lever mechanisms, one for jaw opening and the other for jaw closing. The out-level for both is the total jaw length. The closing in-lever is the articular process, which is where the adductor mandibulae inserts. The opening in-lever is the retroarticular process, which is where the interopercle ligament inserts. The ratio between in- and out-lever lengths can be used to estimate the mechanical advantage (MA) of the system (Westneat 1994). Low MA is typical in fast moving but weak jaw rotation, whereas high MA generally describes slow-moving but powerful systems. Thus, the articular process and length of the mandible would be considered functionally integrated traits, whereas the articular and retroarticual processes would be considered functionally modular. It is important to note that functional modularity does not always translate to phenotypic modularity. For example, Parsons et al. (2012) found that within the Malawi species *Maylandia zebra* these two processes do appear to represent distinct anatomical modules, but within *Labeotropheus fuelleborni* these two processes are integrated. Thus, patterns of covariance can differ between closely related species, which may reflect differences in how each species utilizes its lower jaw (see below), or more fundamental differences in how the lower jaw develops between species.

More complex jaw movements can be described by four-bar linkage models (e.g., Westneat 1990), which often involve the coordinated action of many more skeletal elements, ligaments, and muscles. The opercular four bar system (Fig. 4c) is one such system that has been studied in cichlids, which links the rotation of the operculum to lower jaw depression through a series of moveable elements, or "links" in the system. The combination of epaxial muscle and the levator operculi contraction causes the opercle, which acts as the input link in the system, to rotate caudally relative to the head, pulling the interopercle bone (IOP, the coupler link) posteriorly with it. The interopercle is attached to the retroarticular (RA) process via the interoperclemandibular ligament, which inserts onto the ventral tip of the RA. This ligament pulls the RA posteriorly, which causes the mandible to depress as it rotates around its fulcrum (the mandible–quadrate joint). The movable links in this system (as well as the associated soft tissue) may be considered functionally integrated traits, and we have shown previously that they covary across several cichlid species from multiple genera (*Labeotropheus*, *Maylandia*, and *Tropheops*, Hu and Albertson 2014; more on this below).

Participation in a common task (e.g., jaw depression) is an intuitive way to define functional units of the head, and as described above we often determine this at the anatomical level, albeit through the lens of mechanical engineering. However, a more quantitative and less subjective method would also be useful here. For this, we turn back to Karel Liem's work on cichlid feeding mechanisms. The experimental

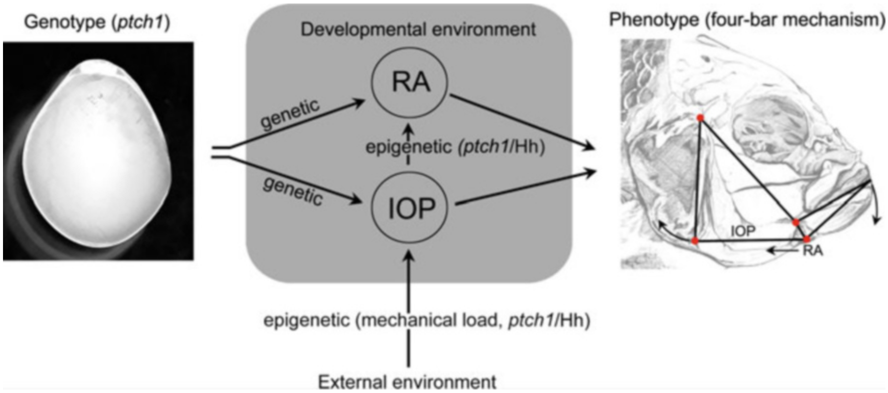

Fig. 4 Genetic and epigenetic mechanisms of phenotypic integration. The retroarticular process (RA) and interopercle (IOP) are two bones that function together in lower jaw depression via the opercle four-bar mechanism (far right). They also covary among closely related cichlid species. The cichlid egg at the far left represents genotype, in this case *ptch1*. Work has shown that allelic variation at *ptch1* mediates variation in both the RA and the IOP through genetic pleiotropy (Roberts et al. 2011; Hu and Albertson 2014). We have also shown that the IOP influences the shape of the RA through epigenetic bone remodeling, possibly via a *ptch1*-mediated mechanism (Hu and Albertson 2017). Moreover, we have shown that the external environment, in particular loading regimes associated with different modes of foraging, influences the growth of the IOP, and that this epigenetic effect is mediated by Hh signaling (Navon et al. 2020). The unfolding of these genetic and epigenetic processes occurs both within the environmental context of the developing embryo (gray shaded area), as well as the external environment that the organism is exposed to. This figure is based conceptually on Jamniczky et al. (2010)

repertoire employed by Liem and other functional morphologists combines a careful evaluation of feeding anatomy with the monitoring of muscle actions with electromyographics during distinct feeding behaviors. While this approach to the study of fish feeding mechanics was/is relatively common, Liem's work stood apart in that he compared kinematic profiles within species, but across different types of feeding behaviors (but see Wainwright and Turingan 1993). Through these studies, he was able to identify kinematic repertoires that were either unique to each feeding mode, or conserved across modes. The example in Fig. 3c shows an electromyogram of various cranial muscles during suction feeding and biting. Whereas some muscles are involved in both functions such as the first subdivision of the adductor mandibulae (am1), other muscles are only involved in biting or suction feeding. Muscles like the am1 would be considered integrated with respect to these functions. Alternatively, muscles such as the second subdivision of the adductor mandibulae (am2) or the adductor arcus palatini (aap) would be considered modular.

Patterns of functional covariation are important because they can influence pattern of phenotypic integration. These muscles originate and insert onto various skeletal elements of the skull. Bone is a dynamic tissue that is able to sense and remodel itself according to its local mechanical environment (e.g., via *phenotypic plasticity*). In other words, forces imposed upon bone by a specific muscle can reshape its geometry in a predicable manner. Muscles that participate in a common function that is distinct from other functions (i.e., are functionally modular), may act to reshape the underlying skeleton in a coordinated fashion. This in turn could result in a measurable pattern of phenotypic integration among skeletal elements associated with that function. Species that perform the same stereotypical function (e.g., algal scraping) throughout much of their lives (i.e., ecological specialists) might be expected to develop a strongly modular skull due to the consistency of the functional demands placed on different region of the feeding apparatus. On the other hand, generalist should exhibit a less modular skull due to the implementation of multiple functional repertoires. Note also that niche shifts over ontogeny could produce dramatic changes in the mechanics of prey capture or processing, which could lead to different patterns of phenotypic integration between life history stages. Depending on when natural selection is acting, one pattern of integration might be far more important than another.

3.4 Evolutionary Modularity

Integration at the evolutionary level refers to patterns of covariation over a phylogeny. When two traits evolve together, they can be considered integrated at this level. While methods have been developed to examine this question in a strict phylogenetic framework (Adams and Felice 2014; Adams 2016), more simplistic models of coevolution can be informative as well. Owing to their rapid speciation and recurrent hybridization, many cichlid radiations lack robust phylogenetic signal, precluding many analyses where variation is mapped onto a phylogeny. In these instances, simple correlations across species can speak to trait coevolution. For example, as mentioned above we have shown that different features of the cichlid skull are correlated across multiple Lake Malawi cichlid species. craniofacial slope and lower jaw shape vary in a correlated fashion among cichlid species, such that species will steep profiles generally have short jaws, whereas species with shallow profiles normally possess longer jaws (Cooper et al. 2011). In-lever and out-lever measures also covary across species (Albertson and Kocher 2006), as do IOP and RA shapes (Hu and Albertson 2014). These trends suggest that these different bones are evolving in a coordinated fashion.

Evolutionary integration may arise due to intrinsic or extrinsic factors. Intrinsic factors include developmental biases such as pleiotropy and functional interactions. For example, if a single genetic polymorphism influences the development of two bones, then it should follow that these bones will evolve together. This is the case for the IOP and RA, which appear to develop under the control of the *ptch1* locus (Hu and Albertson 2014; more on this below). It is also possible that bones that are linked via a common function will grow in a coordinated manner, via plastic responses such as bone remodeling, to accommodate this function. Provided the functional repertoire in sister lineages is the same, these traits should also covary across species. The alternative hypothesis to intrinsic modes of evolutionary

Integration is that patterns of coevolution arise due to a common selective pressure on each trait. Of course, it is difficult to definitively say what is driving integration at the evolutionary level, and it is possible (even likely) that multiple factors are contributing to such trends. For instance, craniofacial profile and jaw length covary across cichlid species (Cooper et al. 2010), and the trend holds even when (the albeit weak) phylogenetic signal is accounted for (Cooper et al. 2011). Variation in these traits was found to have an overlapping genetic basis, which suggests that pleiotropy may underlie the coordinated evolution of these characters. However, we also found that these traits participate in a common function. While a short, stout lower jaw is optimal for the generation of force, a steep skull profile appears to be optimal for absorbing the stresses associated with a powerful bite. Thus, it is possible that overtime the skulls of biting fish remodel themselves to limit the amount of stress that is propagated to the back of the skull (Cooper et al. 2011).

In this section, we have discussed integration and modularity of the skull at multiple levels. The intellectual goal of this type of research is to understand the factors that have shaped cichlid radiations. Pleiotropy and biomechanics represent system inputs, which produce patterns of phenotypic integration, and ultimately shape patterns of morphological evolution (e.g., a system output). This basic line of inquiry has fascinated evolutionary biologists since the time of Darwin, who recognized “correlated growth” as an important influence on evolutionary change (Darwin 1859, p. 146). We maintain that cichlids, which strike an excellent balance between experimental tractably and evolutionary richness, are an ideal system to understand the sources and outcome of phenotypic integration. We highlight recent insights below to underscore this point.

4 Integrating Modularity at Multiple Levels: Lessons from the Hedgehog Pathway

Cichlids exhibit unparalleled morphological diversity among vertebrates. This attribute has fascinated biologists for decades, but is almost overwhelming in its extent. There has been an unspoken sense that cichlids are weird and do not conform to the same set of rules that govern diversity in other systems. In other words, when faced with the dizzying magnitudes of eco-morphological diversity among cichlids, research into the patterns and processes of evolutionary change seems untenable. For this reason, systems with fewer eco-morphs—e.g., stickleback, whitefish, Arctic charr, Anolis lizards—hold great appeal. However, we and others have shown that cichlids do adhere to the same evolutionary patterns as other fish radiation, but have taken it to an extreme with respect to the extent of variation (e.g., Cooper et al. 2010, and references within). This is the definition of a model system—one that exemplifies a process that can be generalized to other systems. The rapid diversification of cichlids seems to occur largely along a conserved eco-morphological axis that distinguishes benthic specialists from pelagic specialists. The notable point here is that this axis is similar to that in many other fish lineages including stickleback (Willacker et al. 2010), whitefish (Praebel et al. 2013), Arctic charr (Jonsson and Jonsson 2001; Skoglund et al. 2015), centrarchids (Smith et al. 2015), and Antarctic notothenioids (Hu et al. 2016). Thus, insights gleaned from the cichlid system are likely to be widely applicable.

The primary assertion of this chapter is that modularity of the cichlid skull promotes, or at least has shaped, patterns of morphological evolution. Cichlids diverge along a benthic-limnetic axis, which has involved concomitant shifts in distinct sets of traits, including characters important for foraging efficiency. As noted above, the IOP and RA accounts for two out of the three moveable linkages in the opercular four-bar linkage mechanism (Westneat 1990). These two bones are therefore integrated at the functional level. We have recently shown that they are also integrated at the genetic level. In particular, genetic variation at the *ptch1* locus influences variation in both the IOP and the RA (Roberts et al. 2011; Hu and Albertson 2014). Thus, genetic pleiotropy likely underlies, at least to some degree, the coevolution of these two traits among closely related cichlid species (Hu and Albertson 2014).

However, we cannot ignore the fact that these two elements are also functionally coupled. In particular, the IOP represents the coupler link that connects to the RA (the output link) via the interopercle–mandibular ligament. As the IOP moves posteriorly, it “pulls” the RA via this ligament. The IOP is a sesamoid bone that develops from within the ligament itself, and thus a deeper IOP bone is associated with a deeper ligament. All else being equal, a larger ligament should be able to confer greater force from one bone to another. This raises the intriguing possibility that variation in the IOP could induce variation in the RA via mechanical load induced patterns of bone deposition. Whereas the linkage between IOP and RA via *ptch1* represents a genetic mode of coupling (i.e., pleiotropy), this kinematic linkage represents an epigenetic (sensu Waddington) mode of integration. A notable observation related to this assertion is that Malawi cichlid larvae (documented in *Labeotropheus*, *Maylandia*, and *Tropheops* genera) exhibit a rather enigmatic behavior at early larval stages. Soon after hatching (~5–6 days post fertilization), the jaw primordium extends, and these fish begin to gape. There is little to no mineralization in the head skeleton at this stage, rather the oral skeleton is entirely cartilaginous. Nevertheless, these larvae initiate a rapid gaping behavior (up to 250 times per minute) at this stage and it continues until the onset of exogenous feeding. The exact role of this behavior is unknown, but it likely has little to do with respiration, as the gill filaments are not developed at this stage and gas and ion exchange primarily occurs via osmosis through the skin, as well as large superficial blood vessels around the yolk (Rombough 2002; Glover et al. 2013). We suggest that this behavior is associated with bone development. Specifically, in a recent paper we hypothesized that this behavior induces stress on the feeding apparatus, which in turn stimulates more extensive early bone development (Hu and Albertson 2017).

In support of this hypothesis, gape frequency was found to be species specific with species that develop more robust bone exhibiting consistently higher rates of gaping over early larval development (6–10 dpf), whereas species that develop more gracile skeletal elements gape at a consistently lower rate. Beyond this observational difference, we found that when this behavior is experimentally altered, bone development changes in a predictable manner. Specifically, when the kinematic link between the IOP and the RA was broken (via surgery) in the fast gaping species, the length of the RA was significantly shorter on the surgery side versus the control side. In addition, when the slow gaping species was made to gape faster (over 4 days), these animals developed statistically longer RAs compared to control animals. Thus, covariation (and coevolution) of the IOP and RA appear to be driven by both genetic (i.e., pleiotropy) and epigenetic (i.e., kinematic coupling) mechanisms, underscoring the complex relationship between genotype and phenotype (Fig. 4).

An outstanding question in this story is the degree to which the *ptch1* locus regulates both genetic and epigenetic mechanisms. As mentioned above, bone is an exquisitely mechanosensitive tissue that is able to sense and remodel itself according to its mechanical environment. The primary cilia on bone progenitor cells are thought to play critical roles in mediating this process (Xiao et al. 2006; Papachroni et al. 2009; Nguyen and Jacobs 2013). Mice lacking functional cilia in bone precursor cells exhibit normal larval skeletal patterning, but impaired growth and remodeling at later stages (Qiu et al. 2012; Temiyasathit et al. 2012). A comprehensive understanding of the molecular basis of bone mechanotransduction is not complete, however the Hedgehog (Hh) signal transduction pathway has been implicated. Members of the Hh pathway localize to the cilium and are intimately associated with cilia-specific proteins (Yuan and Yang 2015; Yuan et al. 2016). Cells lacking cilia are unable to transduce a Hh signal in response to Hh ligand (Haycraft et al. 2005; Berbari et al. 2009). Thus, cilia have been said to constitute the Hh "signal transduction machine" (Goetz et al. 2009). Ptch1 encodes a receptor protein for this pathway and is also a transcriptional target of Hh signal transduction. Thus, it is possible that in addition to its role in the genetic regulation of cichlid bone shape, *ptch1* might also play an important role in mechanical load induced bone formation (Fig. 4).

Consistent with this idea, we have found that when slow gaping animals were made to gape at a faster frequency, not only did their RAs get longer, but levels of *ptch1* in the jaw were also significantly increased (Hu and Albertson 2017). Unfortunately, this difference in expression cannot tell us whether *ptch1*, or the Hh pathway more generally, is responsible for the plastic response, or simply an output. Since Hh signaling participates in bone development (Long 2012), it is possible that increased *ptch1* expression is simply a secondary consequence of developing more bone. However, two recent experiments support the idea that the Hh pathway itself is both necessary and sufficient for craniofacial plasticity. The first involved QTL mapping skeletal and soft-tissue traits in distinct foraging environments (suction feeding versus biting). This work showed that the RA was the most plastic of traits analyzed, and that alternate *ptch1* alleles were differentially sensitively to the environment with respect to RA length (Parsons et al. 2016). The RA was always sensitive to the environment, however, when animals were homozygous for one *ptch1* allele the sensitivity was nearly doubled compared to when they inherited the alternate allele (i.e., differences in mean RA length between foraging environments were nearly twice as large). The second experiment took a developmental genetic approach using both cichlids and zebrafish. Fluorochrome injections were used to label bone and calculate rates of bone matrix deposition (RBMD, following Atkins et al. 2015) under different foraging treatments (again, suction versus biting) (Navon et al. 2020). Both cichlids and zebrafish exhibited different RBMD, especially in the IOP, in different treatments, and higher levels of *ptch1* expression were observed in treatments that resulted in higher RBMD. When Hh was knocked down in zebrafish, using a dominant-negative *gli2* transgene under the control of a heatshock promoter, differences in RBMD were lost. Alternatively, when Hh signaling was elevated, using an active *shha* transgene linked to a heatshock promoter, the plastic response in RBMD was enhanced. These experiments provide strong independent support for the hypothesis that *ptch1* is not simply a transcriptional output of phenotypic plasticity in cichlids, but rather plays an active role in mediating plasticity of the RA and IOP (Fig. 4).

5 Feedback in the System

Ptch1 may be a lynch pin that links variation at multiple levels, from genotype through phenotype and ultimately to function and evolution. This locus also underscores the concept of feedback in a system. In the predominant experimental paradigm, researchers seek to connect genotype to phenotype and ultimately to function, with the implicit assumption that such inquiry will contribute to a better understanding of the factors that influence organismal fitness (Fig. 5). What is not typically incorporated into this paradigm is the concept of feedback. As discussed above, a change in foraging kinematics can lead to a change in morphology. In general terms, this is referred to as phenotypic plasticity. When referring to the skeletal system, this is also called remodeling. Either way, the trajectory from phenotype to function is not unidirectional, and *ptch1* provides a molecular inroad into the mechanisms through which this feedback in can occur.

Functional systems can also feedback directly on genetic systems through cryptic genetic variation (CGV), which refers to variation that does not contribute to the range of phenotypes under “normal” conditions, but has the potential to modify phenotype under novel environmental conditions. A comprehensive understanding of CGV is lacking, but its broad significance is underscored by its roles in affecting the penetrance of complex human diseases, and a population’s ability to respond to changing environmental or genetic conditions (reviewed by Gibson and Dworkin 2004). Many classic examples of CGV come from work in *Drosophila melanogaster*, in which distinct QTL have been discovered for longevity and bristle number in distinct nutrient or temperature treatments (Leips and Mackay 2000; Dilda and Mackay 2002). It has been suggested that CGV is likely to be expressed when an organism faces a rare or novel external environment (Schlichting 2008).

The morphological variation exhibited by cichlid species, and the diverse environments in which they exist, presents an ideal opportunity to study the conditions under which CGV can modify the relationship between genotype and phenotype. To this end, we generated a hybrid mapping population in the lab, split families, and reared them under distinct foraging regimes (biting vs. suction feeding, where the same amount of food is served in two different forms: embedded in agar vs. grounded to small particles, such that nutritional content of diet was held the same). QTL were then mapped for a range of foraging related traits in each environment. Of 22 significant QTL, only one was shared between foraging treatments. Moreover, not all traits exhibited a plastic response, but their genotype–phenotype maps were nevertheless distinct. This suggests that even when the phenotype itself is robust to the environment, there is more than one genetic path leading to its development (Parsons et al. 2016). This work demonstrates that the relationship between genotype and phenotype can be almost entirely dependent upon the environment.

In the case described here, it is the mechanical foraging environment that influences the genetic basis of a trait. Thus, not only can a change in kinematics feedback directly onto skeletal morphology via epigenetic mechanisms, but it can also feedback onto genotype resulting in a wholesale change in the loci that regulate variation in these phenotypes. Since natural selection acts on variation, this consideration is critical to a more comprehensive understand of the genetic features that underlie evolutionary potential in cichlids. It is therefore imperative to expand the current experimental paradigm to include connections and feedback at each level of biological organization (Fig. 5).

6 Conclusions

Although evolutionary biologists have long recognized the joint concepts of integration and modularity (e.g., "correlated growth," Darwin 1859), they have received renewed attention in recent years with new methodologies and their incorporation into modern evolutionary theory (Klingenberg 2008). Being applicable to virtually all levels of biology, they have great explanatory potential to one of the fundamental questions of evolution: how is the diversity of life produced? The cichlid system offers a unique opportunity to explore and shed novel insights into this question, quite simply because they are a suitable model with which to study integration at all levels. Their ecological and phenotype diversity is outstanding and increasingly well understood. Species may be reared in the laboratory, and are large enough for kinematic studies, but small enough to rear large numbers of animals for genetic mapping experiments. Several reference genomes exist. Many species will breed readily in the laboratory, providing material for developmental studies. It is a rare thing to have a system characterized by such a high level of diversity that is also tractable for genetic, developmental, and functional studies. In this way cichlids stand as an important and unique model in which to reveal features that influence

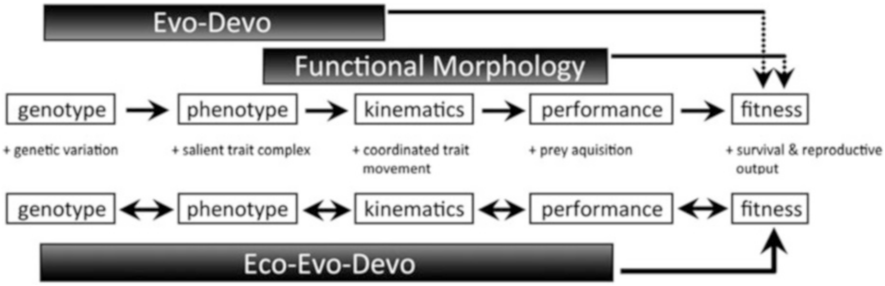

Fig. 5 Linking genotype to fitness. Understanding the factors to contribute to organismal fitness is a major goal of evolutionary biology. Variation at multiple levels of biological organization should contribute to fitness, including genotype, phenotype, kinematics, and performance. Traditionally, few fields in evolutionary biology span all levels. Whereas functional morphology links phenotype to performance, evo-devo is primarily concerned with linking genotype to phenotype (and occasionally to kinematics). The progression from one level to the next is generally considered to be unidirectional in these fields. However, it is increasingly recognized that this is not the case and that each level can feedback on the previous level. For instance, a change in performance can result in a change in phenotype via plasticity and a change in genotype via cryptic genetic variation. We propose that this expanded experimental paradigm, broadly encapsulated by the rising field of eco-devo (or eco-evo-devo), will provide deeper insights into how fitness is determined within a population. In addition, we assert that cichlids are one of few vertebrate systems that offer both experimental tractability and vast evolutionary diversity, making them an ideal model to link variation at each level

organismic Evolvability, and we encourage future generations of cichlid researchers to embrace the system to this end.

Glossary

Evolvability: The potential of biological systems to evolve. Being a relatively new concept in evolutionary biology, the definition of evolvability is not completely settled and depends on context and biological levels of organization. For example, it may refer to a population's ability to respond to selection, or levels of additive genetic variation, or the rate of diversification/speciation in a lineage, or the propensity to produce major evolutionary novelties. For a detailed review, see (Pigliucci 2008).

Craniofacial: All things related to the skull and the face. Historically, craniofacial was predominantly a medical term that referred to the skull and facial structures in humans. Today, this term is widely used in various vertebrate systems to describe features of the head grossly, but often refers specifically to the skeletal system. It is important to note that "craniofacial" is a general term that has been co-opted by evolutionary and developmental biologists in recent years. Craniofacial cannot speak to developmental or evolutionary origins of specific elements of the head. For this, more specific

(continued)

anatomical terminology such as chondro-, splanchno-, and dermatocranium should be applied.

Integration: The relative degree of relatedness within a system. When multiple biological units are related to each other, they are generally considered to be integrated. Integration can occur at many different levels: genetic, developmental, functional, or evolutionarily.

Modularity: The relative degree of independence within a system. A module is a group of units that are related to each other within the group, but relatively independent from units outside the group. Often the degree of "relatedness" between units is assessed via statistical correlation or covariation. The concept of modularity is closely tied to that of integration (see above). It is important to note that these two terms represent opposite extremes of a continuum; in reality systems exhibit a degree of both integration and modularity.

Phenotypic plasticity: The ability of an organism to alter its phenotype in response to environmental cues. In cichlids, both the oral and the pharyngeal jaws (and other suites of traits) have been shown to be plastic when animals are reared on different diets (see Schneider et al. 2014; Parsons et al. 2016). In a broad sense, any variation in phenotype that is caused by environmental factors instead of genes can be considered a plastic response. Since natural selection acts on phenotypic variation, plasticity has important evolutionary implications (Pigliucci 2005). Moreover, that ability of organisms to mount a plastic response varies between closely related species (e.g., Parsons et al. 2014), which suggests that plasticity itself may evolve.

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An Evo-devo View of Post-genomic African Cichlid Biology: Enhanced Models for Evolution and Biomedicine

Kevin J. Parsons, Kirsty McWhinnie, and Tiffany Armstrong

Abstract Major advances towards our understanding of adaptive genetic variation are now readily obtainable in the post-genomic era. Cichlid biology has a continuing history of benefitting from the latest technical advances in sequencing technology. This is now allowing for the discovery of allelic variation related to key evolutionary traits such as colour, morphology, brain and behavioural variation, and sex. However, just as the ability to explore cichlid genomes has increased, it is becoming apparent that phenotypes are influenced by an array of factors, sometimes with environmental conditions determining the genetic basis of traits. This mirrors a growing awareness across biology of the range of mechanisms beyond genetic variation that can be responsible for generating phenotypic variation. Fortunately, cichlids provide a highly tractable study system that can be leveraged to account for such complexity. We outline some of the major findings in cichlid genomics over the past years and provide a framework for effective approaches that can be used to make further discoveries about complex traits within a genomic context. We then move on to some of the core topics facing the field, such as the environmental drivers of phenotypes, sex determination mechanisms, and neurobiology. The utility of a genomic understanding of these traits from cichlids is also clearly relevant within a clinical context, especially as we tackle an understanding of more complex and continuous phenotypic variation.

Keywords Craniofacial genetics · Bone biology · Sex determination · Embryogenesis

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K. J. Parsons (✉) · K. McWhinnie · T. Armstrong
Institute of Biodiversity, Animal Health, and Comparative Medicine, University of Glasgow, Glasgow, UK
e-mail: Kevin.Parsons@glasgow.ac.uk

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1 Introduction

In the decades following both the formulation of the theory of natural selection and the rediscovery of Mendelian inheritance, the modern evolutionary synthesis took shape in the 1940s and 1950s leading to a plethora of investigations into how adaptations and species had arisen (Fisher 1930; Mayr 1959; Provine 1971; see McConnell 2021). Especially during the past three decades, this theoretical basis has allowed us to make tremendous empirical progress on establishing the role of natural selection in evolution (Endler 1986), while also using fish to inadvertently begin scratching the surface of how specific genetic changes contribute to adaptation (Shapiro et al. 2004; Colosimo et al. 2004; Albertson et al. 2003). Adaptive radiations, whereby a number of species evolve rapidly from a common ancestor, have been of particular empirical interest in evolutionary biology with examples coming from Galapagos finches, postglacial fishes, and Anolis lizards of the Greater Antilles (Grant 1987; Robinson and Schluter 2000; Robinson and Parsons 2002; Losos 2009). This was initially because these systems offered a range of phenotypic variations that could readily be related to ecology, providing strong evidence for how natural selection drives evolution (Schluter 2000). Today, research on these systems continues with the focus often extending to modern genetic approaches that seek to directly uncover the molecular basis of adaptation.

Among adaptive radiations, the cichlids of the African Rift lakes, including Malawi, Tanganyika, and Victoria, provide an exemplar system for biologists interested in evolution. African cichlids show the highest rates of speciation known in vertebrates and are famous for their exceptional phenotypic diversity (Turner et al. 2001). Cichlid trophic morphology is especially noteworthy and includes an extensive variety of trophic specializations with species phenotypically matched to the various functional demands of algae grazing, snail crushing, sand sifting, egg predation (including paedophagy), scale eating, and piscivory (Fryer and Iles 1972; Kornfield and Smith 2000). However, even with this high degree of specialization, cichlids show a general replicated pattern of divergence in trophic morphology whereby the primary axis of divergence involves the lengthening and shortening of the oral jaws, which respectively relate to suction and biting modes of feeding (Cooper et al. 2010; Young et al. 2009; Parsons et al. 2011). Besides craniofacial variation, these cichlid systems also display a number of unique and highly specific specializations in behaviour, parental care, morphology, breeding colouration, and sensory systems, which are all active areas of cichlid research (Albertson et al. 2014; Parsons et al. 2015; Nyman et al. 2018). In particular, these attributes of cichlids have made them a major focus for genomic centred approaches to locate and understand the function and organization of genetic variation (Albertson et al. 2003; Parsons et al. 2012, 2015). This has recently culminated in the sequenced genomes of five species of African cichlids (*Oreochromis niloticus, Neolamprologus brichardi/pulcher, Metriaclima zebra*, *Pundamilia nyererei, Astatotilapia burtoni*) a tremendous resource for current and future research (Conte and Kocher 2015; Brawand et al. 2014).

Sequenced genomes are significant for a number of reasons with ‘model’ species often (especially before the wide availability of genomics) informally defined by the availability of a sequenced genome. This is because having such genomic resources (along with other attributes) allows researchers to deduce gene identity and function through experimentation. However, while relatively long-established model organisms such as *Drosophila melanogaster* (fruit fly), *Mus musculus* (mouse), *Gallus* (chicken), *Xenopus laevis* (African clawed frog), and *Danio rerio* (zebrafish) have provided major insights into the underlying genetic basis of major phenotypic traits these systems are not without limitations. Generally, while these organisms can inform us about basic gene function (often through ‘extreme’ tests such as gene knockouts, or obvious mutations) they lack the magnitude and continuum of variation found in natural study backgrounds. In line with this, cichlids can provide a major advantage over traditional model organisms in that they offer a massive increase in the degree and types of phenotypic variation that can be studied.

However, some of the advantages African cichlids extend well beyond their relatively high levels of phenotypic variation. For example, cichlids are usually highly amenable to laboratory conditions, produce embryos regularly for developmental and functional investigations including small molecule experiments and transgenics (Tucker and Fraser 2014; Juntti et al. 2016); and they can often be hybridized to produce pedigrees that allow loci underlying phenotypic traits to be located through QTL analyses—all attributes now enhanced by the availability of sequenced genomes. Cichlids also show an incredibly low degree of genetic variation for such a phenotypically diverse group. Among the major insights from cichlid genomes are evidence that roughly half of the genetic polymorphisms identified among species (descended from a common ancestor ~10 million years ago) display incomplete lineage sorting. This suggests that a significant proportion of ancestral polymorphisms are currently still segregating between species (Brawand et al. 2014; Loh et al. 2013). This explains the persistence of unusually low levels of nucleotide diversity, which is in fact less between species of Malawi cichlids than between different laboratory strains of zebrafish (Loh et al. 2008).

This combination of features made cichlids a valuable target for genome sequencing as the genetic and developmental mechanisms underlying their adaptive divergence are highly tractable (Parsons and Albertson 2009). Therefore, the remainder of this chapter will focus on our current understanding of the genetic basis of phenotypic variation in cichlids, what should motivate this research, and what cichlids can offer as a model organism both for evolutionary biology and beyond. We will begin by providing a broad overview of how cichlid genetics has come to be over the past few decades, and how it is now providing insights into a broad range of topics including, sex determination, behavioural genetics, and morphological evolution with a vision towards how these topics can be expanded.

2 From Past to Present: Ground Breaking Phylogenetic and Genomic Cichlid Studies

The fully sequenced genomes of African cichlids allow for substantial new ground to be broken in our understanding of the evolution of adaptive variation. The roots for the enormous efforts required to obtain these genomes lie in a long history of genetic research. African cichlids, due to their tremendous phenotypic diversity, were a source of great debate for taxonomists making efforts to understand phylogenetic relationships across species. Specifically, it was once suggested on the basis of morphological data that African cichlids from Lake Victoria arose from a number of different ancestors (Fryer and Iles 1972). To address this hypothesis, the mitochondrial DNA of African cichlids was sequenced in a very early application of polymerase chain reactions (PCRs) (Meyer et al. 1990). To the surprise of many, mitochondrial DNA revealed that the hundreds of species found in Victoria all share a common ancestor—a striking discovery at the time. So began the investigation of cichlid diversity from a molecular genetics' perspective. Since then it has become evident that the radiations of Malawi and Tanganyika are also derived from a limited number of ancestors.

Among lakes, Malawi contains the largest adaptive radiation of cichlids, which is composed of 450–1000 species. Evidence of monophyly is present, with the radiation estimated to be occurring in less than 1–2 MYA (Kornfield and Smith 2000; Salzburger and Meyer 2004; Sturmbauer et al. 2001; Turner et al. 2001), but with speciation events still occurring in the very recent past (i.e. less than 1000 ybp, Won et al. 2005). However, recent evidence taking advantage of a wide sampling of nuclear DNA, and including a range of riverine species (putative ancestors), highlights a more complex process for Malawi. Instead, it may be that Malawi was colonized multiple times by several hybrid lineages (Joyce et al. 2011). Nonetheless, a general hypothesis for Malawi is supported whereby a 'hybrid swarm' allowed for rapid divergence into primary sandy and rocky habitats, followed by later morphological specializations, and finally divergence of sexually selected traits (e.g. colour, mating preferences) has been upheld by mounting data (Streelman and Danley 2003). Lake Tanganyika is the oldest of the three Rift lakes and has a more complex evolutionary history. It contains the highest diversity of ancient lacustrine cichlid lineages (12–16) or so called 'tribes'. The basin is believed to have started to form around 20 MYA, initially as an extensive swampland (Tiercelin and Mondeguer 1991), and attaining deep-lake conditions some 6–12 MYA (Cohen et al. 1993). Evidence suggests that cichlids began radiating during the formation of deep-lake conditions. Relationships at basal nodes are somewhat unclear suggesting past hybridization events and rapid adaptive radiation events have contributed to their diversification (Meier et al. 2017).

Following the foundations laid by phylogenetics, a direct understanding of the genetic basis of adaptive traits in African cichlids also started to become an area of interest. Building off microsatellite markers largely developed for tilapia this endeavour began with an experiment involving an investigation of the genetic basis of craniofacial morphology in F2 hybrids of Malawi cichlids possessing differing craniofacial variations (Albertson et al. 2003). While finding loci connected to a number of traits under directional selection, this study opened the door towards understanding connections between genotypic variation and adaptive phenotypes in cichlids. As will be discussed below this type of research has advanced along with other ongoing research that is now pushing the frontiers of evolutionary biology.

3 Cichlid Genomics in the Context of Current Evolutionary Thinking

Currently, evolutionary biology as a whole is arguably at a crossroads (Laland et al. 2014), or alternatively, a point of expansion. From a philosophical perspective evolutionary theory is expanding beyond the limited conventions of the Modern Evolutionary Synthesis of the 1940s to include phenomena that were completely unknown at that time (Pigliucci and Müller 2010). Given the technological limitations, and the division of fields at the time, the conception of the Modern Synthesis focused on population-level changes in allele frequencies. Developmental processes were not incorporated likely because they were seen to happen at the individual level and were incompatible with population-level theory, similarly, genome-level phenomena were largely unknown and excluded. Further, the phenotype was not a focus of the Modern Synthesis leaving a major gap in our understanding of how adaptive variation initially arises (Hamburger 1980; West-Eberhard 2005). This current expansion of evolutionary theory, often referred to as the ‘extended evolutionary synthesis’, is largely driven by findings from evolutionary developmental biology, which matured through the 1990s and early 2000s. However, this extension of evolutionary theory now also coincides with technological advances in DNA sequencing that pervade biology. The ability of these techniques to assess massive amounts of genomic data to uncover tangible and tractable genetic components of evolutionary change was simply inconceivable during the 1940s.

Cichlids hold promise for realizing the full potential of theoretical and technological advances to address the complex realities of evolution. However, this will require careful consideration; if we take on a simplistic view that genomes are the sole cause for phenotypes, we will not realize this potential. For example, it is now widely recognized that environmental conditions can alter the phenotype through phenotypic plasticity, as well as the function and structure of the genome itself through epigenetic change (Parsons et al. 2010; Pfennig et al. 2010; Sultan 2015). Such environmentally induced changes figure prominently in current discussions of evolvability which form a key focus for evo-devo research (Hendrikse et al. 2007; Pigliucci 2008). However, this does not mean that genomes are not a major tool for this research. In fact, with the burden of sequencing cichlid genomes largely lifted, we can focus on the less often appreciated fact that the genetic architecture of a trait, that is, the alleles that determine the phenotype, can change dramatically depending upon environmental cues (Küttner et al. 2014). Indeed, selection can only operate directly on the phenotype and while the genotype-phenotype 'map' (i.e. the G-P map) has become a well-worn metaphor within a broader research programme, there is now a possibility to also extend this to explicitly include environmental effects in a 'G-P-E' map. The aim here would be to determine how the genotype, phenotype, and environment interact to determine what variation is available for natural selection (Sultan 2015).

Such an extension of research to include explicit focus on a G-P-E map would allow us to merge the study of environmental effects with genomics (Sultan 2015). This would provide the potential to answer longstanding questions such as how plasticity contributes to adaptive radiations. More specifically such questions could include: how do genes contribute to plastic responses? Are their effects specific to a given environment? Or is plasticity regulated by the same genes across environments? An understanding of these questions is already beginning in African cichlids. Genetic mapping experiments performed in alternate foraging environments with a focus on craniofacial traits in F3 hybrids has shown that distinct kinematic demands ('biting' and 'suction' modes) rely on an environmentally dynamic genetic architecture (Parsons et al. 2016). Indeed, foraging environment strongly influenced the genetic architecture of traits with only 1 of 22 identified QTL being present in both environments (Fig. 1). This supports the idea that cryptic genetic variation, meaning genetic variation that is not expressed in the phenotype under 'normal' conditions, is widespread in a key anatomical region for cichlid adaptation (Gibson and Dworkin 2004; Paaby and Rockman 2014). Further tests also identified QTL acting across environments with alternate alleles being differentially sensitive to the environment. This suggested that while plasticity was largely determined by loci specific to a given environment, it can also be influenced by loci operating across environments. While a more precise investigation is needed to vindicate both opposing views about the genetics of plasticity (Scheiner 1993; Via 1993). Finally, evidence from fine-mapping suggested a process of genetic assimilation whereby the ancestral alleles occurring at an important regulatory locus for early bone development (Hu and Albertson 2014), *ptch1*, displayed a larger plastic response than derived alleles. While continued efforts are needed to determine the mechanistic basis of such environmental responses (possibly *ptch1* alters the potential for bone growth), this study demonstrates how the environment can be a potent force that interacts with the genome to produce selectable morphological variation (see Hu and Albertson 2021).

4 Combined Approaches Towards Understanding the Genetics of Cichlid Adaptations

While pedigree mapping of quantitative traits (QTL mapping) is a very effective method for linking the genotype to the phenotype that takes on added impact in the context of a reference genome it still suffers limitations. Most noteworthy is the

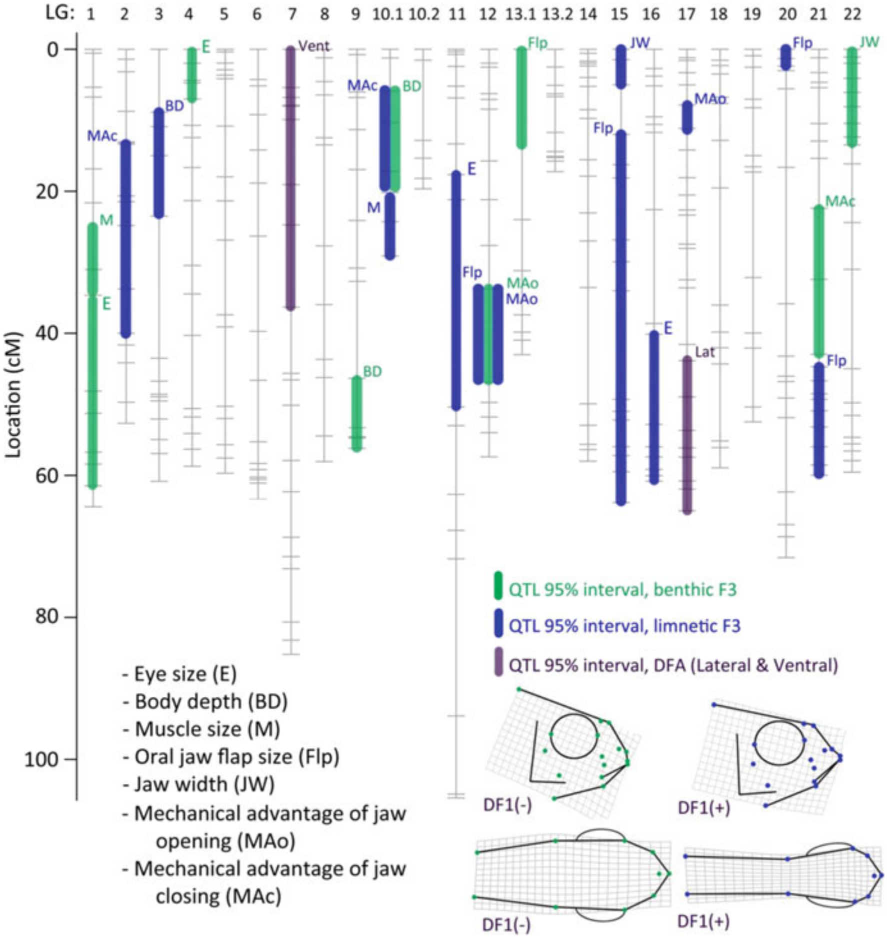

Fig. 1 The genetic basis of trait variation is dependent upon foraging tactics over ontogeny. Here a genetic map represented by 22 linkage groups provides a means to locate regions of the genome that associated with phenotypic variation in F3 hybrids made between *Tropheops* 'red cheek' and *Labeotropheus fuelleborni*. The F3 offspring were equally divided and reared on one of two treatments: a 'benthic' diet (denoted with green) which consisted of food attached to rocks and requiring a biting mode of feeding, and a 'limnetic' diet (denoted with blue) that was nutritionally identical but consisted of same food delivered to the water column requiring a suction mode of feeding. This induced a number of phenotypic changes in shape traits with the overall geometric changes depicted by deformation grids in the lower right panels showing lateral and ventral views of the craniofacial region. Coloured regions on the map depict where traits are mapped and show a genetic architecture that is nearly exclusive to a given treatment. The purple shaded areas show regions that map to the plastic responses of the lateral and ventral views, and hence demonstrate QTLs that relate to plasticity across treatments

difficultly of QTL mapping to identify the precise causative alleles, which can make follow-up fine-mapping studies laborious and expensive due to the need to generate a sufficient number of recombination events (Parsons and Albertson 2013). However, recent research has alleviated this problem by using population genomics in combination with QTL mapping (Fig. 2). While population genomics can efficiently identify loci under divergent selection it cannot link a genotype to a specific phenotype. Yet, the advantage of population genomics is that it takes into account a much larger number of recombination events within natural populations. Thus, using cichlid genomes to cross-reference between QTL and population genomic data can identify phenotypically linked allelic variation undergoing divergence. This can offer a rapid, reliable, and cost-effect means of identifying candidate genes (Parsons and Albertson 2013; Parsons et al. 2015).

Recently, researchers have taken advantage of these combined approaches in cichlids in the form of selection signature QTL or ssQTL (Parsons and Albertson 2013). This begins by creating a genetic map from loci that indicate some degree of divergence between the focal crossed species within natural populations. Thus, any subsequent QTLs identified should be relevant to adaptive phenotypes (Parsons et al. 2015). However, because the process of making a genetic map relies on the amount of recombination occurring within a lab pedigree it can only take advantage of a subset of the genetic markers produced from modern sequencing methods. Conversely, the same markers produced for population genomic analysis are not subject to the same issues because of greatly enhanced recombination in natural populations. This means they can be used to help fine map the most promising candidate regions related to divergence. For example, this approach was recently used to implicate *pax3a* in cichlid colouration (Albertson et al. 2014). Here, QTL mapping was used as a first step to associate a 28-cM genomic region with levels of red/yellow pigmentation. Using the physical map of the *Metriaclima zebra* genome, it was found that this region corresponded to approximately 11 Mb of physical sequence containing 315 genes and 366 genetic polymorphisms—an unmanageable number for follow up. However, population genomic analysis revealed that just 17 genes exhibited high levels of differentiation between the species, suggesting they may be driving the phenotypic differences. One was in the 5′UTR of *pax3a*, which has been previously associated with specification of pigment cells (Minchin and Hughes 2008), and follow-up gene expression assays showed covariance with the development of pigmentation. Thus, the anchoring of markers to the genome provides a way to link different methods to powerfully determine the genetic mechanisms underlying phenotypic variation.

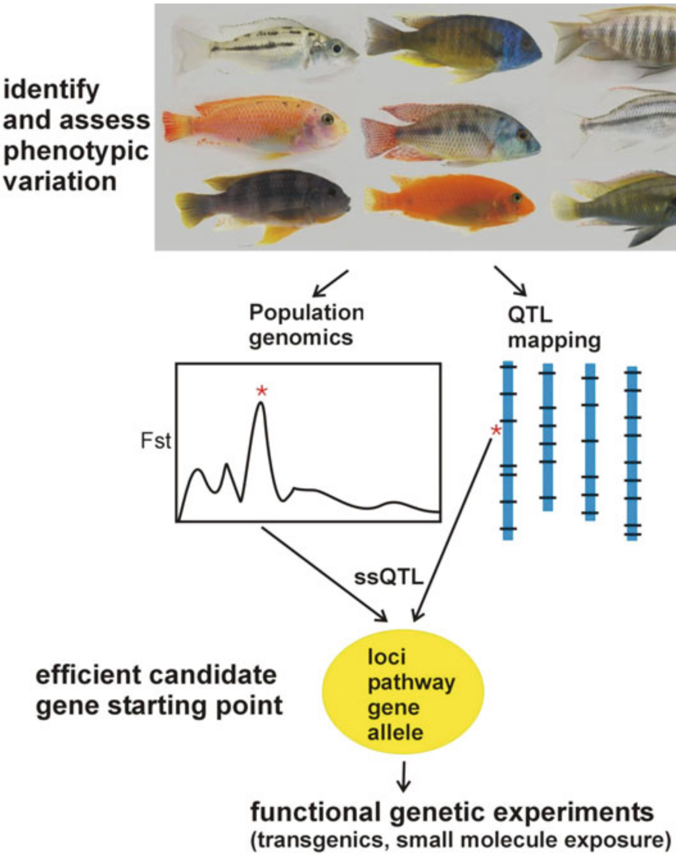

Fig. 2 A generalized approach for the integration of genomic approaches that can be used to understand the evolution and function of African cichlid genetic variation. This approach aims to objectively determine the salient features of the genetic changes underlying cichlid phenotypes. The approach begins by identifying phenotypic variation of interest and then performing population genomics to compare focal species with different phenotypes, concordantly a hybrid cross is made between focal species to perform QTL mapping. This combination leverages the strengths of each approach to mitigate their inherent weaknesses. Specifically, population genomics cannot connect genotypic variation to quantitative phenotypic variation, likewise, QTL mapping using hybrid crosses is limited by fewer recombination events in lab populations. However, population genomic results can take advantage of the vastly increased number of recombination events that occur in wild populations, while QTL mapping can connect genotypic to phenotypic variation. Combining these approaches can therefore identify loci that (1) show signatures of selection, and (2) show connections to phenotypic variation (i.e. selection-signature QTL/ssQTL). These loci can be used to deduce candidate genes efficiently by cross-referencing data sets to provide confirmation, and therefore increasing the likelihood that they are valid. Such loci may lead towards genes within developmental pathways for functional genetic experiments that aim to modify the phenotypes of interest and explain the role of allelic variation

5 The Growing Relevance of Non-traditional Model Organisms for Medicine

We have established that evolutionary biology is being extended to include new theories surrounding the origins of variation, while also incorporating newer techniques to explore variation at a genomic scale. In addition, a genomic understanding of phenotypic variation studied in nature is relevant to medicine (Albertson et al. 2009; Schartl 2014). It is worth noting that during the nineteenth century human and veterinary medicines were one and the same (Dorans 2009; Fisman and Laupland 2010). This means that connections between zoology and medicine were once much stronger than they are currently, and provides proof of concept that they could be strengthened again. The divergence between zoology, veterinary, and human medicine progressed with the separation of training programmes throughout the 19th and 20th centuries to produce a major gap between fields. However, in recent years, prominent veterinarians, doctors, and scientists have called for greater integration of human and animal health research. Specifically, highlighting joint threats posed by several factors and the similarity of disease processes in humans and animals, they have lobbied for the creation of 'One Health' (Dorans 2009). Given the molecular conservation of developmental genes and pathways between humans and animals, as demonstrated by the zebrafish model in translational studies, insights from cichlids are likely applicable to a range of human diseases.

While some of the advantages of cichlids for clinical research, such as an increased range of phenotype variation, have already been mentioned above and reviewed elsewhere (Albertson et al. 2009; Schartl 2014; Powder and Albertson 2016) we will briefly outline some additional points. First, the forward genetic approaches employed with laboratory model organisms show strong biases for extreme phenotypes that are blatantly obvious in researcher screens both when the population has been intentionally mutagenized or the mutation is spontaneous. These extreme phenotypes tend to be directed towards early development and are often lethal but are nonetheless used to model disorders that occur as a complex continuum of phenotypes that appear throughout human lifespans. Second, these mutant lines are biased towards major genes that initiate multiple pathways, or regulate a critical developmental event. Thus, more subtle variations such as those produced by a modifier locus, or those that do not produce a devastating developmental outcome are missed. Indeed, over 75% of mutant alleles identified in standard laboratory screens occur in coding regions and result in severe disruption or complete loss of gene function (Nguyen and Xu 2008). In practice, GWAS approaches in human populations predict that over 80% of causative mutations should lie within non-coding regions. Thus, we can conclude that clinical research would benefit from models and approaches that differ from standard practice and by using naturally varying, closely related species, such as cichlids that are 'screened' by natural selection. Below we describe a number of subjects that are a current focus of cichlid research that provide the bulk of this review. Where possible we point out the clinical relevance even though the motivation for most of this research is to understand basic evolutionary processes. Specifically, we review studies concerning the genetic bases for craniofacial development, mechanisms of sex determination, and brain and behavioural development.

5.1 Craniofacial Genetics in Cichlids: From Embryonic Patterning to Adult Morphology

Variation in craniofacial morphology is a defining feature for many adaptive radiations. This is because craniofacial anatomy provides a direct interaction between the organism and its ecology often through its foraging tactics (Parsons and Albertson 2009; Bright et al. 2016). Conversely, craniofacial variation is prevalent in human disorders as 70% of all known birth defects in humans involve anomalies of the head and neck (Hall 2009). In both cases, the extreme ends of variation have been a focus of research with very little known about what underlies continuous variation. Even for the best-characterized human disorders, the developmental processes involved, and the contributing effects of environmental variation, are virtually unknown. However, recent research on cichlids can contribute towards filling this knowledge gap by providing a focus on continuous variation from embryo to adult. These studies of adaptive variation in cichlids extend to a molecular level allowing them to potentially serve as translational models for human disorders with phenotypic similarity (Powder and Albertson 2016).

This ability to understand the molecular mechanisms underlying phenotypic variation gives cichlids the power to connect to human disorders beyond a superficial level. So far, this research has also provided more examples of how a multipronged approach combining QTL mapping, population genomics, and experimental manipulations can be used. For example, the well-characterized *Wnt* pathway that has a central role in craniofacial development in model organisms has been associated in cichlids with subtle, quantitative variation in bone shape (Hu and Albertson 2014; Loh et al. 2008; Parsons et al. 2014; Roberts et al. 2011). Population genomic scans have identified a highly divergent SNP in *β-catenin* (a core member of *Wnt* signalling pathways) between Malawi cichlids with differing craniofacial shapes (Loh et al. 2008). This SNP is associated with increased levels of *Wnt* signalling and accelerated rates of craniofacial bone deposition in the cichlid (Parsons et al. 2014). The accelerated bone development prevents outgrowth of the preorbital region, effectively ‘locking’ into place an early larval phenotype of a shortened oral jaw demonstrating paedomorphosis (Parsons et al. 2014). This results in a steeper craniofacial slope with an increased mechanical advantage for a species that eats by shearing algae off of rocks (Cooper et al. 2010, 2011; Parsons et al. 2014). In a similar study another major pathway for craniofacial development has been implicated. Using hybrid Malawi cichlids QTL for the shape of the interopercle bone and length of the retroarticular process of the cichlid mandible were mapped to the same genetic interval (Hu and Albertson 2014; Roberts et al. 2011). Follow-up population genomics identified an SNP in this region that resides upstream of the Hedgehog receptor *ptch1*, which is highly divergent between cichlids with alternate morphologies. The evolutionarily derived *ptch1* allele was associated with decreased expression and decreased bone deposition resulting in a shorter retroarticular process and narrower interopercle bone. These anatomical changes conferred a diminished bite force but quicker jaw movements which are adaptive for suctioning food from the water column (Hu and Albertson 2014; Roberts et al. 2011). Together these studies illustrate how well-described processes initiated at early developmental stages are likely used over extended periods to produce adaptive morphologies, but also human disorders (Pan et al. 2013).

Genomic approaches are also revealing new insights into the mechanisms underlying links between tooth and taste bud development. While having very different adult anatomy, teeth and taste buds both originate from placodes (epithelial tissue) during embryonic jaw development. The similarity of teeth and taste buds at early stages suggest that the fate of either structure can be induced by molecular signals (i.e. developmental plasticity). Indeed, using a QTL approach from a hybrid pedigree created from species with different dentition Bloomquist et al. (2015) identified loci that associated (through independent analyses) with both tooth and taste bud density (both are interspersed on fish jaws) suggesting pleiotropy. Candidate genes and core genes belonging to major developmental pathways (*Wnt*, *Hedgehog*, *BMP*s) were shown to be differentially expressed during the initiation of tooth and taste bud development. Similar patterns of expression were found within a mouse model using the jaw and tongue suggesting deep ancestry in the hierarchy of placode development. For cichlids, chemical manipulation experiments showed that *Wnt* signalling coupled tooth and taste bud density while *BMP* and Hedgehog signalling mediated distinct organ identity. These results also suggested that the oral lamina is competent to form either teeth or taste buds. Such manipulative experiments indicate that regeneration of teeth in humans may one day be possible through the modification of developmental pathways that shift regenerating taste buds into teeth.

While some traits have been investigated in great detail, it is important to remember they form only part of the larger craniofacial apparatus. The craniofacial region is among the most complex anatomical structures by requiring a number of traits to work in a coordinated manner (Parsons et al. 2011; Hu and Albertson 2014). Thus, selection that has altered specific traits likely has impacted several others. Such selection should favour a coordination of traits that improves fitness (Parsons and Robinson 2006; Klingenberg 2008). Empirically this can be seen as alterations of the correlation structure reflecting the phenotypic integration of traits. However, ancestral patterns of integration can themselves bias patterns of evolution (Parsons et al. 2018). Conversely, many human disorders (e.g. Marfan syndrome) are associated with phenotypic effects on multiple traits simultaneously. Therefore, it is possible to view many human disorders as the breakdown of phenotypic integration during development (Rickard 2016). But how can we tractably determine the genetic variation that determines the degree and patterns of integration when its measurement requires multiple individuals? It could be that these effects are pleiotropic, or the result of multiple loci that have co-evolved to provide specific patterns of integration. Recent research in cichlids suggests that understanding the genetic basis of phenotypic integration is surprisingly tractable. For example, Parsons et al. (2012) investigated patterns modularity (subsets of integration) in the cichlid mandible and mapped QTL to linkage groups 5 and 19. Findings suggested that the genetic basis of modularity was distinct from that of shape but also surprisingly simple with recessive patterns of inheritance for the type of integration being evident. However, more refined experiments involving several crosses would be useful to more precisely identify candidate genes for assessments of gene function in the formation of integration. Further generalization of the statistical method used called ‘pseudo jack knifing’ has also allowed the genetics of integration for colour and overall head shape to be investigated in cichlids (Albertson et al. 2014; Hu and Albertson 2014). Thus, we can begin to think more broadly about the traits we can investigate at the genomic level and their extended interactions with a broader phenotypic suite.

5.2 Sex Determination: A Genomic Puzzle in Cichlids

The mechanisms of sex determination have captured the attention of evolutionary biologists for decades (McWhinnie 2020). Through their complexity of mechanisms, African cichlid genomes are now quickly enhancing our understanding of the variety of sex determination systems present in nature. Cichlids challenge the main consensus for sex determination which involves separate sex chromosomes (Charlesworth 1991; Hodgkin 1992). Likewise, it can be argued from a range of research that sex determination is not as clear cut in humans as was once thought. For example, differences in sex development in humans are relatively common with a one in 5500 incidence rate with clear chromosomal irregularities being involved in some instances but also a range of genetic and environmental mechanisms contributing to others (Kousta et al. 2010). Thus, with a newly realized range of mechanisms for sex, as well as sex-linked traits in cichlids, these fishes provide potential clinical, as well as evolutionary relevance.

Under the most conventional mechanism, sex chromosomes are structurally different with only minimal opportunity for genetic recombination between them. Most commonly male heterogameity exists; whereby males possess the heterozygous chromosomal combination XY and reduced levels of genetic recombination whereas females are XX and have increased levels of recombination. A possible but less common situation is female heterogameity whereby, females are heterozygous with the chromosomal combination ZW but males are homozygous ZZ. The above conventions are assumed to be the most common, since the genetics of sex determination has so far focused on mammals and model organisms (Bachtrog et al. 2014). However, several other mechanisms for sex determination exist across taxa with fishes (including cichlids) showing a relatively large range of mechanisms. For example, an individual’s sex can also be determined by environmental mechanisms; influences including pH and temperature determine sex in *Apistogramma* cichlids (Roemer and Beisenherz 1996). Sex determination can also be reliant upon a complex of genes (i.e. polygenic sex determination). So far, complex polygenic systems for sex determination have been found in widely different species of fishes. In polygenic sex determination, the genes involved are likely to be spaced across the genome (Liew et al. 2012), while providing more targets for selection this also increases the probability that they interact with a wide range of traits and are subject to environmental influences. For example, polygenic mechanisms for sex determination have been documented in European seabass (*Dicentrarchus labrax*) where a factorial mating study (Vandeputte et al. 2007) showed evidence of a system where there is both a genetic and an environmental component. Similarly, in zebrafish (*Danio rerio*) the exact workings of the sex determination mechanism are relatively unknown; however, a recent study (Liew et al. 2012) suggests a polygenic system which is primarily genetic with a small input from environmental factors. It is clear that perhaps most challenging for future research will be cases whereby complex interactions between genetic and environmental factors determine sex. These few common mechanisms of sex determination remain a largely open set of questions for those using genomic approaches to address such mechanisms in cichlids.

But why do fishes exhibit a more diverse range of sex-determining mechanisms than other groups (e.g. mammals)? So far, this question is largely unanswered, but perhaps the range of mechanisms present within cichlids will provide more comparative power than more distantly related groups. At a basic level, chromosome cytology shows that sex chromosomes are relatively more difficult to distinguish in fishes than in mammals, suggesting perhaps that recombination is more likely to occur. For African cichlids, there are a wide variety of mechanisms of sex determination which can vary between species and in the case of Lake Malawi, have evolved fairly recently in the timeline of the radiation (Ser et al. 2010). Recent findings from seven species of Malawi cichlids suggest that ‘B chromosomes’, revealed by genomic sequencing, are only present in females and therefore could be important for determining sex (Clark et al. 2016). Similarly in Lake Victoria, 12 species have been identified to possess ‘B’ chromosomes in addition to the standard ‘A’ chromosomes that function in sex determination (Yoshida et al. 2011; Kuroiwa et al. 2014). A single B chromosome provides two potential mechanisms for their maintenance in these populations. Specifically, these driving mechanisms are biased towards females in other plants and animals with B chromosomes and include nondisjunction or preferential segregation in a mitotic division prior to the germ line, or another mechanism whereby preferential segregation takes place during meiosis I. Currently, preferential segregation during meiosis 1 appears to be the favoured hypothesis (Kuroiwa et al. 2014) but a better understanding of what causes B chromosomes to be exclusively present in females is needed to appreciate their evolutionary impacts.

For African cichlids, environmental sex determination has been identified in both the Nile tilapia (*Orechromis niloticus*) and the orange chromide (*Etroplus maculatus*) (Barlow 2000). The orange chromide is noteworthy because this species is basal to extant lineages of cichlids which suggests that perhaps environmental sex determination (at least partially) is an ancestral condition. More specifically, the sex determination system of the Nile tilapia is believed to be predominated by male heterogameity with a major sex-determining locus. In addition, it appears that other loci are involved because not all families display evidence of sex linkage to this marker (Lee et al. 2003). There is also evidence that temperature and social conditions can affect sex determination in cichlids. In Nile tilapia, sex determination is not exclusively controlled by genetic factors (Barlow 2000). Work by Baroiller et al. (1995) demonstrated that high temperatures can overrule genetic factors and that sex determination in this species is a combination of environment, sex chromosomes, and interactions between the two. To date, such environmental inputs have surprisingly been largely ignored in favour of genetic cause in studies of sex determination focused on African cichlids from the Rift lakes. We suggest that incorporating the G-P-E view may aid researchers currently undertaking the difficult task of uncovering the mechanisms of sex determination at a genomic level. Indeed, it may be that some genes are only relevant for sex determination within specific environmental conditions.

Currently, studies more specific to Rift Lake cichlids have focused on major sex-determining systems (Gammerdinger and Kocher 2018). For example, Ser et al. (2010) showed that 19 species of Malawi *Maylandia* cichlids exhibit both male and female heterogameity across species. During this study, a single pair of lab-based crosses were made for each species to allow a detailed investigation of the sex determination systems present. Notably, for *Metriaclima pyrsonotus*, they reported that both systems were found to segregate within a single family. In this case, the ZW system is epistatically dominant to the XY system when both of the dominant loci involved in sex determination (Z and W) are present within an individual. Additionally, a number of families of several species showed no linkage of sex to markers at their usual locations on linkage groups 7 (associated with male heterogameity) or 5 (associated with female heterogameity), which suggests that any number of genes on different chromosomes could be controlling sex determination (Ser et al. 2010). Additional genetic mapping studies have confirmed such supplementary mechanisms for sex determination in Lake Malawi cichlids as a study on two mbuna species by Parnell and Streelman (2013) reported the ZW locus on LG5, two XY loci on LG 7, and two additional loci detected on LG 3 and LG 20, which interact with these and influence sex determination. Overall, over a dozen sex determination systems have been identified in African cichlids (Gammerdinger and Kocher 2018).

What would cause such a range of sex-determining mechanisms to evolve in cichlids? It has frequently been suggested sex determination could evolve to resolve sexual conflicts (Gammerdinger and Kocher 2018). Such resolutions are favoured because of sexually antagonistic selection whereby a trait that is beneficial to one sex can have a detrimental effect on the other leading to trade-offs in the form of genetic conflict (Vamosi 2014; van Doorn and Kirkpatrick 2007). To investigate the genetic conflict in Malawi cichlids, Roberts et al. (2009) examined the ‘orange blotch’ (OB) colouration that is present in 20 species. In these cases, the OB phenotype is found almost entirely in females and is considered a method of camouflage by disruptive colouration; conversely this phenotype has a negative effect on males that rely on bright colouration to attract mates. The gene associated with the OB phenotype, *Pax7*, had no differences in coding sequence, causing

Roberts et al. (2009) to test and find that the OB phenotype was the result of cis-regulatory differences in *Pax7*. To resolve sexual conflict, it was suggested that the OB (*Pax7*) locus is tightly linked to a dominant female sex determiner (W). The OB-linked ZW sex determination found on LG5 is epistatically dominant to the male heterogametic system found on LG7, which is understood to be the ancestral condition for sex determination in Lake Malawi cichlids (Ser et al. 2010; Roberts et al. 2009). Since, the linkage between the OB phenotype and ZW locus has been confirmed by Parnell and Streelman (2013).

In the case of the OB phenotype, there are two potential paths to the resolution of the sexual conflict. First, the sexually antagonistic selection at the OB locus could have allowed for the appearance and linkage with a female sex determiner (W) nearby on LG5 to provide a resolution. Or, the OB polymorphism may have emerged near a newly evolving sex determiner which then allowed for the resulting OB-W linkage to evolve and exist alongside the original ancestral system (XY) (Roberts et al. 2009). However, it is also possible that the OB phenotype has evolved subsequently to, rather than driving the evolution of the ZW mechanism (van Doorn and Kirkpatrick 2007). The OB phenotype and its linkage with sex determination have provided a solution to the sexual conflict of this sexually antagonist trait.

Linkage with sex determination could also be the case for a variety of other traits in African cichlids (Roberts et al. 2009). For example, Parsons et al. (2015) found evidence of sexual shape dimorphism in the craniofacial region potentially related to ecologically relevant differences between the sexes; males of a hybrid cross had a steeper craniofacial profile compared to a gradual, sloping profile in females. Furthermore, it was suggested that loci involved with craniofacial shape were often linked to sex-determining loci or were epistatically influenced by sex. For example, QTL for sexual dimorphism in shape were located on LG7, the same linkage group as the sex-determining loci. At this QTL, the *Tropheops* 'Red Cheek' allele (male in the original parental cross) resulted in a steep 'male-like' craniofacial profile whereas the *L. fuelleborni* allele (female in the parental cross) resulted in a more sloping 'female-like' profile. Notably, it has also been suggested that QTLs for phenotypic plasticity in morphology are also linked to sex-determining loci on LG 7 (Parsons et al. 2016). Therefore, cichlids may utilize a number of interactions between sex and morphology to resolve genetic conflict. Although further details have yet to emerge sexual conflict may bias the direction of adaptive divergence as patterns of sexual dimorphism align with the major trajectory of morphological divergence in Malawi (Parsons et al. 2015; McWhinnie 2020). Avoiding such biases could explain why several mechanisms for sex determination persist in African cichlids, and by providing more targets for selection this potentially explains why speciation events in African cichlids have been far more numerous than in other adaptive radiations.

5.3 Genetic and Developmental Basis of Behaviour, Brain, and Neurobiology

Understanding complexity through genomic approaches coincides with an increased interest in understanding the structure and function of the vertebrate brain (e.g. The Brain Initiative: https://www.braininitiative.nih.gov). So far it has been established from model organisms that the brains of fishes and mammals have largely homologous regions, including those involved with social decision making as well as cognitive and locomotive activities (Bshary et al. 2014). The initial embryonic development of these regions is now also understood at a basic level in terms of the genes involved in brain developmental patterning providing a strong basis for extension to organisms showing a wider array of variation in brain anatomy. In line with many of their other features, African cichlids provide an outstanding degree of variation in brain anatomy. In fact, despite a relatively very similar genetic background, the brain variation seen in the Malawi cichlid radiation actually exceeds the variation seen among entire orders of mammals (Sylvester et al. 2010). Therefore, cichlids can provide an unusually tractable system for understanding the mechanisms that create variation in brain anatomy and development.

As mentioned, the major trajectory of morphological divergence across African cichlid adaptive radiations involves craniofacial changes that allow for more efficient foraging on prey that require (1) a biting mode of feeding, or (2) a suction mode of feeding (Cooper et al. 2010; Parsons et al. 2011). While strongly reflected in the craniofacial apparatus, there are corresponding changes to brain anatomy that likely play into foraging mode and habitat choice. Specifically, in Lake Malawi species, brains differ between sand- and rock-dwellers that represent a major habitat divide. These differences are especially prevalent in the telencephalon, which are relatively large in rock dwellers (Fig. 3). This region of the brain is associated with navigation,

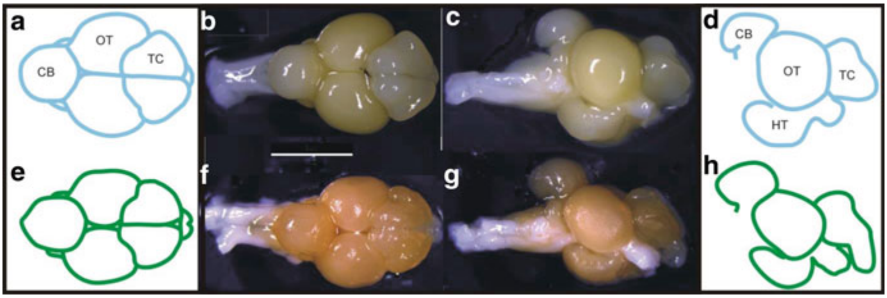

Fig. 3 Brain variation between ‘sand’ and ‘rock-dwelling’ species of Malawi cichlids. The upper panels (**a**–**d**) depict the brain of *Dimidiochromis comprecisseps*, a piscivorous sand-dweller species which likely relies on precise visual cues for successful predation. The lower panels (**e**–**h**) depict the brain of *Labeotropheus fuelleborni*, an herbivorous rock-dweller which mainly scrapes algae from rocks for food. Outlines depict variations between these species with *D. comprecisseps* showing a relatively larger optic tectum (OT), hypothalamus (HT), but smaller cerebellum (CB), and telencephalon (TC) relative to *L. fuelleborni*

and social interaction; hence, the rocky habitats and social hierarchies present in rock-dwelling cichlids would appear to require this adjustment in brain anatomy. In humans, the telencephalon is considered an embryonic stage from which the cerebrum is formed. The cerebrum, with frontal, parietal, temporal, and occipital lobes, is the largest part of the brain that controls all voluntary actions (Judas et al. 1999). Thus, recent experiments exploring the genetic mechanisms of telencephalon variation in cichlids hold broad promise for understanding our own evolution, development, and health.

Specifically, a number of candidate genes and pathways interacts to create telencephalon diversity in cichlids. Using early stages of embryogenesis, Sylvester et al. (2013) recently showed that the expressions of major developmental pathways were responsible for variation in brain patterning. In particular *shh* (hedgehog pathway) showed corresponding changes with *foxg1* expression that dictate much of this variation. In rock-dwellers, the expression of *foxg1* at the initiation of telencephalon development positively relates to increased activity of *shh* by the 4–5 somite stage. However, for sand-dwellers, *foxg1* expression in the presumed telencephalon is delayed until the 8–10 somite stage and *shh* activity is more ventral and slow to expand dorsally. A previous study showed that *foxg1* is a transcription factor that may act as a molecular coordinator for brain development by acting as a key downstream effector for the hedgehog pathway, while also inhibiting Wnt/beta-catenin signalling through direct transcriptional repression of *Wnt* ligands (Danesin et al. 2009). Small molecule experiments show that phenocopies can be induced by altering the timing of major developmental pathways. For example, if *Hedgehog* signalling is upregulated while *Wnt/beta-catenin* signalling is downregulated the early expression of *foxg1* can be induced in sand-dwellers. Conversely, *foxg1* expression can be delayed in rock-dwellers, but if Wnt/beta-catenin is upregulated and *Hedgehog* is downregulated then *foxg1* is induced later (Sylvester et al. 2013). These findings complement earlier findings in cichlids (Sylvester et al. 2010) strongly suggesting that fine adjustments in the expression of *Hedgehog* and *Wnt* pathways are responsible for telencephalon variation in cichlids. While these findings are groundbreaking, the objective use of QTL mapping has yet to be employed to determine the loci that control brain anatomy. Such an approach could leverage genomic resources to make completely new discoveries into how brain patterning is determined in vertebrates, and what alleles involved with this process are targeted by selection.

Variation in brain anatomy is also highly pronounced in the Lake Tanganyika adaptive radiation. Overall, the proportion of forebrain in Tanganyikan cichlids is relatively lower than in Malawi while the proportion of that is midbrain which functions in motor control, vision, hearing is greater (Sylvester et al. 2010). There is also wide variation among species in the size and volume of individual structures that correspond to habitat complexity, sexual selection, and social behaviours (Gozalez-Voyer et al. 2009). The genetic basis of anatomical variation in Tanganyikan cichlids has yet to be explored in detail, but inroads are being made from behavioural genomics, which seeks to link genetic to behavioural variations. Tanganyikan cichlids are particularly noted for their complex social behaviours and mating systems, which have attracted investigation from a genomic perspective. For example, 'brain-gene' expression studies have been used to investigate social dominance (Aubin-Horth et al. 2007) in cooperatively breeding *Neolamprologus pulcher* where males and females display similar behaviours and high testosterone when dominant. Brain gene expression profiles of dominant females also show similarity to those of the males (independent of social rank), indicating that dominant breeder females are masculinized at the molecular level while remaining reproductive. Such sexual variation in brain gene expression would seem to be species specific in Tanganyika as neural gene expression levels between males and females from a pair of sister species of the Ectodini tribe of Lake Tanganyika indicate that only a few genes show conserved expression associated with either sex (Machado et al. 2009). Thus, the complexities of identifying the mechanisms of sexual dimorphism extend to the brain. However, more notably a knowledge gap exists between early embryological stages where a molecular understanding of variation in brain patterning is emerging, and life stages where sexual maturity and social interactions have been established. Therefore, future studies could examine the mechanisms that underlie the ontogeny of such changes in brain and behaviour. This could be especially fruitful for those interested in behaviour as it could point towards the emergence of phenotypic variation rather than the outcome of multiple steps.

6 Conclusions: The Genome as the Basis for a Way Forward

With a collection of cichlid genomic resources (http://em-x1.gurdon.cam.ac.uk; http://cichlid.umd.edu/cichlidlabs/kocherlab/bouillabase.html), we can now move forward with the numerous topics cichlid biology can address (Brawand et al. 2014). From this review, we see that a number of studies are already taking advantage of these resources, while other areas of research can likewise expect an influx of new data and possibilities. We can also begin to ponder how this will fundamentally change both cichlid biology and the larger topics they address as a whole. For example, it is becoming increasingly recognized that understanding the genetic basis of a trait is a challenging proposition. This is in part due to technological advances that allow us to examine the genome at a greater resolution than previously possible (providing more chances for G-P associations), but also because we are now targeting traits with more typical phenotypic distributions. Some traits involved with adaptive divergence stand out as simple, with essentially Mendelian patterns of inheritance (Hoekstra et al. 2006; Shapiro et al. 2004); but these are unusual in natural systems as most adaptive traits display continuous variation (Edwards 2013; Parsons and Albertson 2013). We are now just beginning to embrace the reality that traits are polygenic and interact with the environment in natural populations (West Eberhard 2003; Shapiro et al. 2004; Sultan 2015; Parsons et al. 2016). Adding to this complexity is the notion that heritability can no longer be considered a purely genetic phenomenon as we now recognize that parental effects, epigenetic processes, and environmental conditions provide other mechanisms of inheritance (Laland et al. 2014; Sultan 2015). These shifts in thinking ironically suggest that just as we have grasped the ability to readily sequence genomes, the gene should not take precedence over other factors moving forward. However, this should not reduce the importance of the genome in understanding the processes and mechanisms that shape cichlid variation. We feel that current genomic resources will remain a basis for cichlid research. These resources will inevitably continue to improve to include more species, better coverage, complete chromosome assembly, and perhaps even complete functional annotation as is already being conducted. The research covered in this review shows just some of the ways African cichlids are exemplars for understanding the underpinnings of biological variation found in nature and how this variation enables cichlids to serve as an evolutionary and biomedical model system.

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