Fish & Fisheries Series 39

Andrew M. Muir
Charles C. Krueger
Michael J. Hansen
Stephen C. Riley *Editors*

The Lake Charr *Salvelinus namaycush*: Biology, Ecology, Distribution, and Management

Springer

Fish & Fisheries Series

Volume 39

Series Editor

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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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Michael J. Hansen • Stephen C. Riley
Editors

The Lake Charr *Salvelinus namaycush*: Biology, Ecology, Distribution, and Management

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A lake charr *Salvelinus namaycush* (photo by P. Vecsei—Tlicho Government, Northwest Territories, Canada)

In fond memory of Dr. David L.G. Noakes, the progenitor of this volume. A remarkable man—husband and father, friend, mentor, professor, and inspiration to us all. We will miss you dearly. Charrs/Chars.

Foreword

This volume is a major international accomplishment. Of course, you might expect me to claim this, since I am a coauthor of one of the chapters and of the Introduction. I do take some small credit for that, but the major contributions by a large number of research colleagues are much more important. Full disclosure, I have been involved in research and practical matters with *Salvelinus namaycush* for a number of years, and many of those activities were through contacts with the Great Lakes Fishery Commission (GLFC). In many ways, the GLFC has taken the lead in organizing and producing this volume. I know many of the authors in this volume personally and professionally. I was involved in the organization of the International Charr Symposium held in Duluth, Minnesota (June 2018). That meeting provided much of the basis and impetus for this volume. To my regret I did not attend that Symposium because I was in a different meeting (EEEF, Montreal, Quebec) at exactly the same time.

My claim of international accomplishment for this volume might appear to be yet another example of North American hubris – almost all the authors in this volume are from either the USA or Canada. But the international accomplishment is reflected in both the fact that the Charr Symposium was held in Duluth, Minnesota, and the recognition by international scientists of the significance of *S. namaycush* and the accumulated information on the species.

The International Charr Symposium series originated with a conference on *Salvelinus alpinus* hosted by Lionel Johnson in Winnipeg, Manitoba, in 1981. It has continued from that time, hosted on a voluntary basis by colleagues around the Northern Hemisphere and has usually emphasized *S. alpinus*, even in the name of the Symposium.

One of my Icelandic colleagues is typical of Icelanders in that she has traveled extensively (including study for her doctoral degree in the UK) and collaborated with scientists in a number of countries. However, it was not until she attended the Duluth Charr Symposium that she appreciated the extent of the North American activities with charr. She had not realized that Lake Superior has almost the same surface area as the entire country of Iceland! *S. namaycush* is a dominant species in

Lake Superior, and it is distributed widely in thousands of other lakes across its native range in North America. That includes the other Laurentian Great Lakes, as well as Great Bear Lake and Great Slave Lake, and numerous smaller water bodies. The contrast is not just a North American "Bigger is better" comment; it provides a perspective for both North Americans and those from elsewhere on this volume.

A continuing theme for every Charr Symposium has been the extreme diversity within the genus, mostly focused on *S. alpinus*. For example, Icelanders take great pride in the extraordinary genetic, morphological, and ecological diversity of *S. alpinus* in their lakes and rivers, with the classic example of four quite distinct forms in a single lake, Thingvallavatn (surface area 84 km^2). All evidence points to that, and other Icelandic lakes, as evidence of the process of sympatric speciation. If four distinct forms develop within one lake much smaller than Lake Superior (surface area 82,000 km^2), what can we expect in *S. namaycush* distributed over so many lakes, including truly Great Lakes in North America? The contributions in this volume quite appropriately address that question. Everything from paleoecology to genetic diversity of *S. namaycush* is covered in detail by authorities on a considerable range of subject areas. This is a landmark accomplishment that will be welcomed by international colleagues who have been largely unaware of the wealth of information on this species, for two different reasons. Traditionally much of the literature on *S. namaycush* has been in North American journals, and was mostly directed to questions of management, harvest, and traditional fisheries concerns about a species identified by the common name lake trout. At the same time, most of the people working on *S. namaycush* in North America have not usually considered the International Charr Symposia as a primary meeting venue.

The Duluth Charr Symposium accomplished a great deal, first to draw attention to the ecological and evolutionary significance of *S. namaycush,* and also to provide a very different perspective for North American colleagues. In a different way, this volume is an example of the importance of scientific names in science and the limitations of common names. There is a tradition of using common names of fish species, even in the primary scientific literature. We are all familiar with the standard format: provide both the scientific and common name of each species when first mentioned in the text and thereafter use only the common name. Why default to common names in the scientific literature? And use only English common names—not French, German, Norwegian, or Japanese and certainly none of the names from indigenous peoples who have lived with the fish throughout history. What is gained for science by referring to *Oncorhynchus mykiss*, *S. namaycush*, *Salmo trutta*, and *Salvelinus confluentus* as "trout"?

Yes, I am a coauthor on papers that refer to Icelandic *S. alpinus* by their common Icelandic names or by functional terms used to identify them by their trophic specializations. Those and other studies of *S. alpinus* have emphasized what we recognize as the important distinction between the pattern and the process of evolution. The process is clearly what is important and interesting. The pattern, which is the scientific or common names assigned to particular individuals or groups of individuals, is a necessary convenience but should be understood as only the equivalent of a digital image at one point in time of an active, ongoing ecological and evolutionary process. It is conventional to think in terms of geological time, and such time spans far exceed our ongoing studies and taxonomic discussions. However, the geological evidence from the Icelandic examples of *S. alpinus* suggests that very significant evolutionary changes can take place in only a few thousand years. *S. namaycush* has had at least as much geological time and a much greater and more complex ecological theater in North America in which to develop its evolutionary play. Now we have the details of paleoecology, habitat diversity, and genetic information summarized here to consider this question.

It is fair to ask what should we now expect from the wealth of information about *S. namaycush* in this volume. First and foremost, there will be renewed attention to and analyses of ecological and genetic diversity, prompted by the obvious comparisons to congeneric species. There will be an appreciation of the research potential for this species, given its huge native geographic range and associated life history complexity. The information in this volume already clearly shows that *S. namaycush* is at least as complex and diverse as *S. alpinus*. There are some obvious and important questions. Why (and how) do these fish live to such great ages and grow to such a large size? Why are they relatively intolerant of saltwater and thus restricted to continental North America? The species has very considerable potential for experimental laboratory studies as well as field research. It is produced in large numbers in conventional hatcheries, is harvested as a major commercial and recreational species, and is important for Tribes and First Nations, so it provides a remarkable challenge for those concerned with management, conservation, and restoration. This volume is a major testament to this remarkable species.

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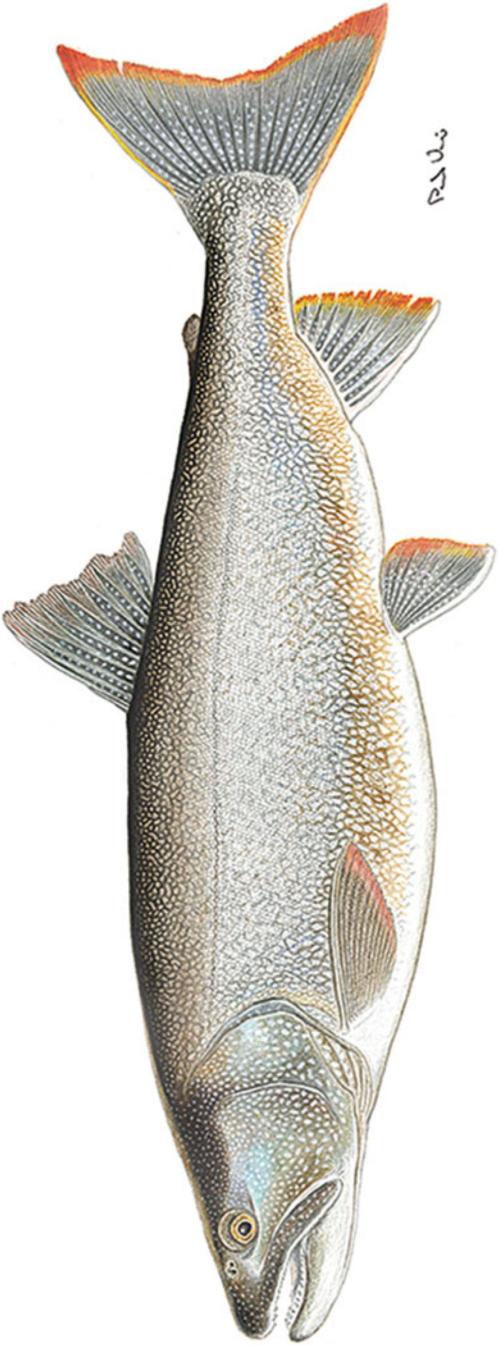
Oregon State University,
Corvallis, USA

David L. G. Noakes

Lake Charr *Salvelinus namaycush* Illustrations



Lean-like (Grey; Piscivore)

Plate 1 NoBeans Island, Smith Arm, Great Bear Lake, NT, Canada, 1141 mm TL

Lean-like

Plate 2 First Bay, Dease Arm, Great Bear Lake, NT, Canada, 675 mm TL

Lean-like

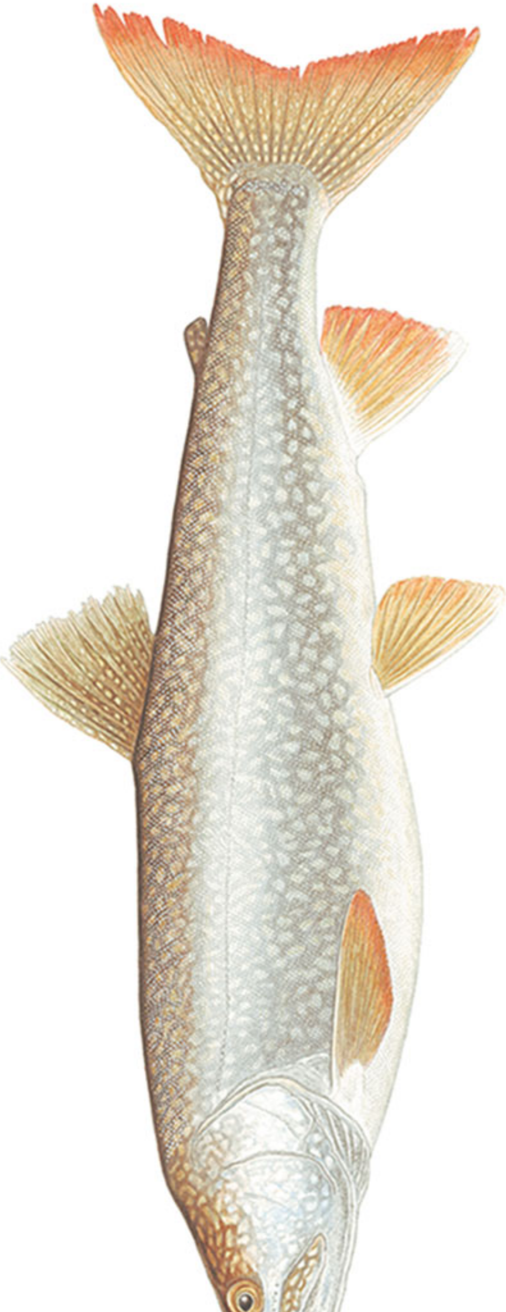


Plate 3 East Arm, Great Slave Lake, NT, Canada, 782 mm TL

Lean

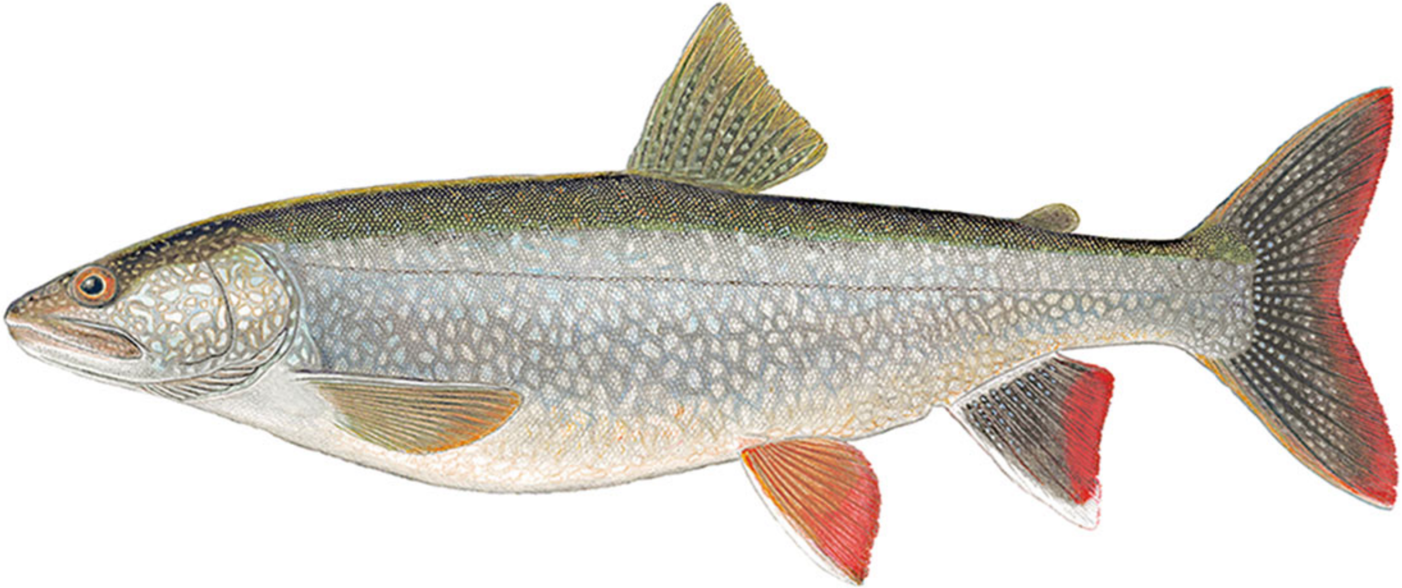


Plate 4 Rock of Ages, Isle Royale, Lake Superior, MI, USA, 508 mm TL

Lean-like

Plate 5 Lake Mistassini, QC, Canada, 504 mm TL

Lean

Plate 6 Rush Lake, MI, USA, 459 mm TL

Humper

Plate 7 Klondike Reef, Lake Superior, MI, USA, 441 mm TL

Humper-like

Plate 8 Lake Mistassini, QC, Canada, 406 mm TL

Humper-like (Huronicus)

Plate 9 Rush Lake, MI, USA, 380 mm TL

Humper-like

Plate 10 Skilak Lake, AK, USA, 360 mm TL

Siscowet-like

Plate 11 East Arm, Great Slave Lake, NT, Canada, 782 mm TL

Siscowet

Plate 12 Lighthouse, Isle Royale, Lake Superior, MI, USA, 602 mm TL

Redfin

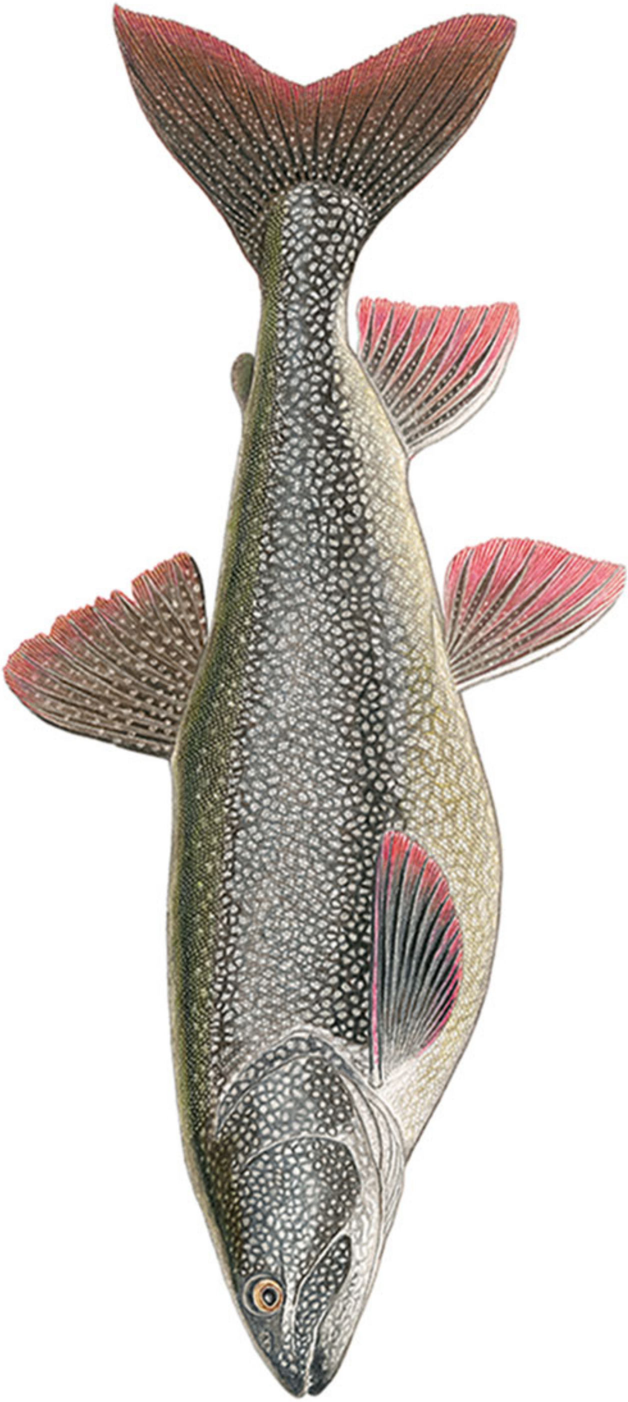
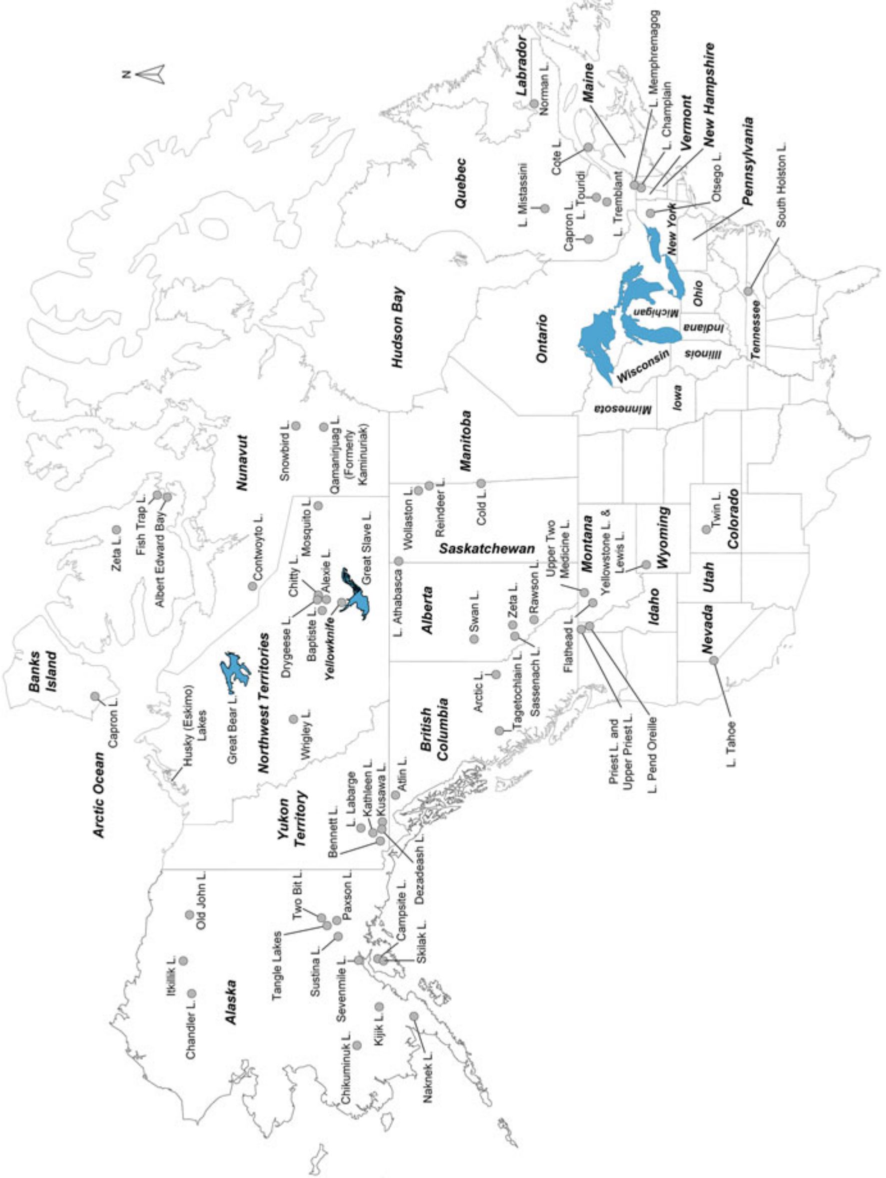


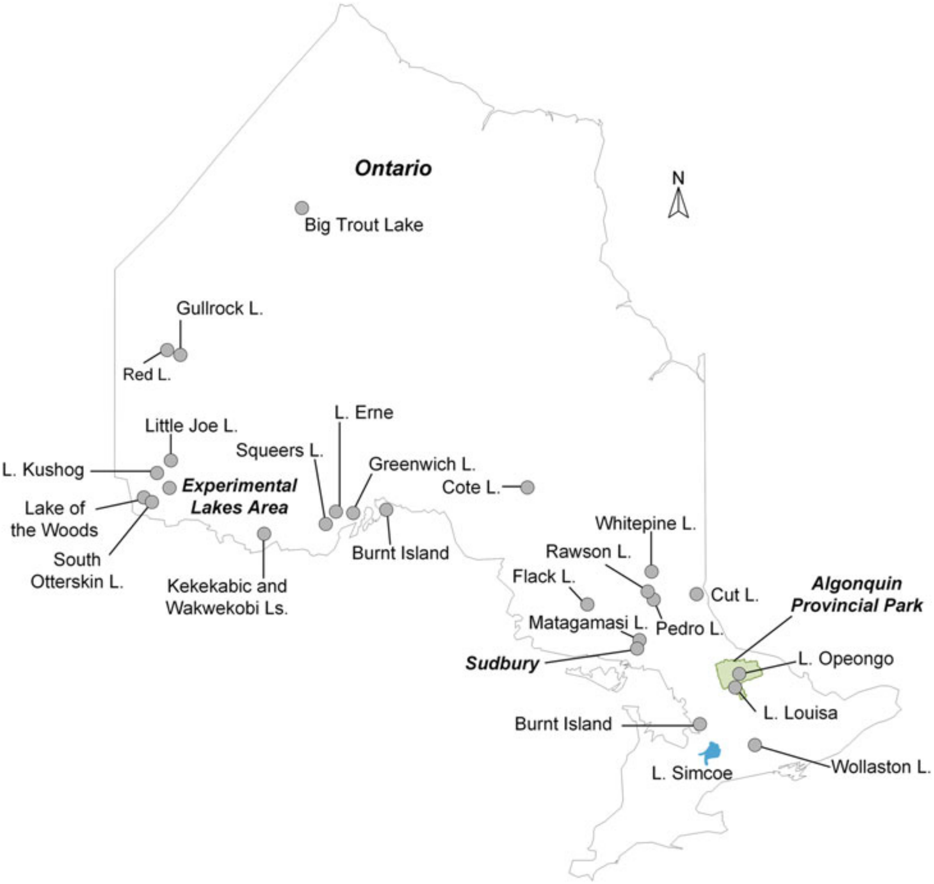
Plate 13 Superior Shoal, Lake Superior, ON, Canada, 867 mm TL

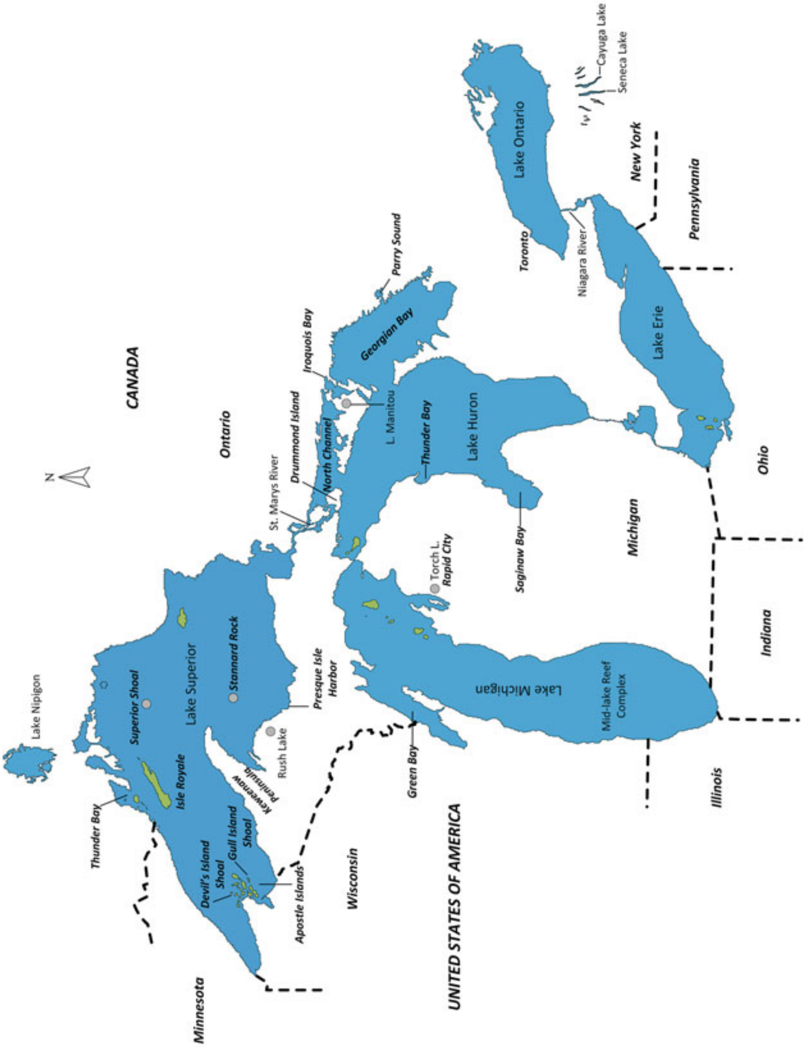
Butterfly (Insectivore)

Plate 14 Shipwreck (PigPen), Dease Arm, Great Bear Lake, NT, Canada, 675 mm TL

Maps of Place Names




Ontario
N
Big Trout Lake
Gullrock L.
Red L.
Little Joe L.
L. Erne
Squeers L.
Greenwich L.
L. Kushog
Experimental Lakes Area
Cote L.
Lake of the Woods
South Otterskin L.
Kekekabic and Wakwekobi Ls.
Burnt Island
Whitepine L.
Rawson L.
Flack L.
Cut L.
Algonquin Provincial Park
Matagamasi L.
Pedro L.
Sudbury
L. Opeongo
L. Louisa
Burnt Island
L. Simcoe
Wollaston L.


N
CANADA
Ontario
Lake Nipigon
Thunder Bay
Superior Shoal
Isle Royale
Lake Superior
Stannard Rock
Presque Isle Harbor
Rush Lake
Keweenaw Peninsula
Devil's Island Shoal
Gull Island Shoal
Apostle Islands
Minnesota
Wisconsin
UNITED STATES OF AMERICA
Green Bay
Lake Michigan
Mid-lake Reef Complex
Illinois
Indiana
Michigan
Torch L.
Rapid City
Saginaw Bay
Thunder Bay
Lake Huron
L. Manitou
St. Marys River
Drummond Island
North Channel
Iroquois Bay
Georgian Bay
Parry Sound
Toronto
Niagara River
Lake Ontario
New York
Pennsylvania
Lake Erie
Ohio
Cayuga Lake
Seneca Lake

Acknowledgments

We thank David Noakes, Oregon State University, for reaching out and encouraging us to take on this project. We are grateful to Alexandrine Cheronet (Senior Editor) and Judith Terpos (Assistant Editor), Springer Nature, for offering us the opportunity to publish a modern synthesis about the lake charr *Salvelinus namaycush* and to Eva Loerinczi (Publishing Editor) and Bharat Sabnani (Production Coordinator) for helping us get the project over the goal line.

We are indebted to the many expert authors who contributed to this volume; without them and their vast experiential knowledge, the book would not have been possible. Several authors also presented their chapters at the 9th International Charr Symposium, July 2018 Duluth, Minnesota (Hydrobiologia (2019) 840:1–398). Our synthesis of modern knowledge on the lake charr's ecology builds off the many pioneers in the field beginning with Louis Agassiz's report of the 1848 expedition to Lake Superior through to Martin and Olver's 1980 synthesis of the lake charr's ecology. These pioneering natural historians paved the way for generations of lake charr biologists.

Color illustrations of lake charr were done by Paul Vecsei–Tlicho Government, Northwest Territories, Canada. Illustrations were created from enhanced high-resolution digital images of live or freshly caught fish. Printed color images were placed on a light table, and body outlines were transferred to cotton archival two-ply vellum (Strathmore™ Artist Papers). Anatomical features (meristic and morphometric variables) were drawn to scale on these outlines. A combination of graphite and polychromos color pencils (Faber-Castell) finished with multiple wash layers of watercolor pencil brought the illustrations to life.

Special thanks to the chapter reviewers: Mike Allen–University of Florida/IFAS, Paul Blanchfield–Fisheries and Oceans Canada, Randy Eshenroder–Great Lakes Fishery Commission, Colin Gallagher–Fisheries and Oceans Canada, John Gunn–Laurentian University, Christopher Guy–USGS Montana Cooperative Fishery Research Unit, Chris Harvey–Northwest Fisheries Science Center, Arne Jacobs–

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Introduction. The Lake Charr: Biology, Ecology, Distribution, and Management

Stephen C. Riley, Michael J. Hansen, Charles C. Krueger, David L. G. Noakes, and Andrew M. Muir

> *This species is well known under the trivial name of "Tyrant of the lakes," because of its size and voracity, and is much esteemed for food in the countries which it inhabits.*
>
> *—Agassiz* 1850

Abstract This volume represents the first synthesis of the biology, ecology, distribution, and management of the lake charr *Salvelinus namaycush* (commonly known as lake trout in North America) in more than 40 years. An updated distribution for the species precedes complete syntheses of the paleoecology, ecological and genetic diversity, habitat, movement and behavior, life history and population dynamics, trophic and reproductive ecology, contaminants and ecotoxicology, and management.

Stephen C. Riley and Michael J. Hansen are retired at the time of publication.

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Finally, a standardized terminology for lake charr early life history is presented in an attempt to correct historical inaccuracies. Our intent is that this volume will serve the next half-century of biologists, ecologists, and fishery managers as the reference for the species—a great icon of the glaciated regions of North America.

Keywords Biology · Ecology · Distribution · Management · Diversity

The Lake charr *Salvelinus namaycush*, the largest and longest-lived of all the charrs (Scott and Crossman 1973; Behnke 1980) is a lacustrine top predator in cold oligotrophic lakes of Canada and the northern United States. Lake charr (commonly known as lake trout in North America) may live more than 60 years and attain sizes exceeding 30 kg and 1.2 m. Consequently, the lake charr is one of the most popular recreational fish species in northern lakes. Lake charr (along with lake whitefish *Coregonus clupeaformis*) were the mainstay of the most valuable freshwater commercial fisheries in North America and have for centuries supported indigenous subsistence fisheries throughout their range (Cleland 1982; Bogue 2000). The last major review of the ecology of lake charr was published more than 40 years ago (Martin and Olver 1980). In addition, the lake charr was the focus of a 1994 international conference to address restoration of the species to the Laurentian Great Lakes—the RESTORE proceedings (Selgeby et al. 1995) contain several review and synthesis papers. The purpose of this volume is to provide a synthesis of scientific information on the lake charr subsequent to Martin and Olver (1980) and RESTORE. The intended audiences for the volume are biologists, ecologists, and fishery managers. The full scope of biology, ecology, distribution, and management of lake charr is synthesized across the North American distribution, including lakes where the species has been introduced. Forty scholars, 25 reviewers, and a host of supporting staff contributed 13 chapters to this volume, each of which is briefly introduced below. Some redundancies occur among chapters—a necessity for each chapter to stand alone—but the editors made relevant connections among chapters and attempted to highlight differences between chapters where appropriate.

The lake charr is restricted in distribution to oligotrophic freshwaters of northern North America largely within the extent of the Pleistocene glaciations (Muir et al. 2021a). Range-wide distribution data were compiled, and existing distribution maps updated to generate a more comprehensive database of native lake charr occurrence in lakes (Muir et al. 2021a). Compared to other freshwater fishes, the lake charr is restricted in its distribution to a narrow set of limnological conditions. While deglaciation shaped dispersal and colonization routes, water oxygen content, temperature, depth, and nutrient content appear to be key limnological variables associated with the lake charr's geographic and bathymetric distribution. Life history variation, physiology (i.e., oxythermal and salinity tolerance), and ecological opportunity (i.e., functional trait variation) likely influenced the lake charr's ability to disperse and colonize newly formed postglacial habitats.

Modern fish communities in streams and lakes of glaciated parts of the northern hemisphere were established after the retreat of the last ice sheets, known as the Wisconsinan glaciation in North America, approximately 10–15 thousand years ago. Prior to the Wisconsinan retreat, freshwater fishes persisted in lakes and rivers south of the glaciers or in unglaciated northern refugia. As Wisconsinan ice sheets retreated, the lake charr and other species dispersed widely through multiple dynamic pro- and periglacial lakes that existed at the edges of the ice sheets (Wilson and Hebert 1998; Wilson and Mandrak 2021). Several Pleistocene glacial cycles preceded the Wisconsinan, and thereby redistributed fish across recently deglaciated landscapes several times, presumably over the past 2.6 M years, and erasing much of the fossil evidence of lake charr evolution (Power 2002; Wilson and Mandrak 2004, 2021). This glacial history selected the lake charr for life in the deep, cold, oligotrophic postglacial environments. The lake charr's physiology allows for growth at low temperatures, and it makes extensive use of cold-water environments, including profundal regions of deep lakes where it feeds on both pelagic and benthic prey. The lake charr is among the few salmonines that spawns primarily in lakes and is relatively intolerant of saltwater, both traits that may be related to its prolonged existence in large inland periglacial lakes. Consideration of the paleoecology of the lake charr may help scientists better understand how the evolution of the lake charr has been shaped by environmental conditions and ecological opportunities related to glacial cycles (Wilson and Mandrak 2021).

The lake charr is one of the most diverse vertebrate species (Muir et al. 2016), and this high intraspecific diversity may have contributed to its ability to thrive in harsh conditions and to quickly recolonize postglacial environments (Wilson and Hebert 1998). Morphology and coloration of the lake charr is particularly diverse, as illustrated by examples in this volume (see Plates 1–14). The most common morph ("morph" in this volume is synonymous with ecotype, ecomorph; ecomorphotype, and morphotype) of lake charr is referred to as "lean" or "piscivore" (Plates 1–6), but several morphs with distinct morphologies and ecologies (Plates 1–14) have been identified throughout the range of the species, particularly in large lakes (e.g., Krueger and Ihssen 1995; Blackie et al. 2003; Zimmerman et al. 2006, 2007; Eshenroder 2008; Muir et al. 2014; Chavarie et al. 2021). Lean lake charr historically coexisted with deepwater morphs throughout the Laurentian Great Lakes (e.g., Brown et al. 1981; Goodier 1981), but deepwater morphs were extirpated from the basin outside of Lake Superior by approximately the 1950s. At least three deepwater morphs are extant in Lake Superior and are referred to as "siscowets," "humpers," and "redfins" (Lawrie and Rahrer 1973; Hansen et al. 1995; Moore and Bronte 2001; Muir et al. 2014). These and other morphs have diverged rapidly since the last glaciation, perhaps because the abundant ecological opportunities (or niches) available in newly formed lakes that had few other species and which promoted diversity in resource use among individuals (Chavarie et al. 2021). Lake charr are in the early stages of diversification, and anthropogenic variables such as climate change, invasive species, stocking of hatchery fish, and fishery harvest may affect future trajectories of this process (e.g., Guinand et al. 2003; Baillie et al. 2016; Chavarie et al. 2021; Wellband et al. 2021).

The astonishing phenotypic diversity of lake charr is a result of interactions between environmental conditions and underlying genetic architecture. Recent research suggests that adaptive variation in this species is distributed along environmental (in particular depth) gradients rather than being focused on specific morphs (Wellband et al. 2021). Furthermore, although heritable differences among morphs have been demonstrated, morphs do not appear highly genetically diverged (Wellband et al. 2021). Most lake charr populations outside the Laurentian Great Lakes show a high degree of genetic diversity among populations, but this diversity has been threatened by human activities such as overharvest and stocking of hatchery fish. Knowledge of lake charr genetics and genomics has expanded greatly and further research may lead to improved understanding of the mechanistic role of plasticity, epigenetic or transgenerational plasticity, and genetics in promoting and maintaining diversity within the lake charr, and the adaptive capacity of the species that will aid in the management of populations across the range.

Habitat use of lake charr within lakes is variable over life stages and across gradients of latitude and lake size (Marsden et al. 2021a). As noted above, the lake charr distribution within lakes is largely controlled by water temperature, because they require cold (<10 °C), well-oxygenated (>6 mg L^{-1}) water, and in stratified southern lakes they primarily reside in hypolimnetic waters during summer. Habitat requirements for adults and juveniles differ, and juveniles at least at the southern edge of the range tend to occupy benthic habitats in deep water (e.g., Elrod and Schneider 1987). Habitat use may also vary among morphs, with the most common form (lean) tending to occupy shallow waters (i.e., <50 m). The lake charr is the least euryhaline of the salmonines, but occurs in brackish or saline waters (6‰ and 9‰ salinity) at some locations in Arctic Canada (e.g., Swanson et al. 2010). Lake charr habitats are susceptible to human activities that may disrupt natural physical and ecological processes, including timber harvest, mining, shoreline modification and hardening, industrial effluents, climate change, and invasive species (Marsden et al. 2021a).

Habitat use, behavior, and movement of lake charr are linked; individual behavior is driven by foraging opportunities, reproduction, predator avoidance, and the physiological need for cool, well-oxygenated water (Binder et al. 2021). Lake charr exhibit variability in behavior among populations, but lake charr behavior is poorly understood compared to the behavior of other salmonines. New technologies, such as acoustic telemetry, video and sonar surveillance, and otolith isotope analysis have provided new insights into lake charr behavior and movement ecology. Juvenile lake charr in southern lakes appear to reside in relatively deep water and begin to disperse as they grow larger. Lake charr may show diel vertical migration, and the nature of these vertical movements may vary among morphs. Adult lake charr may move long distances (>200 km), particularly in large lakes, but most lake charr appear to remain within about 100 km of spawning habitats (Binder et al. 2021). Lake charr may show high site fidelity to spawning habitats, but fidelity varies among populations. Recent evidence suggests that large-scale movements between spawning seasons may be directed migrations to foraging locations rather than undirected nomadic movements. Spawning behavior of the lake charr is unique among salmonines because lake charr typically spawn at night, primarily in lakes, females do not construct redds, and males appear to show little overt aggression toward each other during spawning (e.g., Muir et al. 2012a; Binder et al. 2015).

Animal species show a wide range of life history traits, including growth or size at a given age, age-at-maturity, fecundity, and maximum size and these traits affect the growth and dynamics of populations in complex ways (Roff 1992). Lake charr inhabit the "slow end" of this spectrum, being relatively long-lived (> 60 years) and late to mature (>20 years), but specific life history traits vary dramatically across the species' range and among morphs (Hansen et al. 2016a, b, 2021). Lake charr tend to grow slower in northern lakes but may live longer and reach a larger maximum length, and population density may be higher in smaller southern lakes than in large lakes (>500 km^2; McDermid et al. 2010; Hansen et al. 2021). Life history traits of lake charr make them vulnerable to fisheries and environmental changes but also appear to increase their ability to colonize new systems (Hansen et al. 2021). The lake charr has been introduced into lakes worldwide (Crossman 1995). Many introductions have been relatively unsuccessful, but in western North American lakes, some have resulted in negative interactions with native salmonids, and invasive lake charr have proven difficult to eradicate (Martinez et al. 2009; Hansen et al. 2021).

Lake charr are opportunistic foragers and will consume almost any prey available in both pelagic and benthic habitats, including fishes, invertebrates, zooplankton, terrestrial animals, and plant material (Martin and Olver 1980; Vinson et al. 2021). Trophic specialization is also thought to play an important role in niche diversification among morphs; however, the diet of a specific lake charr population will depend on prey that are available in different parts of a lake, which varies across the species' range. The lake charr is typically a top predator and may play an important role in structuring lower trophic levels and facilitating energy transfer among benthic, pelagic, nearshore, and offshore habitats (Vinson et al. 2021). Lake charr can adapt to feeding on whatever prey are abundant, including newly introduced species, as illustrated by their consumption of rainbow smelt *Osmerus mordax*, alewife *Alosa pseudoharengus*, and round goby *Neogobius melanostomus* in the Laurentian Great Lakes. Young lake charr begin feeding immediately after hatching (i.e., free embryo) on aquatic invertebrates (particularly Chironomids and *Mysis* in the Laurentian Great Lakes) and zooplankton, and typically switch to piscivory (when fish are available) within two or three years in southern lakes. As they grow, lake charr will consume larger prey species and can consume fish more than 50% of their length; they are also cannibalistic, particularly in climax communities (Vinson et al. 2021). Diet varies greatly among life history stages, morphs, and seasons.

The lake charr spawns primarily during autumn, but some morphs, such as siscowet, may spawn during spring and fall in deep waters of Lake Superior (Goetz et al. 2021). Lake charr do not necessarily spawn every year, perhaps due to the difficulty of obtaining sufficient energy resources to support annual gamete production in unproductive oligotrophic systems (Sitar et al. 2014). Age-at-first-maturity ranges from 4 or 5 years in southern lakes to age 15 or older in the north, and males tend to mature before females. Relative fecundity of the lake charr ranges from 718 to 2226 eggs/kg, with no apparent latitudinal differences among populations (Goetz et al. 2021). Fertilized eggs (pre-hatch embryos) are deposited directly onto stony substrates, which usually have relatively large particle sizes. Fertilized eggs typically fall within substrate interstices and incubate over winter, but are vulnerable to predators, fungal infections, sedimentation, low oxygen levels, or physical shock, depending on conditions. The spawning season may last several weeks, and typically free embryos emerge in spring over a period of a month or longer. Some lake charr show high site fidelity to spawning habitats, but fidelity varies among populations (Binder et al. 2016; Pinheiro et al. 2016).

The broad distribution of the lake charr and its position as a top predator makes it a useful sentinel of environmental pollution in aquatic systems (Muir et al. 2021b). In polluted systems, lake charr may contain high concentrations of contaminants, such as mercury and PCBs, which may cause mortality, particularly in early life stages. The concentration of contaminants in lake charr varies widely across the species' range. Contaminants were thought to be a potential cause of the lack of progress during the early years of lake charr restoration in the Laurentian Great Lakes, but subsequent work has suggested that thiamine deficiency and free-embryo predation by non-native fishes has been more important over the past 30 years (see Goetz et al. 2021). High concentrations of some contaminants, particularly mercury (sometimes naturally occurring), continue to be a concern for human consumption of lake charr.

The lake charr has supported fisheries that are large by comparison with other *Salvelinus* species. Commercial fisheries, mostly on large lakes (>500 km^2), were a primary cause (along with sea lamprey *Petromyzon marinus* predation) of the collapse of lake charr populations in the Laurentian Great Lakes (Muir et al. 2012b). Recreational fisheries negatively affected populations in inland lakes, and recreational fishing pressure on some lake charr populations has greatly increased in recent decades (e.g., Martin and Olver 1980; Evans et al. 1991; Gunn and Sein 2000; Post et al. 2002; Olver et al. 2004; Mills et al. 2008; Kaufman et al. 2009; Lester et al. 2021). Subsistence fisheries are common, particularly in remote northern lakes near First Nations communities in Canada, but subsistence harvests tend to be modest (Mills et al. 2008). Sustainable management of fisheries is essential to provide continued fishing opportunities and to sustain lake charr populations. Because stock assessments are not practical to conduct on all lake charr populations, managers rely on models that predict sustainable harvest rates from characteristics of lakes and lake charr life history traits (e.g., Shuter et al. 1998). Based on several large data sets and an innovative synthesis of life history theory and stock assessment models, Lester et al. (2021) developed a series of models to predict and manage the harvest of lake charr populations across the native range. Their models describe across-lake patterns of variation in lake charr habitat and population attributes and facilitates broad generalizations about how, on average, attributes vary across the landscape, thus providing a useful tool for data-limited fisheries.

Lake charr ontogeny and life history literature is confounded by terms that are incorrectly borrowed, used inconsistently, not tied to lake charr developmental stages, not synonymous with formal terminology, not ecologically relevant, and do not reflect differences in behavior between lake charr and their congeners. Marsden et al. (2021b) propose an accurate and informative developmentally based, species-specific terminology for lake charr life stages and their recommendations were adopted throughout the volume. The intent of the proposed terminology is to inspire the use of more accurate terms that conform to ichthyological standards, specify important developmental transitions, and provide useful and identifiable categories that will facilitate clarity in communication and enhanced information transfer.

While considerable research has been undertaken on lake charr biology, ecology, distribution, and management, many key knowledge gaps remain. Geospatial analysis of native and non-native distributions in relation to drivers of dispersal (including movement ecology) and colonization could facilitate risk analysis of future changes to lake charr populations (Muir et al. 2021a). Understanding the extent of local adaptation and adaptive variation of populations or morphs will also be critical to forecasting how these populations will adapt to changing environmental conditions and to better resolve future evolutionary trajectories (Wilson and Mandrak 2021). Identifying the ecological mechanisms responsible for generating within- and among-morph phenotypic diversity and the genomic mechanisms that facilitate divergence among morphs is essential to sustainable lake charr management and restoration (Chavarie et al. 2021; Wellband et al. 2021). Emerging whole-genome sequencing and experimental evidence (e.g., common garden) for the role of plasticity (Chavarie et al. 2021) versus epigenetics or genetics (Wellband et al. 2021) in defining morphological traits could reveal important information about the origins and evolution of the lake charr. The loss of genetic diversity, in Lake Superior, for example, is a major threat to lake charr and should be carefully considered in ongoing management and restoration efforts across the range (Wellband et al. 2021). Research is lacking on juvenile and adult lake charr movements and habitat use, particularly among morphs, in the northern portion of the range where environmental change is rapid, and in small lakes (Marsden et al. 2021a). Binder et al. (2021) identified the need for research to address several questions in three general areas: (1) movement ecology; (2) homing and navigation; and (3) spawning behavior. Future research needs relating to lake charr life history and population dynamics fall in two areas: (1) improving analytical approaches to estimating well-studied metrics focusing on thin-sectioning of sagittal otoliths; and (2) initiating studies of metrics, such as natural mortality and survival from pre-hatch embryo to age 1, that have rarely been quantified (Hansen et al. 2021). Using contemporary tools, better quantification of variability in lake charr diet among morphs, lakes, habitats, life history types, seasons, and years will enhance our understanding of lake charr trophic ecology and ability to generate more informed predictions of how lake charr will respond to change (Vinson et al. 2021). Many knowledge gaps remain with respect to the reproductive ecology of the lake charr. These include environmental variables controlling the seasonal timing of reproduction and skipped spawning, developmental timing of deepwater spawned embryos, sources of pre-hatch embryo mortality, how access to zooplankton affects growth and survival of free embryos, behavior, timing, and physiology related to first filling of the gas bladder, TDC effects on adult, free embryo, and juvenile lake charr, and thiaminase biochemistry in prey fishes (Goetz et al. 2021). The lake charr has not been extensively studied for adverse effects of contaminant exposure, particularly, combined effects chemical mixtures with other stressors, such as increased primary production or shifts in species and prey assemblages, all of which are changing with a changing climate (Muir et al. 2021b). Finally, Lester et al. (2021) identified a number of key research questions specific to their life history-based model for sustainable exploitation of lake charr: (1) further validation of the biomass sub-model for colder northern regions as most of the data used to generate the model came from southern populations; (2) effects of body temperature on natural mortality estimates; (3) refinement of a calibration model so that the biomass of lake charr and other species can be estimated from index netting data across the entire geographic range; and (4) a need to evaluate unexplained variability among lakes to inform a risk assessment for management strategies. The above knowledge gaps, detailed within the chapters of this volume, should help focus another generation of lake charr biologists to provide the information necessary to re-establish this species where lost and conserve pristine populations of lake charr for generations to come.

Lake charr population status varies considerably across their native range. Some populations in remote northern lakes remain in a near-pristine state, but may be affected by a changing climate (e.g., Johnson 1976; Mills et al. 2002, 2008; Environment Yukon 2010), while those at the southern edge of the range, near human population centers, are susceptible to fisheries, habitat degradation, and other anthropogenic stressors in addition to a changing climate. Restoration of naturally reproducing populations in the Laurentian Great Lakes has progressed slowly outside of Lake Superior, but widespread natural reproduction was evident recently in Lake Huron (Riley et al. 2007; He et al. 2012) and to a lesser degree in Lake Michigan (Hanson et al. 2013). Management strategies and stock assessments in inland lakes vary widely among jurisdictions across the range, and little data are available on the status of many populations due to the remoteness and inaccessibility of many northern lakes (Mills et al. 2008).

Martin and Olver (1980) concluded that “It is essential that pristine conditions be maintained for the well-being of this species.” As noted above, the lake charr is slow-growing and requires cold water and high dissolved oxygen, and therefore can serve as an effective indicator of environmental quality in northern lakes. The requirement for cold water also makes the lake charr a valuable sentinel species for monitoring and studying the effects of climate change (e.g., Sharma et al. 2009; Guzzo et al. 2017; Campana et al. 2020). Nearly 50 years ago, Ryder and Johnson (1972) stated that “the future of salmonid communities in North American oligotrophic lakes looks bleak” based on their prediction that anthropogenic threats, primarily eutrophication, would continue to affect these communities. Since then, several lake charr populations have declined in abundance, but many populations remain intact today, and in some cases have recovered (Hansen and Bronte 2019). The wide variety of recent research summarized in this volume is encouraging and will hopefully be useful to fishery managers, but continued research, monitoring, and sustainable management of native lake charr populations will be necessary to ensure their persistence and sustainability for the next 50 years and beyond.

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Distribution

Andrew M. Muir, David Bennion, Michael J. Hansen, Stephen C. Riley, and John M. Gunn

Abstract The lake charr *Salvelinus namaycush* is restricted in its native distribution to oligotrophic fresh waters of northern North America largely within the extent of the Pleistocene glaciations. It is the only freshwater species in northwest North America that does not occur in Siberia. A GIS-based native occurrence map linked to the HydroLAKES database does not extend the lake charr range but provides more comprehensive occurrence data than previous maps. The total waterbody area of lakes occupied by lake charr (451,304 km^2) is 40% of the total waterbody area across the range. Lake charr occur from 42.020901 latitude in the south to 74.420800 in the north and from −62.700000 longitude in the east to −161.173090 in the west. Lake charr lakes range in surface area from 3.4 to 8,210,000 ha (mean = 9715 ha; median = 191 ha), maximum depth from 2.7 to 614 m, and elevation from sea level to 2035 m ASL (mean = 381 m; median = 366 m). Glaciation, water temperature, dissolved oxygen, depth, and nutrient content are the main variables associated with

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lake charr native distribution in lakes. Life history variation, physiology, and ecological opportunity are the most likely drivers of lake charr dispersal and colonization.

Keywords Biogeography · Colonization · Dispersal · Ecological opportunity · Geographic information system (GIS) · Glaciation · Habitat · HydroLAKES · Life history · Map · Native range · Nutrient content · Occurrence · Physiology · Range · Sampling · Temperature

1 Introduction

The lake charr *Salvelinus namaycush* is restricted in its native distribution primarily to oligotrophic freshwaters of northern North America largely within the extent of Pleistocene glaciations (Fig. 1; Lindsey 1964). West of the continental divide, it occurs in British Columbia, Yukon, and Alaska, but is absent from the Columbia River basin (Khan and Quadri 1971; Scott and Crossman 1998), much of western

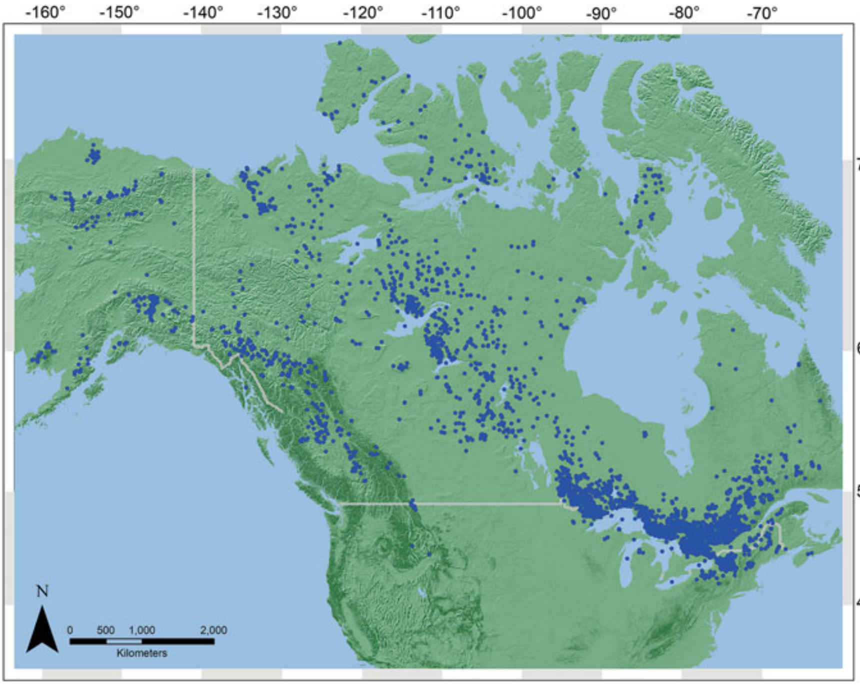

Fig. 1 Native lacustrine distribution of the lake charr *Salvelinus namaycush*. Blue dots ($n = 5110$) represent individual lake occurrences and the x and y axes represent longitude and latitude, respectively

British Columbia, and Pacific drainages north of Cook Inlet, Alaska (Lindsey 1964; McPhail and Lindsey 1970). The lake charr occurs in Bristol Bay and Cook Inlet drainages, Alaska, and several highland drainages north and south of the Brooks Range, but not in Alaska's coastal lowlands. It is the only freshwater species that inhabits the far northwest of North America, but never crossed the Bering Strait to colonize Siberia (Lindsey 1964). East of the continental divide, the lake charr occurs in Montana, Alberta, and throughout much of Canada, but is absent from much of the Hudson and James Bay lowlands and Newfoundland, Prince Edward Island, and much of eastern Labrador (Scott and Crossman 1998). The lake charr distribution extends to ~74° N, including northern Banks, Victoria, Steffansson, and King William islands in the western Arctic and southern Baffin Island in the eastern Arctic (Coad and Reist 2018; Martin and Olver 1980; Sawatzky et al. 2007; Stewart and Bernier 1982). The southern extent of the distribution reaches south to the Laurentian Great Lakes (~42° N) in Minnesota, Wisconsin, Illinois, Indiana, Michigan, Ohio, Pennsylvania, and New York waters of the Great Lakes and inland lakes of Minnesota, Wisconsin, Michigan, and New York. In the southeast, the lake charr occurs in northern waters of New England states, New York, Vermont, New Hampshire, and Maine.

Previous descriptions of lake charr distribution contain some errors. Scott and Crossman (1973) reported lake charr to be native to inland lakes of Pennsylvania, but the species is only native to Lake Erie in that state. Further, Scott and Crossman (1973) did not report the occurrence of lake charr in Illinois, Indiana, or Ohio, where, like Pennsylvania, their distribution is limited to the Great Lakes. Scott and Crossman (1973) erroneously reported the lake charr as native to Idaho. Martin and Olver (1980) corrected the reported occurrence of native lake charr in Idaho, but perpetuated its native status in Pennsylvania, while distinguishing Illinois, Indiana, and Ohio, where the species is limited to the Great Lakes.

The present day distribution of lake charr originated via postglacial dispersal at the end of the last (Wisconsinan) glaciation from periglacial refugia in Atlantic coastal, Mississippi, Missouri, and Pacific basins in the south, and Beringia, Nahanni, and possibly Banks Island basins in the northwest (Lindsey 1964; Crossman and McAllister 1986; Wilson and Hebert 1998; Wilson and Mandrak 2004, 2021). Unlike other charrs, the lake charr primarily inhabits lakes and has primarily lacustrine, and occasionally adfluvial, life histories (Muir et al. 2015). Less commonly, lake charr have a fluvial life history (Evans et al. 2002; Lindsey 1964; Loftus 1958) with some Arctic populations being anadromous or semi-anadromous (Swanson et al. 2010a, b, 2011) and even low salinity brackish resident (Kissinger et al. 2016).

In this chapter, we update the native distribution of the lake charr in lakes and discuss processes and parameters associated with lake charr native distribution and some potential drivers of dispersal and colonization. Our analysis does not extend the historical range presented by Lindsey (1964) but provides more comprehensive occurrence data than previous contributions. To our knowledge, no detailed syntheses of range-wide drivers of lake charr lacustrine distribution have been undertaken. Therefore, we conclude by recommending some fertile areas of research on processes driving geospatial patterns of lake charr distribution facilitated by the dataset assembled and hypotheses generated herein.

2 Methods

2.1 Data Collections

In response to a 14 May 2019 e-mail query and subsequent follow-up queries, we received lake charr occurrence data for each of the states, provinces, and territories across the lake charr distribution (Table 1). Datasets were cross-referenced with available literature to identify additional and erroneous records. In total, data collection resulted in 12 main datasets consisting of 31,387 total occurrence records, which was supplemented by available literature as described below. Removing duplicates, lakes with suspected introduced lake charr, and lotic waterways resulted in native occurrences for 5110 lakes (Fig. 1). Methods for filtering data are described below. Permissions were obtained for inclusion of data contributions in our analysis, but as usual, future use of raw data (Electronic Supplement 1) requires permission from the providing agency or institution for that jurisdiction. All errors or omissions in the compiled dataset are our responsibility.

2.2 Native Versus Introduced Populations

Four types of lake charr occurrence records existed in our compiled dataset: (1) native; (2) native, but historically or currently supplemented by stocking; (3) introduced into non-lake charr lakes within the native range including put-and-grow lakes in Ontario (OMNRF 2015); and, (4) introduced into non-lake charr lakes outside of the native range. Only the type 4 occurrence was relatively easy to detect and several datasets that we received also included records of types 2, 3, and less commonly 4. Lakes identified as put-and-grow populations in Ontario (OMNRF 2015) were removed from the data set if present from another source. Herein, we defined lake charr populations as "native" if source documents or subsequent consultations with local biologists did not define the population as "introduced," which thereby led to their inclusion in our dataset. This conservative definition of "native" underrepresents the true native distribution of the species for some jurisdictions and may overrepresent it for others. For instance, some populations were introduced by stocking (i.e., not native) and are now self-sustaining, and were included as "native" in our database (i.e., false positive; e.g., some Ontario lakes) whereas, in Maine biologists took a conservative approach and removed from the dataset populations that were "native," but are presently or were historically stocked (i.e., false-negative). Our dataset probably contains some occurrences that were: (1) not native, but now self-sustaining populations introduced by stocking

Table 1 Main data sources used to describe the lake charr *Salvelinus namaycush* distribution. Saskatchewan, Manitoba, and Yukon were part of the "North America" jurisdiction records; additional sources were not provided by those jurisdictions. The compiled datasets comprised 31,387 total occurrence records, which were supplemented by additional sources as described in the text. Removing duplicates, lakes with suspected introduced lake charr, and lotic waterways resulted in native occurrences of lake charr for 5110 lakes

Jurisdiction	Source	Number of records
North America	• Global Biodiversity Information Facility (GBIF). https://www.gbif.org/en/occurrence/search?q=, accessed 5/23/19 (Species = *Salvelinus namaycush*; Country or area filter = United States of America and Canada).	13,563
	• Mandrak, N.E., R.A. Curry, P. Dumont, E. Holm, J.D. Reist, and D. Watkinson. (unpublished data). Atlas of the Freshwater Fishes of Canada Annotated with an Illustrated Key. University of Toronto Press.[a]	3658
	• Hansen et al. (2021).	488
Alberta	• Alberta Environment and Parks, Fish and Wildlife Policy Branch—unpublished data.	63
Ontario	• Ontario Ministry of Natural Resources and Forestry. 2015. Inland Ontario Lakes Designated for Lake Trout Management. Peterborough (ON).	2076
Ontario, Quebec, and Northeast United States	• Appendix II. Boreal Shield Watersheds: Lake Trout Ecosystems in a Changing Environment. *Edited by* J.M. Gunn, R.J. Steedmar and R.A. Ryder. Lewis Publishers, Boca Raton.	3771
Northwest Territories & Nunavut	• Sawatzky, C.D., et al. 2007. Distributions of Freshwater and Anadromous Fishes from the Mainland Northwest Territories, Canada. Can. Manuscr. Rep. Fish. Aquat Sci. 2793: xiv + 239 p. • Coad, B.W. and J.D. Reist, 2018. Marine Fishes of Arctic Canada. Toronto (ON, Canada): University of Toronto Press. xiii+618 p. • Unpublished Arctic island data.	1881
Eastern United States	• Carlson, DM, R.A. Daniels, and J.J. Wright. 2016. Atlas of Inland Fishes of New York. New York State Museum Record, The New York State Education Department, Albany. http://www.nysm.nysed.gov/common/nysm/files/atlasofinlandfishes.pdf	5821
	• Maine Department of Inland Fisheries and Wildlife—unpublished data.	21

(continued)

Table 1 (continued)

Jurisdiction	Source	Number of records
Alaska	• Alaska Department of Fish and Game, Alaska Lake Database, http://www.adfg.alaska.gov/index.cfm?adfg=fishingSportStockingHatcheries.lakesdatabase, accessed 5/23/19.	45

[a] Individual data sources compiled in this submission included: University of Alabama Ichthyological Collection (http://uaic.as.ua.edu/); University of Alberta Museum of Zoology, University of Alberta Museums; Canadian Museum of Nature; Fisheries and Oceans Canada, Fisheries Information Summary System (https://cmnmaps.ca/DFO_FISS/; accessed during the early 2000s); Fisheries and Oceans Canada distribution database for eastern Canada compiled by Ken Minns (Retired) during the 1990s (no current source); Ken Stewart's University of Manitoba database (accessed during the 2000s); Province of Quebec database (accessed during the early 2000s; no current source); Royal British Columbia Museum (https://royalbcmuseum.bc.ca/collections/natural-history/ichthyology); Royal Ontario Museum; Saskatchewan Ministry of Environment; and University of British Columbia Museum (https://beatymuseum.ubc.ca/research-2/collections/fish-collection/)

(occurrence type 3 and 4 above); and, (2) excludes some populations that were native but have been subsequently stocked (type 2 above). To illustrate the problem, consider that the lake charr is thought to be native to approximately 100 lakes in Maine (Johnson 2001); however, native status has only been confirmed in 21 of those lakes, which have never been stocked (J. Pellerin, Maine Department of Inland Fisheries and Wildlife, personal communication). Twenty-one lakes likely underrepresent the native distribution of lake charr in Maine because 12 more lakes have no record of stocking and up to 73 lakes that may have contained native populations were stocked at some time but are no longer stocked. This same problem is also true of most provinces in Canada, where native lake charr populations existed in many lakes, along with many other lakes without lake charr that were stocked, some of which are now self-sustaining while others are sustained by stocking. In Ontario, for example, lake charr were introduced into 222 lakes without native lake charr populations, of which 66 are now self-sustaining, and an additional 149 lakes, which are now sustained by stocking (Crossman 1995). A further complication is that the dataset for Ontario identifying native or "natural" lake charr lakes includes lakes that may have lost native populations but have been identified for rehabilitation (OMNRF 2015). In summary, we deferred to local sources to identify "native" lake charr lakes, but how these lakes were classified as "native" differed among jurisdictions, which potentially lead to some inconsistencies in our dataset.

2.3 GIS Mapping

A major challenge of the mapping process was deleting duplicate records and ensuring that all records were spatially accurate. Two factors complicated this process. First, place name conventions were not consistent within and among datasets, and second, accuracy and precision of coordinate pairs representing locations was highly variable. Multiple tools and layers of review were employed to overcome these challenges.

Each individual data source was filtered to only include lakes known to support native lake charr populations, as defined above. Some data sources differentiated native from non-native populations. When this information was available, only records for native populations were included. Datasets were then imported into ESRI's ArcMap 10.7 GIS software package (ESRI 2019) and converted into shapefile format. Records with matching x and y coordinate values were flagged and duplicates removed. Place names were standardized to title case and best efforts were made to limit text to only reflect lake names. Several data sources included various location descriptions, references to alternate names, and inconsistent use of "lake" and its variations in the place name field. Records falling outside of the continental land margins were first corrected if coordinates were associated with a lake name, but otherwise, were excluded. The Spatial Join tool from ArcMap with a 100-m search buffer connected records to lake polygons from the HydroLAKES dataset (Messager et al. 2016), thereby preserving the corresponding unique HydroLAKES id number and waterbody name where available. The HydroLAKES database provides a seamless high-resolution map of the world's lakes ($n = \sim 1.5$ million lakes) and their main characteristics. Next, duplicates within the name field and HydroLAKES id field were flagged. Neither of these attributes alone served as a reliable indication of a true duplicate data point, but we assumed that if both the name and HydroLAKES id were duplicates then the record could reliably be excluded from the dataset.

Individual datasets were then merged into a single file resulting in a dataset containing 5789 lake charr lakes, and the previous process repeated, with a few additional steps as described below. Locations that did not get spatially joined with a lake polygon ($n = 1451$) needed to be checked for spatial accuracy by manual inspection. To minimize the number of records to process, records with names that referenced lotic systems ($n = 177$) and records that did not have an associated name ($n = 250$), were removed because their location could not be verified. Lotic records were omitted because they were: (1) patchy; (2) not represented in the HydroLAKES dataset; (3) verification of lotic residency versus use of the river for part of the life history was not possible; and (4) the point of occurrence in rivers could not be verified due to multiple sampling locations and occurrences reported within a single river. We recognize that exclusion of both estuarine and lotic populations from our dataset under-estimates the native distribution of the lake charr. The remaining 1024 records were individually inspected for location accuracy and adjusted based on comparison of place names with both ESRI's World Topographic Map (ESRI 2019) and Google Maps (Accessed 20 Jan 2020). This process added 843 lakes to the dataset. Adjusted occurrence records were then joined with the HydroLAKES dataset attributes. Working with the full dataset, records with both duplicate name and HydroLAKES id were flagged and removed. Following this step, records with duplicate HydroLAKES ids but different names were inspected and removed when appropriate. This step was necessary due to the way waterbodies are represented in the HydroLAKES database, where large continuous waterbodies that may be practically treated as different lakes are lumped together in a single polygon. Finally, records flagged for name duplication, but with no corresponding HydroLAKES id were manually inspected and removed as appropriate. The dataset was then reviewed by the co-authors and Fig. 1 by four external peer reviewers, resulting in minor adjustments to the final dataset. Adjustments added 47 previously omitted lakes in Alberta, eight lakes from Wilson and Hebert (1993), 20 lakes from Stewart and Bernier (1984), and 7 lakes via personal communications from Alaska Department of Fish and Game biologists (C. Schwanke and L. Stuby, personal communication; Burr 1987). In addition, reviews altered lakes represented in New York (lakes known to be outside the native range, as described below), Maine (only lakes with no possible influence from stocking, as identified by biologists in Maine), and British Columbia (native populations identified by Donald and Alger 1993). This process produced a final dataset with 5110 lake charr lakes, 5010 of which are associated with a polygon from the HydroLAKES database.

2.4 Analytical Methods

The final dataset was used to derive several spatial descriptors of the native range of lake charr. Minimum and maximum depths (m) were from Gunn and Piblado (2004) whereas, mean and median average depths were calculated from the HydroLAKES data set that contains modeled average depths. Minimum and maximum latitude and longitude were taken from coordinates of occurrence records at the extreme north, south, east, and west extent of the dataset. Minimum, maximum, mean, and median elevations were calculated for each lake from elevation values from the GMTED2010 global elevation dataset (Danielson and Gesch 2011). Total waterbody area was calculated by summing the area of the 4717 lake polygons from the HydroLAKES dataset. This total does not include the area of 100 lake charr lakes that were less than 10 ha, and therefore, did not coincide with a feature in the HydroLAKES database. Another caveat to this calculation results from the way waterbodies are represented in the HydroLAKES database—large continuous waterbodies are treated as a single polygon and, therefore, may overestimate total waterbody area. This overestimate is illustrated by the 5010 lakes from our dataset being associated with 4717 polygons in the HydroLAKES database; that is, multiple lakes are treated as a single polygon (i.e., waterbody) in HydroLAKES.

3 Distribution

A range-wide distribution for lake charr was first described by Lindsey (1964) and reproduced by Scott and Crossman (1973, 1998) and Martin and Olver (1980). A distribution for northwestern Canada and Alaska was presented by McPhail and Lindsey (1970), the mainland Northwest Territories by Sawatzky et al. (2007), and coastal Northwest Territories and Nunavut by Reist (2018). The distribution of lake charr in Ontario, Quebec, and the northeastern United States was updated by Gunn and Piblado (2004). None of the above sources shows the full extent of the distribution compiled herein (Fig. 1). Although our analysis does not extend the known native range of the species, we provide more comprehensive native occurrence data than previous contributions and correct some historical inaccuracies largely associated with introduced populations. In the first paragraph of this chapter, we provided an updated description of lacustrine distribution for the lake charr. Below, we explore details of the distribution of the lake charr within jurisdictions where discrepancies exist, where existing datasets contained many non-native populations, and where their occurrence or lack of occurrence is particularly noteworthy. One challenge that we acknowledge and discuss below is that the true native distribution of lake charr can never be accurately known because stocking occurred prior to detailed record keeping.

3.1 Alberta

Lindsey (1964) included several areas of native lake charr populations in Alberta (see his Appendix Sources of Locality Records of *Salvelinus namaycush*): *"(1) headwaters of South Saskatchewan River in Waterton and Minnewanka Lakes (*Cuerrier 1954*); (2) headwaters of North Saskatchewan River in Glacier Lake (*Cuerrier, 1954*) and Swan Lake on the Clearwater River drainage (J. S. Nelson, personal communication); and (3) Athabasca River system in Moab and Pyramid Lakes (*Cuerrier, 1954*), Rock Lake near Hinton (J. S. Nelson, personal communication), and Graham and Legend Lakes (*MacDonald 1951*), formerly present in Lesser Slave Lake.*" The present-day distribution was derived from geospatial maps of lake charr waters in boreal shield (northern and eastern) and alpine (western) ecosystems (https://www.alberta.ca/lake-trout.aspx; accessed December 12, 2019). Supporting data for each map were used to differentiate native from non-native populations (M.G. Sullivan, Alberta Environment and Parks, unpublished data).

3.2 Yukon and Eastern Alaska

Available data indicate a substantial gap in lake charr distribution throughout the western Yukon and eastern Alaska; a question is whether this gap is real, or attributable to a lack of sampling in this remote region of the distribution. Portions of the western Yukon and eastern Alaska (Tanana River north to the Yukon River and the Yukon Flats) are vast with few lakes suitable for lake charr (C. Schwanke, Alaska Department of Fish and Game, personal communication). Alaska Statewide Harvest Survey data show lake trout do occur in 13 lakes in the northern portion of the Yukon Drainage (http://www.adfg.alaska.gov/SF_Lakes/) and lake charr are known to occur in a five lakes in the upper Tanana: Ellis, Beaver, Jatahmund, Braye, and Jack (C. Schwanke, Alaska Department of Fish and Game, personal communication; these lakes are included in Fig. 1). Comprehensive surveys of interior Alaska within National Wildlife Refuges along the Yukon/Tanana River report native lake trout in only one lake (Jatahmund) (Glesne et al. 2011). Taken together, the available data suggest that where habitat is suitable within eastern Alaska and the western Yukon, lake charr have colonized, but that their absence from west central Alaska and large portions of the Yukon is likely real.

3.3 Montana

Lindsey (1964) listed in his Appendix two native distributions of lake charr lakes: "*(1) headwaters of the Missouri River in Lower Two Medicine Lake (*Schultz 1941*) and Elk Lake (*Henshall 1907*); and (2) headwaters of the South Saskatchewan River in Saint Mary Lake, Cosley Lake (misspelled Crossley), and Glenns Lake in Glacier National Park (*Schultz 1941*).*" The lake charr is native in Saint Mary, Lower Saint Mary, Cosley, and Glenn lakes, but whether the lake charr is native to Lower Two Medicine Lake is uncertain (Chris Downs, Glacier National Park, personal communication). On the basis of mtDNA (Wilson and Hebert 1998), Elk Lake and Twin Lakes contain native relict lake charr populations, although successful introductions into both lakes rendered both populations as not pure native stocks (Vincent 1963). Absence of exogenous mtDNA suggests that any introgression that may have occurred was limited (C. Wilson, Ontario Ministry of Natural Resources and Forestry, personal communication).

3.4 Minnesota

According to Eddy and Underhill (1974), "*the lake charr is native to Minnesota waters of Lake Superior and the deep lakes of the northern parts of St. Louis, Lake, and Cook counties and in several lakes in Itasca and Koochiching counties. The lake* *charr is not likely native to the Mississippi drainage in Minnesota, but is native to some lakes in the Arctic and Great Lakes drainages within the state. A small population of hatchery supported lake charr occurs in Lake Pokegama, which is closely connected with the Mississippi River, but it is unknown whether this population is native or remnants of a historical introduction (*Cox 1897*).*" Due to this uncertainty, Lake Pokegama and other lakes outside the native range or known to be of stocked origin were omitted from the dataset (i.e., Big Trout, Roosevelt, and Grindstone lakes).

3.5 Wisconsin

In the Mississippi basin of north-central Wisconsin, at least eight lakes contained lake charr at some point during the last 80 years. In two of the lakes, Black Oak and Trout (Vilas Co.), the lake charr is native as evidence of these populations occurs prior to European settlement (Lyons 1984), which was later confirmed by mitochondrial DNA analysis (Piller et al. 2005). Green Lake was omitted from the database because the population was introduced from a Lake Michigan source (Hacker 1957; Piller et al. 2005).

3.6 New York

According to Smith (1985), Plosila classified the distribution of the lake charr in New York as: "*(1) its relict natural range which includes the border lakes Erie, Ontario, and Champlain, and the Adirondack region, the Finger Lakes, and Otsego Lake in the Susquehanna drainage; (2) its introduced range including lakes in Sullivan, Westchester, and Putnam Counties; and (3) an unclassified area in St. Lawrence and Jefferson Counties for which it could not be determined whether the populations were native or introduced.*" Like other jurisdictions, the native status of several New York populations remains questionable. Lakes from the introduced range in Sullivan, Westchester, and Putnam Counties were removed from our dataset.

4 Processes and Variables Associated with Distribution

Compared to other freshwater fishes, the lake charr is restricted in its distribution to a narrow set of limnological conditions. For example, less than 1% of Ontario lakes are known to support lake charr (Martin and Olver 1976). Total waterbody area occupied by lake charr in our dataset was 451,304 km^2, which was 40% of the total waterbody area across the range (1,118,153 km^2), largely owing to the influence of the Laurentian Great Lakes. Deglaciation shaped dispersal and colonization routes (Wilson and Mandrak 2021), and water oxygen content, temperature, depth, and nutrient content appear to be key limnological variables limiting lake charr geographic and bathymetric distribution. Despite limnological limitations, the lake charr range extends from 42.020901 latitude in the south to 74.420800 in the north and from −62.700000 longitude in the east to −161.173090 in the west (Fig. 1). Lake charr occur in lakes that range in size from Teardrop Lake (3.4 ha; to our knowledge Brewer Lake [2.2 ha] listed by Gunn and Piblado 2004 does not contain lake charr) to Lake Superior (8,210,000 ha) and averaged 9567 ha (median = 192 ha) as calculated from the HydroLakes data set. Maximum depth ranges from 2.7 m for 79 lakes to 614 m in Great Slave Lake, Northwest Territories (mean of average lake depths = 10 m; median = 7.4 m). Lake charr occur in lakes from sea level (0 m) to 2035 m ASL, with a mean elevation of 381 m (median = 366 m).

4.1 Glaciation

Virtually all areas within the native range of lake charr were subject to Pleistocene glaciations, and the most recent glaciation, the Wisconsinan, likely eradicated most evidence of previous glacial cycles (Lindsey 1964; Wilson and Mandrak 2021). Glaciers influenced the current distribution of lake charr in two primary ways: by creating or altering potential distribution pathways during deglaciation, and by creating and leaving behind specific habitats within lakes that might facilitate completion of the lake charr life cycle. The lake charr is thought to have dispersed through proglacial lakes as Wisconsinan ice sheets receded, and the current distribution is the result of colonization dynamics coupled with “opportunities” associated with viable lake habitats linked by dispersal pathways (Wilson and Mandrak 2021). Wisconsinan ice sheets and ice streams also moved and deposited vast amounts of sediment and created a variety of landforms (Eyles and Doughty 2016; Margold and Stokes 2015; Menzies 2002), some of which may be important as lake charr habitat (Riley et al. 2014, 2017, 2019). As evidence of the influence of glacial processes, two large gaps in the distribution of lake charr in the Hudson Bay Lowlands and the prairie provinces of Canada (Fig. 1) are nearly identical to gaps in the distribution of glacially formed eskers in these same areas where no deep lakes occur (Storrar et al. 2013, 2014).

4.2 Water Temperature, Dissolved Oxygen, and Depth

Water temperature, dissolved-oxygen content, and depth are closely linked and primary determinants of lake charr distribution (Evans 2007; Marsden et al. 2021). The lake charr is considered a cold-water stenotherm with bioenergetics requiring an optimal thermal range of 8–12 °C and dissolved oxygen (DO) above 4 mg L^{-1}

Table 2 Frequency distribution of maximum depth (m) for lake charr *Salvelinus namaycush* lakes

	Martin and Olver (1976) $n = 1000$ Ontario lakes		Gunn and Piblado (2004) $n = 1932$ Ontario lakes	
Maximum depth range (m)	Number	Percent	Number	Percent
0–8	1	0.1	11	0.6
8–15	62	6.2	111	5.7
15–23	193	19.3	422	21.8
23–30	211	21.1	431	22.3
30–46	325	32.5	615	31.8
46–61	117	11.7	202	10.5
61–76	53	5.3	75	3.9
76–91	20	2	34	1.8
91–107	11	1.1	20	1
107–122	4	0.4	5	0.3
122–137	0	0	0	0
137–152	1	0.1	2	0.1
152+	2	0.2	4	0.2

(Christie and Regier 1988; Stewart et al. 1983). For example, lake charr yield was correlated with the amount of 10 ± 2 °C habitat in 21 large north-temperate lakes (Christie and Regier 1988). Similarly, in three small Canadian Shield lakes at the Experimental Lakes Area, Ontario, 75–90% of lake charr were captured in waters at >6 mg DO L^{-1} throughout spring and summer (Sellers et al. 1998). Use of habitat by acoustic-tagged lake charr was best predicted by a combination of temperature and DO (Plumb and Blanchfield 2009). In the northern part of the range, isothermal lakes provide appropriate water temperatures year-round, although most lake charr lakes thermally stratify. Shallow isothermal lakes (i.e., <10 m) that occur in the northern part of the distribution are becoming vulnerable to extreme temperature events. For example, a rapid warming event during an El Niño year resulted in bottom temperature exceeding 20 °C in Gullrock Lake, Ontario (max depth 13 m) and caused extensive mortality of all experimentally introduced lake charr (Gunn 2002). During stratification, lake charr distribution varies among and within lakes, and some forms of lake charr are known to vertically migrate daily across the thermocline during stratification (Hrabik et al. 2006). Lake charr can selectively occupy hypolimnetic waters as low as 4 °C, but frequently move into waters as warm as 20 °C (Guzzo et al. 2017; Plumb and Blanchfield 2009; Sellers et al. 1998). In the southern part of the distribution, deep lakes (>30 m) provide more thermally appropriate habitat for lake charr than shallow lakes (Lindsey 1964). Only ~6% of 1932 Ontario lake charr lakes were less than 15 m deep, 76% were 15–45 m, 16% were 46–91 m, and < 2% exceeded 91 m depth (Gunn and Piblado 2004), compared to only 5% of non-lake charr lakes having a maximum depth exceeding 30.5 m (Martin and Olver 1976; Table 2). A warming climate will likely influence how fishes use thermo-physical habitat and likely alter energy pathways and food webs (Campana et al. 2020; Collingsworth et al. 2017; Guzzo et al. 2017) to potentially expand lake charr distribution in the north and contract it in the south. Behavioral thermoregulation in response to changing climate could also influence distributions of lake charr and their prey within lakes, but was predicted via bioenergetics modeling to have only minor effects on lake charr growth in lakes Michigan and Huron (Kao et al. 2014).

4.3 Nutrient Content

Systems supporting lake charr tend to be oligotrophic, nutrient deficient, and supported by deepwater food webs consisting in their unaltered state of a simple complex that include so-called "glaciomarine relicts": opossum shrimp *Mysis relicta*, (now "*Mysis diluviana*") amphipods *Monoporeia affinis* and *Gammaracanthus loricatus*, calanoid copepod *Limnocalanus macrurus*, and the deepwater sculpin *Myoxocephalus thompsonii* (Dadswell 1974; Kontula and Väinölä 2003; Sheldon et al. 2008). About a dozen other deepwater fishes co-occur with lake charr across parts of the native range including: Arctic charr *Salvelinus alpinus*, burbot *Lota lota*, coregonines (whitefishes and ciscoes), and about a dozen other shallow-water fishes. With the exception of Lake Superior, more than 100 shallow-water fishes co-occur with lake charr in the Laurentian Great Lakes. In Ontario, lake charr lakes tend to be larger, colder, deeper, clearer, lower in total dissolved solids (TDS) and lower in littoral zone productivity than non-lake charr lakes (Martin and Olver 1976). Greater than half of Ontario's lake charr lakes surveyed had TDS between 10 and 29 mg L^{-1} and $> 80\%$ had a TDS of less than 50 mg L^{-1} (Martin and Olver 1976). Peak abundance of lake charr occurred in Ontario lakes with Secchi depths greater than 4.6 m (Marshall and Ryan 1987). These limnological conditions translate to a less productive trophic status of lake charr lakes than non-lake charr lakes. An extreme example is Great Bear Lake, Northwest Territories, which is so low in productivity (i.e., low dissolved solids [82 mg L^{-1}]; low total phosphorous [<10 μg L^{-1}]; high Secchi depth ~ 30 m; Johnson 1975; Moore 1980) that fish production and diversity is concentrated in nearshore habitats (Chavarie et al. 2013). On the basis of extensive lower food-web sampling, Miller (1947) concluded that Great Bear Lake's "open waters constitute almost a biological desert." Few freshwater fishes other than the lake charr have specialized to thrive in such low productivity, deep, cold waters.

Recent evidence shows widespread "browning," which is increased terrestrially derived dissolved organic carbon (DOC), of lakes within the lake charr distribution (Monteith et al. 2007; Williamson et al. 2015). Browning could temporarily offset the effects of climate warming by creating more rapid and shallower stratification, thereby capturing more cold-water habitat (Snucins and Gunn 2000). DOC may also represent a source of nutrients in lake charr lakes because concentrations associated with browning of these nutrient poor lakes are usually well below the concentration where productivity is adversely affected (Karlsson et al. 2015; Kelly et al. 2014).

5 Drivers of Dispersal and Colonization

The lake charr has likely gone locally extinct and recolonized waters many times throughout glacial history (Wilson and Mandrak 2021). It occurs in fresh waters of the Canadian Arctic islands and thrives where it is introduced outside of its native range (Hansen et al. 2021), which suggests the lake charr is an effective colonizer under ideal ecological conditions. Conversely, while it occurs in brackish waters of the Arctic Ocean, it has not dispersed across the Bering Strait to colonize Siberia and has not been re-established throughout the Laurentian Great Lakes despite a half century of restoration effort (Muir et al. 2012), which suggests it is a poor colonizer under sub-optimal ecological conditions. Several parameters including life history variation, physiology (i.e., oxythermal and salinity tolerance), and ecological opportunity (i.e., functional trait variation) likely influenced lake charr dispersal and colonization.

5.1 Life History Variation

Strong colonizers and invasive species are generally thought to be r-selected that increase rapidly in abundance to exploit new resources (i.e., fast life history traits), whereas K-selected species maintain relatively stable population sizes and reproduce slowly (i.e., slow life history traits) (Pianka 1970; Wilson and MacArthur 1967). Arguably, the lake charr is closer to K-selected than r-selected because its relatively "slow" life history does not favor rapid colonization. Likewise, its physiology does not promote rapid dispersal (discussed below). However, successful colonization may also be facilitated by high levels of life history variation that allow the charrs to thrive in newly de-glaciated habitats (Gunselman and Spruell 2019). The lake charr shows high intraspecific diversity (Chavarie et al. 2021; Muir et al. 2015), including highly divergent life histories among lakes and among morphs within lakes (Hansen et al. 2012, 2016a, b, 2021) and notable genetic variation (Krueger and Ihssen 1995; Wellband et al. 2021). Life history variation may facilitate colonization of novel environments. The converse is also possible where colonization of new environments facilitates life history diversification. Among about 200 lake charr populations from across the distribution, age at 50% maturity (t_{50}) ranged (0th to 100th percentile) from 2.9 to 27 y and length at 50% maturity (L_{50}) ranged from 208 to 660 mm (see Table 1 from Hansen et al. 2021). A lack of ecological and life history diversity among stocked fish could be hindering lake charr restoration in the Laurentian Great Lakes, where efforts have largely focused on stocking a single form—the lean lake charr (Muir et al. 2012; Zimmerman and Krueger 2009), albeit many lean genetic strains have been stocked (Scribner et al. 2018).

5.2 Physiology

Physiological diversity among deep- and shallow-water lake charr forms (i.e., lean, siscowet, redfin, humper; see Chavarie et al. 2021) likely facilitates dispersal and distribution (Eshenroder et al. 1995; Krueger and Ihssen 1995). Lipid metabolism, which has a genetic basis (Eschmeyer and Phillips Jr 1965; Goetz et al. 2010), is thought to be of particular importance in the ability of lake charr to colonize deep waters (>400 m) (Eshenroder et al. 1995). Homing (Binder et al. 2021), longevity, and age-at-maturity (see Hansen et al. 2021), prey availability (Marsden et al. 2021), and a flexible reproductive strategy that spans multiple habits from deepwater lacustrine shoals to rivers and temporally from April to January (Eshenroder et al. 1995; Goetz et al. 2021) are other important physiological attributes that influence colonization and contribute to the current distribution of the lake charr. These topics are covered in detail in other chapters of this volume—herein we focus on swimming and osmoregulation as key physiological determinants of dispersal.

Swimming ability is an important determinant of dispersal biology, particularly in postglacial environments. The lake charr has a generalist body locomotor type (Webb 1984) that primarily generates propulsion through subcarangiform locomotion (i.e., undulation of the posterior half of the body to generate propulsion; Bainbridge 1963) using a burst-and-glide swimming pattern (Cruz-Font et al. 2016). Swimming ability is a function of scope for activity, defined as the difference between standard (i.e., resting) metabolic rate and maximum sustained metabolic rate (Fry 1971). Scope-for-activity determines the range of energy available for all locomotor activities including active dispersal (Evans 2007). In juvenile lake charr, a ¾ scope-for-activity corresponds to ambient DO of 7.13 ± 0.27 mg L^{-1} at 4–12 °C, which supports most daily life-support activities (Evans 2007) and explains, in part, the habitat requirements and physiological dispersal limitations for the lake charr. In other words, metabolic requirements for cold, well-oxygenated water limits the ability of the lake charr to disperse and colonize via limitations on locomotion.

On the basis of available data and compared to known strong swimmers such as rainbow trout *Oncorhynchus mykiss*, the lake charr is likely intermediate among freshwater fishes in sustained and burst swimming ability. A sustained swimming speed of 0.46 body lengths (BL) per second or 0.36 m s^{-1} for fish averaging 775 mm was obtained from analysis of ultrasonic tag track movement data of six lake charr in Lake Superior (Stewart et al. 1983). In their bioenergetics model, Stewart et al. (1983) reduced their sustained swimming speed estimate by 25% (i.e., to 0.27 m s^{-1}) to compensate for bias associated with tracking spawning fish; they reasoned swimming speed would likely be reduced during the non-spawning period. The lake charr bioenergetics model developed by Stewart et al. (1983), including the swimming speed model was validated for Lake Michigan lake charr (Madenjian et al. 2000). Consistent with Stewart et al. (1983), mean swimming speed of acoustic telemetered lake charr in Lake Opeongo, Ontario was 0.25 m s^{-1} (Cruz-Font et al. 2019; calculation of mean swimming speed provided by L. Cruz-Font, University of Toronto, personal communication). Average burst speeds of 2.8–3.1 m s^{-1} for

460–510 mm lake charr were recorded within the laboratory (Feldman and Savitz 1999). In Lake Opeongo, Lake Louisa, Lake 373 and Lake 626, Ontario, peak swimming speed of acoustic telemetered lake charr was >0.8 m s^{-1} with a maximum burst speed of 1.10 m s^{-1} (Cruz-Font et al. 2019). In a laboratory swim test, 158–258 mm lake charr swam 1–1.15 m s^{-1} continuously for ~10 min, while similar-sized rainbow trout swam the same relative speed for 30 min before exhausting (Jones and Moffitt 2004). In another laboratory study, lake charr maintained sustained swimming speeds of 0.57 m s^{-1} (1 BL s^{-1}) for at least an hour, but were unable to maintain uniform locomotion at ~0.83 m s^{-1} (1.5 BL s^{-1}; Cruz-Font et al. 2016). Converted to body lengths per second, lake charr burst swimming speed of 5–6 body lengths per second is slower than 6.8–8.75 for rainbow trout (Katopodis and Gervais 2016). In spite of intermediate swimming performance, the lake charr distribution suggests that its locomotor capacity would enable it to negotiate movement up proglacial lake outlet channels and through flowing meltwaters during glacial retreat (Wilson and Mandrak 2021), but not likely through highly turbulent spillways associated with deglaciation. The lake charr is known to make long-distance feeding and spawning migrations within large lakes (Binder et al. 2021), and has colonized nearly all lakes in Glacier National Park on the west slope of the Rocky Mountains, via relatively high-gradient mountain streams (Fredenberg 2002; Fredenberg et al. 2007). Further investigation into the lake charr colonization of lakes within Glacier National Park is needed.

Salinity is another potential physiological constraint limiting lake charr dispersal. The lake charr commonly occurs in Arctic waters between 6‰ and 9‰ salinity (Boulva and Simard 1968; Lindsey 1964; Martin and Olver 1980) and have crossed presumably low salinity Arctic waters to reach islands in the Canadian Arctic Archipelago. Physiological evidence suggests that lake charr could survive for relatively long periods of time at low salinity (Hiroi and McCormick 2007; 6–9‰). Recent research has shown that anadromous and semi-anadromous lake charr life histories are more common in the Arctic than once believed and that an estuarine resident life history occurs (Kissinger et al. 2016, 2018; Swanson et al. 2010a, 2011). For example, otolith microchemistry showed that 27% of lake charr >13 years of age from four Arctic lakes made annual marine migrations with 60–66% of migrants diets being marine derived (Swanson et al. 2010a, 2011). Despite the retention of some degree of euryhalinity, full salinity sea water likely presents a barrier to migration and dispersal that contributed to lake charr failing to cross the Bering Strait to reach Siberia. While 80% of lake charr survived direct and gradual transfers to full-strength seawater (30‰), upregulated gill Na+/K+-ATPase activity, and high plasma ion and cortisol concentrations suggested lake charr were stressed under full sea water conditions (Hiroi and McCormick 2007).

5.3 *Ecological Opportunity*

Theoretically, successful colonizers show high levels of generalist traits (e.g., omnivory) or high levels of phenotypic plasticity, defined as the ability of an individual genome to produce different phenotypes when exposed to environmental cues (Pigliucci et al. 2006), or both. High diversity broadens the portfolio (*sensu* Schindler et al. 2015) and facilitates exploitation of novel resources or habitats when ecological opportunities arise (Skulason and Smith 1995). Ecological opportunity via key innovations, access to novel or heterogeneous habitats or trophic resources, or reduced competition, can result in character release and adaptive divergence into new niches (Nosil and Reimchen 2005; Skulason and Smith 1995; Yoder et al. 2010). Intraspecific diversity in functional traits is therefore important in colonization of novel habitats by variants within a species.

The lake charr is considered among the most diverse vertebrates on earth, with as many as 10 intraspecific phenotypes or morphs having been described within a single large (>500 km^2) lake (Goodier 1981; Muir et al. 2015; Chavarie et al. 2021). Many of the phenotypic traits that vary among lake charr morphs have been linked in other fishes to function. For example, eight linear measures of phenotypic traits linked to feeding (i.e., head and eyes) and locomotion (i.e., fin lengths and caudal peduncle shape) varied among four lake charr morphs in Lake Superior, consistent with specialized adaptations for trophic and physical resource use (Muir et al. 2012; see references therein). The capacity of the genotype to flexibly express phenotypic and life history variants has likely played a role in generating the current lake charr distribution.

6 Discussion

Any effort to establish the contemporary distribution of lake charr will be thwarted by history. That is, the true native distribution of lake charr is likely to be challenging to interpret, particularly at the margins of the distribution, because of human introductions, many of which occurred prior to the first documentation of its true native distribution (circa 1925). The examples provided above for Wisconsin, Maine, New York, and Ontario where considerable stocking has occurred highlight the challenge of understanding the true native distribution of the lake charr. Although we were unable to verify all suspected introductions in the data that we received, records were cross-referenced against published sources and against available historical records. Consequently, our dataset may contain some introduced populations, but these are likely few as our criteria for eliminating suspect records was conservative. Likewise, our conservative filtering criteria excluded some lakes that had native populations but were subsequently stocked. The few potential introduced and excluded populations in our dataset are unlikely to influence the range boundary of the species because they are within the native range of the species and not at distributional boundaries.

A warming climate is expected to result in niche tracking (Tingley et al. 2009) by lake charr where its distribution shifts to maintain appropriate physiological conditions (i.e., oxygen, temperature) to thrive. Changing ecological conditions could allow for potential northward expansion of lake charr through either human-assisted movement or direct habitat connections with suitable ecological conditions. In contrast, in the southern part of the distribution, some habitats may become inhospitable. For example, on the basis of a three-dimensional hydrodynamic model, available preferred thermal habitat for lake charr in Lake Superior increased at a mean rate of 6 days per decade (1979–2006) for shallow-water lean lake charr, whereas, deepwater siscowet lake charr lost 3 days of preferred thermal habitat per decade (Cline et al. 2013). Similarly, the number of modeled Arctic lakes that would be habitable to lake charr is predicted to increase by 6.8% ($n = 30{,}832$ lakes) by 2050 (Campana et al. 2020). Despite a modest opportunity for northward expansion of the lake charr range, these new habitats may not be colonized if they lack suitable access conditions.

Fishery monitoring programs are critical sources of data about lake charr occurrence. For instance, since 2008, Ontario’s broad-scale monitoring program has employed standard large- and small-mesh multi-mesh gillnets (13–121 mm increment stretch mesh; Sandstrom et al. 2009) to characterize several hundred lake charr populations throughout the province. Such standardized monitoring programs are not common across North America but provide invaluable data to inventory and evaluate spatiotemporal changes in fish populations, particularly in response to environmental change. A standardized monitoring program in the Arctic could be especially valuable to increase understanding of effects of rapid environmental change on fish populations, albeit logistically and economically challenging to implement.

Despite caveats, the aggregated data presented herein provide the most detailed account of lake charr distribution to date. Linking occurrence data to the HydroLAKES database (Messager et al. 2016) in a GIS context provides a useful tool to explore many questions about lake charr spatial ecology, habitat, colonization, and distribution. Some future areas of research are discussed below.

6.1 Future Research

- ***Historical introductions***—As mentioned above, the true native distribution of the lake charr is uncertain, particularly at the margins of the distribution, due to historical introductions. However, concerted effort to access and analyze historical stocking records, grey literature, and anecdotal accounts could better resolve the true native distribution of lake charr (e.g., Vincent 1963; Lyons 1984) and genetic studies could help confirm status for some questionable populations (e.g., Piller et al. 2005). Additionally, data from Crossman (1995), Evans and Olver

(1995), Nilsson and Svardson (1968), and other sources could be compiled and updated to generate a global introduction map for the species. Establishing accurate occurrence and introduction records would provide a valuable resource to facilitate research recommended below.

- ***Spatial and risk analysis***—Environmental and anthropogenic changes are expected to affect lake charr distribution (Campana et al. 2020; Cline et al. 2013; Collingsworth et al. 2017), potentially through niche tracking (Tingley et al. 2009) if new colonization routes are established. The database assembled herein and put into a GIS platform could facilitate informative spatial analyses of environmental change on lake charr distribution to assess the risk of such changes, particularly in the Arctic, where change is happening rapidly (Campana et al. 2020; Thuiller et al. 2011). Relating occurrence data to physiochemical, fine-scale geological data layers, and isostatic rebound data would facilitate quantitative spatial analysis of variables affecting distribution and allow hypotheses about postglacial colonization (see Wilson and Mandrak 2021), and spawning habitat (see Marsden et al. 2021) to be more fully addressed at the scale of the distribution.
- ***Inventories***—To better quantify the lake charr distribution and project how it may change in response to changing environments, governments should invest in long-term lake charr population and habitat monitoring. Such programs could be piggybacked on contaminant monitoring programs in the Laurentian Great Lakes and Arctic Canada (Muir et al. 2021) or as an expansion to on-going broad-scale monitoring programs such as Ontario's. Large-scale limnological changes, such as brownification (Roulet and Moore 2006; Williamson et al. 2015) and calcium decline (Weyhenmeyer et al. 2019), will likely influence lake charr distribution in the future. Predicting and adapting to changes in lake charr distribution and abundance is critically important to indigenous communities that rely on lake charr for food security (Islam and Berkes 2016). Finally, the lake charr is probably more common in northern rivers and historically, more common in rivers across the range, than previously thought. The lake charr may have evolved in fluvial habitats (Wilson and Mandrak 2021). We removed 177 river occurrences from our dataset. Compiling accurate riverine occurrence data would add an interesting and important element to our knowledge of distribution and could facilitate research on colonization and invasion ecology of the species.
- ***Movement ecology***—Technologies, such as acoustic telemetry, have shown that lake charr movement ecology and behavior is more complex than previously described (see Binder et al. 2021) and some individuals make long-distance (200 + km) movements within a season. However, little is known about lake charr movement or dispersal among ephemerally connected small lakes or how movements contribute to colonization. For instance, hatchery stocked lake charr were found to recolonize and establish reproducing populations in several barren downstream lakes near Sudbury, Ontario after water quality improved (J.M.G., personal observation). Additionally, lake charr have colonized most lakes on the west slope of the Rockies in Glacier National Park upstream from recently colonized Flathead Lake, which demonstrates its ability to move upstream into

new lakes using an interconnected system of lakes. A better understanding of movement ecology within and among lakes could help predict distributional changes, responses to climate and human-mediated change, barriers to dispersal, and identify vulnerable habitats to manage. A first step might be to identify lakes that have recently become colonized and evaluating connections among water bodies at a watershed level. This type of spatial analysis could reveal a better understanding of colonization routes and barriers to movement.

- ***Effects of invasive species and range expansion of native species***—Invasive species continue to threaten the ecology of lake charr lakes (Mills et al. 1993; Ricciardi 2001) and where compounded by other anthropogenic change (Conti et al. 2015) could result in local extirpations. The dispersal and colonization of lake charr lakes by smallmouth bass *Micropterus dolomieu* (Loppnow et al. 2013; Morbey et al. 2007) continues to be a threat that requires continued monitoring. With the opening of the Northwest Passage and increased mining and industrial development in the Arctic, road building will provide new access for humans and thereby human-mediated vectors of colonization (Drake and Mandrak 2010; Kaufman et al. 2009) for both native and non-native species. Likewise, we can learn much by studying the lake charr outside of its native range, where it is often considered invasive (see Hansen et al. 2021). Whether biological invasions or natural colonization differ is a topic of debate (Hoffmann and Courchamp 2016), but both processes threaten the ecology of lake charr, particularly in the northern part of its distribution and is an area ripe for research.

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Paleoecology

Chris C. Wilson and Nicholas E. Mandrak

Abstract The lake charr *Salvelinus namaycush* is an archetypal cold-water species closely associated with Pleistocene glaciations. Although repeated glaciations destroyed most traces of the species' zoogeographic history, its evolutionary and paleoecological legacy can be inferred from its biological attributes. Lake charr fossils are rare, but molecular evidence suggests the species diverged from other charrs during the late Pliocene or early Pleistocene. The lake charr differs from other charrs by its large size, longevity, extreme iteroparity, top predator specialization, reduced sexual dimorphism, and deepwater habitat. Ecological parallels between the lake charr and the taimen *Hucho taimen* suggest the lake charr may have originated as a large-bodied predator in Pliocene rivers, with subsequent lakes formed by glacial expansion and retreat providing novel ecological opportunities. Specialization as an apex predator for oligotrophic environments likely selected for longevity and iteroparity. Exploitation of benthic foods opened new opportunities largely unexploited by other charrs that drove other divergent traits such as vision, coloration, buoyancy, reduced sexual dimorphism, and spawning behavior. Although glacial refugia were highly dynamic environments, lake charr specialized for these conditions persisted in multiple refugia through several glacial cycles. Dispersal from Wisconsinan refugia enabled rapid colonization via vast meltwater lakes into its contemporary range.

Keywords Adaptation · Biogeography · Colonization · Dispersal · Evolution · Forage species · Glacial environments · Glacial refugia · Glacial retreat · Glaciations · Historical demography · Historical environments · Holocene · Ice age · Life history ·

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1 Introduction

As a group, charrs (genus *Salvelinus*) have been strongly influenced by glacial events and conditions (Behnke 1972; Power 2002). The lake charr *Salvelinus namaycush* is limited to habitats created by glacial scouring, and is specialized for ecological conditions created by glacial processes. The species was established in its native distribution via proglacial meltwater lakes and relies heavily on forage like ciscoes *Coregonus*, subgenus *Leucichthys* that similarly evolved in response to glacial events and related opportunities. The lake charr is well known as a large, long-lived top predator in cold, low-productivity systems (Martin and Olver 1980; Eshenroder et al. 1995; Muir et al. 2021). The species' habitat is typically lacustrine, although many northern populations also use rivers, and some populations are known to use brackish-water habitats (Lindsey 1964; Martin and Olver 1980; Power 2002; Chavarie et al. 2021). Although the contemporary niche of the lake charr is largely dictated by temperature, oxygen, and local food webs (Martin and Olver 1980), these factors also reflect the species' evolutionary past.

Reconstructing the origins, Pleistocene history, and paleoecology of the lake charr is difficult at best. The paucity of information on prehistorical environments and communities compared to the present requires a degree of speculation, and piecing together the limited clues available to reconstruct past ecological conditions and selective pressures. Ryder (1972) noted that describing the historical limnology and ecological conditions of North American oligotrophic lakes 200 years ago required an indirect approach, due to the extremely limited data available. Such an approach is even truer for reconstructions of palaeoecological conditions experienced by the lake charr from the late Pliocene to the present, particularly because nearly all of its modern range was repeatedly wiped clean by glacial advances and retreats (Dawson 1992; Wilson and Mandrak 2004).

This chapter complements and expands on previous assessments of lake charr evolutionary history (Lindsey 1964; Behnke 1972; Eshenroder et al. 1995; Wilson and Mandrak 2004) to consider how lake charr may have evolved in response to environmental conditions and perturbations as well as novel ecological opportunities. In writing this chapter, we have attempted to bring together clues from the geological record with zoogeographic evidence from the lake charr and its prey, as well as biological traits of the lake charr itself. Morphological, ecological, and physiological traits of contemporary lake charr reflect its evolutionary legacy, and were used to infer late Pliocene and Pleistocene environments and conditions that may have selected for these traits. We describe potential paleoecological conditions, summarize available information, and outline potential hypotheses or areas for future research to resolve outstanding questions. Hopefully, this chapter will stimulate new research and greater insights into the evolutionary ecology of lake charr past and present, and suggest new avenues for research to help predict future adaptive trajectories.

2 Evolutionary Origins

The evolutionary origins and paleoecology of the lake charr are poorly understood. The species is closely associated with Ice Age events and habitats, but direct evidence of its history preceding the most recent (Wisconsinan) glaciation is extremely limited (Eshenroder et al. 1995). The only known lake charr fossils are very recent, dating back to only 10,500–16,000 years ago [12.5–16 kya (Hussakof 1916; Sullivan et al. 1970) and 10 kya (Gruchy 1968; McAllister et al. 1988)]. Although both fossils confirm the close association of the lake charr with glacial habitats (described in more detail below), they are much too recent to shed light on the species' origins.

The lake charr is generally considered to have evolved in response to Pleistocene glaciation, particularly as it shows extensive adaptation to deep, cold, oligotrophic lakes (Lindsey 1964; Eshenroder et al. 1995; Wilson and Mandrak 2004). Many authors have noted a close fit between the contemporary distribution of the lake charr and the maximum extent of Pleistocene glaciations, with the exception of portions of the Canadian prairies and American Midwest that lack suitable habitat (Fig. 1; Lindsey 1964; Khan and Qadri 1971; Behnke 1972, 1980; Wilson and Hebert 1998). However, early evolution of the lake charr may have occurred during the late Pliocene, before the creation of the continent-wide network of glacial-scour lakes during the Pleistocene.

The three *Salvelinus* subgenera *Salvelinus*, *Cristivomer*, and *Baione* have generally been considered to have diverged during the late Pliocene or early Pleistocene (Behnke 1972, 1980; Grewe et al. 1990), roughly corresponding with the onset of the Pleistocene Ice Age (Dawson 1992). Based on morphological similarities, Lindsey (1964) considered lake charr to have evolved from *Hucho* or a shared primitive salmonid ancestor in the early Pleistocene. Behnke (1972, 1980) disagreed with this interpretation, attributing similarities between the lake charr and *Hucho* as due to ecological convergence between large piscivorous salmonids, and suggested that the lake charr and the brook charr *Salvelinus fontinalis* arose from a common ancestor in eastern North America during the late Pliocene. Multiple studies of salmonid molecular systematics have confirmed the substantial divergence between *Hucho* and *Salvelinus* and clear monophyly of the latter (Grewe et al. 1990; Crespi and Fulton 2004; Crête-Lafrenière et al. 2012). Using an estimated rate of mitochondrial sequence divergence of 2% per million years, Grewe et al. (1990) agreed with Behnke's (1980) interpretation of a late Pliocene or early Pleistocene divergence, and estimated separation of the three subgenera at 1.55 to 1.85 million years ago (MYA). Smith (1992) used fossils to generate a mutation rate of salmonid mitochondrial DNA of approximately 1% per million years, which would double the

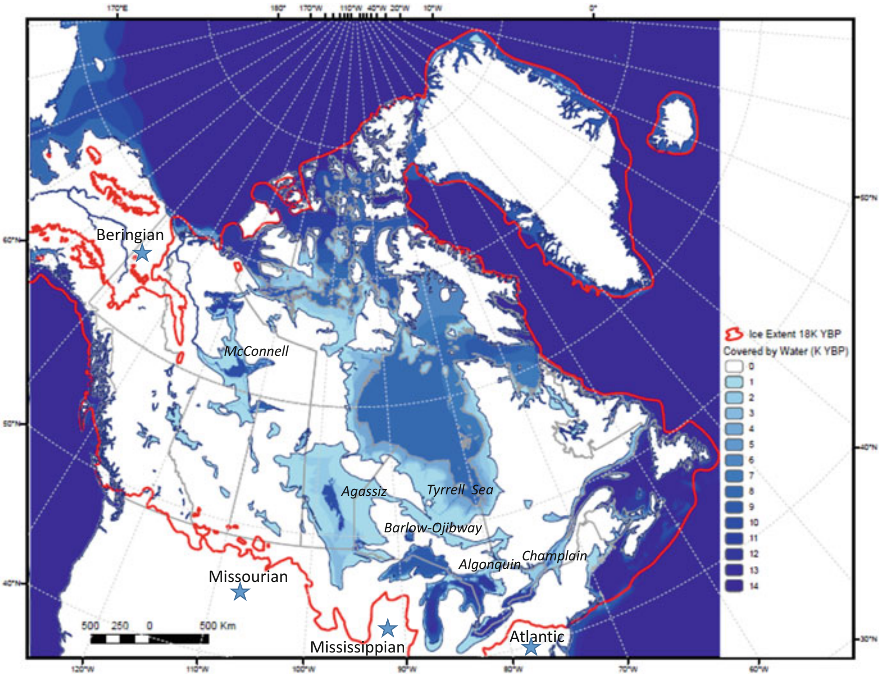

Fig. 1 Map of the native distribution of lake charr (black outline) *Salvelinus namaycush* with respect to maximum ice coverage 18,000 years ago (18 K YBP) and known occupied refugia during the Wisconsinan glaciation (red outline) and the major glacial lakes during glacial retreat at the end of the Pleistocene. Shading shows the duration of the glacial lakes but not their ages; also note that the major lakes were not all contemporaneous

divergence time. A recent holistic examination of speciation and divergence among salmonines places the estimated origins of the lake charr and the brook charr at approximately 3 million years ago (Esin and Markevitch 2018).

Molecular systematic studies continue to shed more light on potential origins of the lake charr. In a study of interspecific relationships among charrs based on nuclear DNA sequences of growth hormone introns, Westrich et al. (2002) showed that ancient hybridization between the lake charr and the Arctic charr *Salvelinus alpinus* or dolly varden *Salvelinus malma*, or both, blurred phylogenetic relationships within the genus. Crespi and Fulton (2004) combined existing mitochondrial and nuclear sequence data to evaluate evolutionary relationships within the Salmonidae and showed that the lake charr and the brook charr were substantially diverged sister species. The authors also noted incongruities between phylogenies based on different genes, and attributed these differences to extensive ancestral hybridization among charr species (Crespi and Fulton 2004), consistent with Holocene and contemporary hybridization (Hammar et al. 1989; Wilson and Hebert 1993; Wilson and Bernatchez 1998). The most comprehensive molecular phylogenetic analysis of salmonid relationships to date employed data from both Westrich et al. (2002) and

Crespi and Fulton (2004) and additional mitochondrial sequence data, and similarly showed ancient divergence between the lake charr and the brook charr after previously splitting off from other *Salvelinus* species (Crête-Lafrenière et al. 2012). Using a low rate of mitochondrial mutation (0.34% per million years), the authors placed the lake charr—brook charr divergence as approximately 7.5 million years ago, in the late Miocene (Crête-Lafrenière et al. 2012), but cautioned against overinterpretation of divergence timing across a broad array of species and genes based on a single molecular clock. Recently, Lecaudey et al. (2018) examined salmonine phylogeny using more than 28,000 nuclear loci and inferred that the lake charr and the brook charr diverged from other congeners and each other approximately 12 and 9 MYA, respectively. However, timing of intraspecific divergences within *Salvelinus* was based on a fossil formerly identified as *Salvelinus larsoni* (Stearley and Smith 1993) dated at 11 MYA, which was subsequently redescribed as *Paleolox larsoni* (Stearley and Smith 2016; see discussion of fossils below). Further, Smith's (1992) estimate of 1% change in mitochondrial DNA per million years based on the salmonid fossil record would place the suggested divergence time of Grewe et al. (1990) at 3.1–3.7 MYA, and that of Crête-Lafrenière et al. (2012) at approximately 2.5 MYA, roughly congruent with estimates by Behnke (1972) and Esin and Markevitch (2018). Similarly, the divergence time of *P. larsoni* from *Salvelinus* species estimated by Crête-Lafrenière et al. (2012) at 24 MYA may indicate an inflated estimate of divergence time by Lecaudey et al. (2018). Correcting for fossil interpretation would bring divergence time estimates in line with other studies described here. Divergence times among species may also have been substantially blurred by hybridization, selection, and rate variation among species and lineages, thereby obscuring when the lake charr first emerged as a species (Crespi and Fulton 2004; Lecaudey et al. 2018).

Although precise timing of the lake charr's origin is unlikely to be resolved, examination of the geological record provides insights into potential paleoecological and zoogeographic drivers of divergence. Throughout the Miocene, much of North America was drained by extensive river systems that traversed what is now Hudson Bay and emptied into the Labrador Sea, with the Bell River being the largest of these (Sears 2013). If the estimated divergence time between the lake charr and the brook charr by Crête-Lafrenière et al. (2012) is correct, lake charr would likely have originally evolved as a large-bodied predator in fluvial habitats similar to those occupied by *Hucho* species in Asia today.

Fossil fish remains from Miocene-age lacustrine sediments in the western Snake River Plain of southern Idaho include an extinct salmonid, *Paleolox larsoni*, with strong similarities to both *Hucho* and *Salvelinus* (Kimmel 1975). Stearley and Smith (1993) placed *P. larsoni* in the genus *Salvelinus* as a basal species, in part due to vomerine characteristics similar to the lake charr and *Hucho*. However, in a more recent publication, based on a greater number of fossils and more complete morphological evidence, the same authors restored *P. larsoni* to its original genus, which they considered intermediate between *Hucho* and *Salvelinus* (Stearley and Smith 2016). *P. larsoni* was a large predatory salmonine, with fossil specimens estimated as having standard lengths between 1.2 and 1.4 m, and a maximum size of 1.7 m total length (Stearley and Smith 2016). Based on the fossil strata in which specimens were found, Smith (1975) considered the species to have occupied lakes and, potentially, riverine habitats. Fossil specimens have been found in Miocene strata 7 and 9 MY old (Chalk Hills formation) and potentially as old as 10 MY (Poison Hills stratum), but to date have not been found in younger Pliocene or Pleistocene strata (Stearley and Smith 2016). For dating species origins and divergences, Crête-Lafrenière et al. (2012) estimated the divergence time of *P. larsoni* from *Salvelinus* species at 24 MYA, a date approximately three times older than the most recent fossil of *P. larsoni* (Stearley and Smith 2016). Other charr-like fossils potentially dated as old as 15–16 MY have been found from a handful of lake basins in western North America extending from northern Idaho to southwestern Nevada (Stearley and Smith 2016; R. Stearley, pers. comm.). Fish fossils are more likely to be preserved in lacustrine versus fluvial sediments due to differing levels of disturbance (Smith et al. 1988).

The lake charr shares a number of ecological traits with *Hucho*; in particular, its large potential size, longevity, posterior placement of the dorsal fin, similar (but reversed) colouration, and reduced dimorphism of secondary sexual characters between the sexes in comparison with other salmonines (Lindsey 1964). In addition, *Hucho* and the lake charr are considered atavistic in being mostly freshwater, non-migratory species (Stearley 1992), although some lake charr populations use brackish-water habitats (Chavarie et al. 2021). Both taxa also have high numbers of pyloric caecae (Lindsey 1964), which increase nutrient uptake capacity and may reflect their trophic position as apex predators or an adaptation to low-nutrient environments (Buddington and Diamond 1986). Whether these similar traits are due to ecological convergence (Behnke 1972) or retention of shared primitive traits (Smith 1975) is unknown, although the former seems more likely. Stearley (1992) and Stearley and Smith (2016) list a number of osteological traits separating *Hucho* from all *Salvelinus* species, and a number of derived traits distinguishing the lake charr from its congeners. These observations, however, still beg the question of what changed to cause the species to evolve, and why the lake charr retained ancestral characteristics that are apparently adapted to riverine environments.

Origins and divergences of charr species were hypothesized to be influenced by climate, hydrogeology, and ecological conditions associated with early glaciations (Lindsey 1964; Behnke 1972; Martin and Olver 1980). Power (2002) listed multiple life-history traits displayed by *Salvelinus* species, including the lake charr, that make them well-suited to periglacial environments, including adaptation to low temperatures, fall spawning, iteroparity with flexible timing between reproductive events, large egg size, and diet flexibility. Several traits listed by Power (capacity to reach large sizes, longevity, cryptic colouration, ability to live in dark conditions), apply more to the lake charr than other members of the genus, whereas others (habitat generalists, migratory behavior, and use of redds) are the reverse (Martin and Olver 1980). These traits reflect the species' specialization as a top predator in low-productivity systems (Martin and Olver 1980; Vinson et al. 2021) and its evolutionary history adapting to novel cold, deepwater habitats intimately linked to glaciation events.

The initial shift of the lake charr or its precursor from a large riverine predator to a cold-water lake specialist may have been triggered by a glacial event in the late Pliocene. Although North American glaciations are not generally thought to have occurred until the start of the Pleistocene approximately 2.6 MYA (Dawson 1992), geological evidence suggests that a major ice sheet formed in northern Quebec and expanded across what is now Hudson Bay at least as far as Manitoba and Ontario approximately 3.5 MYA (Gao et al. 2012). The expanding ice sheet would have dammed the Bell River and other Pliocene rivers flowing into the Labrador Sea (Sears 2013) and created novel cold-water lacustrine habitats along glacial termini (Ashley 2002; Carrivick and Tweed 2013). Bedrock scouring and plucking by the ice sheet would have created local depressions, which became lakes after the ice retreated (Dawson 1992; Ashley 2002). This early glaciation was likely short lived, because the late Pliocene was considerably warmer than today and showed a general warming trend (Melles et al. 2012; Brigham-Grette et al. 2013). The late Pliocene glaciation was thought to have had an extent comparable to later (Pleistocene) Laurentide ice sheets (Gao et al. 2012) that extended as far south as Iowa (Calkin 2002), and may have provided the original impetus for the lake charr to diverge in response to changed ecological conditions. The scenario described above would be consistent with Behnke's (1972) and Esin and Markevitch's (2018) assertions of the species' late Pliocene divergence from a common ancestor in eastern North America, and more contemporary evidence of glaciation events providing novel ecological opportunities (Skulason and Smith 1995) that act as drivers for speciation (April et al. 2013).

3 The Pleistocene

Although the lake charr may have been a product of the Pliocene, the Pleistocene was its playground. The Pleistocene was characterized by multiple glaciation events, with the first major event occurring approximately 2.6 MYA (Balco and Rovey II 2010; Dredge et al. 2015). Between 2.6 MYA and 800 kya, glacial advances and retreats predominantly occurred at approximately 41 ky intervals, consistent with Milankovitch cycles associated with angular variation (tilt) of Earth's rotational axis (Dredge et al. 2015). Over the past 800 ky, glaciations tended to follow a 100 ky cycle corresponding to the planet's orbital eccentricity (primary Milankovitch cycle; Calkin 2002). The latter glaciation cycles consisted of several waves of glacial advance and partial retreat over ~80 ky, followed by abrupt deglaciation at an interglacial interval of approximately 22 ky (Dawson 1992; Calkin 2002).

Reconstructing the extent of older paleo-ice sheets is difficult, because each glacial advance obliterated most evidence of preceding advances and retreats (Stokes et al. 2015). The oldest major expansion of the Laurentide ice sheet that occurred approximately 2.4 MYA (Balco and Rovey II 2010) may have been an important event for the origins of several species described as glaciomarine relicts (Dadswell 1974) and deepwater specialists that subsequently formed a novel forage base for the lake charr (see below). Subsequent major glacial advances occurred during the mid-Pleistocene, approximately 1.3 MYA, and several between 800 kya and the present (Balco and Rovey II 2010), the most recent occurring during the late Wisconsinan (Calkin 2002). At least three earlier glaciations had ice coverage comparable to or greater than the most recent (Wisconsinan) glaciation, based on geological evidence beyond the maximum extent of the Wisconsinan ice sheets (Calkin 2002; Dredge et al. 2015). Of these, at least one glacial advance displaced glaciomarine relict taxa as far inland as northern Montana and resulted in their becoming freshwater species (see below).

One question repeatedly raised is why native lake charr is limited to North America and absent from Siberia (Lindsey 1964; Muir et al. 2016, 2021). Lindsey (1964) suggested that marine Pacific lamprey *Entosphenus tridentatus* in the North Pacific may have served as a formidable biological barrier westward colonization by the lake charr, in addition to potential competitive interactions with *Hucho* occupying a similar trophic niche in Siberian rivers. A simpler explanation may be the coverage and extent of ice sheets during each glaciation event: while North America had extensive coverage by the Cordilleran, Laurentide, and Innuitian ice sheets, Siberia did not due to lower levels of precipitation (Dawson 1992). The supply of meltwater (livable habitat) would have largely been limited to ice margins, and isostatic depression of continental features from the weight of ice sheets would have caused meltwater flows toward the North American ice sheets rather than westward toward Siberia. A meta-analysis of phylogeographic data of multiple Beringian species showed that colonization was predominantly eastward (Waltari et al. 2007). Although Lindsay's (1964) reasoning may be correct, glacial coverage and associated physical processes may have confined the lake charr to North America (see Muir et al. 2021). Furthermore, a recent paleodrainage map of Beringia, ca. 18,000 YBP, indicates that its lakes were shallow, possibly wetlands, and drained south into the Pacific Ocean or north into the Arctic Ocean, not east-west (Bond 2019).

During each cycle of advance and retreat, ice sheets were much more dynamic than previously recognized (Stokes et al. 2015). In addition to multiple lobes and ice streams, ice sheets also have their own subglacial hydrology and meltwater outflows (Storrar et al. 2014; Stokes et al. 2015; Margold et al. 2018). Subglacial lakes and outflows at glacial termini can cause rapid advances due to reduced friction, thereby causing ice surges that further challenge reconstructing paleoecological conditions at glacial margins (Menzies 2002; Stokes et al. 2015). Ice streams and subglacial meltwater flows, the latter evidenced by large-scale networks of eskers radiating from ice dome centers (Storrar et al. 2014), highlight how dynamic ice sheets and their margins were.

4 Pleistocene Refugia and Lakes

Highly dynamic glacial systems resulted in formation of proglacial lakes along ice margins, which served as refugia for many aquatic species (Crossman and McAllister 1986; Lindsey and McPhail 1986). Refugia for aquatic species started as proglacial lakes and extended through meltwater overflows into unglaciated drainage basins. However, these proglacial lakes were likely the extent of southern refugia for cold-water species such as the lake charr, because few large, cold lakes are present in Atlantic coastal, Mississippi, Missouri, and Pacific basins in the south, and Beringia, Nahanni, and possibly Banks Island, basins in the northwest (Fig. 1). The lake charr may also have survived in cold-water riverine habitats in refugial areas close to the ice margins. If so, the highly disturbed nature of proglacial riverine habitats makes it unlikely that fossil evidence of lake charr presence will be found (Smith et al. 1988). Lake charr occupied most and potentially all these refugia during Pleistocene glacial maxima, although evidence of lake charr using a Pacific refugium is lacking (Fig. 1). As subsequent glacial advances erased many traces of conditions at ice margins, paleoecological reconstructions of proglacial lakes are mostly limited to conditions during late and end stages of the Wisconsinan glaciation (e.g., Teller and Clayton 1983; McAllister et al. 1988; Karrow et al. 2001). Vivid reconstructions of proglacial lake conditions are provided by Pielou (1991), Power (2002), and Carrivick and Tweed (2013). Proglacial lakes varied considerably in size and likely underwent different dynamic processes during glacial advance, maxima, and retreat (Carrivick and Tweed 2013), with some dwarfing contemporary freshwater lakes (Teller and Clayton 1983; Dawson 1992). Dammed by glacial fronts and fed by glacial meltwater, ice streams, and subglacial flows (Storrar et al. 2014; Margold et al. 2018), ice-dammed lakes could be quite deep close to ice margins due to isostatic depression of underlying ground (Teller and Clayton 1983; Ashley 2002; Carrivick and Tweed 2013). Surficial glacial ice streams and subglacial flows provided substantial sediment and till deposits (Storrar et al. 2014; Margold et al. 2018) that resulted in high sediment load, low light conditions, and submerged eskers and drumlins (Carrivick and Tweed 2013; Riley et al. 2014, 2017). Refugia were not static or stationary environments, but highly dynamic systems subject to changing conditions and locations, sometimes with abrupt and violent transitions. Lakes shifted in size, extent, and location with movements of glacial fronts, ice streams, and neighboring topography (Ashley 2002; Carrivick and Tweed 2013), and were subject to rapid and sometimes catastrophic drainage or changes in depth. Some of the best known recent examples toward the end of the Pleistocene were the emptying of Glacial Lake Missoula, the abrupt drainage of Glacial Lake Algonquin via spillways to the St. Lawrence River and formation of the Champlain Sea, and the emptying of Glacial Lake Agassiz and Barlow-Ojibway when the Laurentian Ice Dome collapsed over Hudson Bay (Pielou 1991).

Proglacial lakes may have largely been isothermal, particularly during glacial advances and maxima, with meltwater inputs from subglacial flows, surficial ice streams, glacial meltwater at 0 °C, and calving icebergs along ice fronts (Ashley

2002). Thermal stratification would also have been impeded by strong katabatic winds flowing off ice sheets onto surrounding warmer and lower elevation lands (Ashley 2002). Evidence of wind strengths and iceberg contributions are provided by iceberg scour tracks along former lake bottoms, which can be seen on top of the Scarborough Bluffs near Toronto, Ontario (Karrow et al. 2001) and on the former bed of Glacial Lake Agassiz in southern Manitoba (Dredge et al. 2015). Stratification in proglacial lakes would more likely have been due to sediment stratification than to thermal gradients (Ashley 2002; Carrivick and Tweed 2013), and may have been more prevalent during glacial retreat and mostly limited to areas near ice margins in large lakes. Evidence from contemporary populations shows that lake charr can use turbid waters close to ice margins (Northrup et al. 2010). Regardless of whether stratification occurred, proglacial lakes likely had abundant dissolved oxygen year-round due to their cold temperatures, great depth, low productivity, and surface disturbance due to katabatic winds.

Analysis of fossil plant and animal remains has provided windows into paleo-ecological conditions in proglacial lakes. For example, at the end of the last glaciation, Glacial Lake Agassiz was at the epicenter of the distribution and postglacial dispersal of the lake charr and served as a major nexus for refugia from all directions (Fig. 1; Stewart and Lindsey 1983). During its existence, ca. 11,700–7700 YBP, Glacial Lake Agassiz went through five major phases (Teller 1985). The initial Cass and Lockhart Phase commenced as the southern portion of the Agassiz basin became ice free and began to fill with cold, turbid glacial meltwaters from melting ice sheet and overflow into the Mississippi basin. Shores were dominated by boreal and tundra vegetation and roamed by woolly mammoth (Ashworth and Cvancara 1983; Ritchie 1983). During this phase, Glacial Lake Agassiz grew into a massive, deep (>170 m; Teller 1985) lake until it became much reduced in size and depth (~20 m; Teller 1985) during the Moorhead Phase, ca. 10,675 YBP (Fisher 2003). Shallowing of Lake Agassiz was the result of either the receding ice sheet exposing a lower outlet to the Superior basin that led to a catastrophic outflow and extensive draining of the lake (Teller 1985) or evaporation during the dry, cold Young Dryas period (Leydet et al. 2018). Increased salinity during this dry period caused turnover in mollusc and diatom species and spruce forest gave way to mixed deciduous and prairie vegetation (Ashworth and Cvancara 1983; Ritchie 1983). The Moorhead Phase of the lake continued to drain to the Superior basin until a glacial readvance closed the outlet and re-established a southern outlet to the Mississippi basin during the Emerson Phase, ca. 9600 YBP. During this phase, Agassiz was the largest lake known to have existed in North America, covering over 350,000 km^2 and exceeding 200 m in depth (Teller 1985). The lake drained for the last time as the melting ice sheet re-established outlets to the Superior basin, Nipigon Phase ca. 9500 YBP, with a series of catastrophic outflows exceeding 100,000 m^3 s^{-1} and 4000 km^3, then into proglacial Lake Ojibway, Ojibway Phase ca. 8500 YBP, and finally into the Tyrell Sea, ca. 7700 YBP (Fig. 1). Paleoclimatic reconstruction from biostratigraphic data in southwestern Manitoba indicate a gradual increase in mean summer temperature from ~4 °C in 11,000 YBP to ~15 °C by 9000 YBP, followed by a brief cold period, then a fluctuating increase to ~20 °C by the end of Lake Agassiz' existence (Ritchie 1983). Similar paleoecological transitions occurred in the Laurentian Great Lakes basin, with lake areas and depths varying widely (e.g., Karrow and Calkin 1985) and bordering terrestrial environments shifting from tundra to boreal to prairies and mixed woodland vegetation based on pollen data (e.g., Karrow et al. 1995, 2001, 2007). Despite these marked changes, the lake charr would have been among the first teleost to colonize both Lake Agassiz and the Great Lakes basin based on phylogeographic data (Wilson and Hebert 1996, 1998).

The only known lake charr fossils also provide clues to its late Pleistocene environments. Lake charr fossils described by Hussakof (1916) provide the only physical evidence of their presence in a Mississippian refugium and suggest that lake charr lived close to the ice-sheet margin. The clay layer of lacustrine sediments where the fossil was found is comprised of finely stratified silt, sand and clay, consistent with glacial deposition in a proglacial lake (Ashley 2002; Carrivick and Tweed 2013), and also contained fragmented mammoth, mastodon, caribou, and spruce fossils (Hussakof 1916). The clay layer was overlain by sand and gravel glacial outwash sediments (Hussakof 1916; Sullivan et al. 1970) that reflect dynamic conditions at the edge of the Laurentide Ice Sheet. Champlain Sea fossils from multiple fish species including lake charr (Gruchy 1968) enabled McAllister et al. (1988) to describe the fish community and probable paleoecological conditions. Fossils of multiple cold-water fish species including coregonines (either *C. artedii* or *C. zenithicus*), deepwater sculpin *Myoxocephalus thompsonii*, other sculpins, and suckers (e.g., Catastomidae), showed a cold-water fish community with the lake charr as the apex predator. Based on the median latitudes of the species' contemporary distributions, McAllister et al. (1988) interpreted the paleoclimatic conditions as comparable to southern Labrador, or subarctic conditions approximately 8.1° latitude north of the actual geographic location.

5 Pleistocene Interglacial Periods

The conception of lakes as stationary, stable environments is misleading, as most lakes are ephemeral from an evolutionary perspective, with lifespans of 20,000–30,000 years (Wetzel 2001). Despite this, for most of their existence, oligotrophic lakes provide consistent habitat with only seasonal variation (Wetzel 2001). By specializing for low-productivity, well-oxygenated lacustrine habitats, the lake charr is able to exploit a unique niche that few other salmonines or apex predators are able to use (Colinvaux 1978). In the absence of major competitors or predators, its potential and realized niche (sensu Hutchinson 1965) would have been virtually the same for most of the species' evolutionary history.

In the absence of serious interspecific competition or predation, lake charr would have thrived in oligotrophic lakes for the duration of interglacials throughout the Pleistocene, and during cycles of partial advances and retreat during the Wisconsinan and other major (100 ky) glaciations. With each renewed glacial advance, however, most lake charr populations would have been lost. Based on the dynamics of ice-sheet expansion (Menzies 2002; Stokes et al. 2015), populations in small lakes would likely have been extirpated by the influx of glacial till and sediment or displaced into unsuitable habitat by sudden flooding or drainage. Populations in large lakes would have been buffered to some extent by lake size, underlying topography, and connecting tributaries, and may have been entrained into proglacial lakes along the leading edge of the ice sheet.

Based on the presence of sympatric morphs within the Laurentian Great Lakes, Great Bear and Great Slave lakes, and lacs Mistassini and Albanel in Quebec (Muir et al. 2016; Chavarie et al. 2021), similar specialized morphotypes may have existed in deepwater glacial refugia, glacial lakes, or during previous interglacials (Eshenroder et al. 1995). To date, however, fossil and genetic evidence documenting the existence of specialized morphs before the current interglacial is lacking. Postglacial origins of contemporary sympatric ecotypes (Eshenroder 2008; Harris et al. 2015; Marin et al. 2016; Wellband et al. 2021) reflect the ability of lake charr to rapidly adapt to available trophic niches and ecological opportunities (Baillie et al. 2016; Muir et al. 2016; Chavarie et al. 2021).

6 Pleistocene Lakes as Novel Environments for Lake Charr

The formation of proglacial lakes and glacial-scour lakes during interglacial periods would have created novel habitats and ecological opportunities for species evolution and adaptation. Environmental conditions in lakes vary with depth from surface to bottom, with gradients equivalent to several orders of magnitude greater differences in elevation for terrestrial habitats, make lakes significant evolutionary arenas (Hutchinson 1965). This idea was further developed by Skulason and Smith (1995) and Schluter (1996), who argued that ecological release in these novel habitats was a primary driver in diversification and speciation in northern temperate freshwater fishes. Deep, cold, low-productivity lacustrine habitats provided novel conditions for aquatic species, with differences in light penetration, pressure, and benthic production that contributed to the formation of new species and species complexes, some of which provided a unique forage base for lake charr. Dadswell (1974) and Carter et al. (1980) described a freshwater assemblage of so-called "glaciomarine relict" crustacean and fish species in oligotrophic lakes (*Limnocalanus macrurus*, *Diporeia* sp., *Mysis relicta*, deepwater sculpin *Myoxocephalus thompsoni*, and others) that were derived from ancestral marine species displaced inland by expanding ice sheets. These "relict" species adapted to conditions in freshwater proglacial environments that are now confined to oligotrophic North American glacial-origin lakes (Dadswell 1974; Carter et al. 1980). Molecular systematic studies have shown that several of these species are North American endemics that diverged from their marine ancestors during the early to mid-Pleistocene (deepwater sculpin, Kontula and Väinölä 2003, *Mysis relicta* Audzijonyte and Väinölä 2005; Dooh et al. 2006) or even earlier (*Diporeia* taxa, Väinölä and Varvio 1989; Usjak 2009). By contrast, inland populations of *Limnocalanus macrurus* appear to have diverged from their marine ancestors during the late Pleistocene (Dooh et al. 2006). Based on divergence timing and geographic distributions, *Mysis* and deepwater sculpin were likely sluiced inland during major glaciation in the late Pliocene or early Pleistocene (Kontula and Väinölä 2003; Audzijonyte and Väinölä 2005, 2006). Subsequent phylogeographic analysis of both species and *Diporeia* showed the presence of intraspecific lineages with differing zoogeographic distributions in North American lakes, which suggests their divergence and subsequent expansion from allopatric refugia in the mid- to late Pleistocene (Dooh et al. 2006; Sheldon et al. 2008; Usjak 2009).

In their earliest stages, productivity in cold, ice-dammed lakes may have been strongly driven by benthic taxa. A number of these species, particularly *Diporeia* sp., *Mysis relicta*, and deepwater sculpin form key elements of the lake charr diet (Martin and Olver 1980) and have important roles in connecting benthic productivity with higher tropic levels in proglacial and subsequent lacustrine food webs (Vander Zanden and Vadeboncoeur 2002). Other species associated today with glacial meltwater lakes, such as lake whitefish *Coregonus clupeaformis*, ciscoes (*C. artedi* and relatives), and sculpins *Cottus* spp., are important prey species for lake charr (Dadswell 1974; Ryder 1972; Martin and Olver 1980; Scott and Crossman 1998). Of these, the origin of coregonines and freshwater cottids preceded the Pliocene and Pleistocene glaciations (Stearley and Smith 2016), but these taxa diversified and thrived in glaciolacustrine environments (Behnke 1972; Eshenroder 2008). Using these novel benthic and pelagic forage bases would have created ecological opportunities for the lake charr, despite the low productivity of these oligotrophic environments (Colinvaux 1978; Wilson and Mandrak 2004; Brodersen et al. 2018).

Novel ecological conditions in proglacial lakes and glacial-scour lakes likely had a profound influence on lake charr life history and adaptive traits that potentially reinforced some existing traits and drove selection for others. The lake charr is a cold-water specialist with a preferred temperature range of 8–12 °C (Martin and Olver 1980; Plumb and Blanchfield 2009), and comparative thermal physiology trials on populations from Canadian Shield lakes have shown remarkably little variation among populations (McDermid et al. 2013; Kelly et al. 2014). Contemporary populations of lake charr require cold, well-oxygenated water that does not drop below 4 mg/L of oxygen (Evans 2007; Marsden et al. 2021). Although contemporary populations typically occur in clear oligotrophic habitats, the lake charr is able to exist in lakes with high turbidity from suspended silt and rock flow from glacial inflows (Northrup et al. 2010) and to use habitats close to glacial margins (Power 2002). Adapting to low-light conditions at greater lake depths, as well as from glacial sediments and turbidity, has resulted in lake charr expressing a different eye pigment in addition to that shared with other charrs (Ali and Wagner 1980), enabling it to see at depths >300 m (Harrington et al. 2015). The lake charr is unusual among salmonines in relying extensively on benthic food resources (Vander Zanden and Vadeboncoeur 2002) such as *Diporeia*, *Mysis*, deepwater sculpin, and other benthic species where present (Martin and Olver 1980; Scott and Crossman 1998; Vinson et al. 2021). Specialization as a top predator in low-productivity environments is also reflected by the lake charr's high number of pyloric caecae (Vladykov 1954; Martin and Olver 1980), which aid in nutrient uptake (Buddington and Diamond 1986) and may have benefitted or facilitated energetic conversion in low-productivity habitats or food webs. The radiation of the cisco species complex in large lakes (>500 km^2; Todd and Smith 1992; Muir et al. 2014) may also have acted as a driver for parallel diversification of lake charr ecotypes (Eshenroder 2008; Brodersen et al. 2018), with both groups partitioning by depth and diet (Eshenroder et al. 1995, 1998; Eshenroder 2008; Muir et al. 2016).

Adaptations to deepwater habitat and low-light conditions may have driven or reinforced the evolution of other traits, such as the lake charr's reduced sexual dimorphism, less vivid colouration, and spawning at night. In turn, these traits have likely influenced sexual selection and mate choice in the lake charr compared with other charrs, as evidenced by lack of redd use, instead spawning in lakes over rock rubble (including submerged drumlins and eskers; Riley et al. 2017, 2019; Marsden et al. 2021). Icy temperatures and low productivity of proglacial environments would have required substantial time for lake charr to grow to adult size and reach reproductive maturity as a large-bodied top predator. The lake charr is among the longest-lived salmonines and shows the highest degree of iteroparity (Martin and Olver 1980; Fleming and Reynolds 2004). As a large-bodied top predator in low-productivity habitats, the lake charr has a much older age at maturity than most congeners (Vladykov 1954; Scott and Crossman 1998) and also exhibits skip-spawning in both very large (>500 km^2) and small inland lakes (Johnson 1972; Martin and Olver 1980; Goetz et al. 2011, 2021; Morbey and Shuter 2013; Sitar et al. 2014). In a stable population (lifetime replacement = 1), long life and late maturity would also indicate relatively few recruits per year and low survival to adulthood, with populations dominated by old age classes (Mills et al. 2002). In addition to its extreme iteroparity, the lake charr is remarkable among charr species in its sharply reduced sexual dimorphism of secondary sexual characters (Fleming and Reynolds 2004) and is also the only charr species that does not exhibit maturation at the juvenile stage (Esteve 2005). This reproductive strategy is energetically expensive (Fleming and Reynolds 2004) and could be risky in a cannibalistic species. A lack of fixed redd locations for spawning in the lake charr might also make precocious maturation risky. Whether any or all of these factors contribute to the lack of precocious maturation, reproduction in the lake charr is bioenergetically expensive and size driven (Morbey and Shuter 2013). Thus, longevity may have been important for enabling the lake charr to achieve the large body size needed as a top predator.

Although glacial cycles have been linked to speciation events (Hewitt 1996; April et al. 2013), the lake charr shows remarkable ecological and morphological consistency across its range (Lindsey 1964; Behnke 1972, 1980; Martin and Olver 1980), with specialized morphotypes and sympatric forms largely limited to large lakes (Muir et al. 2016; Chavarie et al. 2021). Therefore, selection for novel ecological traits possessed by the lake charr likely happened early in the species' evolutionary history, based on the remarkable stability of morphological, physiological, and life-history traits across the species range (Lindsey 1964; Khan and Qadri 1971; Behnke

1972, 1980; McDermid et al. 2013; Evans 2007; Kelly et al. 2014). If so, the ecological factors and evolutionary opportunities that gave rise to the lake charr as a species probably occurred soon after initial formation of lake environments and evolution of forage species adapted to these novel environments, which led to its specialization for deep, oligotrophic habitats. In turn, some specializations, such as long generation time and requirements for low temperatures and high levels of dissolved oxygen (Evans 2007; Kelly et al. 2014), may limit its ability to persist in modern, changing environments (Martin and Olver 1980; Wilson and Mandrak 2004).

7 Pleistocene Zoogeography of Lake Charr

Intraspecific phylogeographic divergences in the lake charr provide evidence of repeated vicariant divergences caused by glaciations throughout the Pleistocene (Grewe and Hebert 1988; Wilson and Hebert 1996, 1998). Although contemporary data are limited to identifying fish descended from Wisconsinan refugia (Wilson and Hebert 1996, 1998), three major lineages originally described by Grewe and Hebert (1988) and Grewe et al. (1990) correspond with vicariant divergences driven by glacial advances during the mid-Pleistocene. Assuming a mitochondrial mutation rate of 1% per million years Smith (1992), major vicariant divergence events occurred approximately 800 kya and 400 kya (Wilson and Hebert 1996, 1998). More recent divergences within two of the major lineages likely occurred in allopatric refugia during the Illinoian glaciation for the Nahanni and Atlantic lineages, and separation in northwestern, Missourian, and Mississippian refugia for the mitochondrial “C” lineage (Wilson and Hebert 1998). Accordingly, evidence from extant populations is clear that lake charr were repeatedly isolated in multiple allopatric refugia during at least four glaciation events. Given the substantial difference in levels of mitochondrial divergence among lake charr lineages (<1%; Wilson and Hebert 1996, 1998) versus the substantial divergence of the lake charr from its congeners (Grewe et al. 1990; Crespi and Fulton 2004; Crête-Lafrenière et al. 2012), entire evolutionary lineages of lake charr from previous glaciation events were probably eliminated by glacial advances, died out in insufficient refugia, or went extinct. However, additional lineages may be extant in populations that have not been genetically surveyed, particularly in non-glaciated or isolated areas such as Banks Island in the western Arctic (Fig. 1), or have not been assessed for their phylogeographic ancestry (Crane et al. 2015).

Based on contemporary secondary contact among extant lineages in areas formerly covered by proglacial lakes at the end of the Wisconsinan glaciation (Wilson and Hebert 1996, 1998), similar secondary contact among dispersing refugial populations probably also occurred at the end of previous glaciations. Clear segregation of mitochondrial types in separate refugia during the last glacial maximum (Wilson and Hebert 1998) underscores the extent to which displaced populations were decimated and the severity of bottlenecks preceding or during establishment of different refugia, as well as long-term constraints on refugial populations over evolutionary timescales (Bernatchez and Wilson 1998; Wilson and Hebert 1998). Given that some of the initially displaced populations would likely have had levels of diversity comparable to those in major lakes today (Wilson and Hebert 1998; Harris et al. 2015; Baillie et al. 2016; Wellband et al. 2021), the reciprocal monophyly and low diversity among Wisconsinan refugial populations is a testament to the severity of impacts of glaciation events on lake charr populations (Power 2002). Repeated cycles of vicariant displacement, isolation, and re-expansion through the Pleistocene have left lasting signatures on contemporary populations of many northern species, but particularly for the lake charr (Bernatchez and Wilson 1998).

At the end of the Wisconsinan glaciation, lake charr dispersed from six known refugia in Beringian, Missourian, Mississippian, and Atlantic drainages, by utilizing giant meltwater lakes fed by the melting Laurentide Ice Sheet (Fig. 1). The dynamic nature and spatial and temporal extent of proglacial lakes enabled contact among different lineages, which followed retreating ice margins closely (Wilson and Hebert 1996, 1998; Wilson and Mandrak 2004). Phylogeographic reconstructions of lake charr persistence in Wisconsinan refugia and their Holocene postglacial colonization have provided insights into their late Pleistocene and Holocene zoogeography (Wilson and Hebert 1996, 1998; Wilson and Mandrak 2004), but are likely oversimplified. Previous analyses of lake charr zoogeography have relied on methods such as geographic distribution (Lindsey 1964), morphometric analysis (Khan and Qadri 1971; Crossman and McAllister 1986), and parasite distribution (Black 1983a, b). All of these were necessarily limited to assessing dispersal from Wisconsinan refugia, and information on deeper vicariant and evolutionary events was limited at best (Wilson and Mandrak 2004). Similarly, phylogeographic analyses by Wilson and Hebert (1996, 1998) relied on coarse-grained analysis of mitochondrial DNA (mtDNA) using restriction enzymes. Reliance on a maternally (uniparental) inherited genetic marker substantially underrepresented secondary contact among dispersing refugial populations, as suggested by morphometric and parasite analyses (Khan and Qadri 1971; Black 1983a, b). More recent phylogeographic studies of other species revealed the presence of multiple, previously cryptic refugia or subrefugia, and hidden complexity in dynamics, dispersal, and secondary contact among refugial groups (e.g., Brunner et al. 2001; Turgeon and Bernatchez 2001; Bernatchez and Dodson 1994; Witt et al. 2011; Moore et al. 2015; Morgan et al. 2017). As mentioned above, additional evolutionary linages of lake charr may wait to be discovered in nonglaciated portions of the species range, such as the Old Crow basin in the Yukon Territory and Banks Island in the western Canadian Arctic, and areas with complex and understudied deglaciation histories such as the Yukon River Basin in Alaska (Crane et al. 2015), northern Quebec, and mainland Nunavut. Combined mitochondrial and nuclear analyses can also provide more nuanced insights into secondary contact among refugial lineages (Wellband et al. 2021), and the advent of large numbers of genomic markers promises to provide further resolution of the lake charr's phylogeographic history. In addition, historical occupancy of candidate refugia and dispersal pathways by lake charr could be evaluated by testing paleolacustrine sediments for ancient DNA (Pederson et al. 2016) to potentially fine-tune timing estimates of dispersal events.

8 Historical Demographics

Despite their limitations, existing phylogeographic data provide some insights into historical environmental conditions. The lake charr has one of the lowest evolutionary effective population (N_e) estimates of North American freshwater fishes studied to date (estimated evolutionary female effective population size (N_{ef}) of 3.4×10^4; Bernatchez and Wilson 1998) that reflects multiple severe demographic impacts relating to Pleistocene events. The vicariant separation among mtDNA lineages in allopatric refugia also enables some speculative reconstruction of ancestral population sizes. The low N_{ef} of contemporary lake charr populations reflects repeated cycles of population displacement and loss during ice advances (Wilson and Hebert 1996, 1998; Bernatchez and Wilson 1998; Power 2002). Most inland lake populations were likely extirpated by glacial advances, as they would either have been obliterated by advancing glacial fronts, catastrophically inundated with sediment-laden glacial meltwaters or proglacial lake outflows or displaced to waterbodies along glacial margins. Founding diversity within each refugium may have been a diverse mix of surviving refugees (i.e., displaced survivors). Subsequent diversity over time would have been influenced by population size that, in turn, would have been limited by habitat size and quality, food-web productivity, and local carrying capacity. Other limiting factors influencing N_e included recruitment, variation in reproductive success, and genetic drift across multiple generations (Avise et al. 1984; Avise 2000), which would have had pronounced effects in peripheral refugial populations (Wilson and Hebert 1998; Wilson and Mandrak 2004).

Using restriction site data, Wilson and Hebert (1998) constructed a mutation network or minimum spanning tree among lake charr haplotypes. In addition to showing relationships and diversity within and among different refugial lineages, the same data can be used to construct a mismatch distribution among lake charr haplotypes. The resultant multimodal mismatch distribution supported repeated vicariant divergence that reflects the persistence of lake charr in multiple refugia and exhibits hierarchical divergence among the different lineages (data not shown).

For most of the refugial lineages observed by Wilson and Hebert (1998), the apparent loss of diversity within allopatric refugia was severe: examining each lineage separately, only the main Mississippian (A) lineage had sufficient variation to assess the diversity that refugial environment might have supported. Comparing the number and relative abundance (haplotype richness and nucleon diversity) of different extant group A haplotypes with these same metrics in contemporary populations, independent of lineages from which haplotypes of the latter populations originated (i.e., comparing diversity metrics within the A lineage to those for all haplotypes present in modern populations), showed that haplotype richness and diversity of the A lineage was comparable to contemporary populations in lakes with surface areas of approximately 10,000 ha (C. Wilson, unpublished data). Although admittedly a crude measure, this surprisingly low value may reflect long-term constraints on population size in the Mississippian refugium over thousands of years, as well as likely disruptions to the local environment that may have impacted the refugial population. Re-examining this question using combined mitogenomic and nuclear data (Wellband et al. 2021) to test coalescent simulations of refugial populations would likely substantially improve understanding of prehistoric population dynamics in glacial refugia.

9 From Pleistocene to Holocene

As the Laurentide ice sheet started to recede, ca. 18,000 YBP, meltwaters formed proglacial and glacial lakes along the southern margin of the ice sheet Dyke et al. (2003), which flowed into southern, or out of northern, refugia (Fig. 1). These glacial lakes and outlets formed dispersal corridors for lake charr to colonize recently deglaciated areas. At their maxima, a series of large glacial lakes extended from the Mackenzie Valley in the north, southeast through the great lakes of central Canada and Laurentian Great Lakes basin (Fig. 1), although not all of these lakes were contemporaneous. The spatial and temporal extent of these large glacial lakes varied with position of ice sheets and isostatic rebound Dyke et al. (2003) to allow lake charr to broadly disperse throughout northcentral North America until contemporary drainages formed about 6000 YBP and prevented further dispersal. These recolonization patterns have been well documented (e.g., Wilson and Hebert 1998; Wilson and Mandrak 2004). Wilson and Mandrak (2004) hypothesized that smaller, dynamic proglacial lakes along the edge of the ice sheet also played an important role in postglacial dispersal of lake charr, with cold-water fish dispersing closely with the receding ice sheet. These lakes would have been the primary means for dispersal from the Missourian, Nahanni, and Atlantic refugia into areas that were not covered by large proglacial lakes, such as central British Columbia, the Ungava Peninsula, and Acadia (Fig. 1). As the locations and depths of proglacial and glacial lakes changed in response to inflows, outflows, glacial movements, and isostatic adjustments, lake charr would have been isolated in local depressions that became contemporary lakes.

Dispersal through glacial or proglacial lakes would have been complemented by local colonization of newly available habitats, not covered by glacial or proglacial lakes (e.g., at higher elevations), via meltwater streams (Power 2002). The esker networks described by Storrar et al. (2014) demonstrate the abundance of flowing waters during glacial retreat of the Laurentide Ice Sheet, with similar processes also acting on local scales. Although lake charr were able to actively disperse using postglacial flows to colonize newly exposed habitats, not all forage species were able to do the same (Dadswell 1974). The distribution of *Mysis* and *Diporeia*, in particular, were dictated by glacial movement and retreat patterns, particularly for meltwater lakes. These macroinvertebrate species are weak dispersers whose distributions reflect direct coverage by meltwater lakes at the end of the Pleistocene and early Holocene (Dadswell 1974; Carter et al. 1980).

After glacial meltwaters receded, lake charr were isolated into local finite populations. Except for a few very large lakes, such as Great Bear Lake, Great Slave Lake, and the Laurentian Great Lakes, postglacial ecological conditions would have been markedly different from those in proglacial lakes. Once isolated, the same ecological and demographic constraints described earlier would have limited local population sizes (Martin and Olver 1980; Mills et al. 2002), with subsequent effects on N_e and population divergence (Hill 2018; Wellband et al. 2021). These conditions may have been more pronounced during the warmer Hypsithermal interval approximately 8.5–6 kya (Pielou 1991; Teller et al. 2017), but many lake charr populations were able to persist for millennia in the absence of harvest exploitation and competition from warmer-water species.

Zoogeographic reconstruction of postglacial colonization at finer scales is more readily undertaken with modern geographic information systems and biological inventory data. As an example, Ridgway et al. (2017) combined fine-scale mapping of surficial geological features, a digital elevation model, and isostatic rebound rates with species occurrence data to reconstruct postglacial colonization of the Algonquin Park region in central Ontario by aquatic species. The occurrence of *Mysis* in Canadian Shield lakes within Algonquin Park is limited to Glacial Lake Algonquin and its main outflow, the Fossmill Outlet, areas directly covered by proglacial flows (Dadswell 1974; Carter et al. 1980). By contrast, the more extensive distribution of native lake charr populations in Algonquin Park, combined with geological data, indicates that they were able to colonize lakes not directly covered by outflows from Glacial Lake Algonquin (Ridgway et al. 2017). The distribution of Atlantic refugium haplotypes in Petawawa watershed lakes below 385 m elevation (Wilson and Hebert 1996, 1998; Halbisen and Wilson 2009; Ridgway et al. 2017) indicates colonization from the east likely occurred after the closure of the Fossmill Outlet, ca. 10,400 YBP, via the Champlain Sea or Lampsilis Lake (McAllister et al. 1988; Pielou 1991), rather than by fish of Mississippian origin from Glacial Lake Algonquin outflows as originally posited (Wilson and Hebert 1996, 1998; Halbisen and Wilson 2009). Combining surficial geology, temporal glacial coverage, and isostatic rebound data could similarly be applied elsewhere to test predictive colonization scenarios by mapping genetic relationships among local populations and comparing identified structure to contemporary and historical watersheds.

10 Conservation Implications

The same characteristics that made the lake charr highly adapted to Pleistocene lacustrine conditions make it vulnerable to anthropogenic and emerging environmental pressures (Gunn et al. 2004). Life-history and ecological traits that were previously beneficial for bet-hedging in cold, low productivity habitats limit the lake charr's ability to adapt to rapidly changing environmental conditions. Ecological constraints imposed by its temperature and oxygen requirements largely limit lake charr to the hypolimnion in the mid- and southern areas of its distribution (Evans 2007; Plumb and Blanchfield 2009) and seasonally isolate them from forage species in productive littoral habitats, as well as making them vulnerable to oxygen depletion through eutrophication and longer summer stratification (Evans 2007). As a long-lived top predator with a long generation time, the lake charr has only limited opportunities for juvenile recruitment (adult replacement) in stable populations, with resultant low rates of population growth or recovery that make lake charr populations vulnerable to overexploitation (Martin and Olver 1980; Mills et al. 2002; Lester et al. 2021). Depositing eggs over rock rubble instead of burying them in redds leaves lake charr eggs and pre-hatch embryos vulnerable to predation by invasive species such as round goby *Neogobius melanostomus* (Fitzsimons et al. 2009) and rusty crayfish *Orconectes rusticus* (Jonas et al. 2005) and expanding warm-water native species such as centrarchids and percids into lake charr habitats (Vander Zanden et al. 1999). Its evolution in species-poor environments leaves the lake charr vulnerable to competition, as it is ill-equipped to compete with other predators such as esocids *Esox* spp. or bass *Micropterus* spp., particularly in small inland lakes (Vander Zanden et al. 1999, 2004). Adaptive limitations imposed by its long generation time, longevity, and trophic position as an apex predator are compounded by low genetic effective population sizes, especially for inland lake charr populations (Mills et al. 2002; Hill 2018; Wellband et al. 2021).

11 Areas for Future Research

Understanding the potential resilience and adaptive potential of lake charr populations would be valuable and timely. With many emerging environmental stressors, important questions for lake charr management include:

- The extent of local adaptation is still poorly understood for inland populations in general, in contrast to specialized ecotypes in the Laurentian, northwestern, and Quebec great lakes (Eshenroder et al. 1995; Muir et al. 2016; Chavarie et al. 2021). Given the physicochemical stability of deepwater habitat in many inland lakes, the extent of local adaptation or specialization is an open question, and very relevant for restoration or reintroduction efforts. For example, the extent of ecological equivalency among inland populations may be important to know, to reverse local losses or extirpations.
- How able are local populations to cope with and adapt to changing environmental (e.g., temperature, oxygen) regimes? Similarly, how flexible are lake charr populations for phenological changes in reproductive timing in response to increasing temperatures, delayed fall turnover, and earlier ice-out, and what are the consequences of phenological changes for lake charr recruitment? As environmental conditions continue to change rapidly, populations may need to cope

with persistent directional selection over the short-term by acclimation, as well as long-term adaptation. Understanding the rate and potential for acclimation and adaptive responses may become important for predicting the probability of population viability and persistence.

- What is the standing adaptive variation within and among lake charr populations? As new challenges increase, a knowledge of the adaptive potential of lake charr populations at local, regional, and range-wide scales may become increasingly important for their sustainable management. This would include identifying populations with potential cryptic diversity (e.g., long isolated lakes) through a combination of postglacial geology, genetic, and trait analyses. The advent of more sophisticated genomic tools also holds promise for more nuanced and comprehensive understanding of the genetic architecture underlying adaptive traits from historical and contemporary environments, as well as the deeper evolutionary history of lake charr at both species and population levels (Wellband et al. 2021).

12 Take-Home Messages

Contemporary populations of lake charr reflect the rich evolutionary and paleoecological legacy of the species. Despite rapid environmental change and concern about future sustainability of populations in a warming and increasingly crowded world, the lake charr has persisted through multiple glacial and interglacial intervals over its evolutionary history, including several periods with warmer temperatures than today (Ritchie 1983; Karrow et al. 2001; Wilson and Mandrak 2004; Teller et al. 2017). In their synthesis of lake charr biology, Martin and Olver (1980) paint a somewhat gloomy outlook for the lake charr, due to its extreme sensitivity to anthropogenic disturbances such as pollution, development, introduction of exotic and native species, and exploitation. While we agree that its biological traits combined with its dependence on pristine cold-water habitats makes the lake charr vulnerable to contemporary stressors, our improved knowledge of the species' history and biology should help inform policy and management decisions that ensure this iconic Ice Age fish has a future as well as a past.

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Ecological Diversity

Louise Chavarie, Colin E. Adams, Heidi K. Swanson, Mark S. Ridgway, William M. Tonn, and Christopher C. Wilson

Abstract Lake charr, *Salvelinus namaycush,* ecological and phenotypic diversity within and among populations was reviewed from empirical and conceptual perspectives. The species is generally the top predator in oligotrophic lakes, with diversity either constrained, or promoted by, habitat depth and complexity, available forage species, and presence or absence of competitors. Diversity in smaller lakes is generally limited to forage-based life-history variation. Large, complex lakes provide a greater array of available resources, thereby enabling diversification to capitalize on increased ecological opportunities. Morphological and ecological differentiation is common between deep-water (humper-like or siscowet-like) and shallow-water (lean-like) ecotypes, consistent with the hypothesis that foraging opportunities and selection pressures vary with lake depth. Sympatric lake charr assemblages of deep- and shallow-water ecotypes in multiple lakes (Great Slave

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Lake, Lake Superior, Lake Mistassini, and Rush Lake) likely arose independently in response to parallel ecological opportunities. Diversification also occurs in small lakes and within shallow-water habitats. Research is needed on (1) how habitat size, complexity, and trophic coupling affect diversity and adaptive capacity, (2) the extent of heritable versus plastic responses of lake charr to ecological opportunities and selective pressures, and (3) the ability of lake charr populations and ecotypes to respond to stressors in ecological time.

Keywords Intraspecific diversity · Phenotypic plasticity · Genetics · Evolution · Morphology · Resource partitioning · Postglacial lakes

1 Introduction

The ecological diversity of the lake charr *Salvelinus namaycush* is a study in contrasts. In some ways, the lake charr seems to embody multiple paradoxes that defy simple categorization, while other aspects of its biology are highly conserved. Lake charr occupy a variety of habitats across a broad native distribution (Muir et al. 2021) but are almost exclusively limited to cold, low-productivity systems with simple biological communities (Martin and Olver 1980). Although the lake charr is well-adapted as an apex predator in these oligotrophic lakes, this niche is expressed in a variety of ways across habitats and communities. Physical descriptions of the lake charr range from a morphologically invariant and highly specialized species (Behnke 1972; Martin and Olver 1980; Gunn and Pitblado 2004), to a group of phenotypically diverse ecotypes displaying a range of traits (Muir et al. 2015; see illustrations, Plates 1–14, this volume). Neither characterization fully encompasses the ecological, phenotypic, and trophic diversity of the lake charr, which reflect its responses to historical and contemporary ecological opportunities (Wilson and Mandrak 2021).

Intraspecific diversity, both within and among lakes, in fishes that inhabit postglacial lakes reflects different evolutionary trajectories that result in a continuum of patterns of expressed phenotypes and genotypes. These patterns of observed phenotypic and genotypic diversity are often complex. Individuals may vary considerably within a population in a single lake. In some lakes, that variation may be continuous, whereas, in other lakes, variation may be manifest as discrete or partly overlapping (multi-modal) phenotypic and/or genotypic groups. Variation within lakes may also be relatively constrained and may be expressed similarly among multiple lakes. Thus, across this single species, a variety of divergence patterns are evident among populations (Figs. 1 and 2; Seehausen and Wagner 2014).

Several models have been proposed to explain observed patterns of intraspecific diversification in teleost fishes. Common components include ecological opportunity, phenotypic plasticity, and intraspecific competition in species-poor environments (Fig. 2; Skulason and Smith 1995; Smith and Skulason 1996; Skúlason et al. 2019). For discrete variation, two general patterns of sympatric divergence between ecotypes occur in post-glacial lakes: (1) divergence by habitat use and foraging ecology, and (2) migratory (anadromous) versus resident forms (Taylor 1999). The

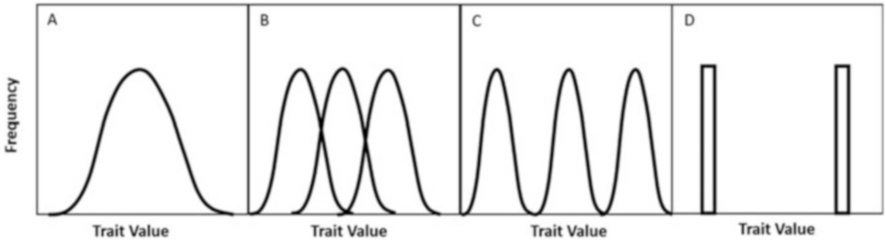


Fig. 1 Patterns of intraspecific phenotypic variation representing a continuum of phenotype-frequency distributions ranging from (**a**) continuously varying traits, (**b**) multi-modal traits with overlapping continuous variations (**c**) discrete (non-overlapping) multi-modal traits with continuous variations within each distribution (**d**) discrete traits with no or little variation within each phenotype. Figure was modified from Wennersten and Forsman (2012)

most frequently described pattern in lacustrine systems is paired benthic and pelagic ecotypes (Schluter 2000). Benthic ecotypes usually specialize to forage in the littoral zone on benthic macro-invertebrates such as insect larvae and crustaceans and are typically characterized by a robust head and jaw structure, a deep and wide body, blunt snout, and small eyes. In contrast, pelagic ecotypes specialize in feeding on zooplankton or fish in the limnetic zone and are usually more fusiform in body shape, with delicate mouth and head structures, and large eyes (Skulason and Smith 1995; Schluter 2000).

Although the lake charr exhibits divergence in habitat use, foraging ecology, and life-history tactics, it seems to do so to a lesser extent than some species at lower trophic levels or with shorter generation times. In several species, such as sticklebacks *Gasterosteus aculeatus* and cisco *Coregonus* spp., ecological speciation is thought to have occurred (Schluter 1996), whereas lake charr have not ecologically speciated, and little or no genetic divergence is evident between sympatric ecotypes (Box 1; Wellband et al. 2021). An apparent contrast in phenotypic and ecological variation between lake charr populations from large (>500 km^2), deep versus small lakes is consistent with predictions from ecological and evolutionary theory (Skúlason et al. 2019). The diversity expressed within and among lake charr populations mirrors many key elements of evolutionary processes that have driven intraspecific divergence in other postglacial fishes, including other salmonids (Skúlason et al. 2019).

In this chapter, we describe the ecological and phenotypic diversity of lake charr populations across their range (see patterns in the wild) as a continuum of variation (Fig. 1), from monomorphic populations with relatively little variation among lakes, to multi-modal populations living within single lake. The latter pattern includes depth as the primary axis of divergence within a lake, but also less-frequent divergence frameworks, such as shallow-water divergence, piscivorous vs. planktivorous divergence, and alternate life-histories. We then present ecological and evolutionary conceptual models for how intraspecific diversification emerges in postglacial lakes and link them with observed patterns of intraspecific diversity in lake charr (see Box 1). We aim to resolve apparently conflicting views of either constrained or diverse variation within and among lake

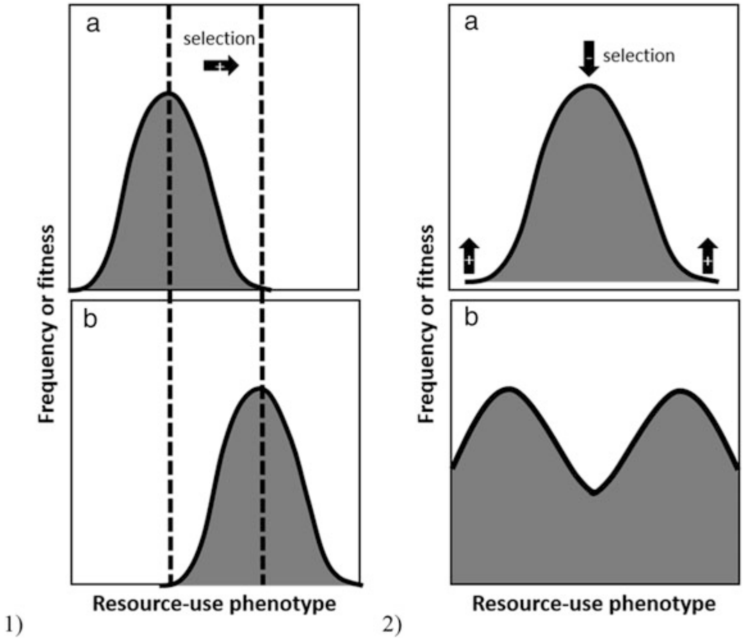


Fig. 2 Continuous variation resulting from directional selection (i.e., along an environmental gradient) (1) vs. discrete (i.e., polymorphic variation) resulting from disruptive selection (2). Directional selection (1) begins with a unimodal range of quantitative trait variation. If a trait is under directional selection, the mean phenotype expressed will change as a function of the strength of selection on that trait, both within or among populations, as shown in panels (**1a**) and (**1b**). In disruptive selection, continuous variation (**2a**) becomes discrete variation (**2b**) as two alternative fitness peaks emerge, each exploiting an alternative resource. The shaded area represents a hypothetical population's distribution of resource-use phenotypes (shown as a quantitative trait). Initially, a population is exploiting a range of resource types that are normally distributed (e.g., a range of prey sizes), and selection favors individuals that use the most common resource type (e.g., intermediate prey size). Under disruptive selection (**2a**), this resource type results in low fitness under conditions of high competition, resulting in negative selection for that phenotype compared to the more extreme, but underexploited, resource types (e.g., very small or very large prey items; positive selection). Under these conditions, disruptive selection will promote the development of alternate phenotypes that will specialize in different resource types. Figure was modified from Pfennig and McGee (2010)

charr populations and show how observed patterns are consistent with eco-evolutionary model predictions.

2 Patterns in the Wild: A Diversity of Lake Charr Intraspecific Variation

Viewing populations along a gradient of ecological trait divergence, as presented in Fig. 1, helps to visualize the wide variation in phenotypic patterns that can occur within a species. Here we describe these patterns of variation among and within lake charr populations in North America.

2.1 Continuous Variation Among Lakes

Most lake charr populations in small and medium lakes (≤500 km^2) across the species' range consist of one phenotype (i.e., monomorphic), albeit with some level of continuous variation among lakes (Fig. 1a). Monomorphic populations are broadly characterized as either piscivorous ("large-bodied") or planktivorous ("small-bodied") (Martin 1952, 1966). Despite genetic evidence showing that the lake charr colonized its current range from multiple allopatric refugia (Wilson and Mandrak 2021; Wilson and Hebert 1998), the lack of major differences in phenotypes in lakes across North America (i.e., geographical variation) suggests that expression of alternative lake charr phenotypes may be constrained by local ecological and environmental conditions (Fig. 2; McDermid et al. 2010).

Patterns in food-web structure underlying these trophic phenotypes were first defined by Rasmussen (1990), who classified lake charr populations based on their prey base, trophic level, and ecology (Fig. 3). Lake charr in Class 1 populations are secondary consumers relying on invertebrates, whereas Class 2 and Class 3 populations are piscivorous, with Class 3 populations including *Mysis diluviana* (hereafter *Mysis*) in the food web (Fig. 3). The small-sized prey of Class 1 populations, as well as the more active foraging required, results in slow-growing small-bodied lake charr, with small size at maturity and short lifespan (Vander Zanden et al. 2000; Pazzia et al. 2002). Forage fishes that may be present in littoral habitats are largely inaccessible, especially where seasonal stratification provides a thermal barrier to movement (Vander Zanden and Rasmussen 1996; Vander Zanden et al. 1999b, 2000). In contrast, Class 2 and Class 3 populations have access to both benthic and pelagic forage fishes due to longer food-webs, but the greater prey-size spectrum and food availability for lake charr at smaller life-stages leads to faster growth and larger asymptotic size in Class 3 populations (Pazzia et al. 2002; Morissette et al. 2018). The classification system described by Rasmussen (1990)

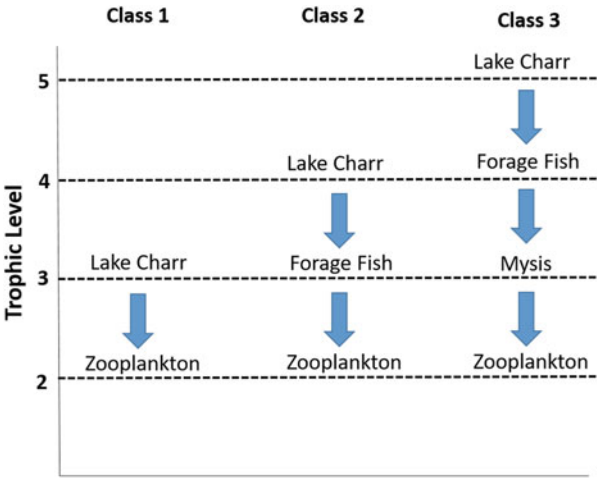


Fig. 3 Classification of lake charr *Salvelinus namaycush* trophic status based on diet and food chain length (modified from Vander Zanden et al. 1999b)

that focused on pelagic food webs can be extended to lakes in which lake charr make use of benthic productivity (Scott and Crossman 1998; Vander Zanden and Vadeboncoeur 2002). Lake charr in Class 1 lakes rely heavily on benthic invertebrates, whereas deep-water prey fishes, such as sculpins (Cottidae), can be a significant prey in Class 2 and Class 3 lakes. Accordingly, for monomorphic lake charr populations, growth as a function of prey size and habitat appears to be a key driver of phenotypic diversity among lakes (Vander Zanden et al. 2000; Pazzia et al. 2002; Bernatchez et al. 2016; Morissette et al. 2018).

Native lake charr populations in Ontario's Algonquin Park illustrate continuous trophic phenotypic variation independent of geographic distance or phylogeographic ancestry (see Wilson and Mandrak 2021). The postglacial history of the park landscape established different food-web structures among lakes largely based on the presence or absence of *Coregonus* spp. (ciscoes) and *Mysis* (Ridgway et al. 2017), which in turn, largely determines the distribution of Class 1, 2, or 3 populations. Class 1 lakes lack *Coregonus* as prey. Class 2 lakes are all located above 381 m elevation and have *Chaoborous punctipennis* rather than *Mysis* as the predominant diel migrator in the planktonic community. Class 3 lakes contain *Mysis* and were directly influenced by the drainage of Glacial Lake Algonquin (below the 381 m elevational contour and with sufficient water depth; Ridgway et al. 2017). For lake charr in each of these different trophic classes, body size and growth propensity have both plastic (environmental) and heritable components (Matuszek et al. 1990; McDermid et al. 2007; Houde et al. 2016).

2.2 Multi-modal Patterns of Variation

2.2.1 Depth-Based Divergence

Typical lacustrine divergence in fishes is between individuals specializing in either pelagic or littoral-benthic habitats (see Sect. 1 Introduction). A less common habitat on which fish specialize is the profundal zone (i.e., layer of deep, open water; Robinson and Parsons 2002; Præbel et al. 2013; Hooker et al. 2016). Because depth, which is correlated with temperature, oxygen concentration, and linked with differences in habitat and foraging opportunities, is the main axis of divergence for lake charr, the expression of divergent ecotypes is frequently associated with large, deep lakes (Table 1; Eshenroder 2008; Muir et al. 2015; Chavarie et al. 2016d). Large aquatic environments provide greater complexity than small ones, support more ecological opportunities across greater distances, and thereby facilitate more phenotypic variation in response to a range of resources (Recknagel et al. 2017). Shallow- and deep-water habitats (i.e., vertical resource-axis) can provide different ecological opportunities, which can promote and maintain rapid postglacial adaptive divergence (Zimmerman et al. 2009; Goetz et al. 2010; Baillie et al. 2016a; Chavarie et al. 2016d). Although research on sympatric diversification in lake charr has focused on isolation-by-depth in large and deep lakes (without excluding isolation-by-adaptation), diversification can also occur in small lakes or within shallow-water habitats (see Table 1 for examples).

2.2.1.1 Phenotypic and Ecological Characteristics

Some generalities can be drawn from documented examples of lake charr differentiation, where three common ecotypes occur in multiple lakes in North America: the lean-, humper-, and siscowet-like ecotypes (Fig. 4). Evidence from Lake Superior, Great Slave Lake, Lake Mistassini, and Rush Lake suggests a prevalent pattern of ecological divergence of co-occurring deep-water (humper- and/or siscowet-like) and shallow-water (lean-like) ecotypes. Multi-modal populations in these lakes seem to have evolved independently (Chavarie et al. 2016d), albeit in a repeatable fashion, under similar ecological conditions (e.g., foraging opportunities associated with different depths; Rundle et al. 2000; Faria et al. 2014). For these morphologically similar ecotypes found in multiple lakes (e.g., independent of phylogeographic ancestry), ecological and evolutionary processes appear to act in the same way, thereby resulting in parallel divergence associated with depth gradients.

Recurrent morphological variation displayed by sympatric deep- and shallow-water ecotypes of lake charr is consistent with a hypothesis that foraging opportunities and selection pressures differ along a depth-related niche axis (as a gradient; Eshenroder 2008). Ecotypes can overlap along the depth gradient, but the degree of overlap differs among lakes. Specific to deep-water morphological variation, the humper-like lake charr has a small head, short snout and maxillae, large eyes, and a generally elongated body with a short and narrow caudal peduncle. The humper-like ecotype is only slightly fatter (lipids and plumper) than the lean-like ecotype (Moore and Bronte 2001; Muir et al. 2015). The siscowet-like ecotype, also found in deep-water, has a large head, short snout, long maxilla, large eyes, short and deep caudle peduncle, and moderately long paired fins (Moore and Bronte 2001; Bronte and Moore 2007; Muir et al. 2015). The siscowet-like ecotype is the fattest lake charr ecotype. As a result of the strong link between locomotion and feeding in deep-water habitats, this deep-water ecotype displays an enhanced ability to migrate vertically (compared to the shallow-water lean-like ecotype; Videler 1993; Henderson and Anderson 2002; Blake 2004), and has longer paired fins and a higher lipid content than the shallow-water ecotype, which improves buoyancy regulation associated with hydrostatic lift (Sideleva 1996; Eshenroder et al. 1999). As visual predators, deep-water ecotypes tend to have eyes that are larger and higher on the head than those of the shallow-water ecotype, a characteristic likely connected to feeding on *Mysis* and deep-water ciscoes (*Coregonus artedi* complex) (Hrabik et al. 2006; Muir et al. 2014a; Hoffmann 2017). Large eyes positioned high on the head are known to improve binocular vision and light gathering, which are needed to feed at night or in deep habitats with low light levels (Van Der Meer and Anker 1983; Bond 1996). Although humper-like and siscowet-like ecotypes generally exploit deep-water environments (>50 m), they vary in their depth distribution and diet where they co-exist. In Lake Superior, for example, siscowet occupy deeper-water (>100 m)

Table 1 Diversity currently known in lake charr *Salvelinus namaycush* populations across North America

Localities	Axis of divergence	Morphology	Diet	Habitat	Life-history (means or medians for length, weight, and age)	Genetic difference
Superior	Depth segregation: shallow-watervs.profundal; insectivory vs. piscivory	**Lean**: streamlined, long head, narrow caudal peduncle, short paired fins, and low body lipid content **Humper**: small head, short snout, short maxilla, large eye, and short and narrow caudal peduncle **Redfin**: deeper body, large head, longest and deepest caudal peduncle, and long fins **Siscowet**: large head, short snout, large eye, short and deep caudle peduncle, moderately long paired fins, and high body lipid content	Trophic overlap = degree of generality **Lean**: fish **Humper:** *Mysis* **Siscowet**: deepwater cisco **Redfin**:?	**Lean**: shallow water $\leq$70 m **Humper**: offshore, mid-water shoals, or banks **Siscowet**: deep-waters >100 m **Redfin**: moderate depths ~80 m	**Lean**: 479 mm; 854 g; 13 years **Humper**: 443 mm; 697 g; 17 years **Siscowet**: 519 mm; 1221 g; 19 years **Redfin**: 544 mm; 1481 g, 22 years	Present
Great Slave	Depth segregation: shallow-water vs. profundal	**Lean-like**: streamlined, long head, narrow caudal peduncle, short paired fins, and low body lipid content **Siscowet-like**: large head, short snout, large	Trophic overlap = degree of generality **Lean-like**: fish **Siscowet-like**: *Mysis* & deepwater cisco	**Lean-like**: shallow-water $\leq$50 m **Siscowet-like**: deep-water $\geq$50 m	**Lean-like:** 568 mm; 1838 g; 20.2 years **Siscowet-like**: 583 mm, 2319 g; 24.9 years	Unknown

		eye, short and deep caudle peduncle, moderately long paired fins, and high body lipid content				
Mistassini	Depth segregation: shallow-water vs. profundal	**Lean-like**: dark, streamlined, long head, narrow caudal peduncle, short paired fins, and low body lipid content **Humper-like**: small head, short snout, short maxilla, large eye, and short and narrow caudal peduncle, high body lipid content	Trophic overlap = degree of generality **Lean-like**: fish **Humper-like**: *Mysis*	**Lean-like**: shallow-water $\leq$50 m **Humper-like**: deep-water $\geq$50 m	**Lean-like**: 525 mm; 1210 g; 21 years **Humper-like**: 474 mm; 852 g; 27 years	Partial
Rush	Depth segregation: shallow-watervs.profundal; insectivory vs. piscivory	**Lean-like**: streamlined, long head, narrow caudal peduncle, short paired fins, and low body lipid content **Humper-like**: deep body, small head, higher eye position, deeper peduncle, and high body lipid content	**Lean-like**: Rainbow smelt **Huronicus**: *Mysis*	**Lean-like**:shallow-water~28.8 m **Huronicus**:deep-water ~85.1 m	**Lean-like**: 430 mm; 687 g; 11.7 years **Huronicus-like**: 393 mm; 580 g; 16.8 years	Absent
Flathead	Depth segregation: shallow-watervs.profundal; insectivory vs. piscivory	**Lean-like**: streamlined, smaller eye and lower position on the head, and longer caudal peduncle	**Lean-like**: chironomids, fish **Deep-water individuals**: *Mysis*, fish	**Lean-like**: shallow-water $\leq$25 m **Deep-water individuals**: deep-water 60–100 m	**Lean-like** 50% length-at-maturity = 574 mm **Deep-water individuals** 50% length-	Absent

(continued)

Table 1 (continued)

Localities	Axis of divergence	Morphology	Diet	Habitat	Life-history (means or medians for length, weight, and age)	Genetic difference
		Deep-water individuals: deep body, large eye with a higher position on the head, and shorter caudal peduncle			at-maturity = 481 mm	
Great Bear	No depth segregation; weak benthic vs. pelagic and insectivory vs. piscivory	**Ecotype 1**: small head, small jaw, moderate body depth, and intermediate fins **Ecotype 2**: streamlined, long head, narrow caudal peduncle, short paired fins **Ecotype 3**: deep body, deep caudle peduncle, and long fins **Ecotype 4**: streamlined, curved and thick lower jaw	3 generalists vs. one pelagic specialist **Ecotype 1**: generalist **Ecotype 2**: generalist, piscivorous-oriented? **Ecotype 3**: generalist, benthic-oriented? **Ecotype 4**: pelagic specialist	Shallow-water ≤30 m	**Ecotype 1**: 641.7 mm; 20 years **Ecotype 2**: 670.8 mm; 22 years **Ecotype 3**: 644 mm; 29 years **Ecotype 4**: 683 mm; 26 years	Partial
Southern Quebec (typically among lakes, in sympatry: Maganasipi and Mondonac)	No depth segregation; planktivory vs. piscivory	**Planktivorous**: streamlined body, small head, narrower caudal peduncle, small caudal fin **Piscivorous**: deeper body, long head,	**Piscivorous**: fish **Planktivorous**: zooplankton	Unknown	**Piscivorous:** 487.96 mm; 11 years-average 5 lakes **Planktivorous**: 400 mm; 10 years	Present in among lakes

		deeper caudal peduncle, and larger caudal fin				
Atlin	No depth segregation; two morphological groups	**Group 1**: long heads and narrow caudal regions **Group 2**: deeper heads and bodies overall *Variation in color independent of the two groups: dark shading vs. sliver-white shading	Unknown	Unknown	Unknown	Partial
Algonquin Park (among lakes)	No depth segregation; planktivory vs. piscivory	**Planktivorous:** smaller body size **Piscivorous:** larger body size	**Piscivorous**: fish **Planktivorous**: zooplankton	**Piscivorous**: all depths from thermocline to bottom with 50% of time on bottom **Planktivorous**: all depths from thermocline to bottom with 30% of time on bottom	**Piscivorous:** 518 mm; 1768 g; 11 years **Planktivorous**: 431 mm; 1032 g; 11 years	Unknown
Mishibisu lakes, Dog and Montreal rivers, Northern Canada	No depth segregation; adfluvial or riverine	Unknown	Unknown	Unknown	River spawner: male mean age at maturity = 7 years, ~635 mm Female mean age at maturity = 8 years, ~723 mm	Unknown

(continued)

Table 1 (continued)

Localities	Axis of divergence	Morphology	Diet	Habitat	Life-history (means or medians for length, weight, and age)	Genetic difference
High Arctic Canada	No depth segregation; semi-anadromous vs. landlocked	Unknown	**Semi-anadromous**: fish and invertebrates **Landlocked**: fish and invertebrates	**Semi-anadromous**: lakes and estuaries **Landlocked**: lakes	**Semi-anadromous**: 604 mm, mean age of first migration = 10-17 years **Landlocked**: 439 mm	Present

This table is a synthesis of the following sources: Loftus (1958), Power (2002), Wilson and Mandrak (2004), Zimmerman et al. (2006, 2007, 2009), Bronte and Moore (2007), Eshenroder (2008), Sitar et al. (2008, 2014), Goetz et al. (2010, 2011, 2013, 2017), Northrup et al. (2010), Swanson et al. (2010, 2011), Hansen et al. (2012, 2016b), Chavarie et al. (2013, 2016a, b, c, 2018), Stafford et al. (2013), Muir et al. (2014a, 2015), Harris et al. (2015), Marin (2015), Baillie et al. (2016a), Bernatchez et al. (2016), Kissinger et al. (2016, 2017a, b), Marin et al. (2016), Hoffmann (2017), Perreault-Payette et al. (2017), Jones et al. (2018), Morissette et al. (2018, 2019)

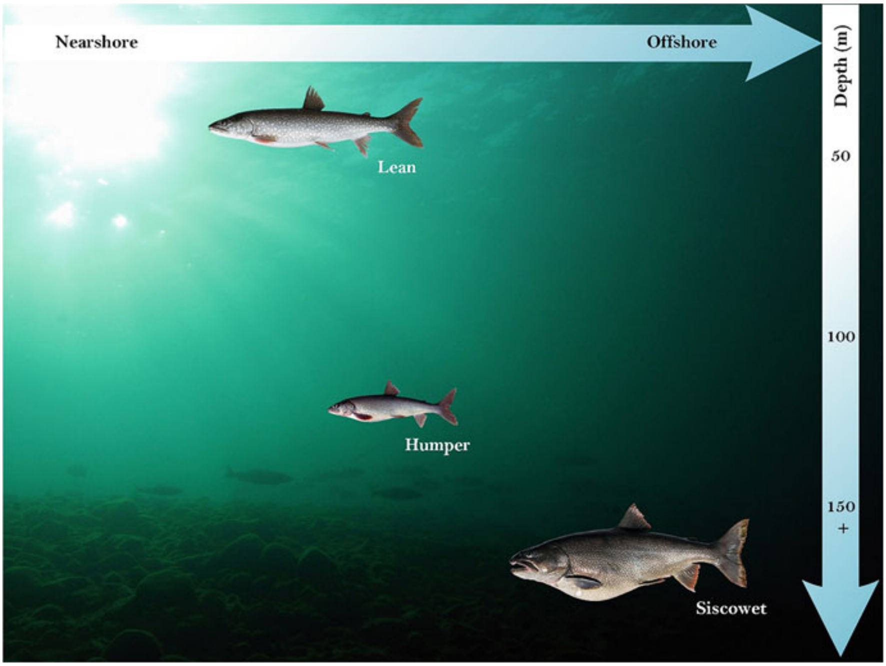


Fig. 4 The main niche dimension driving lake charr *Salvelinus namaycush* differentiation is associated with depth, with individuals diverging to occupy shallow vs. profundal environments, and partitioning prey resources within and between those habitats (Eshenroder 2008; Zimmerman et al. 2009). Some morphological generalities can be drawn from documented lake charr differentiation into three ecotypes occurring in multiple lakes in North America (lean-, humper-, and siscowet-like ecotypes). Deep-water ecotypes are characterized by deeper bodies and caudal peduncles and greater buoyancy (lipids), whereas shallow-water ecotypes have a streamlined body, smaller fins, and larger head that reflect locomotion-related traits associated with trophic differentiation

and move off the bottom at night to prey on vertically migrating ciscoes. In contrast, humper lake charr are thought to inhabit offshore, midwater shoals, or banks, where their small head and gape facilitates feeding on small prey (Krueger and Ihssen 1995; Eshenroder 2008; Muir et al. 2014a).

In contrast, the shallow-water ecotype has a long, narrow, and pointed head, long snout, long maxillae, small eyes, long and narrow caudal peduncle, short paired fins, and low body lipid content. It also has a streamlined body and tends to have silvery and light overall color, with a white ventral aspect, and little or no vermiculation (i.e., cryptic pattern) (Khan and Qadri 1970; Endler 1978; Moore and Bronte 2001; Muir et al. 2014a). The shallow-water ecotype is adapted for daytime predation on pelagic fishes in shallow-water habitats (piscivorous feeding strategy; Harvey and Kitchell 2000; Harvey et al. 2003; Janhunen et al. 2009). One of the main benefits of the streamlined body typified by the shallow-water ecotype, in contrast to the deep body of the deep-water ecotype, is that it reduces drag, thereby decreasing swimming costs for cruising predators (Webb 1984; Pakkasmaa and Piironen 2001; Gillespie and Fox 2003). These more pelagic predators, rely more on hydrodynamic (versus hydrostatic) lift for sustained swimming and greater reliance on the swim bladder rather than lipid content to maintain neutral buoyancy (Webb 1984; Muir et al. 2015).

2.2.1.2 Life-History

The concept that ecological and evolutionary dynamics influence each other reciprocally (Turcotte et al. 2011) is illustrated by differences in life-history characteristics among lake charr ecotypes. Parallel life-history variation between deep- and shallow-water ecotypes is found in several North American lakes (Hansen et al. 2012, 2016a; Chavarie et al. 2016d), which reflects similar ecotype-specific patterns of resource use among lakes. In general, deep-water ecotypes (i.e., siscowet-like or humper-like) are not only heavier, plumper, more buoyant, and longer-lived than the shallow-water ecotype (i.e., lean-like), they are also slower growing early in life and achieve shorter asymptotic length (see Hansen et al. 2012, 2016b, 2021).

Relatively little is currently known about the reproductive biology of sympatric lake charr ecotypes in North American lakes, except in Lake Superior. The lean and siscowet ecotypes in southern Lake Superior have similar timing of gonad maturation, although the timing for spawning (i.e., release of gametes) can differ. Although siscowet reproduce during both spring and autumn, lean, humper, and redfin (a third deep-water ecotype in Lake Superior; Muir et al. 2014a) ecotypes are only known to reproduce in autumn at Isle Royale (Lake Superior; Bronte 1993; Goetz et al. 2017, 2021). Therefore, some siscowet populations differ in spawning times from other ecotypes in Lake Superior, which can increase reproductive barriers and divergence (Klemetsen et al. 1997; Telnes and Sægrov 2004). Isolation resulting from a spatial or temporal reproductive mismatch could be a mechanism involved in the origin and maintenance of lake charr divergence in Lake Superior (Goetz et al. 2017, 2021).

2.2.1.3 Genetics

Lake charr genetic patterns are shaped by biogeographic history, landscape features, ecological opportunity, and human impacts (Wilson and Mandrak 2021; Wellband et al. 2021). Uncertainty about origins of divergence (i.e., sympatric vs. allopatric) remain for several lakes, but the general lack of evidence for allopatric origins of co-occurring ecotypes favors an argument for in situ differentiation. In some lakes, such as Great Slave Lake, population genetic studies have yet to be conducted on lake charr ecotypes. In general, in lakes sustaining depth-based intraspecific diversity, genetic divergence between deep- and shallow-water ecotypes range from high gene flow to some level of genetic differentiation (Wellband et al. 2021). In general, genetic divergence among co-occurring ecotypes appears to be weak, although recent applications of genomic markers are improving our understanding (Morissette et al. 2018, 2019; Wellband et al. 2021). Rush Lake and Lake Mistassini are among lakes lacking apparent genetic differences associated with depth (Chavarie et al. 2016d; Marin et al. 2016). As a caveat, an absence of genetic divergence may result from a lack of power of the genetic discrimination technique employed, especially because genomic studies of lake charr are in their infancy. Nevertheless, Rush Lake, with its small size (1.3 km^2), would seem unlikely to be able to generate and maintain differentiation because isolation-by-distance is likely to be an important component maintaining lake charr intraspecific diversity. In some instances, a single ecotype differs genetically among locations (e.g., sampling locations or depth strata) more than the differences among ecotypes within a lake (Wellband et al. 2021; Baillie et al. 2016a; Marin et al. 2016; Perreault-Payette et al. 2017). This highlights the contribution of both spatial isolation and local adaptation in shaping genetic variation of lake charr in large, deep lakes (Baillie et al. 2016a; Marin et al. 2016; Perreault-Payette et al. 2017). Lake Superior seems to be the lake with the highest degree of genetic differentiation among lake charr ecotypes, with several studies demonstrating genetic differences between lean and siscowet ecotypes, although differences are weak compared to ecotypes from other species (Wellband et al. 2021; Krueger et al. 1989; Krueger and Ihssen 1995; Page et al. 2004; Goetz et al. 2010). A recent genomics study also provides evidence of divergent selection among lake charr ecotypes in Lake Superior (Perreault-Payette et al. 2017). However, due to major human-induced impacts, introgression among lake charr ecotypes appears to have increased over time, thereby reducing the magnitude of genetic divergence (Guinand et al. 2012; Baillie et al. 2016b).

2.2.2 Shallow-Water Divergence

Shallow-water divergence presents a distinct ecological context for lake charr differentiation relative to the better-studied depth-based divergence. With shallow-water lake charr diversity having been extirpated in Lake Superior (Goodier 1981), the primary example of sympatric divergence independent of depth is from Great Bear Lake (Chavarie et al. 2013). The vertical distribution of lake charr in Great Bear Lake is not limited by thermal barriers (relative to more southern lakes), which provides conditions favorable for divergence in shallow-water habitats ($\leq$30 m) (Johnson 1975, 1976; Chavarie et al. 2013). Compared to depth-based divergence, body shape variation is less distinct among shallow-water ecotypes, with morphological differences primarily associated with head shape and fin size (Chavarie et al. 2013). The extent and relative importance of trophic factors that influence patterns of diversity in shallow-water habitat are not well understood, although the expressed phenotypic diversity appears to reflect a complex array of processes (co-existence of multiple generalists, Fig. 5, see Sect. 4.3 trophic overlap versus phenotypic variation; Chavarie et al. 2016b).

Consistent with predictions about trade-offs linked to exploitation of different resources and environments, shallow-water ecotypes differ in adult growth rates, age- and size-at-maturity, and survival rates (Chavarie et al. 2016a). In contrast to

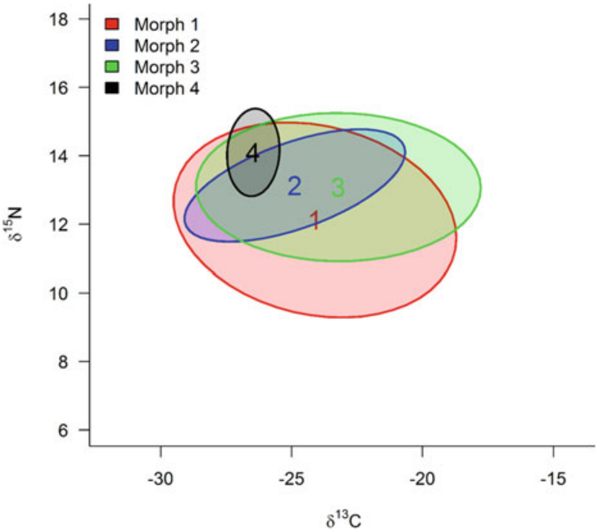


Fig. 5 Probabilistic (95%) niche regions of carbon (δ^{13}C ‰) and nitrogen (δ^{15}N ‰) stable isotope ratios for four shallow-water ecotypes of lake charr *Salvelinus namaycush* in Great Bear Lake, Northwest Territories. Figure adapted from Chavarie et al. (2016b) to illustrate trophic overlap and degree of generality of lake charr ecotypes in this system

other studies of lake charr that showed differences in juvenile growth among ecotypes (Hansen et al. 2012, 2016b; Chavarie et al. 2016d), juvenile growth was similar among shallow-water ecotypes (Chavarie et al. 2016a). Similar juvenile rearing environments, including similar prey spectra, might explain this similarity (Andersen et al. 2009).

Shallow-water lake charr ecotypes in Great Bear Lake are weakly differentiated genetically, with existing divergence among the four ecotypes apparently occurring in sympatry, subsequent to postglacial colonization (Harris et al. 2015). The lack of a link between morphological and genetic differences of shallow-water ecotypes with spatial variation within a lake suggests a plastic morphological response to differing environmental conditions (Chavarie et al. 2015; Harris et al. 2015).

Great Bear Lake has sufficient depth (maximum depth = 450 m) to drive and sustain lake charr diversity across a vertical resource axis (Eshenroder 2008; Wellborn and Langerhans 2015). Why phenotypic divergence in Great Bear Lake is focused in the shallow-water habitat, while deep-water diversification is less pronounced than in other large deep lakes is unknown, especially when the potential for depth divergence seems high. As such, Great Bear Lake is an exception. Potential reasons for lack of depth-based divergence in Great Bear Lake include: (1) a relatively weak opportunity for divergent selection (e.g., low productivity in deepwaters due to northern location), (2) high gene flow, and (3) insufficient time to diversify (Hendry et al. 2013).

2.2.3 Piscivorous Versus Planktivorous Divergence

Another ecological pattern of lake charr divergence is the co-occurrence of piscivorous and planktivorous ecotypes (two lakes, see Bernatchez et al. 2016). The expression of discrete piscivorous and planktivorous ecotypes is a common axis of sympatric divergence in northern freshwater fishes (Gíslason et al. 1999; Robinson and Parsons 2002) that seems to occur less often in lake charr populations than other salmonids. Sympatric piscivorous and planktivorous lake charr differ in body condition, body shape, body size, gill raker number, caudal fin length, caudal peduncle depth (females only), and head length (males only) (the latter two are rare examples of sexual dimorphism in lake charr; Bernatchez et al. 2016). Overall, planktivores have a more streamlined body, a narrower caudal region, and a higher number of gill-rakers than piscivores. Genomic markers indicate ongoing gene flow between these sympatric ecotypes (Bernatchez et al. 2016).

2.3 Alternative Life-History Forms

2.3.1 Adfluvial or Riverine Lake Charr

Most lake charr spawn in lakes, although adfluvial forms that live in lakes and spawn in streams occurred in the Dog and Montreal Rivers, Lake Superior (Loftus 1958). Adfluvial lake charr also occur in the Mishibishu lake chain in northeastern Ontario, where populations were founded by introductions from two river populations (Loftus 1958). These introductions were intended to guard against the extirpation of river populations due to sea lamprey predation in Lake Superior. River-spawning behavior appears to be heritable because reintroductions from the Mishibishu lake chain led to successful re-establishment of wild populations in both the Dog and Montreal Rivers (Jones et al. 2018).

The number of riverine or adfluvial populations existing in northern Canada is unknown, but anecdotal observations suggest their presence in northern systems (Power 2002), such as in the Great Bear River (Great Bear Lake; L. Chavarie, unpublished data) and Stark River (Great Slave Lake; C. C. Krueger, unpublished data).

2.3.2 Anadromous Lake Charr

The lake charr is generally viewed as a saltwater-intolerant lacustrine species, with fluvial populations persisting in shallow rivers and streams in the north of their range (~60–73 °N, e.g., Scott and Crossman 1973). However, anecdotal reports of lake charr inhabiting brackish coastal waters in the Canadian Arctic (reviewed in Martin and Olver 1980) suggested that lake charr may have some capacity for anadromy. More recently, two new life-history types have been documented: (1) semi-anadromous (Swanson et al. 2010); and (2) brackish-water resident (Kissinger et al. 2016).

Partially migrant populations of salmonids include genetically similar sympatric anadromous and freshwater-resident individuals that can each produce freshwater-resident progeny (Nordeng 1983; Hindar and Jonsson 1993; Hendry et al. 2004; Chapman et al. 2012). Partial anadromy migrants are semi-anadromous, with a protracted period in freshwater before first migration, annual overwintering in freshwater, and a likely preference for brackish rather than full-strength seawater, where they feed in large, brackish estuarine areas (Swanson et al. 2010), much like coastal Arctic charr *Salvelinus alpinus*. The frequency of semi-anadromous individuals in populations varies, and the age of first migration to the sea for semi-anadromous lake charr is older than for anadromous Arctic charr (Table 2). General benefits of anadromy include increased resource availability, increased growth, larger asymptotic size, decreased intraspecific competition, and parasite shedding (Gross 1987; Swanson et al. 2010).

Semi-anadromous lake charr also occur in sympatry with brackish-water residents (Kissinger et al. 2016). In a series of five interconnected lakes located east of the Mackenzie Delta (Husky Lakes) that vary in salinity from 1 to 17 psu, 14% of captured lake charr were semi-anadromous, whereas 86% were brackish-water residents (Kissinger et al. 2016). The latter appear to spawn, grow, and complete their life cycle entirely in brackish water. Brackish-water residents also live longer than semi-anadromous individuals (Kissinger et al. 2017b). Greater resource availability in brackish-water habitat than in freshwater habitat likely contributes to the maintenance of these two life-histories.

In contrast to species with predominantly anadromous life histories, such as pink salmon *Oncorhynchus gorbuscha*, which can gain >95% of their mass while at sea (Schindler et al. 2003), flesh of semi-anadromous lake charr comprises both marine- and freshwater-derived material, with marine-derived prey estimates considerably lower than for sympatric semi-anadromous Arctic charr (Table 2; Swanson et al. 2011). This interspecific difference is likely attributable to the relatively larger age- and size-at-first-migration for lake charr than for Arctic charr, and that migrating lake charr feed during winter in freshwater lakes (H. Swanson, unpublished data), whereas Arctic charr do not (Johnson 1980). Furthermore, although 29–55% of the biomass of freshwater-resident lake charr was derived from freshwater pelagic prey, semi-anadromous lake charr had no isotopic signature consistent with foraging on such prey. To date, data are lacking on the trophic ecology of brackish-water resident lake charr.

Table 2 Mean age of first sea-migration, and 95% credible interval estimates from MixSIR models presented in Swanson et al. (2010, 2011), respectively

Species	Lake	Mean age of first migration	Lower 95% CI marine source contribution	Upper 95% CI marine source contribution
Arctic char	Hovaktok	5 ($n = 9$)	0.85 ($n = 15$)	0.95 ($n = 15$)
	Roberts	4 ($n = 13$)	0.85 ($n = 9$)	0.96 ($n = 9$)
Lake charr	Glenn	10 ($n = 14$)	0.60 ($n = 9$)	0.67 ($n = 9$)
	Nauyuk	17 ($n = 9$)	0.57 ($n = 8$)	0.64 ($n = 8$)
	Roberts	13 ($n = 10$)	0.58 ($n = 6$)	0.73 ($n = 6$)

2.4 Summary

Patterns of phenotypic variation observed in the lake charr illustrate a gradient of ecological trait divergence, ranging from continuously varying traits (Fig. 1a) to multi-modal traits with overlapping and non-overlapping distributions (Fig. 1b, c). Discrete traits with little or no variation among phenotypes (Fig. 1d) have not yet been documented in the lake charr. Rather, a phenotypic cline seems to exist within each ecotype, including overlapping phenotypic and ecological characteristics (e.g., see Sect. 4.3 trophic overlap versus phenotypic variation). This suggests that phenotypic diversity in the lake charr, whether adaptive or not, is distributed along ecological and environmental gradients (Baillie et al. 2016a; Chavarie et al. 2018).

3 Models of Intraspecific Diversity Emerging in Postglacial Systems

Models of intraspecific diversity emphasize important elements that facilitate evolutionary divergence in post-glacial fishes (see Dieckmann and Doebeli 1999; Skúlason et al. 2019). These elements include access to ecological opportunity (provided by alternative resources in depauperate systems), a capacity for phenotypic diversity in the population, and a heritable basis to diversify adaptive traits, with high intraspecific but low interspecific competition and predation (Adams et al. 2003; Garduño-Paz and Adams 2010; Knudsen et al. 2011). A critical stage in the divergence process is how and when gene pools start to segregate, thereby allowing potential genetic differentiation. Alternative phenotypes can have selective advantages under high levels of intraspecific competition, with each phenotype having alternative fitness maxima that establish elements necessary for disruptive selection (Fig. 2; Dieckmann and Doebeli 1999). This may result in gene pool segregation under a number of scenarios, particularly when mate choice is based on phenotypes that have functional significance in resource exploitation (Dieckmann and Doebeli 1999). The stepwise progression of likely processes applied to lake charr is depicted in Box 1, based on evidence from the literature (but also see Box 2).

Box 1 The ABCs of Lake Charr Divergence

A combination of field studies, laboratory experimentation, and theoretical modeling have established a likely sequence of events and processes involved in the formation of intraspecific diversity expressed in many postglacial fishes. Although much of the understanding of these mechanisms has come from other species (e.g., Arctic charr *Salvelinus alpinus*), these events and processes have likely also shaped diversity in lake charr *Salvelinus namaycush*.

Colonization: The fish that initially enter freshwater systems, as they emerged from the Pleistocene glaciation, are assumed to have high levels of phenotypic plasticity that enable strong colonizing ability and rapid establishment in these new environments. Postglacial environments are species poor with low levels of interspecific competition that facilitate high levels of ecological opportunity for colonizers. Prevailing knowledge suggests that lake charr colonized from multiple glacial refugia into systems with considerable ecological opportunity (Wilson and Mandrak 2021).

Ecological specializations emerge: As newly established populations grow, species-poor environments offer opportunities for individuals to diversify into novel niches. Specialization is more likely to emerge under conditions of increased intraspecific competition (Skulason and Smith 1995). Morphologies that are suboptimal when intraspecific competition is low within a system may gain significant fitness advantage when intraspecific competition is high, thereby allowing individuals to exploit resources associated with reduced competition (Dieckmann and Doebeli 1999). For the lake charr, the prevailing consensus is that commonly adopted alternative niches included those provided by occupying different depths (see Sect. 2 patterns in the wild).

Alternative phenotypes expressed: Plasticity can also allow for the expression of alternate phenotypes by two (or more) specialists resulting from exposure to different environments and foraging opportunities (West-Eberhard 1989). Plastic responses can be rapid (occurring within a single generation) and laboratory experiments have shown that phenotypes expressed by two foraging specialists can be: (a) different from each other (Adams et al. 2003) and (b) adaptive (Adams and Huntingford 2002; Goetz et al. 2010, 2013). In lake charr, little knowledge exists about how phenotypically plastic they are currently, or were historically following dispersal into postglacial environments.

Divergent selection: The expression of different phenotypes resulting from exposure to differential environmental gradients provides multiple phenotypic nodes (Fig. 1) upon which selection may act differentially (West-Eberhard 1989). Divergence occurs because phenotypes evolve toward two or more distinct fitness peaks in the adaptative landscape, with different phenotypic means (Schluter 2000). Stabilizing selection should occur when phenotypes come close to their corresponding adaptative landscape peaks, with higher

(continued)

Box 1 (continued)

fitness than other phenotypes. For some habitats occupied by alternate ecotypes of lake charr, divergent selection likely occurred and may still be in action, although the heritability or genetic architecture of adaptive phenotypic traits in the lake charr is largely unexplored (Krueger and Ihssen 1995).

Gene pool segregation: The presence of a fitness minimum within the range of phenotypes in a system is an important element of disruptive selection (Schluter 2000). Disruptive selection will favor traits in the population that are adaptive for emerging specializations, whereas intermediate forms will be selected against, and ultimately will decrease in frequency. Selection pressures for assortative mating may emerge alongside disruptive selection, which may result in a decrease in intermediate phenotype frequencies (Dieckmann and Doebeli 1999). At this point, different genetic groups may be detectable, initially with some gene flow between them, but if gene flow is reduced, then full reproductive isolation may emerge (Hendry et al. 2009). In the lake charr, no evidence exists that divergent populations have reached the stage of strong genetic divergence, although some divergence can exist.

Reversibility: At all steps during divergence, processes may operate in reverse. Thus, diverging phenotypes with limited gene flow may revert to a monomorphic population (McKay and Zink 2015). If a reversal occurs, re-emergence of divergence may or may not be possible (Taylor et al. 2006; Jacobs et al. 2019). In the lake charr, introgression among ecotypes from Lake Superior has likely increased over time due to major anthropogenic and ecological changes (Baillie et al. 2016a, b).

4 Linking Ecological and Evolutionary Processes to Lake Charr Diversity

General mechanisms of evolutionary divergence (Sect. 3; Box 1) that result in phenotypic and genetic diversity observed in postglacial fishes (salmonids specifically) should also operate to generate phenotypic diversity observed in the lake charr and described in Sect. 2. In this section, we identify similarities and differences of interest.

4.1 Bimodal Versus Multi-modal Diversification

Salmonids in general, and lake charr in particular, do not always follow the bimodal benthic-pelagic habitat diversification model that is typical of other fish species (e.g., three-spined stickleback, sunfish *Lepomis* spp., and perch *Perca* spp.; Robinson and Parsons 2002). Additional patterns of diversification, such as littoral-profundal divergence, have been observed in salmonids, thereby resulting in repeatable divergences of up to four sympatric ecotypes. Arctic charr, whitefishes, and ciscoes *Coregonus* spp., brown trout *Salmo trutta*, and lake charr are all known to sustain quadrimorphic diversification in multiple systems (Snorrason et al. 1994; Turgeon et al. 1999; Chavarie et al. 2013; Muir et al. 2014a, b; Kahilainen et al. 2017; Piggott et al. 2018). To date, examples of quadrimorphic populations of lake charr include Great Bear Lake and Lake Superior (Chavarie et al. 2013; Muir et al. 2014a). Such quadrimorphic populations demonstrate more complexity than the bimodal axis of diversification, not only with respect to the diversity expressed but also in the mechanisms that led to divergence. Despite their complexity, the emergence of tri- and quadrimorphic populations should result from the same fundamental processes that drive simpler bimodal divergence (Box 1; Wellborn and Langerhans 2015). A common feature of habitats in which multi-modal divergence occurs is high levels of ecological opportunity (Boxes 1 and 2). A number of salmonid examples of quadrimorphic diversification are located in high latitude (or altitude) systems, which might indicate that more ecotypes can be sustained in systems that are depauperate due to recent glaciation (and also related to low productivity, at least indirectly; Schluter 2015). However, this latitudinal pattern remains to be robustly tested (Box 3).

Box 2 Generalists, Specialists, Plasticity, and Genetics: Are the Dynamics of Diversification Linked with the Spatiotemporal Structure of Ecological Opportunity?

Fishes that colonized freshwater systems as they emerged from the Pleistocene glaciation are typically assumed to have been generalists (e.g., in foraging and habitat use) at the time of colonization (Snorrason and Skúlason 2004). After colonization, diversification is often linked to the emergence of foraging specialist ecotypes that use different foraging opportunities associated with discrete habitats; intraspecific competition likely helps to drive this specialization process (Skulason and Smith 1995). A possible alternative is that the colonizer is a resource-use specialist and divergence occurs through the development of novel specializations (i.e., a specialist to specialist divergence). In this case, initial specialization is not an impediment to ecological diversification (Schluter 2000; Levis et al. 2017).

Where intraspecific divergence occurs in a single waterbody, alternate ecological opportunities are an important precursor to divergence into ecotypes, which is thought to begin through phenotypic plasticity acting upon traits that enhance resource use efficiency (see Box 1; Futuyma and Moreno 1988; West-Eberhard 1989; Skulason and Smith 1995). Ecological opportunity is intrinsically coupled with environmental conditions to which species colonizing new systems are exposed. The specific nature of that opportunity may also facilitate divergence and subsequent persistence of ecotypes within a

(continued)

Box 2 (continued)

system. Ecological opportunity arises from the availability of unexploited resources, whereby individuals using such resources are likely to experience a relaxed selection in the face of abundant available resources (Losos 2010). In these circumstances, a population can express a new phenotype and persist in the presence of novel resources. Two components that appear to be important in driving divergence of a single monomorphic population into multiple ecotypes are the population's ability (through plasticity) to respond to environments to which it is exposed and the spatiotemporal structure of resource availability (Knudsen et al. 2010, 2011). This spatiotemporal structure of ecological opportunity helps to define the form, direction, and intensity of selection, and the scope of divergence (see Figs. 1 and 2, and Box 3; Seehausen et al. 2008; Wellborn and Langerhans 2015).

Mechanisms that allow flexibility in the expression of phenotype, such as phenotypic plasticity (West-Eberhard 1989), are thought to be evolutionarily costly, so that as ecosystems stabilize and become more predictable, a general tendency should be that a population's capacity for phenotypic plasticity should be reduced (Fig. 6). If the move toward specialization involves multiple expressed specializations, then genetic divergence should increase (Bolnick et al. 2003; Svanbäck et al. 2015; Dermond et al. 2017). If the environment remains sufficiently stable, plasticity may be less advantageous and traits associated with emerging specializations may begin to become genetically determined, often described as "genetic assimilation" (DeWitt 1998). Once genetic assimilation begins, disruptive selection should favor extreme traits in the population that are adaptive for emerging specializations, and intermediate forms should be selected against and decrease in frequency. At one extreme, flexible and highly plastic populations occur in unstable systems, and several alternate (but overlapping) states are possible with varying degrees of restricted gene flow (Hendry et al. 2009). At the other extreme, genetically distinct ecotypes occur in stable systems that, through adaptation to niche use and reproductive isolation, and have lost their original capacity for plasticity (Snorrason and Skúlason 2004; Nosil 2012; Oke et al. 2016).

Regarding diversification in the lake charr, an intriguing question is how was ecological diversity shaped by ecological opportunity and adaptational constraints?

Bimodal populations of lake charr that have diversified on a resource axis associated with depth appear somewhat straightforward, e.g., shallow-water- vs. deep-water ecotypes exploiting fish (piscivory) vs. *Mysis* (although some trophic overlap can exist; Zimmerman et al. 2006, 2007; Eshenroder 2008). Additional axes of diversification could be linked to ecological opportunities provided by prey species, which leads to the question of whether adaptive radiation of prey may lead to diversification of predators (adaptive radiation cascades; Brodersen et al.

2018). Several lake charr diversifications occur in association with coregonine divergence along a depth gradient, such as in Lake Superior, Lake Mistassini, and Great Slave Lake. Accordingly, cisco divergence could result in novel additional resources in a system, which could lead to additional ecological opportunities and niche expansion for lake charr (Brodersen et al. 2018). If a species has the evolutionary capability of diversifying to exploit an increased variety of resources (Stroud and Losos 2016), this diversification is a type of "ecological release" (Wellborn and Langerhans 2015).

4.2 Processes Linked to Phenotypic Diversification

4.2.1 Heterochrony and Ontogeny

Phenotypic plasticity is primarily a mechanism operating through ontogeny (Skúlason et al. 2019). Two routes through which phenotypic plasticity may operate include heterochrony and epigenetic effects. Heterochrony is widely regarded as an important mechanism in morphological divergence within *Salvelinus* and occurs when changes in developmental timing or rate of life-history events lead to changes in size and shape (Mabee et al. 2000; McPhee et al. 2012). In Arctic charr, inherited differences in gape and head size have arisen from differential rates of growth of anatomical features relative to body size (Skúlason et al. 1989; Hindar and Jonsson 1993; Adams and Huntingford 2005). In the case of lake charr, juveniles show little phenotypic variation compared to adults (Zimmerman et al. 2006, 2009; Chavarie et al. 2013), which raises questions about the interplay between ontogenetic niche shifts and environmental feedback in shaping divergence (e.g., Parsons et al. 2011).

Whether phenotypic diversification in lake charr is mediated by epigenetic processes is unclear. Epigenetic effects can be caused by conditions encountered in early life history, but can also be trans-generational, and reflect conditions experienced by parents (Wellband et al. 2021; Jonsson and Jonsson 2014). Common garden experiments demonstrate a heritable basis for phenotypic differentiation (e.g., condition factor, morphology, and lipid levels) between siscowet and lean charr ecotypes from Lake Superior (Wellband et al. 2021; Eschmeyer and Phillips 1965; Krueger and Ihssen 1995; Goetz et al. 2010). Transgenerational epigenetic programming is unlikely to be the sole causal influence on phenotypic variation among sympatric ecotypes, because the process would need to be repeated in each generation in perpetuity. Instead, potential epigenetic influences on phenotypic diversification would more likely occur during the early stages of sympatric differentiation, with alternate mechanisms of heritable adaptation increasing in importance in later generations (Fig. 6). Due to the long generation time of lake charr, however, experimentally testing questions about phenotypic plasticity and genetic influences on phenotypic traits would be challenging. More knowledge in this area is critically needed.

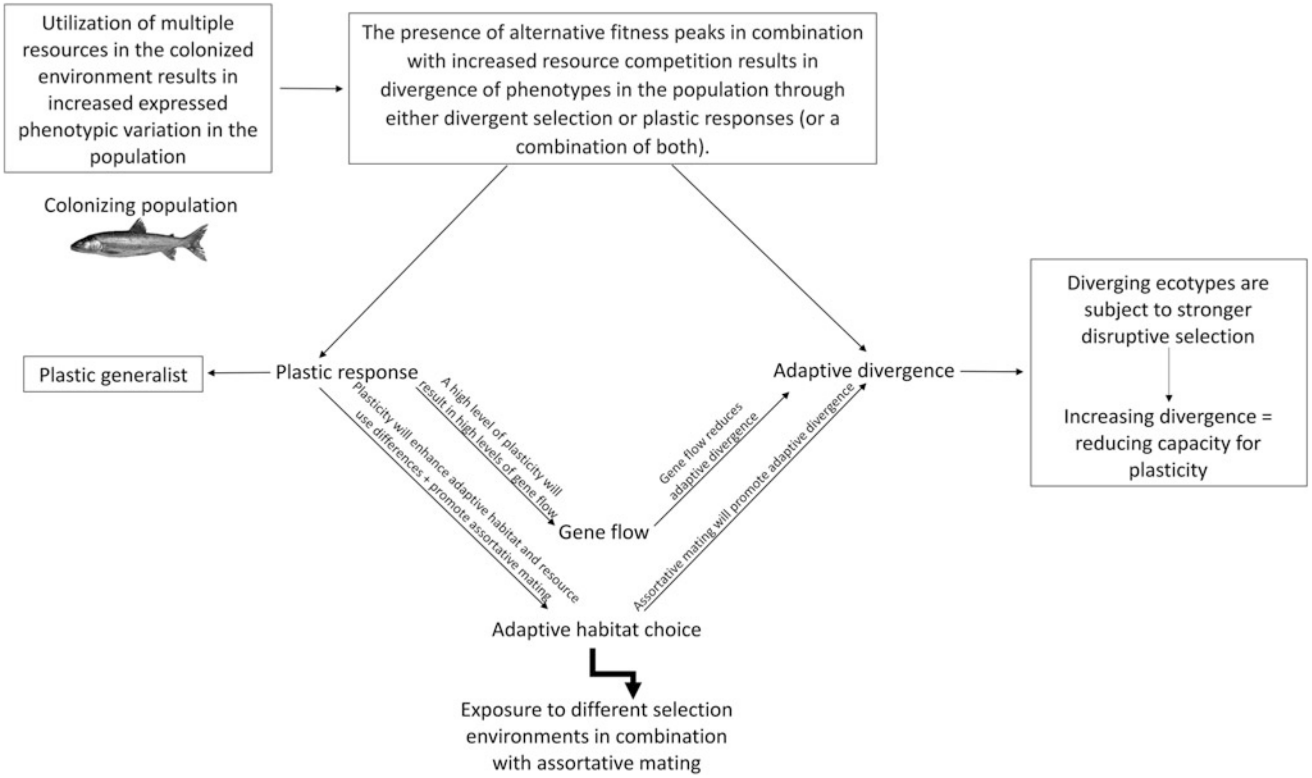


Fig. 6 Summary diagram of processes of adaptive diversification (figure modified after Nonaka et al. 2015). Phenotypic plasticity can potentially both promote evolutionary divergence and act against it, with effects that vary depending upon steps in the divergence

The relationship between resource partitioning and ontogeny is rarely examined in studies of resource polymorphism in wild populations, but this relationship is particularly relevant for lake charr because trait divergence in individuals generally begins at ca. 430–450 mm (Zimmerman et al. 2006; Chavarie et al. 2013). For example, juvenile lean-like and siscowet-like ecotypes in Great Slave Lake overlapped in habitat and resource use, with juveniles from both ecotypes inhabiting the same deep-water benthic habitat (Zimmerman et al. (2009). Juveniles differed slightly in head shape, with siscowet-like charr having deeper head profiles, blunter snouts, and eyes higher on their heads than small lean-like charr (Zimmerman et al. 2009). This contrasts with the concept of resource polymorphism that assumes habitat partitioning at comparable ontogenetic stages, as is commonly observed in other polymorphic species, such as European whitefish *Coregonus lavaretus* (Kahilainen et al. 2003).

4.2.2 Rapid Divergence

Divergence within ecological time scales (e.g., within a few generations) illustrates intraspecific flexibility of the lake charr. Some of the best cases that demonstrate contemporary changes of lake charr in response to novel environments are found in introduced populations. Many of these populations have shown rapid phenotypic divergence from their source populations (Box 4). For example, lake charr introduced into Flathead Lake (USA) in the late 1800s showed rapid phenotypic divergence after the establishment of *Mysis* in the 1980s (Stafford et al. 2013). Sympatric differences in morphology, ecology, and life-history quickly emerged, with deep-water individuals feeding heavily on *Mysis* (Stafford et al. 2013). However, lake charr from the two depth zones (shallow-water, 0–25 m and deep-water, 60–100 m) did not differ genetically at ten microsatellite loci (Stafford et al. 2013). This finding is consistent with observed rapid shifts in trophic level and body size in other lake charr populations after the establishment of centrarchid competitors (Vander Zanden et al. 1999a, b, 2000), and supports the inference that phenotypic and life-history traits of lake charr can be plastic. Similar rapid phenotypic divergence has been observed for introduced populations in California (from Lake Michigan), where differences in life-history among populations were extensive (McDermid 2007). Whether these phenotypic differences have any heritable basis is currently unknown.

4.3 Trophic Overlap Versus Phenotypic Variation

How do lake charr fit into conceptual models of divergence processes and trophic specialization, given the contrasting patterns of phenotypic variation and the capacity to display opportunistic and flexible feeding behavior? Ecological opportunities that drive divergent selection of traits to enhance efficient use of resources are hypothesized to be an initial step toward intraspecific divergence (e.g., niche specialism; Skulason and Smith 1995; Svanbäck and Persson 2004; Knudsen et al. 2010). In several lakes, lake charr morphological heterogeneity is apparently disconnected from the apparent trophic mechanisms underlying the process of divergence (Chavarie et al. 2016b; Marin et al. 2016; Hoffmann 2017). This observation of trophic overlap and divergent morphology (see Fig. 5 for an example and Chavarie et al. (2020a); the degree of trophic overlap among ecotypes changes among lakes) contrasts with more typical patterns observed in salmonids where: (1) the emergence of distinct sympatric specialist phenotypes is often rapid in postglacial lakes (Gíslason et al. 1999; Hudson et al. 2011; Elmer 2016) and (2) morphology is a good proxy for diet specialization due to known form-function relationships (Bolnick and Paull 2009; Bolnick et al. 2010).

Several recent examples of generalists displaying specialized morphology across taxa are challenging long-standing hypotheses that specialized morphology corresponds to a specialist diet (Chavarie et al. 2016b; deVries 2017; Figgener et al. 2019). Trophic overlap among lake charr ecotypes may consist of subsets of differently specialized individuals that produce a broad ecotype-level niche as an overall outcome (see Bolnick et al. 2002, 2003 for a discussion of individual specialization within a generalist population). Depauperate environments and large, bathymetrically complex habitats, common for lake charr populations, can promote the use of spatially separated resources or variable use of resources among years, which are known to favor individual specialization (Svanbäck and Persson 2004; Costa et al. 2008; Quevedo et al. 2009).

Due to a presumed homogeneity of resource use within an ecotype, few studies have investigated dietary patterns within a lake charr ecotype. However, for at least one lake, among-individual resource specialization within an ecotype is evident (Great Bear Lake; Chavarie et al. 2020b). Cryptic eco-evolutionary outcomes are often overlooked despite their potential importance within an ecosystem. Thus, trophic specialization and generalization across multiple hierarchical levels within lake charr (e.g., a continuum of intraspecific trophic specialization within and among ecotypes) present a far more complex view than suggested by trophic and functional ecology of intraspecific diversity (Figgener et al. 2019). Ecological opportunity may not wholly explain diversification because of several examples of failure to diversify in the presence of ecological opportunity (Losos 2010), which suggests that currently unrecognized factors may promote phenotypic divergence in lake charr.

4.4 Does Observed Overlap Imply Intermediate Phenotypes?

Although different patterns of phenotypic divergence can represent different stages of evolutionary processes, intermediate phenotypes between well-defined ecotypes have been presumed to be rare in nature due to assumed low fitness when resources accessed by alternative ecotypes are also discrete and where intraspecific competition is high (see Box 1; Schluter 2000). Yet, intermediate phenotypes occur in the lake charr (Zimmerman et al. 2006, 2007; Northrup et al. 2010; Marin et al. 2016;

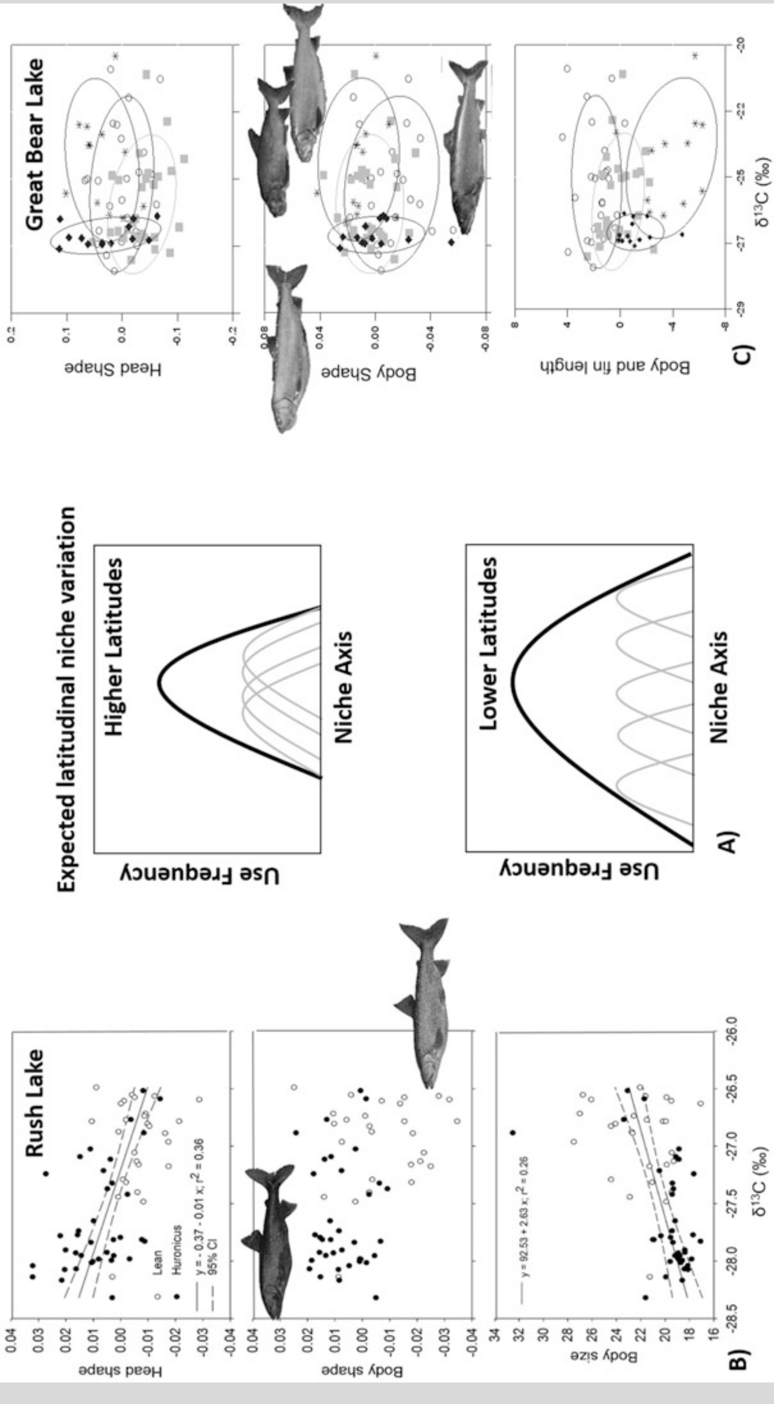
Chavarie et al. 2018). Although more frequent in lake charr, other salmonids such as whitefishes also display intermediate phenotypes (Harrod et al. 2010; Siwertsson et al. 2010). Phenotypic traits in lake charr may display continuous, clinal, or multimodal variation, rather than strong discontinuities among well-defined discrete ecotypes (Fig. 1b, c; Wellband et al. 2021). In such cases, lake charr display morphological or niche overlap and may operate as flexible generalists (Box 3), which results in difficulties classifying individuals that fall outside the "extreme phenotype." Competition in post-glacial systems could be low enough that intermediate phenotypes persist even if they exploit available resources less effectively (Schluter 2001). Intermediate phenotypes may also reflect insufficient time for divergence, weak isolating mechanisms, presence of other undescribed ecotypes, high levels of phenotypic diversity in combination with subtle local environmental influences on phenotypic expression, or a combination of these (Zimmerman et al. 2006, 2007; Chavarie et al. 2020c).

Box 3 The Importance of Niche Variation in Lake Charr Intraspecific Diversity?

Spatial and temporal variation in resource availability and use should influence the stability of individual specializations within a species and thereby influence the origin and maintenance of intraspecific diversity (Costa et al. 2008; Quevedo et al. 2009; Knudsen et al. 2010). At higher latitudes, niches occupied by individuals in a population may become larger so overlap between individual increases, while overall population niche width decreases. The opposite occurs at lower latitudes (panel a below). For example, the form-function covariance (i.e. morphological variation in relation to diet and habitat partitioning) in lake charr ecotypes from Rush Lake (southern population, panel b) was higher than that for Great Bear Lake ecotypes (northern population, panel c). Rush Lake ecotypes displayed a high level of ecological specialization, with a strong linear relationship between morphological variation related to trophic ecology and depth-related habitat use (e.g., small individual niches, high specialization). In contrast, Great Bear Lake supports multiple generalists displaying concurrent lines of diversification that exploit multiple niche axes (large individual niches, low specialization). However, population niche width between Rush Lake and Great Bear Lake did not follow latitudinal expectations, with greater population niche width for Great Bear Lake than for Rush Lake (perhaps influenced by the large difference in lake size). This and other system-level comparisons could demonstrate a latitudinal structure of niche variation (e.g., individual specialization) linked with diversification, but more systems with similar numbers of ecotypes and lake size are needed to assess if a latitudinal gradient exists and how it operates.

(continued)

Box 3 (continued)



(continued)

Box 3 (continued)

Figure adapted from Araújo and Costa-Pereira (2013), a conceptual representation of the increase in niche variation from lower vs. higher latitudes (a). Black thick lines represent the population use frequency along an arbitrary niche axis and individuals are represented as thin gray lines. Two lake charr examples illustrate different form–function relationships linked to trophic specialization between two populations that differ in latitude. For Rush Lake (b), the form–function relationship is shown as a linear relationship with 95% confidence intervals for the first principal component of head shape, body shape, and body size associated with carbon ($\delta^{13}C$) isotope signatures (representing shallow- vs. deep-water habitat use) for lean (open dots) and huronicus (solid dots) lake charr ecotypes; adaptation from Chavarie et al. (2016d). For Great Bear Lake (c), the form-function relationship of four shallow-water lake charr ecotypes is illustrated as 68.3% confidence ellipses for the first principal component for head and body shape, and fin and body lengths plotted against carbon ($\delta^{13}C$ ‰) stable isotope values. The four shallow-water ecotypes are: open circle = Ecotype 1, light gray square = Ecotype 2, X = Ecotype 3, and black diamond = Ecotype 4.

5 Does Lake Charr Capacity for Divergence Differ from Other Post-Glacial Fishes?

Behnke (1972) speculated that evolutionary specialization in the lake charr as a long-lived top predator in highly stable habitats may have resulted in limited variation in morphology across populations. Long-lived species, such as the lake charr (more than 60 years; Hansen et al. 2021), have fewer generations over time and lower effective population sizes (N_e) with concomitant reduction of standing genetic variation, which potentially reduces local adaptive potential compared to other salmonids with shorter generation times such as the Arctic charr and the whitefishes. This in turn could hinder diversification, because heritable change can be limited by lower spawning frequency, fecundity, and recruitment (Latta 2008; O'Grady et al. 2008; Wilson et al. 2014).

Some evidence suggests that among-individual variation, which can lead to phenotypic divergence, is highest for individuals that occupy intermediate trophic positions (Svanbäck et al. 2015). Piscivory might therefore limit the scope for morphological variation in the lake charr (Collar et al. 2009). Specifically, if lake charr adopt piscivory early in development, exposure to fish prey at a young age may limit exposure to alternative prey, thereby making them less likely to specialize on alternative prey than other species (Andersson et al. 2007). Lake charr generally fill foraging niches at a higher trophic level than Arctic charr, brook charr *Salvelinus fontinalis*, and whitefishes, which could limit their opportunity for diversification. However, one aspect of piscivory that could lessen this diversification limitation is cannibalism, especially in early life stages. Within a population, cannibalism on small-sized individuals can indirectly increase the availability of planktonic and benthic resources for larger-sized individuals, thereby expanding their resource base and ultimately leading to the development of resource polymorphism (Persson et al. 2004; Andersson et al. 2007; Chavarie et al. 2016b).

Another possible reason why divergence within lake charr in small lakes (<500 km^2; but see Table 1 for examples) is relatively rare might be that lake charr have a greater ability to range over multiple habitats within a small lake (habitat coupling) compared to a large lake. This coupling results in an evolutionarily stabilizing effect that reduces the probability of unused foraging habitat into which lake charr may diverge. The lake charr is a mobile predator that displays flexible foraging behavior by moving across spatially disparate habitats (e.g., shallow- vs. deep-water habitats), albeit requiring cold-water habitat in the southern part of its range during thermal stratification (Guzzo et al. 2017). Mobile predators may couple relatively discrete habitats in small ecosystems and thereby reduce the possibility of foraging niche specializations while enhancing habitat generalization (McCann et al. 2005). Conversely, if lake size is correlated with a more reticulated lake shape, with consequently larger littoral zones, large lakes ought to reduce the degree of habitat coupling by lake charr (Dolson et al. 2009) than small lakes. Consistent with this prediction, lake charr inhabiting small lakes have shown pronounced higher levels of omnivory (i.e., less specialization) than those in large lakes (Post et al. 2000; McCann et al. 2005; Dolson et al. 2009). Future research should seek to determine if lake charr are inherently more likely to function as habitat couplers than other salmonids.

Finally, divergence into multiple specialist foraging ecotypes may be less common in small lakes than in large lakes if selection for different levels of phenotypic diversity varies with lake size. For example, a capacity to express high levels of plasticity could have a larger positive selection advantage in small than in large lakes. The advantage could derive from a need to respond to environmental changes in less stable environments of small lakes (Snorrason and Skúlason 2004). High levels of plasticity, in combination with a fluctuating environment, may prevent evolutionary divergence in favor of temporal variation in phenotypic expression (Fig. 6; West-Eberhard 1989; Nonaka et al. 2015; Chavarie et al. 2020c). This may favor the expression of a plastic generalist, and thereby prevent the evolution of niche specialization (Chavarie et al. 2015, 2016b; Marin et al. 2016; Perreault-Payette et al. 2017).

Alternatively, lake charr in small lakes may express lower levels of plasticity than in large lakes. Plasticity is an important element of the process of ecologically driven diversification (West-Eberhard 2003; Pfennig et al. 2010; Nonaka et al. 2015). A capacity for plasticity, in combination with moderately stable but more diverse environments in large lakes, provide conditions that permit expression of a range of phenotypes and promote diversification (Fig. 6; Snorrason and Skúlason 2004). Altogether, the question might be whether the lake charr's capacity for plasticity is high or low? The capacity of lake charr to express different plasticity among lake types or sizes has not yet been studied, so these two alternative explanations for differences among lake charr in large and small lakes have not yet been disentangled. This subject would be a fruitful area for future research.

On one hand, high levels of phenotypic variation have been found repeatedly in the lake charr (Box 4; Chavarie et al. 2015; Marin et al. 2016; Perreault-Payette et al. 2017), whereas on the other, the lake charr is found in tens of thousands of lakes, but sympatric ecotypes have been documented in only a handful of lakes. Yet, the congeneric Arctic charr, despite being renowned for sympatric ecotypes, are similarly known for a small number of cases of lacustrine intraspecific diversity in North America (excluding diversity related to anadromy, only four cases of sympatric polymorphism in the Arctic charr have been reported in Canada: Lake Hazen, Gander Lake, Lake Aigneau, and Lake Matamek; Saunders and Power 1969; Reist et al. 2013). A key point here is that *Salvelinus* intraspecific diversity within lacustrine systems in North America is still under-studied, primarily because of the number of populations and their remote locations. Consequently, the full extent of intraspecific diversity in North American *Salvelinus*, including the lake charr, is unknown. Alternatively, lacustrine divergence of *Salvelinus* in North America may be more limited than in Europe. Such discrepancies between geographic regions might be explained by their degrees of environmental seasonality (and stability) or variation of latitudinal environmental gradients (e.g., temperatures; Chavarie et al. 2010). The inventory of lake charr intraspecific diversity urgently requires more work, particularly in the context of a rapidly changing climate in the Arctic that could modify existing diversity levels.

Box 4 Are Lake Charr Variable?

1. Multiple examples indicate that lake charr display high intraspecific flexibility and can show rapid phenotypic change in response to shift in ecological conditions
    (a) Lake charr sympatric diversification in Mondonac Lake (QC) was artificially induced by the construction of a hydroelectric reservoir in the 1940s. Maintenance of significant genetic separation suggests some degree of reproductive isolation and/or disruptive selection exists (Bernatchez et al. 2016).
    (b) Lake charr introduced into Montana approximately 100 years ago exhibited rapid phenotypic divergence (shallow-water vs. deep-water phenotypes) from source population when *Mysis* were introduced 40 years ago (Stafford et al. 2013). Similar rapid phenotypic divergence has been observed in introduced populations among lakes in California (McDermid 2007).
    (c) Following the establishment of rock bass *Ambloplites rupestris* in Canadian lakes, littoral prey species abundances were sharply reduced and lake charr shifted from being the top piscivore feeding on nearshore prey fishes to a pelagic planktivore, with concomitant decreases in body size and longevity (Vander Zanden et al. 1999a). This abrupt change from a Class 2 to Class 1 phenotype demonstrates that lake charr are

(continued)

Box 4 (continued)

capable of quickly shifting foraging specialization with consequent effects on growth. Similar findings have been reported for other lake charr populations following the establishment of smallmouth bass (Morbey et al. 2007).

(d) In response to temperature variation observed in a lake over 11 years, lake charr shifted from littoral to pelagic habitat use and from piscivory to planktivory (Guzzo et al. 2017).

2. Two lakes, Lake Superior and Great Bear Lake, support four sympatric ecotype populations of lake charr (Chavarie et al. 2013; Muir et al. 2014a).
3. Lake charr can diverge on multiple niche axes: shallow-water vs. deep-water; piscivorous vs. insectivorous or planktivorous; and littoral or benthic vs. pelagic.
4. Examples of parallel expression of lake charr ecotypes are found across North America: (1) Lake Superior, Great Slave Lake, Lake Mistassini, and Rush Lake for lean-like (shallow-water ecotype) and humper- or siscowet-like ecotypes (deep-water ecotypes) and (2) piscivorous and planktivorous ecotypes in Laurentian Shield lakes in Southern Québec and Ontario.
5. Lake charr display high levels of morphological variation within a single ecotype within large and complex lakes (spatial morphological variations in Great Bear Lake and Lake Superior). Lake charr also display a high level of morphological variation in Lake Mistassini, although it was not linked to spatial patterns.
6. Lake charr display variation of different traits (see table below, based on Klemetsen (2013)), where intraspecific variation of ten variable traits were compared among ten highly variable species (in species other than the lake charr). Variability of lake charr is demonstrated by variation in geographic range, migration pattern, habitat type, body size, diet, and genetic variation.

Measure of variation	Comparing and ranging
Variation in geographic	Continent: Nearctic (native), Palearctic (introduced), Neotropical (introduced), Australian (introduced) Ocean: Arctic Max latitude: 73 °N
Variation in migration pattern	Anadromous: (+), Lake-lake: +, Lake resident: ++, River-lake: +, River resident: (+), assumed to be present in the Arctic rivers, but status currently unknown
Variation in habitat type	Sea: (+), River: (+), Littoral:++, Pelagic:++, Profundal:++, Shift:++
Variation in body size (mature)	Variation (mm): 212–1575 mm
Variation in diet	Drift: not present, Pleuston: ++, Plankton: ++, Benthos: ++, Fish: ++
Genetic variation (among ecotypes)	F_{st}: 0-0.029 (microsatellite); 0.001-0.1 (SNPs)

(+) barely present, + present, ++ strongly present

6 Conservation and Management Implications

Management of lake charr should reflect the extent of ecological and phenotypic diversity within and among populations across the species range. Not considering units of management below the species level would risk overlooking a component of diversity that can be vulnerable to extinction (Taylor et al. 2006; Etheridge et al. 2012). Intraspecific diversity can be lost through stressors, such as habitat loss, stocking, overfishing, or invasive species (Orlane et al. 2015), which have interacted to impact historical lake charr populations in the Laurentian Great Lakes (Krueger et al. 1995). The original diversity of lake charr ecotypes in the Laurentian Great Lakes is difficult to determine but has undoubtedly declined greatly. Up to ten visually distinct ecotypes of lake charr were reported to occupy specific depths (e.g., including shallow-water intraspecific diversity) and spawn at different times in Lake Superior (Goodier 1981), compared to the four ecotypes currently documented. Combined anthropogenic and ecological stressors also caused a loss of genetic diversity (genetic homogenization) among extant lake charr ecotypes (Guinand et al. 2003, 2012; Baillie et al. 2016a, b; Wellband et al. 2021). Other consequences reflecting ongoing changes in the lake charr include dramatic declines in the fat content of the siscowet ecotype in Lake Superior, which have been attributed to increases in siscowet abundance and changes in depth distribution resulting from declines in cisco diversity and abundance, their main prey species (Bronte et al. 2003, 2010; Bronte and Sitar 2008; Muir et al. 2014a). Altered siscowet habitat use may increase distributional overlap with other ecotypes and could lead to a breakdown of ecological drivers that maintain the expression of intraspecific diversity (Guinand et al. 2012). Altogether, a key relevant observation is that the amount of introgression among ecotypes has likely increased over time, as a reflection of either ongoing ecological breakdown (Guinand et al. 2012; Baillie et al. 2016b) or resurgence of different ecotypes despite introgression at neutral genetic markers. On a smaller scale, the recent invasion of Rush Lake, Michigan by rainbow smelt has the potential to disrupt partitioning of resources and ecological barriers between lake charr ecotypes and result in a homogenization of diets and habitat use (Chavarie et al. 2016d), a process that has been described for other divergent ecotype pairs (Taylor et al. 2006).

Why does maintenance of intraspecific diversity in lake charr matter? The diversity of an ecosystem is generally linked to its stability and resilience to disturbance from natural or anthropogenic sources (Bolnick et al. 2011; Davies et al. 2016). In particular, throughout much of its range, the lake charr is experiencing dramatic and rapid changes in climate (Poesch et al. 2016) to which populations need to adapt if they are to survive (Guzzo et al. 2017; Campana et al. 2020). Intraspecific diversity will likely be important for maintaining the resilience of this species to coming changes. Plasticity and a high diversity of heritable traits should increase the probability that novel variation may emerge, thereby facilitating persistence and adaptation of populations to changing environmental conditions (Ghalambor et al. 2007; Campbell et al. 2017; Skúlason et al. 2019). Thus, understanding processes that favor phenotypic and genetic variability that underlie adaptation to environmental changes will help identify management options to help populations cope with these and future environmental challenges (Reist et al. 2013).

7 Conclusion

In this chapter, we reviewed a wide range of topics related to the intraspecific diversity of the lake charr, the patterns it can take, and the mechanisms that have likely resulted in these patterns. Below are several conclusions from this synthesis that we believe are important to those interested in lake charr for management or as a study species:

1. A consistent trait of the lake charr is its specialization in cold, highly oxygenated, and oligotrophic habitats. Other aspects of the lake charr's biology, such as its longevity, trophic position as an apex predator, and capacity for habitat coupling, may also act as possible factors constraining diversification.
2. Lake charr exhibit trophic differences among populations in a variety of lakes, and in some lakes, different phenotypes differ ecologically. These can be described as sympatric ecotypes that exhibit both similarities and differences with polymorphic salmonids described elsewhere. One notable difference observed in the lake charr is that phenotypic and genotypic variation along ecological and environmental gradients, which appears to be less discrete than in other salmonids (e.g., Fig. 1b vs. c; whitefish and Arctic charr).
3. Although not identical or uniform, sympatric polymorphisms have been described in at least 14 systems. Most cases show some differences in foraging ecology and in habitat use, but also a few in migratory behavior.
4. Evidence indicates that observed patterns of sympatric diversity in the lake charr are the result of rapid (<10,000 years) *in situ* divergence, and key elements (e.g., see point 6) that enable and maintain intraspecific diversity were found in areas they re-colonized.
5. Most explanations of evolutionary mechanisms that enable rapid ecotypic divergence come from theoretical and empirical studies of other post-glacial fishes, not directly from the lake charr. Key elements of these models describing mechanisms of disruptive selection and divergence where ecology is a large component include high levels of phenotypic plasticity, ecological opportunity in colonized habitats, and strong intraspecific competition (at least at times).
6. Although few studies have directly tested evolutionary models in lake charr populations, circumstantial evidence suggests that these or similar evolutionary mechanisms are relevant to diversification in the lake charr. This is an area that clearly needs research.
7. General mechanisms of evolutionary divergence in other post-glacial fishes are also likely operating in the lake charr, although some differences are of interest. Arguably, the most common ecological divergence in other sympatric post-

glacial fishes is between pelagic feeders and littoral or benthic feeders. In the lake charr, however, the most common axis of sympatric divergence lies along a depth gradient. A second, potentially linked difference is that sympatric polymorphisms in the lake charr are relatively rare in small lakes.

8. Future research—Many knowledge gaps remain for characterizing lake charr diversity in terms of both patterns of intraspecific diversity and mechanisms that drive and maintain that diversity. The lake charr has the potential to be a model species for addressing fundamental questions about the origins and mechanisms of evolutionary divergence. Here, we identify a non-exhaustive list of questions that could be addressed using the lake charr:

    - Are there other, yet undocumented patterns of intraspecific diversity among and within lakes?
    - Is cryptic diversity evident among lake charr populations?
    - Can patterns of sympatric divergence in the lake charr tell us something about underlying ecological, evolutionary, or genetic mechanisms?
    - How phenotypically plastic or heritable are adaptive traits in the lake charr?
    - How does the divergence of phenotypic traits relate to genetic differences among diverging groups?
    - What is the genetic architecture underlying the expression of different functional groups in lake charr?
    - Can functional genes be identified as responsible for functional adaptive trait differences in the wild?
    - Is phenotypic diversification in the lake charr mediated by epigenetic processes?
    - Can we test specific component parts of evolutionary models (see for example Skúlason et al. 2019)?

We hope that others will pick up the challenges presented here to use the lake charr as a model to develop a deeper understanding of ecological and evolutionary processes that promote ecological diversity, as well as to ensure the sustainability of the species.

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Glossary[1]

Adaptation The evolution of heritable traits in a population that result in higher fitness of individuals with those traits.

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[1] Glossary is a synthesis of the following sources: Skulason and Smith (1995), Allendorf et al. (2001), Glossary (2001), Malats and Calafell (2003), Kuparinen and Merilä (2007), Metcalf and Pavard (2007), Bolnick et al. (2011), Violle et al. (2012); Richardson et al. (2014).

Adaptive divergence The evolution of differences between populations as a result of adaptation to different environmental conditions and divergent natural selection.

Allopatry Geographical separation, such that members of two or more populations fail to encounter one another.

Continuous variation Variation that follows a normal distribution in the population.

Discrete variation Variation that is discontinuous in the population.

Disruptive selection Natural selection within a single population toward two or more different phenotypes, for example, when large or small individuals have an advantage over those of intermediate size.

Divergent selection Natural selection in different directions within each of several populations, for example, when large size is favored in one population, whereas small size is favored in another.

Eco-evolutionary dynamics Effects of ecological changes on evolutionary dynamics or the effects of evolutionary changes on ecological dynamics; feedbacks arise when a loop links both directions of effect.

Ecological speciation The evolution of reproductive isolation caused ultimately by divergent natural selection on traits between populations (or disruptive selection between phenotypes of a single population) in different environments (including use of different resources).

Ecotype An ecologically and phenotypically distinct group of individuals that belong to the same species.

Effective population size (N_e) The size of an "ideal" (stable, random mating) population that results in the same degree of genetic drift or inbreeding as observed in the actual population.

Functional trait Any trait affecting, directly or indirectly, individual performance and fitness of species.

Genotype The genetic constitution of an organism, which is modulated by the environment before being expressed as a phenotype.

Intraspecific diversity Variation occurring within a species.

Introgression Gene flow between populations whose individuals hybridize.

Phenotype The outward expression of an individual's genotype as affected by the environment (see "trait" below).

Phenotypic variation Variation within or among populations for an expressed trait that can be due to either phenotypic plasticity or genetic variation.

Phenotypic divergence Divergence of trait means between two or more populations or subpopulations.

Phenotypic plasticity The ability of the same genotype to produce or express different phenotypes.

Reproductive isolation Absence or severe restriction of gene flow between populations whose members are in contact with one another.

Resource polymorphism Occurrence of different phenotypes associated with segregation in habitat and diet.

Sympatry Absence of geographical separation, such that all individuals have the same chance of meeting each other.

Trait Any morphological, physiological, phenological, or behavioral feature measurable at the individual level.

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Genetic Diversity

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Abstract The use of genetic information in fishery management has become increasingly valuable as input to decision making. The lake charr *Salvelinus namaycush* represents an important model species of management concern for studying ecological divergence. We compiled a comprehensive assessment of the knowledge of lake charr genetic diversity. The following topics were reviewed: spatial patterns of genetic diversity, the relationship between genetic and morphological distinctiveness of ecotypes, heritability of phenotypes, evidence for "reverse speciation," and genetic effects of hatchery stocking. Important patterns that emerged were: strong divergence and high genetic uniqueness for most inland lake populations; evidence for heritability of traits associated with lake charr ecotypes; inconsistent support for genetic differentiation of ecotypes; an emerging view that lake charr diversity is distributed along a depth gradient in large lakes rather than discrete ecotypes; and hatchery supplementation and stocking have had profound but highly variable impacts on genetic diversity of populations. Knowledge gaps were identified to guide future research and to assist lake charr management and include investigations into the molecular mechanisms and evolutionary processes generating phenotypic diversity.

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1 Introduction

Molecular ecology and its associated evolutionary concepts and principles (e.g., variation, genetic drift, inbreeding, selection, connectivity; see Box 1) are increasingly being integrated into sustainable fishery management and aquatic ecosystem conservation, with recent developments in genomics technologies giving rise to a set of powerful, precise, and cost-effective genetic tools (Hendry et al. 2011; Ovenden et al. 2015; Casey et al. 2016; Bernatchez et al. 2017). The potential for molecular ecology to provide significant added value to fishery stock assessments and species rehabilitation programs has been recognized by fishery scientists and managers internationally, including the bilateral United States–Canada Great Lakes Fishery Commission, since the 1980s (Billingsley 1981). The lake charr *Salvelinus namaycush* is a major resource for both recreational and commercial fisheries, and is a treasured subsistence fishery of Indigenous Nations, particularly in large northern lakes (e.g., Great Bear Lake, Great Slave Lake). As an ecologically, economically, and culturally important species throughout its range, effective conservation and management of the lake charr requires knowledge of the distribution of genetic diversity within and among populations. The lake charr is also a species of tremendous interest in applied and fundamental research, notably for understanding the genomic basis of phenotypic variation, local adaptation, and origins of species. Due to its propensity for forming multiple morphological and life history variations (hereafter referred to as ecotypes), the lake charr is an interesting and exceptional model for studying eco-evolutionary processes involved in phenotypic divergence.

The first lake charr genetic studies focused on comparisons of allozyme variation among lake charr populations (Dehring et al. 1981; Krueger et al. 1989). Subsequently, studies concerned with lake charr re-establishment investigated postglacial colonization lineages using mitochondrial DNA restriction fragment length polymorphisms (RFLP; Wilson and Hebert 1996 1998), ecotype distinction and genetic impacts of human activities and stocking using microsatellite DNA markers (e.g., Page et al. 2004; Piller et al. 2005; Halbisen and Wilson 2009; Guinand et al. 2012; Valiquette et al. 2014; Baillie et al. 2015, 2016b; Harris et al. 2015), adaptive immune gene diversity and copy number variation in major histocompatibility complex (MHC) genes (Dorschner et al. 2000; Noakes et al. 2003; Baillie et al. 2018), gene expression to identify traits underlying phenotype (Goetz et al. 2010), and genome-wide scans of single nucleotide polymorphisms (SNPs) to investigate population structure and genomic variation among ecotypes (Bernatchez et al. 2016; Perreault-Payette et al. 2017; Perrier et al. 2017; Ferchaud et al. 2018). As part of a long-term project, the lake charr genome is currently being sequenced and annotated

(L. Bernatchez, unpublished data). Such knowledge will permit a deeper understanding of the structure of the lake charr genome, the genetic basis of ecologically relevant traits, and the consequences of human activities on patterns of genomic diversity.

Lake charr phenotypic diversity has traditionally been conceptualized using discrete ecotypes (e.g., lean, humper, siscowet, butterfly, redfin). Recent studies by Baillie et al. (2016a) and Chavarie et al. (2018) generated an emerging view of lake charr genetic and phenotypic diversity where adaptive variation is distributed along ecological and environmental gradients, rather than as discrete ecotypes. This information alters the conceptual model that fishery managers have been working under where "ecotypes" follow a genetically pre-determined developmental plan. Phenotypic clines within each ecotype also suggest that environmental conditions (i.e., phenotypic plasticity) interacts with genetic variation to determine morphological and life-history traits (Chavarie et al. 2021).

The genetic diversity of lake charr populations has also been dramatically re-shaped by human activities over many decades. Lake charr were severely reduced in abundance in the Laurentian Great Lakes by the mid-twentieth century and became extirpated from all lakes except Lake Superior and one small region of Lake Huron (Zimmerman and Krueger 2009). The combined effects of overfishing, the introduction of invasive species, water quality degradation, and hatchery supplementation influenced the genetic diversity of lake charr populations. Genetics and genomics can now provide more than biological stock structure information (see Ovenden et al. 2015) and we feel that empirical, theoretical, and applied genomics research must be embraced together if we are to understand the adaptive capacity of the lake charr, and how to manage it, in the face of ongoing natural and human-induced environmental change (McMeans et al. 2016).

The objectives of this chapter are to review the accumulated knowledge of genetic variation within and among lake charr populations, review evidence for the genetic basis of phenotypic divergence of lake charr populations, and to synthesize knowledge relevant for management and conservation of lake charr genetic diversity. We address these objectives with a series of questions on the diversity of postglacial genetic lineages observed in lakes today, the relationship between genetic and morphological distinctiveness among ecotypes, ecological axes of genetic divergence among lake charr populations, the genetic basis of lake charr phenotypes, evidence for losses in genetic and morphological diversity in the human-altered Laurentian Great Lakes and potential for "reverse speciation," and effects of hatchery supplementation on lake charr genetic diversity. We first introduce and present literature from an ecotypic perspective, then consider recent evidence in support of ecological-gradient-based genetic divergence, followed by case examples of human impacts on lake charr. The final section highlights emerging (epi)genomics approaches and technologies that may help resolve questions regarding the relationship between phenotype and genotype in lake charr and their genetic associations with habitat and evolutionary trajectories.

Box 1: Population Genetics Principles and Glossary

For those unfamiliar with the terms or concepts discussed in this chapter, we provide a brief primer on molecular ecology and population genetics concepts relevant for understanding the content discussed herein. Molecular ecology is an interdisciplinary field of study that applies molecular genetic markers to ecological questions. The variation of molecular genetic markers (for the purposes of simplicity: genes) are governed by Mendel's principles of inheritance and various evolutionary concepts collectively under the umbrella of population genetics. For diploid organisms like humans, or functionally diploid organisms like lake charr,[1] individuals carry two copies of each gene that are called alleles. One copy is inherited from the organism's mother and the other from its father. Mendel's principles of inheritance state that alleles are inherited randomly with equal probability and alleles at different genes are inherited independently. In the context of a population of organisms, this generates predictions that link the frequency of an allele in the population with the expected frequencies of combinations of alleles (genotypes) carried by individuals. Deviations from these expectations in real samples can be used to make inferences about various evolutionary forces influencing populations.

Four major evolutionary forces generate, maintain, and shape molecular diversity in natural populations. They are: mutation, migration (or gene flow), genetic drift, and selection. Mutation is the source of all variation and occurs spontaneously through errors in DNA replication and the action of selfish DNA and RNA elements (e.g., viruses and transposable elements). The remaining forces simply shape the variation created by mutation. Directional and divergent selection and genetic drift tend to erode genetic diversity through either the stochastic loss of variation due to finite population sizes (drift) or selection for, or against, specific variants in certain environments. These forces result in the genetic subdivision or structuring of groups of organisms when interbreeding between these groups is low. Migration that results in interbreeding between the groups is known as gene flow and works in the opposite direction from selection to homogenize genetic variation among structured groups. Similarly, balancing selection will favor the maintenance of genetic variation within populations.

Glossary

(continued)

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[1] All salmonid fishes, including the lake charr, are descended from an ancestral species that experienced a genome duplication at least 60 to 88 million years ago (Allendorf and Thorgaard 1984; Crête-Lafrenière et al. 2012; Macqueen and Johnston 2014). This duplication resulted in an organism whose cells had four copies of the genome rather than the normal two. Over time these duplicated genes may have become non-functional or evolved new functions such that most modern lake charr only carry two copies of each gene, although some regions (~15% of the genome) show residual tetraploidy.

Box 1 (continued)

Allele: One of the possible variant copies of a locus.

Allelic richness: The sample size corrected the number of unique alleles found in a group of samples.

Genetic divergence: Differences in allele frequencies among groups of organisms that are greater than those that could be explained by sampling artifacts.

Genotype: The combination of alleles that an organism carries at one or more loci.

Haplotype: Series of physically linked alleles belonging to the same strand of DNA.

Heterozygosity: The frequency of individuals in a sample that possess two different alleles at a specific locus.

Marker, Locus (singular), Loci (plural): Specific region or location in a species' genome.

Microsatellite: Type of variable genetic marker used for population genetic inference characterized by short (2–6 base pairs) tandemly repeated DNA sequences.

Mitochondrial DNA (mtDNA): DNA contained within the mitochondrial organelle that is maternally inherited.

SNP: Single Nucleotide Polymorphism, the most common class of genomic variation, characterized by the presence of two (or more) alternate base pairs at a specific genomic location.

2 Geospatial Patterns of Lake Charr Genetic Diversity

Contemporary geospatial patterns of lake charr genetic diversity are shaped by biogeographic history, landscape features, ecological opportunity, and the influence of human activities. Lake charr expanded their range from multiple refugia after the last glacial maximum and today are distributed across many thousands of North American lakes that formed as the ice retreated (Wilson and Hebert 1996; Wilson and Mandrak 2021). As a "nearly obligate" lake-dwelling species, except in the very northern part of its distribution, lake charr populations have experienced limited connectivity over the last few thousand years. This limited connectivity has led to spatial patterns of genetic diversity where local populations harbor subsets of a larger regional gene pool (Perrier et al. 2017).

Landscape genetics provides a framework of testable expectations or predictions (e.g., genetic diversity is positively correlated with lake size) often used in evolutionary and conservation biology to understand factors and mechanisms that affect the distribution of genetic variance, and hence local adaptation, in spatially fragmented and complex systems (Manel et al. 2003; Storfer et al. 2007). Basic assumptions of landscape genetics theory are that patterns of population genetic structure should reflect geographical features, such as physical distance separating populations, lake surface area, and elevation. In this section, we briefly review relationships between lake size and lake charr genetic diversity, as well as elevation and dendritic patterns. As more sophisticated genetic marker panels are developed in the coming years, more detailed relationships between genomic and habitat variation will be resolvable.

2.1 Refugial Origins, Postglacial Dispersal, and Secondary Contact

Like many North American boreal freshwater species, the spatial genetic structure of the lake charr was profoundly shaped by Pleistocene glaciations (Bernatchez and Wilson 1998; Wilson and Mandrak 2021). Repeated glacial advances and retreats alternated between destroying and revealing suitable habitats and, when combined with dispersal largely restricted to freshwater habitats, impacts on species' ecology and genomes have been especially pronounced (Pielou 1991; Wilson and Mandrak 2021). In a comprehensive project to reveal historical biogeographic origins and patterns of re-distribution of the lake charr, Wilson and Hebert (1996, 1998) tested alternate dispersal hypotheses using restriction fragment length polymorphism (RFLP) analysis of mitochondrial DNA (mtDNA). The contemporary distribution of four major mtDNA lineages observed following screening of 1416 lake charr from 93 populations across the species' range showed that extant populations of lake charr originated from at least five glacial refugia (Fig. 1).

The work of Wilson and Hebert (1996, 1998) provided clarity to the multitude of glacial refuge hypotheses that had been previously proposed, including several

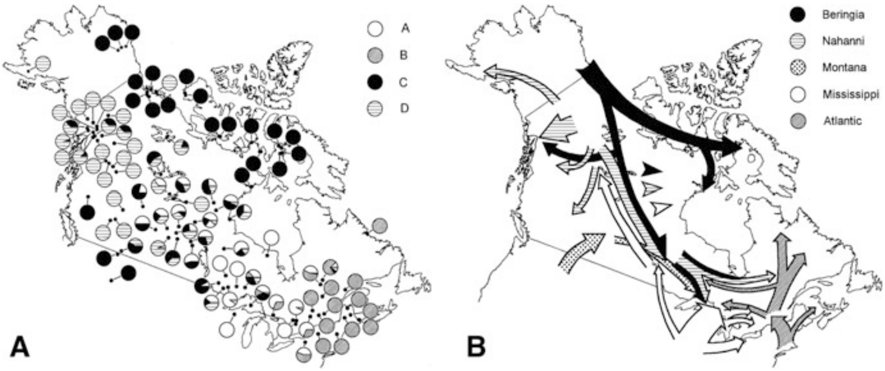

Fig. 1 Distribution of lake charr *Salvelinus namaycush* glacial refugia mtDNA RFLP lineages (**a**) and hypothesized refugial origins and patterns of dispersal for extant lake charr populations based on distributions of mtDNA haplotypes (**b**). From Wilson and Hebert (1998)

single refugia scenarios and various combinations of two or more (reviewed in Crossman and McAllister 1986). Current distributions of refugial lineages are best explained by the dynamics of proglacial lakes that formed along edges of the Wisconsinan ice sheet. Patterns and timing of connections between proglacial lakes changed dynamically as ice sheets receded to facilitate large-scale dispersal from multiple refugia. Long-distance dispersal is particularly evident from the Mississippian refuge in all directions and the eastward spread of lake charr from northwestern refuges. Dispersal through proglacial lakes also enabled extensive secondary contact among refugial groups.

2.2 Genetic Diversity Patterns in Large Lakes, Small Lakes, and Streams

Low rates of dispersal and a lack of suitable connectivity between most inland lakes during the past 6000–9000 years has led to high levels of differentiation among populations that reflect strong effects of genetic drift and a lack of migration among populations (Fig. 2; Halbisen and Wilson 2009; Valiquette et al. 2014; Perrier et al. 2017). In an extensive study of small lakes in Québec, lake charr genetic diversity was positively correlated with lake size and likely reflected initial founding events for these populations and effects of genetic drift in years since population establishment (Perrier et al. 2017). In small lakes, within-population genetic diversity was typically low and populations harbored a restricted subset of regional allelic diversity (Ihssen et al. 1988; Halbisen and Wilson 2009; Valiquette et al. 2014; Perrier et al. 2017). Consistent with evidence for lower diversity in smaller lakes, inbreeding was higher in smaller lakes (Perrier et al. 2017). Under these conditions, populations might be expected to have a reduced ability to adapt to changing climate or other factors, such as anthropogenic impacts because of insufficient genetic variation.

While increased levels of inbreeding and reduced genetic diversity appeared to limit adaptation for the most highly inbred populations (Fig. 3; Perrier et al. 2017), inbreeding was negatively correlated with the probability of deleterious genetic variants in inland lake charr populations and predicted that inbreeding may facilitate purging of deleterious variants (Perrier et al. 2017). A similar pattern was observed in pristine lakes in Labrador, where lake charr genetic diversity was positively correlated with lake size (McCracken et al. 2013). Inbreeding can lead to genetic purging because it raises the likelihood of homozygous individuals for recessive deleterious mutations. This exposes deleterious variants to selection and they are rapidly removed from the population. While genetic purging can cause short-term benefits by reducing populations' genetic load from deleterious mutations, purging is expected to come with negative long-term fitness costs due to loss of linked adaptive variation during these selective sweeps. Thus, increasing inbreeding should not be considered an optimal strategy for reducing maladaptation in the lake charr.

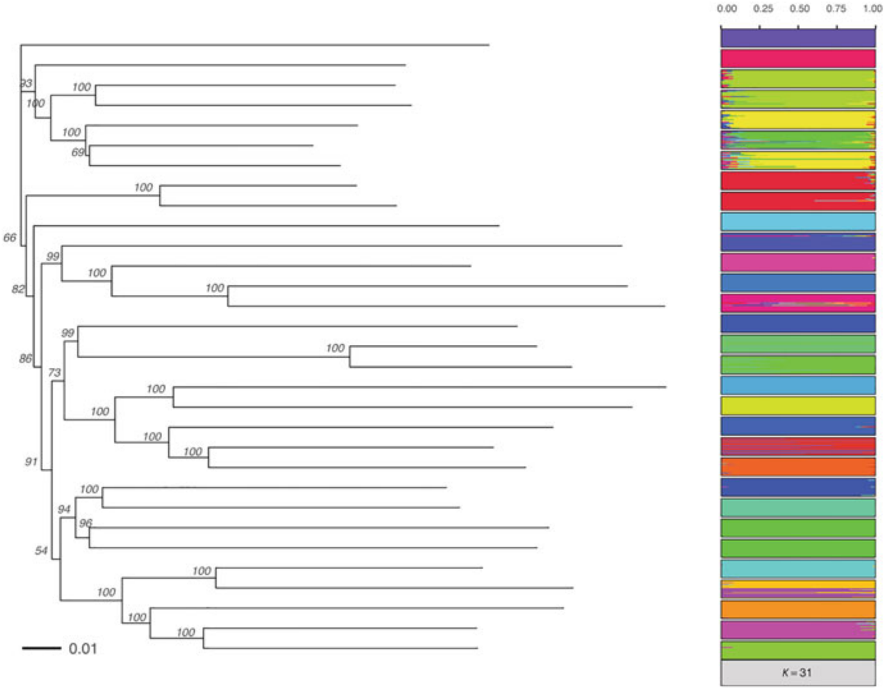

Fig. 2 Neighbor-joining tree based on Nei's genetic distance and structure plot for 31 populations of lake charr *Salvelinus namaycush* from Québec. Populations exhibit effects of strong genetic drift and limited gene flow as evidenced by long branch lengths and limited evidence for admixture in the structure plot. From Perrier et al. (2017)

As a consequence of pronounced genetic drift and limited connectivity, lake charr populations typically do not show a pattern of isolation by distance or regional hierarchical structuring according to hydrological connections (Halbisen and Wilson 2009; McCracken et al. 2013; Valiquette et al. 2014; Perrier et al. 2017), a pattern that may be unique to the lake charr among postglacial fishes. The exception to this lack of a spatial structuring pattern is for lakes at the southeastern edge of the distribution of lake charr in Vermont (Baillie et al. 2015). Here, variation is best explained by contemporary drainage basins, not proglacial drainages, and genetic differentiation increases with increasing elevation that suggests connectivity among these populations after postglacial colonization.

In large lakes, (>500 km^2), the situation is more complicated. Large lakes harbor higher levels of genetic diversity than small inland lakes (Ihssen et al. 1988; Halbisen and Wilson 2009), but landscape genetics patterns are not as clear due to the natural complexity of large lakes. Large lakes vary in both surface area and depth, which influences suitable habitat for and population sizes of lake charr. Lake

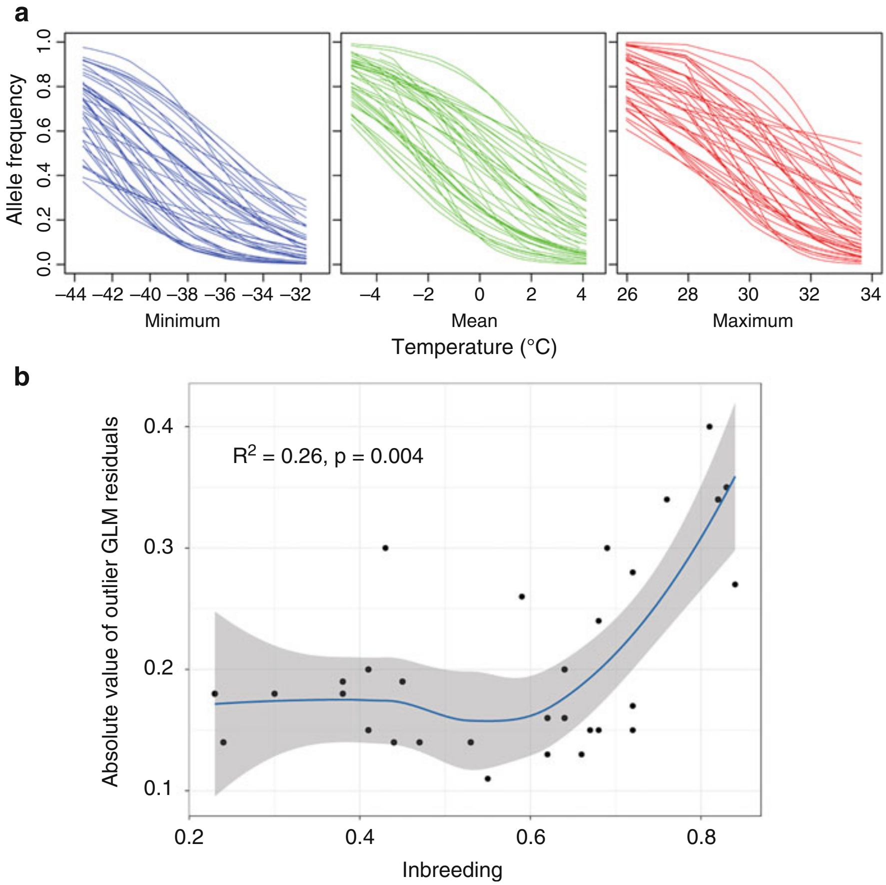

Fig. 3 Clinal association of allele frequency of 44 SNPs with minimum, mean, and maximum annual temperature for 31 populations of lake charr *Salvelinus namaycush* from Québec (**a**). Residuals from the GLM of outlier allele frequencies with temperature as a function of the population inbreeding coefficient (**b**). Higher levels of inbreeding increase the deviation of populations from the model fit suggesting increased inbreeding may be limiting adaptation. From Perrier et al. (2017)

charr populations in large lakes also tend to have within-lake geographical genetic structure (Guinand et al. 2003, 2012; Page et al. 2004; Harris et al. 2015; Baillie et al. 2016b; Marin et al. 2016; Perreault-Payette et al. 2017; Chavarie et al. 2018) that suggests the species may form a meta-population composed of multiple semi-independent gene pools in large lakes that confound whole-lake comparisons of diversity.

3 Comparative Genetic Diversity Among Ecotypes

The lake charr's extensive phenotypic diversity within- and among-lakes (Chavarie et al. 2021; Muir et al. 2016) has historically been characterized using a "discrete ecotype" conceptual model (e.g., lean [various lakes], humper, siscowet, redfin [Lake Superior], huronicus [Rush Lake, Michigan, U.S.A.], butterfly [Great Bear Lake, Northwest Territories, Canada], and many others). While Chavarie et al. (2021) contains a detailed treatment of the full range of morphological and ecological variation present in the lake charr, we provide a brief overview here to contextualize the patterns of genetic variation discussed below. Lean lake charr are the archetypal form found throughout the species' range and are characterized by long, fusiform bodies presumably adapted for a pelagic lifestyle. In large, deep lakes, lean lake charr are primarily found in shallow surface waters (<80 m depth) while several different forms (i.e., humpers, huronicus, siscowets) are more commonly found in deep waters (>80 m depth) and developed traits associated with life in deep water (e.g., short, deep bodies, and long paired fins).

The origin of ecotype variation has been of great interest to fishery managers and evolutionary biologists alike. For managers, knowledge of whether ecotypes reflect unique stocks or populations with potentially different dynamics, habitat requirements, and susceptibility to stressors (e.g., fishing mortality, invasive species) is important for appropriate conservation, restoration, and management planning. For evolutionary biologists, the evolutionary forces and genetic mechanisms that generated and maintain divergent ecotypes are interesting for understanding of adaptive processes and speciation.

Simple quantitative models describe phenotypes as resulting from the joint action of an individual's genotype and its environment. At the two extremes, lake charr ecotypes result entirely from exposure to different environmental conditions (e.g., prey communities, depth), or, alternatively, are completely genetically determined at birth. While neither of these extreme scenarios are likely, the relative contribution of genotype and environment to ecotype differentiation has important implications for stock delineation, fishery management, and prediction of evolutionary responses to changing environments. For example, conservation of biological (ecotype) diversity when a predominantly genetic basis exists for an ecotype might emphasize conservation of unique spawning populations of each ecotype, while a predominantly environmental basis for ecotype might emphasize maintenance of high-quality habitat types that give rise to each ecotype.

Many lake charr ecotypes were initially described, and were once believed, to represent different species (Brown et al. 1981; Goodier 1981). Early molecular genetic work found that lake charr in Lake Superior were structured primarily based on ecotype and secondarily among geographically dispersed populations within each ecotype (Page et al. 2004). The genetic distinctiveness of ecotypes in the lake has consequential effects on management recommendations. For example, Page et al. (2004) stated that in light of the evidence of significant genetic differentiation among morphotypes, lake charr morphotypes should be managed as distinct units in a manner like that advocated for imperiled Pacific salmon. This context of reproductively isolated ecotypes shaped much of the subsequent thinking about lake charr ecotype divergence.

For the purposes of discussing lake charr ecotypes, we will make use of a "biological species concept" which defines species based on the principle of reproductive isolation (Coyne and Orr 2004). Under this paradigm, ecotypes represent incipient species that fall somewhere along a continuum of reproductive isolation from complete panmixia to complete reproductive incompatibility (Hendry 2009; Chavarie et al. 2021). Two main possible evolutionary routes exist for the origin of ecotype variation: (1) allopatric divergence of ecotypes in geographic isolation (e.g., separate glacial refugia) where reproductive isolation developed and has subsequently been maintained following secondary contact of these diverged forms after dispersal from glacial refugia, or (2) multiple instances of sympatric divergence where divergence occurred along parallel environmental gradients found in multiple lakes throughout the species' range.

Molecular genetic data have shed light on the debate between allopatric versus sympatric divergence of lake charr ecotypes. Different ecotypes share the same mitochondrial haplotypes within each of the Great Lakes across continental North America (Burnham 1993) and ecotypes are generally more genetically similar to one another within lakes than when populations of the same ecotype are compared among lakes (Dehring et al. 1981; Krueger et al. 1989; Guinand et al. 2012; Baillie et al. 2016a, b; Perreault-Payette et al. 2017; but see Page et al. 2004). Collectively, this pattern suggests that independent divergence of ecotypes multiple times since the last glaciation is a more plausible explanation for observed patterns of phenotypic diversity than allopatric divergence of lake charr ecotypes during previous glacial cycles.

Ecological speciation, where divergent selection on populations exploiting different habitats or resources leads to reproductive isolation and eventual reproductive incompatibility (Schluter 1996, 2001; Rundle and Nosil 2005), provides a useful framework to conceptualize parallel evolutionary divergence of lake charr ecotypes in multiple lakes. Putative examples of ecological speciation are common for fishes colonizing postglacial habitats (Behnke 1972; Taylor 1999; Noakes 2008; Bernatchez et al. 2010). For these species, divergence in parallel at multiple locations is driven by selection along similar environmental axes (e.g., benthic versus limnetic). Thus, conserved phenotypic parallelism of lake charr ecotypes (e.g., between deep-water versus shallow-water forms) in geographically distant lakes provides evidence for similar ecological conditions driving ecotype divergence.

While molecular genetic data has proven useful for addressing questions of allopatric versus sympatric divergence, teasing apart potential reproductive isolation of lake charr ecotypes in several lakes has been more difficult using neutral markers (Northrup et al. 2010; Marin et al. 2016; Chavarie et al. 2016, 2018). This difficulty raises important questions about the genetic basis of ecotype divergence and mechanisms responsible for driving and maintaining ecotype divergence. In the sections below, we review hypothesized axes of ecotype divergence, evidence for reproductive isolation of ecotypes, and alternatives to the leading hypothesis of ecological speciation for explaining lake charr ecotypic differentiation.

3.1 Genetic Evidence for Ecotype Reproductive Isolation

Based on observed patterns of genetic variation among ecotypes and available data on the heritability of lake charr phenotypes (Sect. 5), Eshenroder (2008) developed an eco-evolutionary conceptual model to explain the evolutionary origins of lake charr ecotypes. The model proposed a resource-driven basis for ecotype polymorphism and thus divergent ecotypes only occur where an appropriate ecological opportunity exists. In particular, the model stipulates that divergence occurs in large, deep lakes (e.g., Great Slave Lake, Laurentian Great Lakes) with appropriate deep-water prey species to facilitate feeding resource polymorphism (Eshenroder 2008). The model postulates that a lean-like piscivorous form of lake charr is the ancestral form that survived glaciation and recolonized North America during the last glacial retreat. This form, driven by intense intraspecific competition, diversified into various deep-water forms specialized for feeding on deep-water invertebrates (e.g., humper-like) or deep-water fish (siscowet-like). While Eshenroder's (2008) model was largely influenced by observed genetic and heritable differences in phenotype between lean and siscowet ecotypes in Lake Superior, small inland lakes harbor phenotypic variation in the form of piscivorous and planktivorous ecotypes that are also compatible with this ecologically driven basis for evolved morphological divergence (Bernatchez et al. 2016).

Eshenroder's eco-evolutionary model drew heavily from some of the earliest studies of genetic variation in the lake charr. Surveys of allozyme variation among lean, humper, and siscowet lake charr forms from three locations in Lake Superior revealed significant divergence in allele frequencies among both ecotypes and sites (Dehring et al. 1981). Numerous subsequent studies also supported the partitioning of genetic variance among ecotypes in Lake Superior using allozymes (Krueger et al. 1989), microsatellites (Guinand et al. 2003, 2012; Page et al. 2004; Baillie et al. 2016a), and single nucleotide polymorphisms (Perreault-Payette et al. 2017), although the relative importance of sampling site over ecotype for partitioning variation varies among studies. Furthermore, genetic differences have also been demonstrated among multiple shallow-water ecotypes in Great Bear Lake (Harris et al. 2015) and between piscivorous and planktivorous lake charr in inland lakes of Québec (Bernatchez et al. 2016). The genetic differentiation among ecotypes in these studies rejected the null hypothesis of panmixia, but the generally weak genetic differentiation of ecotypes at neutral markers raises questions about the degree of reproductive isolation among lake charr ecotypes across the range.

Baillie et al. (Fig. 4; unpublished data) specifically tested hypotheses that lake charr ecotypes are reproductively isolated and comprise discrete genetic clusters. They sampled tissue from ecotypes within four large lakes, Great Bear Lake, Great Slave Lake, Lake Mistassini, and Lake Superior, and one small lake, Rush Lake.

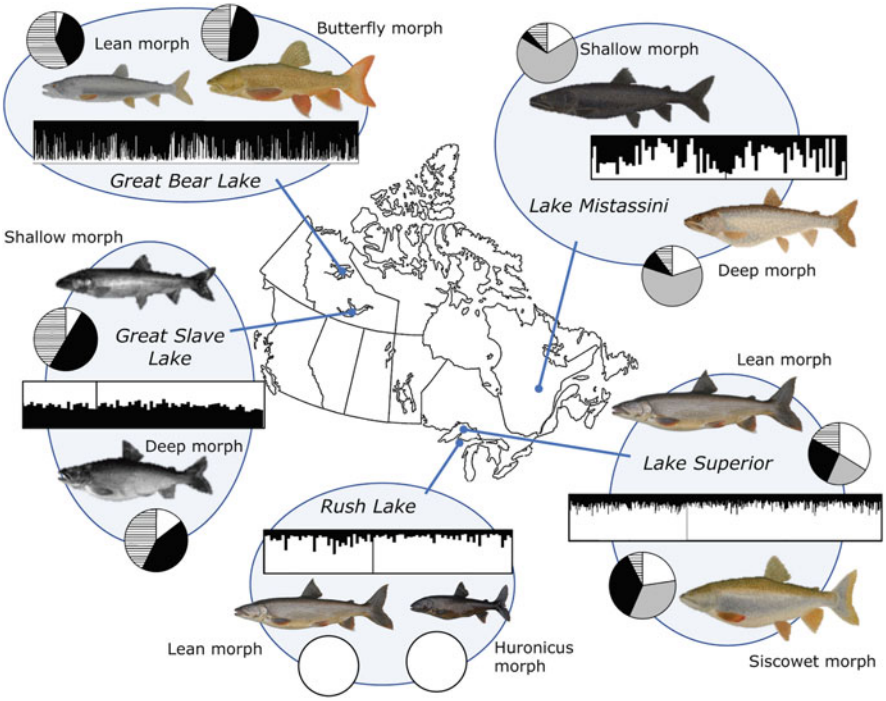

Fig. 4 Different lake charr *Salvelinus namaycush* ecotypes in the same lake share the same mitochondrial haplotypes (pie charts: white, gray, black, and horizontal lined slices represent Mississippian, Atlantic, Beringian, and Nahannian glacial refugia lineages, respectively) across continental North America and do not exhibit strong genetic distinction based on data from microsatellite markers (bar plots generated in Program STRUCTURE). The size of fish is to scale within but not among lakes. Baillie et al. unpublished data

Results from mitochondrial and microsatellite DNA analyses supported the hypothesis that ecotypes arose independently in lakes after postglacial colonization (Fig. 4). In contrast to previous studies, morphologically and ecologically differentiated lake charr ecotypes within lakes were largely genetically indistinguishable using neutral microsatellite markers and conventional population genetic analyses (Fig. 4). A lack of strong support for reproductive isolation among ecotypes was not likely due to a lack of power in genetic markers and statistical techniques previously used, but rather likely reflects ongoing gene flow between ecotypes. These results collectively suggested that lake charr ecotypes were at an early stage of divergence with incomplete reproductive isolation.

Genomic perspectives on ecological speciation with gene flow suggest that during the early stages of divergence, selection will heterogeneously influence divergence throughout the genome (Feder et al. 2012; Nosil and Feder 2012). Divergent selection on ecologically relevant genomic variation will be opposed by forces of gene flow and recombination that will break up ecologically favorable combinations of alleles. Where selection on genomic variation is stronger than these opposing forces, "genomic islands of divergence" will develop to explain phenotypic polymorphism despite apparent panmixia in regions not influenced by selection (Feder et al. 2012; Nosil and Feder 2012). All studies that have failed to identify strong genetic divergence between ecotypes have employed microsatellite markers, and while effective and powerful markers for estimating gene flow, they offer a selectively neutral perspective of genome-wide patterns used to infer adaptive divergence between ecotypes. Given the lack of strong evidence for reproductive isolation among ecotypes, genomic data appear poised to make significant contributions to our understanding of lake charr ecotype divergence and ecological axes driving divergence (e.g., Larson et al. 2014).

3.2 Genomic Architecture of Parallel Divergence

Species that exhibit repeated parallel divergence in phenotypes across locations raise questions about whether the genetic basis of such divergence reflects the same, or different, genetic architectures (i.e., the same or different sets of genes). Where genomic data were available, the genetic basis of such parallel divergence resulted from both shared (Colosimo et al. 2004; Hohenlohe et al. 2012; Laporte et al. 2016) and unique genetic architectures (Gagnaire et al. 2013; Elmer et al. 2014; Laporte et al. 2016). Recent advances in next-generation sequencing techniques now provide genomic tools with the resolution required to investigate divergence at adaptive loci in the face of gene flow (Feder et al. 2012). Applications of genomic approaches to the question of lake charr ecotype divergence have the potential to provide insight into both ecotype divergence in the face of gene flow and potential genome-wide parallelism among lakes with similar ecotypes. Thus far, only two studies have investigated the genome-wide basis of ecotype divergence: one in Lake Superior, and one in inland lakes of Québec.

In Lake Superior, reduced representation genome sequencing (RADseq) of four ecotypes (lean, humper, siscowet, redfin) from four locations tested for parallelism at the genomic level (Perreault-Payette et al. 2017). Several outlier loci among ecotypes were consistent with known differences between Lake Superior ecotypes (e.g., lipid metabolism, visual acuity), although results did not support parallel genomic changes underlying repeated phenotypic divergence among sites (Fig. 5). Different genetic architectures may explain phenotypic parallelism among Lake Superior ecotypes at different sites. In support of this hypothesis, morphology could also be used to discriminate fish among sampling sites, which may reflect subtle differences in convergent evolution of forms at each site based on different genetic architectures (Perreault-Payette et al. 2017). Alternatively, reduced-representation sequencing used by Perreault-Payette et al. (2017) may have lacked the resolution to survey important areas of the genome involved in divergence among ecotypes. In the face of ongoing gene flow, the existence and size of islands of divergence for important loci underlying the ecotype will depend on the amount of gene flow, the strength of selection, and the frequency of recombination (Feder et al. 2012; Nosil and Feder

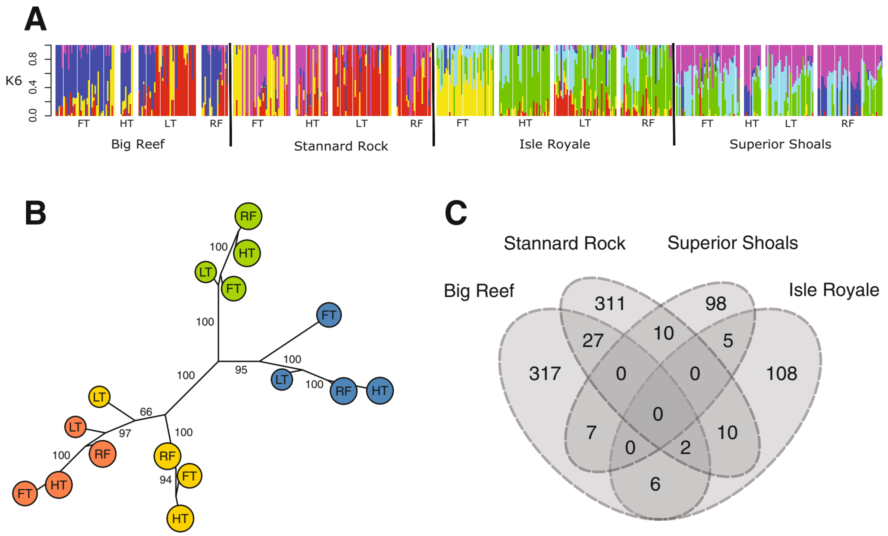

Fig. 5 Patterns of genomic variation in Lake Superior lake charr *Salvelinus namaycush*. (**a**) Admixture plot based on 486 individuals and 6822 SNPs (including outliers) for $K = 6$. Individuals are shown by sites and ecotypes. (**b**) Neighbor-joining tree based on 486 individuals and 6822 SNPs. Yellow circles represent Big Reef, orange circles Stannard Rock, blue circles Isle Royale and green circles Superior Shoals. Bootstrapping support is indicated on each branch. The four ecotypes are: lean (LT), humper (HT), redfin (RF), and siscowet (FT). (**c**) Venn diagram of the number of outlier SNPs among ecotypes that are shared among sites. From Perreault-Payette et al. (2017)

2012). Improved genetic resources, including a reference genome (currently in preparation; L. Bernatchez, unpublished data; see Sect. 8), will be essential for identifying the genomic architecture of adaptive traits of lake charr ecotypes. Finally, considering the likely polygenic basis for divergent adaptive traits, improved models describing the link between genotypes and phenotypes are required to properly address the mechanistic basis of phenotypic parallelism in the lake charr (Bernatchez 2016).

Small Canadian Shield lakes support ecologically divergent populations of lake charr (Wilson and Mandrak 2021; Bernatchez et al. 2016). In Québec, striking phenotypic parallelism in traits was associated with the foraging strategy of piscivorous and planktivorous ecotypes that occurred in both sympatry and allopatry (Bernatchez et al. 2016). Where these ecotypes occurred in sympatry, genetic divergence was consistently observed between ecotypes within lakes (Fig. 6). Furthermore, ecotype discriminating loci identified by means of a multivariate (polygenic) statistical framework correctly predicted ecotype assignment for seven of nine allopatric populations when they were not included in the training set (Bernatchez et al. 2016). These results provided the first evidence of a parallel genomic basis for parallel ecotypic divergence of lake charr. The inconsistent assignment results for two of the sympatric populations most likely reflected ongoing gene flow between

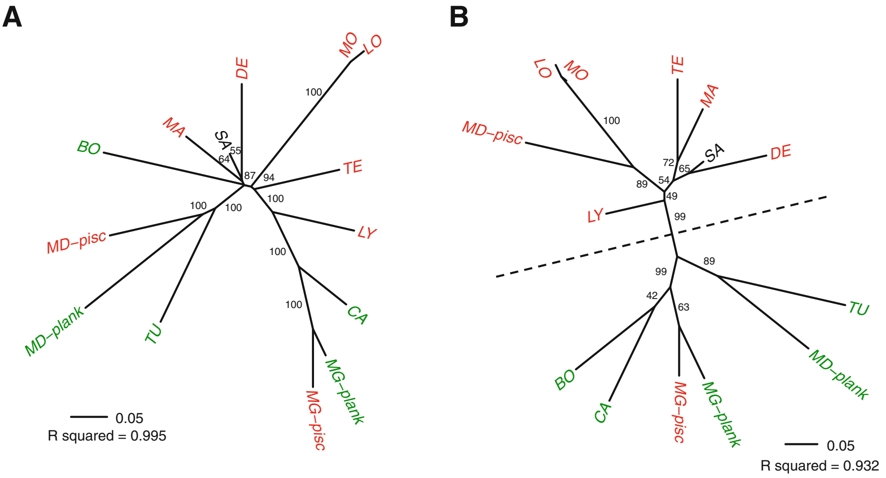

Fig. 6 Genomic parallelism underlying piscivorous (red) and planktivorous (green) ecotypes of lake charr *Salvelinus namaycush* in Québec, Canada. (**a**) Neighbor-joining tree constructed with pairwise F_{ST} values among the 14 lake charr groups based on 3925 SNPs. (**b**) Neighbor-joining tree constructed with pairwise F_{ST} values among the 14 lake charr groups based on 48 outlier SNPs between piscivorous (red) and planktivorous (green) ecotypes. Bootstrap values are indicated on the branches based on 1000 replicates. The dashed line shows the major split between planktivorous and piscivorous ecotypes. From Bernatchez et al. (2016)

ecotypes that reduced the strength of differentiation within lakes but could also reflect plasticity or different genetic architectures for ecotypes in lakes. Much remains to be discovered about the maintenance of lake charr ecotypic diversity in the face of gene flow.

3.3 *Functional Inferences from the Major Histocompatibility Complex (MHC) Genes*

In addition to genomic techniques, other “functional” genetic markers show promise for improving genetic discrimination of lake charr ecotypes. Major histocompatibility genes (MHC) critical for vertebrates’ (including fish) adaptive immune systems involved in pathogen detection are known to experience positive selection (Bernatchez and Landry 2003). MHC genes are also known to be involved in mate choice through disassortative mating in salmonids (Landry et al. 2001). Functional loci, such as this, that have direct sequence-specific effects on organismal survival can provide complementary information to neutral markers for delineating important groups of organisms and environmental forces driving divergence. Studies of the lake charr investigated variation in the peptide-binding region (PBR) of the Major Histocompatibility Class IIβ (MHCIIβ) gene (Dorschner et al. 2000; Noakes et al.

2003; Baillie et al. 2018). Diversity at the MHCIIβ locus is higher for lake charr than other salmonids and a large proportion of private, ecotype-specific alleles exist (Dorschner et al. 2000; Baillie et al. 2018). Results suggest that different ecotypes may experience different pathogen communities and that the MHCIIβ locus may provide higher resolution for differentiating lake charr ecotypes than neutral markers.

The parallel sequencing technique recently used by Baillie et al. (2018) provided greater quantitative power of MHCIIβ variation than in past studies and suggested the presence of up to four alleles within individuals. This observation is the first time that putative copy number variation had been detected in the lake charr. Phylogenetic and principal component analyses on MHCIIβ sequences clearly showed two major groups of lake charr MHC alleles and were supported by the degree of change (DOC) statistical method used to call individuals' genotypes (Baillie et al. 2018). Taken together, the results of Baillie et al. (2018) indicate that lake charr may have a duplicated MHCIIβ locus. However, 96% of successfully genotyped lake charr showed evidence of only one copy of the MHC locus (one or two alleles). The number of alleles per individual was scored conservatively and the number of individuals with three or more alleles was likely underestimated. Further work is required across lakes within the species range to test the hypothesis of lake charr MHCIIβ copy number variation and its relevance for ecotype differentiation in other lakes.

3.4 Ecotype Divergence and a Role for Phenotypic Plasticity

In addition to weak differentiation of lake charr ecotypes throughout the range, no genetic divergence was found between lean and humper-like ecotypes from Lake Mistassini (Marin et al. 2016), Rush Lake (Chavarie et al. 2016), and a recently introduced population in Flathead Lake (Stafford et al. 2014). Genetic divergence was also lacking between a lean and an undefined deep-water form of lake charr in Atlin Lake (Northrup et al. 2010). Phenotypic plasticity has been proposed by many of these authors as a possible mechanism to explain the presence of divergent ecotypes in these lakes. Phenotypic plasticity, the ability of a genotype to be expressed in different phenotypes due to different environmental stimuli, has been hypothesized to play a role in driving population establishment, local adaptation, and speciation (West-Eberhard 2003; Pfennig et al. 2010). Surprisingly, experimental evidence directly testing the role of plasticity in explaining differences between ecotypes of lake charr is lacking. As such, the relative importance of divergent natural selection versus phenotypic plasticity in lake charr ecotype divergence remains unclear, as for many systems (Perry et al. 2018). Salmonids are thought to be highly phenotypically plastic and responsive to environmental variables (Hutchings 2011). Furthermore, in a closely related species, the Arctic charr *Salvelinus alpinus*, a substantial amount of plastic variation contributed to ecotype differences (reviewed in Klemetsen 2010). The role of plasticity in generating and maintaining lake charr ecotype variation is an under-developed area of research that could benefit from further investigation using controlled mating and common-garden rearing experiments (but see Goetz et al. 2010, 2014 discussed below).

4 Genetic Evidence for Ecological Axes of Adaptive Divergence

Recent genetic data have challenged the discrete ecotype conceptual model (Baillie et al. 2016a, 2018) and incited a view of lake charr genetic and phenotypic diversity where diversity is distributed along environmental gradients, rather than by reproductively isolated divergent ecotypes. On the basis of genetic evidence, water depth is an important ecological variable that promotes and maintains lake charr diversity (Baillie et al. 2016a, 2018). Genetic variation was more strongly partitioned among depth strata than among ecotypes. These genetic differences correlated with morphological and life-history traits and also varied along a depth gradient. Additionally, the immunogenetic diversity of lake charr was examined to ascertain whether immune genes would be useful for current and future lake charr habitat-genetic studies (Baillie et al. 2018). Immune genes are often closely tied to habitat because pathogen diversity varies greatly among local environments. Consequently, major histocompatibility complex (MHCIIβ) gene diversity better reflected habitat (water depth) differences than microsatellite markers (Baillie et al. 2018).

4.1 Parallel Patterns of Divergence in Lake Charr

To understand mechanisms and potential for future divergence within any species, adaptive diversification should be examined in parallel among independent populations in similar environments and ecological niche axes. Independent populations that colonize similar environments and evolve similar traits provide evidence for nonrandom processes responsible for divergence driven by changes in gene frequencies (Endler 1977; Schluter 2001; Kaeuffer et al. 2012). Evidence required to conclude adaptive diversification involves detection of sources of divergent selection, such as competition for habitat or food, ultimately leading to reproductive isolation (e.g., partially restricted gene flow, complete isolation), and correlations between sources of divergent selection and reproductive isolation (Rundle and Nosil 2005; Østbye et al. 2006). Simple habitat category contrasts, such as lake versus stream, benthic versus limnetic, or high predation versus low predation, provide important starting points for investigations of more nuanced ecological axes of divergent selection (Kaeuffer et al. 2012; Stuart et al. 2017).

Lake charr water-depth clinal patterns were consistent in replicate at multiple spatial scales within a sampling site (e.g., Isle Royale; Baillie et al. 2016a) and among multiple sampling sites within a lake (e.g., Lake Superior; Perreault-Payette et al. 2017). Phenotypic clines present within each ecotype clearly suggest that environmental conditions influenced genetic control of morphological and life-history traits. Local adaptation and maintenance of intraspecific genetic diversity are important to a species' persistence in the face of rapidly changing environmental conditions. Where human activities impede the conservation of genetic diversity, habitat heterogeneity is thought to play a major role in the maintenance and promotion of diversity (Larkin et al. 2016). This work provides a framework for understanding the evolutionary potential of lake charr for managers and conservation programs seeking to re-establish declining or extirpated populations.

4.2 Nonparallel Patterns of Divergence

Where traits diverge in different directions along similar niche axes for different populations, the niche axes in question do not fully explain variation or intraspecific biological diversity, and traits are considered nonparallel traits. Therefore, nonparallel and parallel patterns of divergence across populations are important to recognize and better understand the conservation and restoration of biodiversity (Arendt and Reznick 2008; Kaeuffer et al. 2012). In Lake Superior, despite generally high parallelism for locomotive traits, several patterns were not parallel among geographically disparate populations. Morphological variables related to feeding traits showed low to no parallelism along a depth gradient across shoals and this non-convergence could be explained principally by differences among ecotype (Baillie et al. 2016a). Key differences in trait variation with depth occurred among ecotypes. For instance, the lean ecotype had longer and leaner bodies than humper, siscowet, and redfin ecotypes. The fusiform body of the lean ecotype may be more constrained than deep-water ecotypes with depth variation. This result is supported by previous studies of lake charr depth distribution data, which show that siscowets are often observed in shallow water during summer while leans are rarely found in deep water (Moore and Bronte 2001). The large amount of unexplained variation in morphology may be attributable to prey assemblage overlap within depth strata, which maintains variation in foraging traits through disruptive selection even within ecotypes (Kaeuffer et al. 2012; Chavarie et al. 2018).

4.3 Conclusions

Phenotypic clines in morphology within ecotypes followed a depth gradient, despite ecotypes having morphological traits best suited to shallow or deep depths (Baillie et al. 2016a). This observation suggests that a degree of phenotypic plasticity likely operates in the lake charr system as a result of resource plasticity. Furthermore, awareness that environmental conditions can influence genetic control of life-history traits has increased over the last few decades (Gutteling et al. 2007). Environmental variables may affect ontological processes after egg fertilization, which subsequently may influence phenotypic expression (Stearns 1976; Moran 1994; Sinervo and Svensson 1998; Bailey et al. 2015). Growth rates and age-at-maturity are correlated with temperature, with northern populations growing slower and maturing later than southern populations (Redick 1967; Allen et al. 2005). Therefore, variation in water temperature at different depths may affect growth. Based on available data, we hypothesize that lake charr variation is shaped initially by phenotypic plasticity and genotype-by-environment effects, and second, divergent natural selection operated on plastic phenotypes, thereby leading to adaptive divergence and partially restricted gene flow.

5 Heritable Basis of Phenotype

An alternative way of interrogating the evolutionary basis of lake charr phenotypic diversity is to assess the heritability of traits associated with major axes of variation among ecotypes. The strongest evidence for a heritable basis of traits associated with lake charr ecotypes comes from quantitative genetic experiments where divergent lake charr ecotypes were bred and reared in common environments. Beginning in the mid-1900s, the culturing of lake charr for stocking provided opportunities to investigate the heritability of lake charr phenotypes. Rearing offspring of artificial breeding crosses, where the parental ecotypes were known, under the same environmental conditions allowed investigators to rule out effects of phenotypic plasticity due to differences in environmental exposure and thus isolate genetic contributions to the variance in phenotype between ecotypes. These experiments broadly support a heritable basis of many important phenotypic differences among ecotypes and populations of lake charr.

5.1 Common Garden Experiments with Reared Lake Charr

Morphology has been the primary axis on which forms of lake charr have been identified (Chavarie et al. 2021). First-generation crosses between wild-caught lean and siscowet lake charr reared in a common environment exhibited heritable growth and morphological differences (Goetz et al. 2010). Morphological differences were detectable as early as age-1 (Goetz et al. 2010) and trajectories of divergence in head shape and caudal peduncle length were consistent with morphological divergence observed between wild adult forms (Khan and Qadri 1970; Moore and Bronte 2001). These results indicated the morphological differences between lean and siscowet were both heritable and likely maintained throughout ontogeny. These results confirmed that phenotypic variation among lake charr ecotypes was not purely plastic, but also has an additive genetic component.

Heritable differences in morphology, in particular paired fin size, are of important consequence because of hydrodynamic and hydrostatic swimming modes employed by different lake charr ecotypes (Eshenroder et al. 1999; Muir et al. 2014). Hydrodynamic swimming achieves greater speed and horizontal acceleration, whereas hydrostatic swimming provides greater maneuverability vertically through the water column. Two ecotypes (siscowet and redfin) of Lake Superior have long gliding fins, and increased fat content (discussed below), that promote buoyancy primarily through hydrostatic swimming. In contrast, the streamlined lean ecotype has hydrodynamic adaptations for fluvial and pelagic swimming and is not often found in deep water. Humpers inhabit moderate depths at offshore shoals with strong current and show characteristics adaptive for hydrodynamic lift (Muir et al. 2014).

Other common garden experiments have revealed heritable differences in developmental rate among different hatchery and wild populations of lake charr reared under similar laboratory conditions (Horns 1985) and a heritable basis for both growth rate and age-at-maturity for purebred crosses of fish from Lake Opeongo and Lake Louisa in Ontario reared in a common environment (McDermid et al. 2007). Hybrid crosses of males from Lake Louisa with females from Lake Opeongo produced offspring that were intermediate to parental purebreds (McDermid et al. 2007), which suggests phenotypes result from additive inheritance of these traits (where the effect of each allele contributes additively to the inheritance of phenotypic traits as opposed to the influence of dominance or epistatic effects). Collectively, heritability of developmental rate and age-at-maturation are consistent with observations of population-specific differences in age-at-maturation that have been reported (Krueger and Ihssen 1995).

Fat content has long been recognized as an important and defining characteristic that distinguishes lean and siscowet charr ecotypes in Lake Superior (Goodier 1981). Eschmeyer and Phillips (1965) were the first to quantitatively demonstrate that muscle fat content was consistently higher for wild-caught siscowet charr compared to lean charr. They further demonstrated that humpers had intermediate fat content closer to lean ecotypes than siscowet. These differences between lean and siscowet were subsequently shown to be maintained when pure-type breeding crosses of lean and siscowet ecotypes were raised in a common hatchery environment (Eschmeyer and Phillips 1965). The offspring of hybrid lean x siscowet breeding crosses exhibited intermediate fat contents, and for the single size category where comparison was possible, fat content appeared to be inherited in an additive manner.

The early work of Eschmeyer and Phillips (1965) on body fat differences was corroborated and expanded upon by recent studies of Goetz et al. (2010, 2014). Siscowet were again found to have higher lipids in whole body analyses (Goetz et al. 2010), and in a more detailed tissue-level analysis, siscowet had higher lipids in both muscle and liver tissues than lean lake charr (Goetz et al. 2014). Hybrid crosses of lean and siscowet showed intermediate lipid contents between the two ecotypes (Goetz et al. 2014), which further suggested that lipid content is inherited through the additive effects of alleles. The composition of lipid differences between ecotypes are characterized by a higher proportion of polyunsaturated fatty acids (PUFAs) in the lipid profile of siscowet that could not be explained by differences in diet (Goetz et al. 2014). Increased levels of PUFAs may reflect an adaptation for maintaining membrane fluidity at lower temperatures for siscowet but the significance of these differences for wild populations is uncertain (Goetz et al. 2014). In contrast to results for muscle and liver tissues, leans have higher circulating levels of lipids in their blood plasma, higher glycogen levels in muscle and liver tissues, and higher blood glucose than siscowet. Goetz et al. (2014) concluded that lean and siscowet represented different "metabolotypes" that differed considerably in the way they process and store energy.

Metabolic differences between siscowet and lean charr are likely mediated through differential regulation of gene expression. Genes related to lipid processing and transport and immune response were differentially expressed in livers of siscowet and lean charr reared in the same environment (Goetz et al. 2010). Transcriptional patterns suggested that leans maintained greater lipid storage in liver tissue while siscowet exhibited greater transport and deposition of lipids in peripheral tissues (Goetz et al. 2010). These gene expression patterns were partially congruent with physiological differences (Goetz et al. 2014). In particular, higher expression of myostatin proteins was demonstrated in siscowet muscles (Goetz et al. 2014). These proteins play a role in the positive regulation of adipose tissue mass and were consistent with higher levels of lipids in muscle tissue of siscowet than lean ecotypes. The two results differed, however, in predictions of lipid levels in livers of leans. Transcriptome data suggested that leans were storing fat in this tissue, but physiological data indicated that siscowets had fattier livers. The RNA sequencing work of Goetz et al. (2010) represented a very early application of this technique to characterize gene expression. Improved sequencing technologies and analysis methods for this type of data are now available that would facilitate a more complete characterization of lake charr transcriptomes and provide further insight into differential metabolic regulation exhibited by these ecotypes.

High lipid levels in siscowet (Eschmeyer and Phillips 1965; Goetz et al. 2010, 2014) and differences in buoyancy between ecotypes in Lake Superior (Muir et al. 2014) and other lakes (Zimmerman et al. 2006, 2007) have been speculated to represent adaptations for maintaining buoyancy at different preferred depths (Henderson and Anderson 2002). In support of this hypothesis, swim bladder gas retention has a heritable basis for lake charr from inland Ontario lakes (Ihssen and Tait 1974). Fish from Lake Simcoe that evolved with access to deep habitats retained their buoyancy better than fish from shallow Lake Louisa when reared in a common environment. Reciprocal hybrid crosses between the two populations showed intermediate buoyancy to further support a heritable basis for this trait.

Finally, other physiological differences with a heritable basis have been observed between siscowet and lean ecotypes in Lake Superior. Despite sharing the same tanks as siscowet, lean charr showed higher constitutive expression of certain immune system transcripts (complement proteins; Goetz et al. 2010). These differences may reflect adaptation to a greater pathogen diversity in warmer surface waters for the lean ecotype than the siscowet ecotype, which spend most of their time in deeper, colder water (Goetz et al. 2010). While this hypothesis remains to be tested, studies of MHC loci also support differentiation of Lake Superior lake charr along a depth gradient (Baillie et al. 2018; see Sect. 3.3) that may also be indicative of adaption to alternative pathogen pools.

5.2 *Experimental Stocking of Lake Charr*

Further indirect evidence of heritable differences for phenotypes relevant to the survival of lake charr is based on the assessment of stocking efforts. Locally sourced strains out-perform non-local strains in experimental stocking of inland lake systems (Plosila 1977; Siesennop 1992). Mechanisms that underlie differential survival of strains are unclear but may be related to behavioral differences or competitive abilities that are as yet uncharacterized (Siesennop 1992). In the Great Lakes, recapture data and genetic stock assignment of wild-spawned progeny have been used to assess the performance of various hatchery strains. In lakes Huron, Michigan, and Ontario, the Seneca strain, derived from lake charr from Seneca Lake in New York, has consistently been represented at higher proportions than expected among wild produced progeny of stocked fish (Marsden et al. 1993; Grewe et al. 1994; Eshenroder et al. 1995; Perkins et al. 1995; Page et al. 2003; Roseman et al. 2009; Scribner et al. 2018). The specific mechanism for this performance difference has never been elucidated, although Seneca strain fish suffered lower sea lamprey *Petromyzon marinus* wounding rates in Lakes Ontario (Schneider et al. 1996) and Huron (Madenjian et al. 2006) than other strains. The progenitors of the Seneca hatchery strain are known to have co-existed with sea lamprey for over a century and may have evolved an adaptation that allows them to escape lamprey predation, possibly by suspending off the bottom, thereby reducing vulnerability to sea lamprey depredation. Mortality after lamprey attacks in the laboratory that are similar for Seneca and Lake Superior strains suggest that behavioral differences or environmental preferences may explain this strain's reduced incidence of sea lamprey wounding in the wild (Swink and Hanson 1986).

5.3 *Transgenerational Plasticity*

While the kinds of common garden experiments described above provided strong evidence that divergence of traits associated with lake charr ecotypes is heritable and not strongly influenced by phenotypic plasticity in the F1 generation, a potential role for transgenerational plasticity exists for determining ecotypic differences in the F1 generation. Adults used to produce breeding crosses in many studies were sourced from wild populations that may have passed on heritable but nongenetic markers to influence their offspring's development. For example, short-term heritable epigenetic marks (e.g., DNA methylation) can produce heritable phenotypes in offspring without affecting the DNA sequence (Verhoeven et al. 2016). The role of epigenetic modifications in producing adaptive (or mal-adaptive) phenotypes is an emerging area of research that may have important relevance for understanding lake charr ecotypic divergence. For instance, migratory (steelhead) and nonmigratory rainbow trout *Oncorhynchus mykiss* differed in many methylated regions (DMRs), which is the first evidence of a relationship between epigenetic variation and life history divergence in salmonids (Baerwald et al. 2016). Recent studies of sticklebacks Gasterosteidae spp. have also provided clear evidence for DMRs as a result of developmental acclimation to different temperatures (Metzger and Schulte 2017). These differences were stable through ontogeny (larvae to adult) and had corresponding effects on gene expression (Metzger and Schulte 2018). Furthermore, studies of coral reef fishes have demonstrated that transgenerational acclimation to temperature was mediated by the transmission of parental methylation profiles (Ryu et al. 2018). If ecotypic differences initially arise or are maintained as a result of phenotypic plasticity as some authors have speculated (Marin et al. 2016; Chavarie et al. 2016; Chavarie et al. 2021), heritable epigenetic variation may initiate the divergence process. Multigenerational common garden experiments are needed to investigate potential transgenerational plasticity, and epigenetic studies are needed to provide important insight into fundamental questions on the origin and maintenance of ecotype diversity.

6 Temporal Trends in Laurentian Great Lakes Lake Charr Population Genetic Diversity and Structure After the Fishery Collapse

After the collapse of lake charr populations in the Laurentian Great Lakes during the 1950s, the species was extirpated from lakes Michigan, Ontario, and Erie, only remnant populations survived in Lake Huron, and population sizes were depressed in Lake Superior. To investigate temporal changes in genetic variation in the Laurentian Great Lakes over the span of this event, “ancient” DNA extracted from 40-year-old lake charr scale samples collected during years before, during, and after the collapse (c. 1940–1959) in lakes Michigan, Huron, and Superior was genotyped using five microsatellite loci and then compared to samples collected during 1995–1999 from lakes Huron and Superior where lake charr populations had persisted (Guinand et al. 2003). Extinct Lake Michigan lineages harbored most of the Laurentian Great Lakes meta-population genetic diversity and gene diversity decreased in populations from lakes Superior and Huron over time (Guinand et al. 2003). Naturally reproducing populations from Lake Superior, believed responsible for the resurgence of lake charr abundance and distribution, were probably affected by hatchery supplementation (Guinand et al. 2003; see Sect. 7). Thus, past demographic declines in abundance and the extirpation of native lake charr populations between 1954 and 1999 appeared to have resulted in a dramatic decline in the amount of standing genetic variation in the lake charr (Guinand et al. 2003).

6.1 Reductions in Genetic Diversity Within Ecotypes in Lake Superior

Temporal changes in genetic diversity and structure of three sympatric lake charr ecotypes (lean, siscowet, and humper) in Lake Superior at three points in time (1948 = pre-collapse period of intensive fishing, 1959 = collapse due to sea lamprey, and 1990s = recovery) confirmed that lean and siscowet ecomorphs lost substantial genetic diversity (23 and 21%, respectively) from pre-collapse levels (Guinand et al. 2012). Lean charr were affected more heavily and declined quicker after the collapse than siscowet charr (Guinand et al. 2012). Significant genetic differentiation was also evident among ecotypes historically, prior to declines in abundance, and among contemporary populations, which suggests that periods of population decline and resurgence in abundance and distribution did not result in loss of genetic distinctiveness among morphs (Guinand et al. 2012).

Recent work using samples and genotypes from these previous studies, while adding contemporary samples across Lake Superior and additional microsatellites, indicated that lake charr may still be losing allelic richness today (Baillie et al. 2016b), in spite of the tremendous recovery efforts where Lake Superior lake charr were declared restored by the 1990s (Muir et al. 2012). Although both the census size of lake charr populations and the effective number of breeders (a population genetic estimate of the number of reproductive adults efficiently contributing to a cohort) in Lake Superior have made spectacular recoveries, lake charr in Lake Superior have lost 6% allelic richness and 41% private allelic richness since the 1990s, and possibly 30% of overall neutral genetic diversity since the 1950s (Fig. 7; Baillie et al. 2016b).

Functional genetic data from Major Histocompatibility Complex class IIβ gene (MHCIIβ) diversity provided similar evidence of genetic diversity loss. Data from three studies of lake charr MHCIIβ variation in Lake Superior on samples from different periods provide insight into temporal trends in allelic variation at this important immune locus (Dorschner et al. 2000; Noakes et al. 2003; Baillie et al. 2018). While these three studies used different approaches to genotyping, thereby preventing direct comparison of specific allele identities, the number of MHCIIβ alleles detected per individual in contemporary samples (2006–2007) was lower (0.41 alleles/ind; Baillie et al. 2018) than from the 1990s (0.58 alleles/ind; Dorschner et al. 2000; Noakes et al. 2003). Next-generation amplicon sequencing methodology is likely more sensitive than previous electrophoretic (e.g., single-strand conformational polymorphism analysis) and cloning methods, which suggests this difference may be an underestimate of the MHCIIβ allelic diversity lost since the 1990s (Baillie et al. 2018). Erosion of MHC diversity can represent a serious risk to populations by increasing disease susceptibility (Garrigan and Hedrick 2003; Goyette et al. 2015; Rico et al. 2016), which may be particularly important considering the influx of invasive species in recent decades (Holeck et al. 2004). More high-resolution genomic studies (i.e., whole-genome resequencing) will allow the investigation of patterns of heterozygosity across the genome to give more comprehensive insights into the loss of genetic diversity in functional genomic regions.

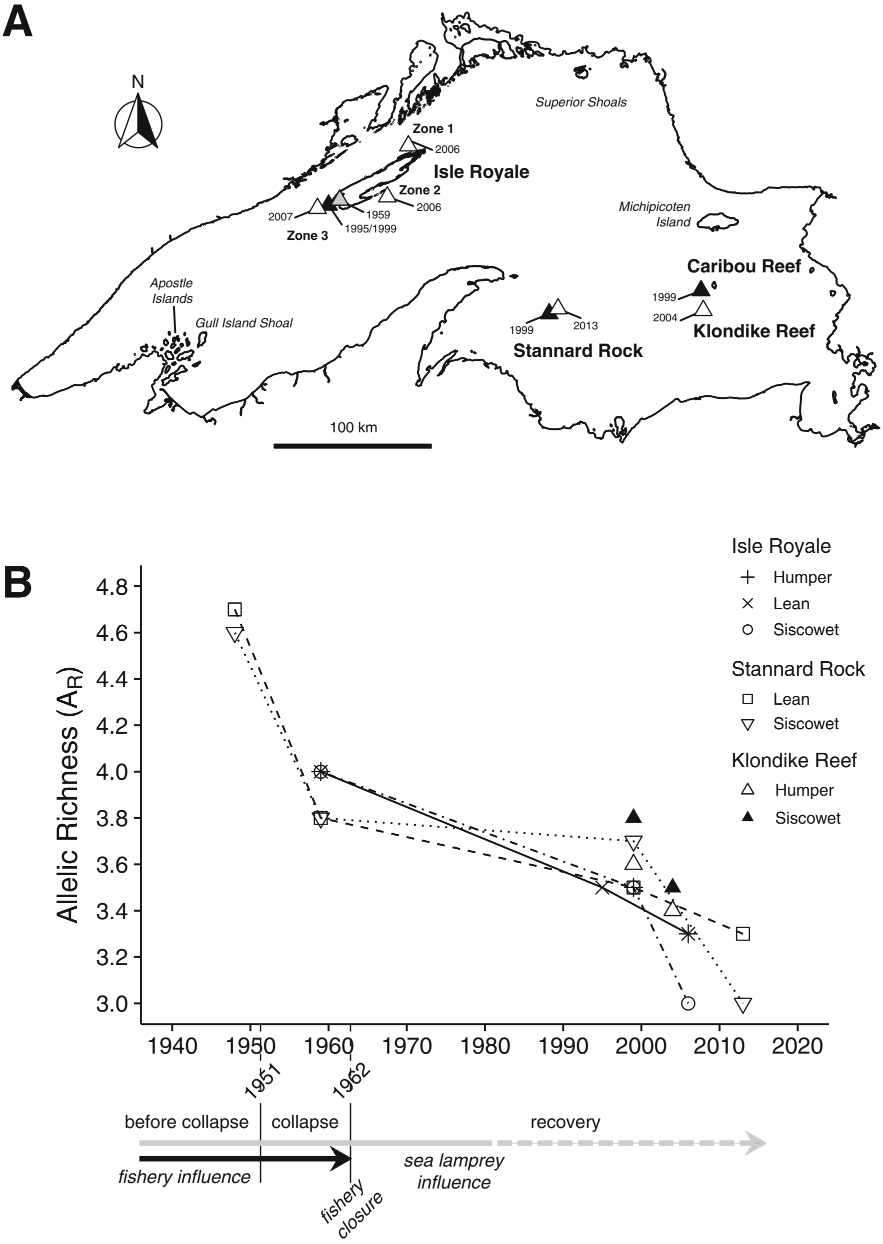

Fig. 7 Lake charr *Salvelinus namaycush* genetic data collection sites within Lake Superior representing three main locations, Isle Royale, Stannard Rock, and the Caribou Reef/Klondike Reef area (**a**) and temporal trends in allelic richness (**b**) of lake charr ecotypes: lean, humper, and siscowet from 1948 to 2013. Open, black, and dark gray triangles on the map represent contemporary, recovery, and historical samples, respectively. Points represent previously published data from Guinand et al. (2012) collected during 1948, 1959, and 1995–1999 as well as data collected during 2004–2013 by Baillie et al. (2016b). Arrows below the graph indicate three management periods (in bold) and represent dominant influences during pre-collapse and recovery management (gray arrow is dotted to symbolize reduced sea lamprey influence after 1980). From Baillie et al. (2016b)

6.2 Reductions in Genetic Distance Among Ecotypes in Lake Superior

The loss of allelic diversity through time within lake charr populations in Lake Superior has been paralleled by changes in among-population variation. As detailed in Sect. 3, genetic differentiation of ecotypes had been reported in early molecular genetic work conducted on lake charr from Lake Superior. Microsatellite genotypes from lake charr samples collected during the 1990s indicated that lake charr in Superior were structured primarily based on ecotype and secondarily among spatial sampling sites (Page et al. 2004; Guinand et al. 2012). While ecotypes could be differentiated genetically (Guinand et al. 2012), genetic distinctiveness among ecotypes apparently collapsed (Baillie et al. 2016b). Lake charr clustered together by ecotype across geographic locations during the recovery period (1990s) but clustered together by location in the contemporary period (2000s) (Fig. 8). Re-analysis of data from Guinand et al. (2012) and Page et al. (2004) in direct comparison with contemporary data using multiple population genetic methods (e.g., tree clustering, AMOVA, hierarchical FST tests, multiple co-inertia ordination analyses) provided strong corroborative proof that ecotypes could be discriminated genetically during 1995–1999, but not during 2004–2013 (Baillie et al. 2016b). The five-locus data set reproduced the same population genetic structure as when 18 loci were used. The overall reduction in genetic distance among ecotypes was ~60% (averaged among all pairwise ecotype comparisons at Isle Royale).

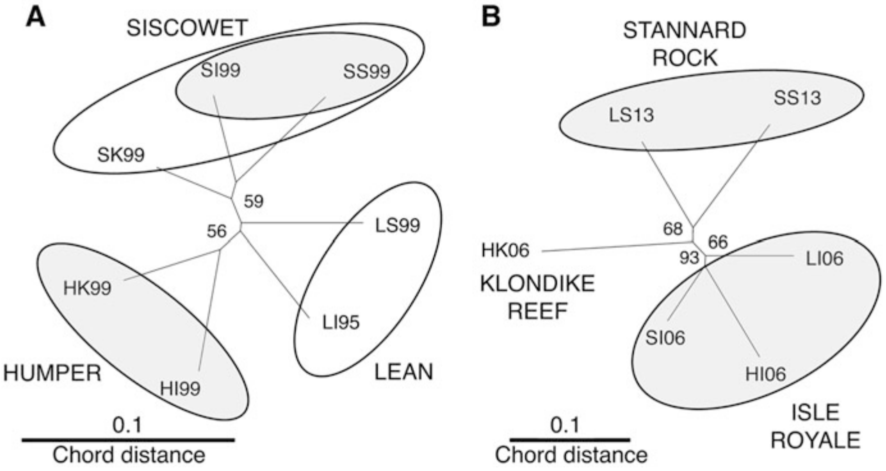

Fig. 8 Neighbor-joining tree of Cavalli-Sforza and Edward's chord distance based on Lake Superior lake charr *Salvelinus namaycush* recovery period samples genotyped at five microsatellite loci (**a**) and contemporary period samples genotyped by 18 loci (**b**). Sample codes indicate ecotype (L, lean; H, humper; S, siscowet), sampling location (I, Isle Royale; S, Stannard Rock; K, Klondike Reef), and year, e.g.,99 = 1999, 13 = 2013. Numbers on branches represent bootstrap values greater than 50% (100 replicates). From Baillie et al. (2016b)

The MHCIIβ data from Lake Superior reinforced findings based on microsatellite markers that differentiation among Lake Superior ecotypes decreased greatly since the 1990s. The number of MHCIIβ alleles shared by both lean and siscowet increased over time (Baillie et al. 2018). The number of shared alleles increased from 20% overlap in the 1990s (Noakes et al. 2003) to 35% overlap in contemporary samples (Baillie et al. 2018). Despite the overlap between lean and siscowet, almost half of MHC alleles were unique to ecotypes. Thus, Lake Superior lake charr ecotypes, except for redfins, can still be distinguished by immunogenetic differences despite no longer being distinguishable with microsatellites. These results are generally consistent with the hypothesized collapse of lake charr ecotypes based on morphological and microsatellite studies (Muir et al. 2014; Baillie et al. 2016b) and may reflect a reversal of the speciation process.

6.3 Reverse Speciation

Striking instances of collapse or homogenization of diverging ecotypes in fishes are numerous, especially during the early stages of diversification—this process is referred to as speciation reversal (Taylor et al. 2006; Seehausen 2006). Speciation reversals can occur when gene flow, which was previously restricted, increases among ecological variants. In some cases, phenotypic plasticity, or environmental responsiveness of traits, can increase susceptibility to reversals of divergence (Taylor et al. 2006; Seehausen 2006). For example, in once-heterogeneous environments that become homogenized, speciation reversal can occur through the adaptive convergence of genes under selection. Hybridization of formerly reproductively isolated populations represents another mechanism potentially driving speciation reversals (Ribeiro and Caticha 2009). In particular, hybridization may contribute to speciation reversal when ecotypes cross habitat “barriers” (Camacho et al. 2016) or results from dramatic changes in abundance or population dynamics (Bhat et al. 2014) as hypothesized for bloater *Coregonus hoyi* in Lake Huron (Eshenroder et al. 2016). A successful “re-speciation,” after a collapse of diverging ecotypes, is thought to involve restoration of the selection regime that historically allowed for diversification in heterogeneous habitats and along environmental gradients (e.g., habitat restoration, translocation of former species assemblages; Hirsch et al. 2013; Jacobs et al. 2019). A growing body of research indicates that the ebb and flow of speciation, and its reversal, may naturally characterize evolutionary dynamics of adaptive radiations and may increase the adaptability of genomes (Turner 2002; Taylor et al. 2006; Seehausen 2006).

Based on previously observed losses in neutral genetic diversity and increased overlap among ecotypes in MHCIIβ alleles, a genetic collapse in differentiation among ecotypes may be occurring in lake charr from Lake Superior. The apparent homogenization of genetic and morphological variation indicates a possible reversal in the lake charr evolutionary trajectory of sympatric adaptive diversification in Lake Superior. Speciation reversal and loss of biodiversity are often difficult to detect because ecotypes can homogenize rapidly and without major changes in the species distribution (Vonlanthen et al. 2012). In principle, divergent natural selection could maintain ecotype differences despite low genetic diversity at neutral genes (Feder et al. 2012). Data for Lake Superior suggests, however, that reproductive and ecological niche spaces have been altered to a degree that selection may not be able to counteract the homogenizing effects of gene flow. Already extirpated from lakes Michigan, Erie, and Ontario by the combined effects of overfishing and sea lamprey predation, the lake charr of Lake Superior are a considerable conservation and management concern as the last remaining stronghold for the species in the Laurentian Great Lakes. Understanding lake charr diversity and niches that ecotypes occupy is a top priority for rehabilitation and re-establishment of deep-water food webs (Zimmerman and Krueger 2009). Conservation approaches for this species could focus on managing ecological habitats by depth, in addition to regulating fisheries specific to ecotypes. Preserving ecosystem function requires maintaining the selective environment offered by functional ecosystems, which in turn require protection of ecological conditions and evolutionary mechanisms that generate and maintain species diversity (Vonlanthen et al. 2012).

7 Genetic Effects of Hatchery Stocking

Lake charr populations have experienced variable intensities of stocking throughout North America with the most severe and extensive stocking efforts concentrated in lakes of the eastern half of the continent. Stocking has the potential to alter the genetic composition of populations when individuals have been sourced from genetically divergent populations or when source populations for stocking have experienced domestication selection. For much of the twentieth century, lake charr were stocked indiscriminately with little apparent consideration of the origins of source populations. Negative effects of stocking on wild salmonid populations have been demonstrated in recent decades (Araki et al. 2007; Frankham 2008; Christie et al. 2014) and drove interest in understanding the influence of stocking history on the genetic integrity of extant native populations of lake charr.

In most cases, early stocking (pre-1950s) of lake charr was too poorly documented to enable assessment of stocking intensity and its effects on native population genetic diversity. For lakes where records of the number of fish stocked and their origins exist, a more controlled assessment of genetic effects of stocking on native populations has been possible (Halbisen and Wilson 2009; Valiquette et al. 2014). Spatial coverage of studies investigating genetic effects of stocking on natural lake charr populations is widespread for inland lakes (Wisconsin: Piller et al. 2005; Saskatchewan: Giroux et al. 2009; Ontario: Halbisen and Wilson 2009; Quebec: Valiquette et al. 2014; Vermont: Baillie et al. 2015), while less is known about genetic effects of stocking in the Laurentian Great Lakes (Grewe et al. 1994; Page et al. 2004). Phylogenetic and population genetic approaches have both been used to characterize influences of stocking on extant lake charr populations. Mitochondrial

DNA (mtDNA) combined with biogeographical expectations of the postglacial distribution of mtDNA lineages have been used to identify the presence of putatively stocked fish or their descendants (e.g., Giroux et al. 2009) and mtDNA combined with population genetic analyses based on microsatellite markers have been used to investigate patterns of genetic diversity within and among un-stocked, stocked, and putative source populations.

Typical lake charr populations of inland lakes are characterized by low within-population genetic diversity and high genetic divergence from other populations that reflect isolation after postglacial dispersal (Ihssen et al. 1988; Halbisen and Wilson 2009; Valiquette et al. 2014; Perrier et al. 2017). In contrast to expected native patterns, lake charr populations with a strong stocking history show elevated levels of within-population genetic diversity (in particular allelic richness), reduced genetic differentiation from other stocked lakes, reduced genetic differentiation from source populations used for stocking, and evidence of admixture between hatchery and native gene pools (Fig. 9; Halbisen and Wilson 2009; Valiquette et al. 2014; Baillie et al. 2015). Despite differences in stocking histories and source populations, these patterns have been consistently observed in populations from Québec, Ontario, and Vermont. For heavily influenced populations in lakes surveyed by these studies, the effects of stocking have acted to homogenize genetic diversity and erode distinct genetic signatures of original native populations compared to un-stocked populations.

Further effects of stocking have been revealed through more detailed genomic analyses of stocked populations by using genotype-by-sequencing to characterize deleterious variation (SNPs) in stocked and un-stocked lake charr populations in

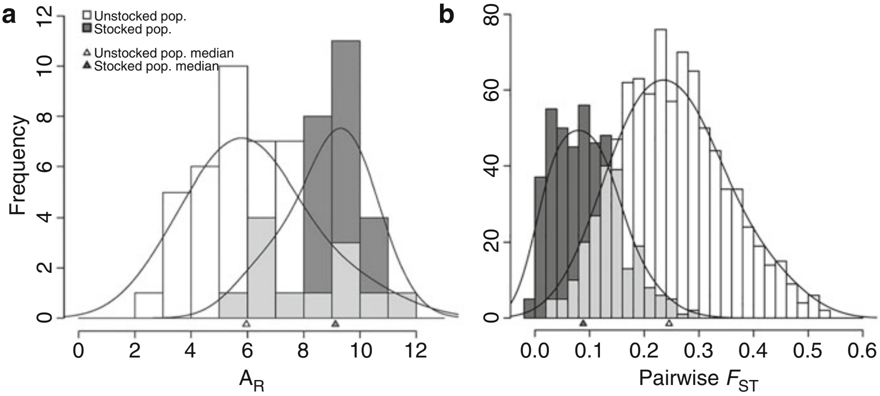

Fig. 9 Distribution of allelic richness (A_R) for un-stocked populations ($N = 42$; white bars) and stocked populations ($N = 30$; dark gray bars) of lake charr *Salvelinus namaycush* where triangles indicate median A_R value for each distribution and light gray is the overlap between the two distributions (**a**). Distribution of pairwise genetic divergence (F_{ST}) among un-stocked (N comparisons $= 861$; white bars) and among stocked populations (N comparisons $= 435$; dark gray bars) where triangles indicate median F_{ST} for each distribution and light gray is the overlapping between the two distributions (**b**). From Valiquette et al. (2014)

Québec. Deleterious variation is genetic variation that is predicted to cause an amino acid change in a functional protein that will adversely affect its function (Ferchaud et al. 2018). Negative effects of deleterious variation on populations would generally be expected to be counter-acted by stocking because stocking should reduce the effects of genetic drift as described above. Remarkably though, one source population for stocking in Québec had a high proportion of deleterious variation compared to most populations and had certain deleterious sites that were fixed (invariant) (Ferchaud et al. 2018). Thus, not only is stocking possibly eroding local adaptation through outbreeding depression, stocking is actually introducing deleterious variation into populations that previously did not exist. Future management of stocking activities should take note of this fact and screen potential source populations carefully for their suitability.

Despite the influence of stocking on genetic diversity in some lakes, variable effects of stocking on genetic diversity of recipient lake charr populations have been reported by multiple studies (Piller et al. 2005; Giroux et al. 2009; Halbisen and Wilson 2009; Valiquette et al. 2014). In some cases, heavily stocked lakes in Ontario (>100,000 released fish) appear to have resisted the effects of stocking and retained their historical genetic distinctness and lower diversity (Halbisen and Wilson 2009). In Québec, higher stocking densities and greater numbers of releases are associated with increased genetic impact but genetic effects on recipient populations are highly variable below a stocking threshold of approximately 45 fish/hectare (Valiquette et al. 2014). Populations in Saskatchewan (Giroux et al. 2009) and Wisconsin (Piller et al. 2005) have retained historical genetic signatures despite large introductions and only show residual evidence of stocking in the form of non-native mtDNA haplotypes or individuals with genotype assignment to stocking source populations. These examples represent different management jurisdictions, geographic locations, and stocking source populations suggesting variable effects of stocking on genetic diversity of lake charr populations are the norm rather than the exception.

Failure of stocking to have universal effects on the genetic diversity of recipient populations is undoubtedly linked to the adaptive suitability of stocking source populations and ecological and environmental conditions of a particular recipient lake (Halbisen and Wilson 2009; Valiquette et al. 2014). Even regionally or locally sourced populations for stocking fail to leave a signature in the genetic diversity of recipient populations in some lakes, which suggests either stocked fish do not survive or they do not contribute to reproduction (Valiquette et al. 2014). These observations may reflect important local adaptions of lake charr populations that are unique to each lake. Inland lakes represent genetically distinct systems that have been isolated since the last glacial period, and while populations variably experience negative effects of drift and inbreeding, much adaptive variation is retained (Perrier et al. 2017). Alternatively, just one generation of captive rearing is associated with reductions in fitness for other salmonids due to exposure to artificial hatchery environments (Araki et al. 2007; Christie et al. 2012). Lower fitness of stocked lake charr may thus result from either adaptive mismatch or from domestication effects associated with artificial rearing. Stocked fish generally grow faster to larger sizes than native wild fish (Morissette et al. 2018). Lakes with a native planktivorous ecotype that are stocked with a piscivorous ecotype exhibit hybrids that outgrow either pure-type but have reduced body condition, which suggests they are maladapted to planktivorous type lake prey communities (Morissette et al. 2018). The results discussed above highlight the risks of outcrossing different lake charr ecotypes.

Encouragingly, preliminary evidence suggests that native populations in inland lakes can recover local genetic signatures over time after cessation of stocking. The average proportion of non-local genetic ancestry decreased from 95% in lakes with recent stocking to 20% in lakes with no stocking inputs for 15 years (Valiquette et al. 2014). These findings suggested that, once stocking has been stopped, the "wild" genetic makeup of populations that had been stocked could be reestablished, presumably by purging alleles from populations contained within fish used for stocking. Longitudinal studies of these lakes are needed to confirm reductions occur, but this observation supports the interpretation that non-local genotypes have reduced fitness and provides hope for recovering local native gene pools of inland lake charr populations.

In the Laurentian Great Lakes, the effects of stocking on native genetic diversity are less clear. Human exploitation and sea lamprey predation severely reduced or eliminated native populations from the majority of the Great Lakes prior to the development of molecular genetic tools (Hansen et al. 1995). Archival samples allowed assessment of some historical genetic diversity and comparisons demonstrated that populations today have less genetic diversity than those prior to the Lake Superior population crash during the 1950s (Guinand et al. 2003, 2012; Baillie et al. 2016b). Hatchery supplementation played an important role in the recovery of these populations (Hansen et al. 1995). Only a fraction of the total lake charr genetic diversity of the Great Lakes is represented in current hatchery broodstocks (Page et al. 2004) where progenitors of stocked hatchery strains are largely derived from collections of the lean ecotype (Krueger et al. 1983).

In Lakes Michigan, Erie, and Ontario, where lake charr populations were completely extirpated, all wild production, and thus genetic diversity, is derived from previously stocked hatchery sources. In these lakes, as well as Lake Huron, proportions of wild-spawned juvenile fish attributable to hatchery strains by genetic assignment do not conform to expected proportions based on stocking rates and estimates of known-hatchery-origin adult fish present on spawning reefs (Marsden et al. 1989; Grewe et al. 1994; Page et al. 2003; Roseman et al. 2009; Scribner et al. 2018). The Seneca Lake strain out-performs other hatchery strains in these lakes (see Sect. 5.2 for a discussion of the reasons). Thus, genetic diversity in all Great Lakes, except Superior, likely reflects only a fraction of the genetic diversity that has been stocked due to the disproportionate contribution of certain strains to natural reproduction.

Lake Huron is the only lake, other than Superior, to possess remnant native populations of lake charr. These remnant native populations are restricted to two areas of Georgian Bay and are believed to have largely retained their distinct genetic signature (Guinand et al. 2003). Recent supplementation used hatchery stocks derived from these remnant populations (Iroquois Bay and Big Sound). These locally sourced stocks appear to contribute disproportionately more to natural production than non-native stocks that were released (Stott et al. 2004; Scribner et al. 2018). Unfortunately, extensive evidence of interstrain hybridization exists in naturally produced fish in Georgian Bay, and potential fitness consequences of outbreeding depression that may result from these crosses are unknown.

Splake (F1 hybrid of lake charr and brook charr, *Salvelinus fontinalis*) were stocked in Lake Huron during the 1960s and 1970s and splake backcrossed with lake charr comprised the majority of stocking in Ontario waters of Lake Huron until the early 1990s (Eshenroder et al. 1995). The splake initially used for stocking was the result of a broodstock highly selected for several traits (e.g., rapid growth, early-maturation, and deep-swimming ability) to provide increased chances of reproducing before being killed by sea lamprey or fisheries (Tait 1970). This high level of artificial selection undoubtedly altered the genetic composition of these fish and although splake backcross fish had lower survival in matched plantings (Anderson and Collins 1995) splake backcrosses interbreeding with stocked fish from other sources and remnant wild populations comprised up to 30% of fish from certain sites in Lake Huron (Stott et al. 2004). A large proportion of lake charr in Lake Huron could have one-eighth brook charr ancestry. Consequences of this ancestry for the genetic diversity of extant lake charr are unclear, although the proportion is likely to diminish over time because these hybrids do not naturally occur and stocking of splake and their backcrosses ceased in the early 1990s, in part due to concerns about negative genetic effects (Krueger and May 1991). In contrast, splake continue to be stocked in Lake Superior, where they pose risks to both brook charr and lake charr populations (Feringa et al. 2016).

In Lake Superior, ongoing declines in genetic diversity have been observed despite population census sizes that have recovered to near pre-crash levels (see Sect. 6; Guinand et al. 2012; Baillie et al. 2016b). These declines are inconsistent with ongoing genetic drift and sampling effects and may reflect the effects of stocking (Baillie et al. 2016b). Of lean-type fish collected at two Lake Superior sites in 1995, 50–70% traced ancestry to a hatchery population rather than wild samples collected from the same sites in 1959 (Guinand et al. 2003). This result is not surprising given that most fish stocked into Lake Superior from the 1950s to the 1990s were of the lean ecotype (Krueger et al. 1983). Gene flow between ecotypes within sites and decreasing genetic differentiation between ecotypes (see Sect. 6.3; Baillie et al. 2016b) suggest that stocking may have eroded not only the native diversity of lean ecotypes but may also be affecting that of other ecotypes as well.

Despite the utility and widespread use of genotype assignment approaches for characterizing stocking influences on genetic diversity in inland lakes, Guinand et al. (2003) and Scribner et al. (2018) are the only published studies to have explicitly investigated hatchery influences in this way for any of the Great Lakes (but see Stott et al. 2004). This may be, in part due, to the low resolution among several genetically similar stocking source populations used in the Great Lakes. Improved genetic and genomic tools that provide greater resolution among hatchery stocks and interstrain hybrids as is currently being done for Lake Michigan (W.Larson, NOAA, personal communication) will improve the assessment of stocking contributions to recovering lake charr populations. An opportunity also exists for more extensive sampling of archival samples to better characterize historical patterns of native lake charr genetic diversity and the contributions of hatchery stocks to genetic diversity of extant lake charr populations in the Great Lakes.

8 Future Directions

Throughout this chapter, we have provided suggestions for future studies to improve knowledge of various aspects of lake charr biodiversity. Ultimately, a critical need exists for improved genomic resources to support future lake charr genetic work. Here, we summarize future research and monitoring directions and possibilities contingent on rapidly emerging genomics and bioinformatics technologies of today to provide a roadmap for future genetic studies of the lake charr.

8.1 Whole-Genome Sequencing

A chromosome-level reference genome is currently being produced by an international collaboration (L. Bernatchez, unpublished data). A double haploid lake charr was generated and its genome sequenced to a coverage of approximately 90X using Pacific Biosciences (PacBio) Sequel long-read sequencing. Initial assembly of the PacBio reads generated a genome of approximately 2.3 billion base pairs (Gb) in length organized into 340 continuous sequences, which were then assembled into scaffolds using a recently published high-density linkage map (Smith et al. 2020). The current assembly is near chromosome-level, with more than 77% of the genome anchored to chromosomes and has a scaffold N50 of 39.7 million base pairs (i.e., more than half the genome is organized into pieces longer than ~40 Mb), making it a very high-quality fish genome. As of publication of this volume, polishing and annotation of the genome are in progress with its publication anticipated in 2021.

This reference genome will provide numerous opportunities to investigate the genomic and epigenomic basis of lake charr phenotypes, clarify the major ecological axes driving phenotypic and genomic divergence, and the extent to which parallel genomic changes underlie convergent phenotypes both with and among lakes. A high-quality reference genome will create possibilities for use of low-coverage whole-genome sequencing for population genomic studies. Low coverage sequencing (1–2X) provides a cost-effective solution for obtaining whole-genome data that will be especially suited to addressing many unresolved population genomic questions for the lake charr (Therkildsen and Palumbi 2017) and development of analytic approaches and software tools specifically designed for low coverage data will open new possibilities for understanding patterns of connectivity and reproductive isolation (Korneliussen et al. 2014). Additionally, low coverage sequencing is effective with small amounts of DNA (Therkildsen and Palumbi 2017) that will make it suitable for use with archival samples to improve the resolution of temporal losses of lake charr genetic diversity and its consequences for populations in the Great Lakes.

An interesting possibility exists that large structural rearrangements (e.g., chromosomal inversions) are partially responsible for determining lake charr ecotypes. Structural variation of this kind suppresses recombination within the inverted region of a chromosome and causes the inverted region to be inherited in a large chunk that can function as a kind of "super-gene" (Wellenreuther and Bernatchez 2018). Chromosomal inversions are known to underlie important adaptive phenotypes in a wide range of organisms including some well-known ecotypic differences such as migratory and nonmigratory forms of rainbow trout and Atlantic cod *Gadus morhua* (see review by Wellenreuther and Bernatchez 2018). Currently available genomic datasets have an estimated resolution of one SNP per 450–700 Kb (i.e., ~3 Gb genome size / 4000–7000 SNPs), which suggests even reasonably sized inversions could have been missed. A reference genome and whole-genome sequencing data will allow for the characterization of structural variation and an assessment of its relevance for lake charr ecotype differentiation.

A high-quality reference genome will also support the fine-scale genomic assessment of the effects of stocking introgression on wild populations. New tools and analytic approaches based on the length and frequency of hatchery origin haplotypes have the power to improve the resolution of ancestry inference and resolve complex patterns of stocking influences (e.g., Leitwein et al. 2018). Further knowledge of deleterious genetic variation provided by a reference genome will improve management by selecting, where necessary, appropriate populations as stocking sources that closely match genetic-environmental signatures of recipient populations, while minimizing risks of introducing deleterious variation (Ferchaud et al. 2018).

8.2 Common Garden Experiments and Transgenerational Plasticity

The mechanistic basis of lake charr phenotypic diversity remains unresolved. While compelling evidence exists for a heritable basis for certain phenotypic traits, a role for transgenerational plasticity has not been ruled out. Multigenerational breeding experiments with controlled environmental conditions will be essential to assess the influence of transgenerational plasticity on lake charr phenotypes. These experiments would simultaneously provide an opportunity to conduct genome-wide association studies for important traits. Divergence at multiple sites within Lake Superior (Perreault-Payette et al. 2017) and throughout inland lakes (Bernatchez et al. 2016) allows replication across sites when investigating a shared genomic basis for convergent phenotypes.

The role of epigenetic mechanisms (e.g., DNA methylation, histone modifications) in facilitating transgenerational plasticity is an emerging area of research that holds great promise for understanding the mechanistic basis of lake charr ecotypes.

Epigenetic mechanisms play important roles in regulating gene expression and are especially important during development and tissue differentiation (Jones 2012). While many epigenetic changes are genetically encoded, they can also be altered in response to different environmental conditions and persist through an organism's life (Metzger and Schulte 2017). In exceptional cases, epigenetic variation has been shown to be stably transmitted over multiple generations and provides a mechanism that environmental influences can be transmitted across generations (Klosin et al. 2017). Epigenetic variation thus has the capacity to regulate environmentally-induced adaptive phenotypic variation and meets requirements to be acted on by natural selection, thereby suggesting it could facilitate rapid adaptation to environmental change (Rey et al. 2016). Growing evidence shows that epigenetic mechanisms are involved in the adaptive phenotypic variation of fishes. Recent work has identified epigenetic differences between migratory ecotypes of rainbow trout (Baerwald et al. 2016) and epigenetic divergence was found even when no divergence was identified at genetic markers between hatchery and wild populations of both coho salmon *Oncorhynchus kisutch* and rainbow trout (Le Luyer et al. 2017; Gavery et al. 2018).

A conceptual model for the origin of lake charr ecotypes could reasonably involve both genomic and epigenomic mechanisms. Given differential gene expression between lake charr ecotypes (Goetz et al. 2010) and within-ecotype morphological trait variation along depth gradients (Baillie et al. 2016a), divergence of lake charr ecotypes may first occur as a result of epigenetic changes caused by different developmental or rearing environments. For example, pressure or temperature effects during incubation (Ryu et al. 2018), or morphologically plastic responses due to different diets like those observed in cichlid fishes (Gunter et al. 2013) could be maintained by transgenerational plasticity or result from natural selection acting on genomic variation to fix these traits through a process called "genetic accommodation" (West-Eberhard 2003). The relative importance and interactions between each of these mechanisms will be of great interest in decoding the origins of lake charr ecotypes.

A reference genome for lake charr will facilitate whole-genome sequencing techniques to characterize epigenetic variation (e.g., bisulfite sequencing for methylation, chromatin-immunoprecipitation sequencing for histone modifications) and assess their contribution to ecotype divergence. Further expanding this work to include convergent phenotypes from other systems will enhance the ability to characterize the extent of genomic or epigenomic parallelism across the geographic range of the lake charr. Integrative work that compares the mechanistic basis of phenotypic parallelism across systems is sorely lacking from the lake charr literature. In particular, recently diverged phenotypes of lake charr (e.g., Flathead Lake, Montana) and lakes where divergent phenotypes exist but genetic differentiation is lacking (e.g., Rush Lake, Lake Mistassini) will be particularly important for contrasting the relative importance of selection, gene flow, and plasticity to phenotype divergence.

8.3 Archival Samples as Baseline for Contemporary Levels of Genetic Diversity

Investigations into the loss of genetic diversity in lake charr would not have been possible without archived scale collections (e.g., United States Geological Survey, United States Fish and Wildlife Service, and Ontario Ministry of Natural Resources and Forestry). Such archives remain a valuable resource for additional samples (Baillie et al. 2016b). Historical samples provide a reference point from which contemporary levels of genetic diversity can be interpreted (Bouzat 2001; Matocq and Villablanca 2001). In 2016, Baillie et al. (unpublished) were successful in genotyping MHC (using next-generation Illumina sequencing technologies) from archival scale samples dating back to 1948, which demonstrates the use of archival samples as a plausible tool for genetics studies that aim to investigate historical genetic patterns in the lake charr.

One potential limitation is that certain SNPs are more sensitive to DNA degradation and thus older samples may have lower genotyping success (Johnston et al. 2013). For example, accurate allele frequency estimation at these loci may require a greater number of individuals (Johnston et al. 2013). This could pose a problem if archival collections have limited numbers of samples. Nevertheless, historical samples have enormous potential to provide insight into the dynamics of lake charr genetic diversity in the Great Lakes. Genomic characterization of lake charr archival samples has yet to be done but will provide a clearer picture of historical patterns of native lake charr genetic diversity within and among sampling locations and depths.

Studies that use archival samples of lake charr will allow assessment of the contributions of hatchery stocks to the genetic diversity of extant lake charr populations and a more detailed assessment of demographic changes through time for lake charr populations in Lake Superior. Knowledge of historical patterns of genomic diversity throughout the Great Lakes will be important for informing recovery and re-introduction of lake charr throughout the Great Lakes.

8.4 eDNA

The environmental DNA (eDNA) field is a revolutionary cross-disciplinary area of biological science that uses genetic material, shed by living organisms, extracted from environmental samples, such as water, to determine organism presence and other population parameters (Lodge et al. 2012). The rapid expansion of eDNA technologies has generated an unprecedented ability to detect species and conduct genetic analyses. Therefore, careful inclusion of eDNA in studies of fishery resources can enhance the understanding and sustainability of aquatic resources and ecosystems. Exciting developments have occurred in the use of eDNA technology to assess lake charr populations. Lake charr abundance could be predicted simply by quantifying lake charr DNA from a water sample, which opens up possibilities to assess and monitor population status in more lakes with less effort than conventional methods (Lacoursière-Roussel et al. 2016). Further development and validation of these kinds of approaches have the potential to revolutionize lake charr management.

9 Conclusions

The past, present, and future research discussed in this chapter contributes to an evolving framework that integrates molecular ecology studies into fishery management practices and permits insight into the evolutionary potential of the lake charr for managers and conservation programs seeking to re-establish declining or extirpated populations. Lake charr survived the last glacial maximum in at least five separate refugia and dispersed north and east through large proglacial lakes that followed the melting ice (Wilson and Mandrak 2021). As levels of these large proglacial lakes dropped, lake charr became distributed across smaller lakes that remained. With some exceptions, most of these populations have since been isolated for thousands of years. Finite population sizes in postglacial lakes and a lack of connectivity led to significant genetic drift and deep neutral divergence among inland lake charr populations. Low genetic diversity, and for some populations elevated inbreeding, suggests many populations may have difficulty adapting to changing climate.

Many inland populations, especially those near human habitation and recreation areas, have been stocked. For these populations, the genetic legacy of past stocking is obvious, and studies have indicated stocking negatively affected native populations, particularly where one ecotype (e.g., piscivorous) was stocked into a lake with only the opposite ecotype (e.g., planktivorous). However, genetic evidence also suggests that stocking effects are probably transient and populations are resilient to genetic changes in most lakes. Studies reviewed in this chapter highlight the importance of using molecular genetic tools to screen potential source populations for future supplementation or enhancement stocking. The choice of source populations should prioritize local sources that experience similar climatic and ecological variation, have similar patterns of genetic variation, and low levels of deleterious genetic variation.

In large lakes (e.g., Laurentian Great Lakes, Great Bear and Great Slave Lakes, Lake Mistassini), inconsistent support occurs for genetic differentiation of lake charr ecotypes. Furthermore, studies reviewed in this chapter challenged the traditional view of lake charr ecotypes and demonstrated that divergence along ecological gradients better explains contemporary patterns of genetic diversity. Open and important questions for understanding ecotypic variation in lake charr include identifying ecological forces responsible for generating within and among ecotype phenotypic diversity and genomic mechanisms that facilitate this divergence. Despite inconsistent support for genetic differentiation of ecotypes, strong evidence exists for heritability of many ecotypic traits. Emerging whole-genome sequencing datasets and experimental evidence for the role of plasticity in ecotype defining traits will reveal important information about the origins of lake charr ecotypes that will improve the management of ecotype diversity.

Temporal loss of genetic diversity from Lake Superior populations, combined with reduced genetic differentiation among ecotypes, suggests that fisheries and invasive species (sea lamprey predation) reduced population sizes that led to a breakdown of reproductive barriers among ecotypes. Populations sizes have since stabilized, stocking has ceased, and sea lamprey is well controlled, so conditions for re-diversification now exist. Ongoing efforts to restore lake charr throughout the rest of the Great Lakes basin should focus on introducing deep-water ecotypes, consistent with those that are known from historical records, to speed recolonization of these habitats and realize the full range of lake charr diversity in these lakes.

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Habitat

J. Ellen Marsden, Thomas R. Binder, Stephen C. Riley, Steven A. Farha, and Charles C. Krueger

Abstract Lake charr *Salvelinus namaycush* habitat is defined by the presence of cold (<15 °C), oligotrophic, oxygen-rich (>4 mg L^{-1}) waters where rocky substrates suitable for spawning and forage is available. At low elevations and latitudes, lake charr habitat is confined to the hypolimnion of stratified lakes in summer, though river-spawning occurs at a few locations (e.g., Lake Superior). Description of spawning habitat has previously emphasized the importance of rocky shoals with steep bathymetric relief and deep, silt-free interstices. Recent work, including research in lakes invaded by lake charr, has broadened this view to include boulder and gravel habitat areas with little to no relief and emphasized the role of currents in spawning site suitability. Spawning habitat choice by lake charr is adaptable, such that charr readily spawn on new sites if previously used sites are degraded. Many nearshore structures such as breakwalls and water intake lines attract spawning lake charr. Advances in telemetry technology and work in invaded lakes have broadened understanding of the variability of habitat use by lake charr. Additional work is

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needed to describe the use of deepwater habitats in lakes and focus on habitat preferences of juvenile lake charr.

Keywords Contour · Currents · Dissolved oxygen · Forage · Predators · Spawning · Substrate · Temperature

1 Introduction

Habitat, broadly defined, encompasses physical, chemical, and biological components of the environment that allow a species to live, grow, and reproduce. The relative importance of components of habitat can be viewed as a hierarchy of physical and biotic characteristics that determine distribution and occupancy. Temperature and dissolved oxygen (DO) are primary determinants of the lake charr *Salvelinus namaycush* geographic range and distribution within lakes because lake charr are physiologically constrained to temperatures less than 15 °C and DO above 4 mg L^{-1} (Evans et al. 1991), with an optimum habitat boundary at 10 °C and 6 mg L^{-1} (Dillon et al. 2003). The native range is confined to northern latitudes within the range of Pleistocene glaciations, in cold, oligotrophic lakes of North America (Muir et al. 2021). In seasonally stratified lakes, lake charr spend most of the summer in the hypolimnion. Unlike most salmonine species, lake charr live primarily in lakes, although some populations move into rivers or brackish water (Martin and Olver 1980; Swanson et al. 2010, 2011; Kissinger et al. 2016). Rocky substrates are considered essential spawning habitats, so lake charr are confined to lakes with suitable geological features. Availability of prey may also be an important predictor of habitat use of lake charr within morphotypes (Vinson et al. 2021).

Within the physiochemical and biological limits outlined above, the lake charr appears highly adaptable with respect to habitat use, particularly in their selection of spawning habitats. Consequently, the lake charr is a successful invader, having been introduced widely in the western United States and elsewhere (Crossman 1995; Martinez et al. 2009). This observation presents a conundrum: how can a species that rapidly establishes populations and flourishes in novel waters fail to re-establish in previously occupied lakes within its native range (notably the Laurentian Great Lakes and Lake Champlain), despite decades of stocking and restoration efforts? Early hypotheses focused on effects of loss or degradation of spawning habitat (e.g., Christie 1974), but lake charr use a variety of spawning substrates (Binder et al. 2017; Simard 2017) and will readily adopt new spawning sites in small lakes with abundant spawning habitat (McAughey and Gunn 1995). Colonization of new spawning sites in lakes where spawning habitat is less contiguous, however, maybe a slow process (e.g., Marsden et al. 2016).

The biotic community in lakes is an important predictor for successful colonization. Lakes with few fish species are more susceptible to invasion than those with a richer fish community (Evans and Olver 1995; Martinez et al. 2009). Similarly, the diversity and abundance of predators appear to be inversely related to pre- and post-hatch embryo survival (Marsden et al. 2005). Lake charr need adequate prey resources accessible within their thermal range, particularly small prey for newly hatched free embryos and post-embryos. The absence of pre-hatch embryo predators, particularly interstitial predators, maybe a critical component of invasion success. For example, an invasive lake charr population in Yellowstone Lake expanded exponentially despite sustained, intensive suppression efforts, perhaps because no early life stage predators were present in the lake (Simard 2017). By contrast, the biotic community of the Laurentian Great Lakes has changed substantially since lake charr populations were extirpated in the 1950s, with the addition of over 85 exotic species (Mills et al. 1993; Ricciardi 2006), and new and complex biotic interactions may contribute to slow progress toward restoration.

Habitat requirements change throughout the ontogeny of lake charr, so different life stages—pre-hatch embryos, free embryos, post-embryos, age-0, juveniles, and adults—occupy different regions of lakes. The characterization of lake charr habitat has been refined and expanded since the 1994 International Conference on Restoration of Lake Trout in the Laurentian Great Lakes (RESTORE) (Selgeby et al. 1995; Marsden et al. 1995a) with advances in technology (e.g., high-resolution sonar, acoustic telemetry, modified remotely operated vehicles), dive surveys, and construction of research-based artificial reefs. Expansion of research to northern Canadian Great Lakes (Great Bear and Great Slave lakes; Zimmerman et al. 2006, 2009; Chavarie et al. 2016a, b, 2019), other North American lakes (e.g., Lake Champlain, Otsego Lake, Alexie Lake, Mistassini Lake; Ellrott and Marsden 2004; Tibbits 2007; Blanchfield et al. 2009; Callaghan et al. 2016), and western lakes that lake charr have invaded has highlighted the commonalities that define basic habitat requirements and also revealed exceptions that demonstrate behavioral plasticity in the lake charr.

In this chapter, we review what is known about lake charr habitat at each life stage (adult, spawning, free embryo, and juvenile habitats) primarily focusing on freshwater lacustrine habitats, and discuss anthropogenic effects on habitat. We discuss variables that influence habitat use by lake charr and provide a schematic to describe lake charr foraging habitat selection across their native range (Fig. 1).

2 Adult Habitat Preferences and Foraging Habitat

The lake charr evolved during the Pleistocene Era (2.5 million to 12,000 years ago) in glacial refugia, from which they radiated to colonize their current native range (chapter "Paleoecology" by Wilson and Mandrak 2004). Although the lake charr is probably best adapted to survive in low-productivity northern habitats with simple fish communities and limited competition (Snucins and Gunn 1995; Gunn and Pitblado 2004; Muir et al. 2016), the species has been able to take advantage of thermal refugia in the form of lake hypolimnia and groundwater springs to persist in lakes as far south as the southern extent of the Laurentide Ice Sheet, approximately latitude 38°N (Gunn and Pitblado 2004; Muir et al. 2016, 2021). In addition, individual lake charr populations show diverse morphological, life history, behavioral, and physiological traits that make them well-adapted to survive in their local environments (Martin and Olver 1980; Muir et al. 2016; Chavarie et al. 2021).

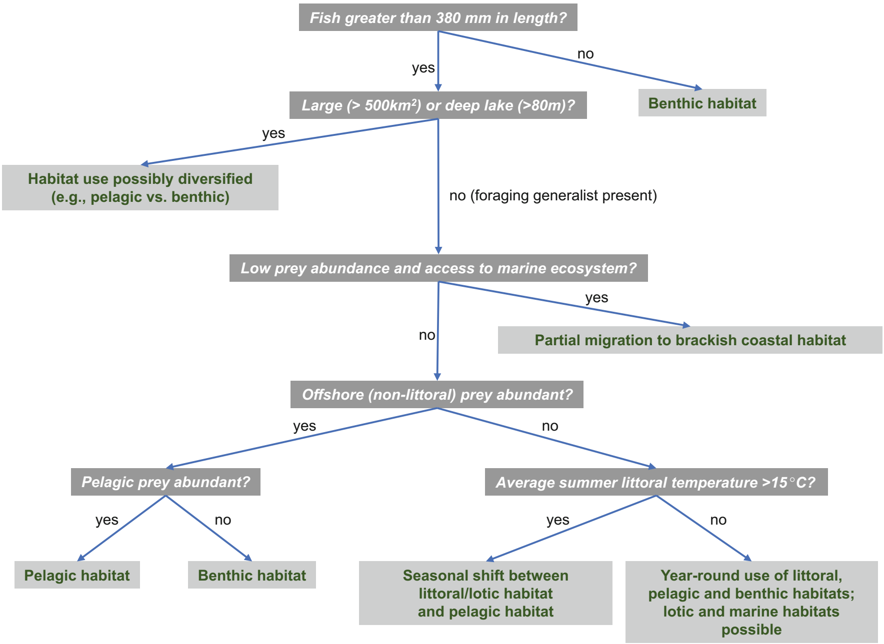

Fig. 1 Schematic of lake charr *Salvelinus namaycush* foraging habitat selection

The most commonly occurring form of lake charr is the lean, shallow-water morphotypes (Chavarie et al. 2021), a trophic generalist that forages on most available food items including plankton, crustaceans, insects, mollusks, and fishes (Martin and Olver 1980; Vinson et al. 2021). However, some large (>500 km^2) or deep lakes also contain sympatric deepwater morphotypes, i.e., siscowets, redfins, and humpers, which presumably developed as a result of resource specialization in lakes with few competitors, low predation risk, diverse forage, and available habitat (Zimmerman et al. 2006; Eshenroder 2008; Chavarie et al. 2021). Deepwater morphotypes are known to exist currently in five lakes (Lake Superior; Great Slave Lake, Northwest Territories, Canada; Lake Mistassini, Quebec, Canada; and Rush Lake, Michigan, USA), but were also present in Lakes Ontario, Erie, Michigan, and Huron prior to their extirpation from the Laurentian Great Lakes (Eshenroder et al. 1995; Krueger and Ihssen 1995; Zimmerman et al. 2006). Multiple shallow-water lake charr morphotypes are also known from Great Bear Lake (e.g., Chavarie et al. 2017).

Foraging behavior and habitat use differ considerably among the four primary lake charr morphotypes. Siscowets, with a deeper body and higher fat content than lean lake charr, typically reside at depths >100 m and, as adults, make vertical migrations to forage on pelagic prey (Zimmerman et al. 2006; Muir et al. 2016). By contrast, humpers, which are smaller than lean lake charr, have intermediate lipid content, feed on zooplankton, insect larvae, and small benthic fishes (Muir et al.

2016), and are usually restricted to high-relief offshore shoals surrounded by >100 m of water (Zimmerman et al. 2006). Redfins reside at intermediate depths of 50–100 m and have a more robust body size and much larger pelvic and pectoral fins than the other morphotypes, but little is known about their behavior (Muir et al. 2014, 2016). The shallow-water, lean lake charr usually reside at depths <70 m (Zimmerman et al. 2006) and use a more diverse range of foraging habitats than their deepwater counterparts. Habitat use in lean lake charr has been widely studied, especially near the southern extent of the species' range, but relatively little is known about the behavior and habitat use of deepwater morphotypes. Consequently, this review focuses primarily on habitat use by lean lake charr, beginning with variables that dictate the range of lake charr and then describing variables that affect their use of habitat within that range.

2.1 Habitat Boundaries

Upper and lower lake charr depth habitat boundaries in lakes are defined by water temperature and dissolved oxygen (DO) concentration (Ryan and Marshall 1994; Clark et al. 2004). Generally, areas with temperatures less than 10 °C and DO greater than 6 mg L^{-1} have been considered preferred habitat, while usable habitat has been defined as having a temperature less than 15 °C and DO greater than 4 mg L^{-1} (Evans et al. 1991; Dillon et al. 2003; McDermid et al. 2013). However, broader use of oxythermal habitat in many lakes likely reflects the occupancy of suboptimal habitats for behaviors such as foraging and predator avoidance. For example, short-term forays into epilimnetic water greater than 15 °C occurs in lakes that thermally stratify (Morbey et al. 2006; Guzzo et al. 2017), but exposure to these temperatures is usually brief, sometimes related to foraging forays, and may have limited metabolic consequences because the rate of thermal exchange between environment and fish is slow (e.g., 35–41 min for a 1100 g lake charr to equilibrate to a 2 °C temperature gradient) and scales with body size (Snucins and Gunn 1995). Extended residence at temperatures greater than 15 °C appears to be rare but can occur seasonally in some lakes. For example, internal lake charr body temperatures were sustained between 16 and 18 °C in Pedro Lake (Ontario, Canada), a small lake that becomes isothermal during late summer (Snucins and Gunn 1995). However, some individuals in that population, usually the largest, exploited a shoreline plume of cold-water discharge (behavioral thermoregulation) to lessen the thermal burden, a behavior that has also been observed in Dezadeash Lake (Yukon Territory, Canada; Mackenzie-Grieve and Post 2006), and inferred from recordings of body temperatures in Gullrock and Michaud lakes, Ontario (Gunn 2002). Epilimnetic residence at temperatures up to 21 °C was observed in Lake 468 (Experimental Lakes Area, Ontario, Canada), despite fish having access to cool hypolimnetic water, perhaps because the greater metabolic cost of extended epilimnetic residence in that population was offset by greater foraging opportunities in warm surface waters (Sellers et al. 1998).

In lakes that thermally stratify during summer, hypolimnetic DO depletion appears to be a significant factor in determining colonization success by lake charr. For example, few of the 163 lakes examined in northwestern Ontario that experienced >40% DO depletion of thermally suitable habitat supported lake charr populations (Ryan and Marshall 1994). Similarly, colonization failed most frequently in 183 small, shallow, eutrophic lakes (having high autotrophic biological oxygen demand) with high species diversity in Ontario where lake charr were introduced (Evans and Olver 1995). Seasonal variation in hypolimnetic DO concentrations within a lake can limit lake charr access to thermally favorable habitat during summer months. For example, an acoustic telemetry study on lake charr seasonal habitat use in Lake 373 (Experimental Lakes Area, Ontario, Canada) indicated a minimum DO threshold of 4 mg L^{-1} for usable habitat, with only 0.03–0.3% of positions, depending on year, occurring at depths with lower DO concentrations (Plumb and Blanchfield 2009). Consequently, DO set a lower boundary for habitat occupancy that became shallower as summer progressed, and fish became 'squeezed' into a shrinking layer between low DO below and high temperature above as summer progressed. In small (16–54 ha) boreal lakes, increasing summer air temperatures led to periodic loss of optimum oxythermal habitat for lake charr, longer spring temperatures (>15 °C), and delayed onset of autumn (Guzzo and Blanchfield 2017). Ultimately, a changing climate may result in the loss of lake charr from some small lakes.

Salinity is also an important boundary to habitat use by lake charr. Lake charr are the least euryhaline salmonine species and appear to be precluded from residing in water with salinity greater than 13‰ (Martin and Olver 1980). Nonetheless, historical observations of lake charr in Arctic marine bays and river mouths suggest that the movement of individuals into coastal marine zones with salinity between 6 and 9‰ may be common (Martin and Olver 1980). Osmoregulatory capacity in the lake charr is poor relative to the brook charr *Salvelinus fontinalis* and the Atlantic salmon *Salmo salar*, but the lake charr should be capable of long-term survival in salinities less than 10% (Hiroi and McCormick 2007). Indeed, recent studies indicated that partial anadromy to brackish coastal habitats was common among Arctic lake charr populations in low productivity lakes with access to the marine environment. For example, based on otolith microchemistry, 27% of individuals from four Arctic populations made annual migrations to brackish water to feed (Swanson et al. 2010). Downstream migrations as far as 50 km to coastal brackish water have been observed in one Arctic population (Harris et al. 2014). Lake charr in the Husky Lakes, Northwest Territories, largely resided in brackish water, but a small proportion (18% of a sample of 58 fish) were semi-anadromous (Kissinger et al. 2016). In anadromous lake charr, marine prey comprised between 60 and 66% of the total diet (Swanson et al. 2011). Length-at-age did not differ between anadromous and non-anadromous lake charr, but anadromous lake charr were in significantly better condition than their non-anadromous conspecifics, likely reflecting greater food availability in the marine environment (Swanson et al. 2010).

2.2 Variables Governing Habitat Selection

Within constraints imposed by temperature and dissolved oxygen, and within trophic morphotypes of lake charr, prey availability appears to be the primary factor determining habitat use (Dux et al. 2011; Bergstedt et al. 2012). In large lakes, such as the Laurentian Great Lakes, lake charr prefer to reside and forage in cool, offshore habitats. Juveniles reside in deep water (>35 m), where they feed almost exclusively on benthic invertebrates during their first year (Martin and Olver 1980) or *Mysis diluviana* (Marshall et al. 1987; Marsden unpublished data), and then at age-1 or 2 begin to incorporate small fishes, such as sculpins *Cottus* spp., rainbow smelt *Osmerus mordax,* and alewife *Alosa pseudoharengus*. The diet gradually shifts to complete piscivory after lake charr reach a length between 300 and 490 mm (Zimmerman et al. 2009; Muir et al. 2016, Marsden unpublished data; Vinson et al. 2021). Pelagic fishes are the preferred prey for adult lake charr (Martin and Olver 1980), but in lakes with a low abundance of pelagic prey fish, adults forage in alternate habitats, including offshore benthic habitats (Rush et al. 2012; Colborne et al. 2016), nearshore littoral habitats (Morbey et al. 2006; Dolson et al. 2009; Guzzo et al. 2017), and coastal brackish-water habitats (Swanson et al. 2010; Harris et al. 2014; Fig. 1). Habitat selection depends largely on opportunities presented by the food-web composition and physical properties of the lake that can vary seasonally (Fig. 1). In contrast, lake charr in small lakes and in northern parts of their distribution use habitat more flexibly, with less distinction between epilimnetic and hypolimnetic occupancy of deep versus shallow waters due to near isothermal conditions (Sellers et al. 1998; Fig. 1). In small lakes, littoral habitats are closer to pelagic habitats and are a higher proportion of total lake volume, so lake charr spend proportionately more time foraging in shallow nearshore areas (e.g., Morbey et al. 2006). Some juvenile lake charr in Great Bear Lake, for example, do not go to deep water but may remain inshore where temperatures rarely exceed 6–8 °C during summer (Chavarie et al. 2019).

In small lakes, particularly those that thermally stratify during summer and that lack a pelagic prey fish community, pelagic–littoral habitat coupling (Schindler and Scheuerell 2002) is common. In these systems, temperature is the primary driver of seasonal habitat selection because lake charr must balance access to energy-rich nearshore prey against the increased metabolic cost of residing at higher temperatures (Morbey et al. 2006; Cruz-Font et al. 2019). In general, littoral habitat is used least in summer when surface temperatures are $\geq$15 °C but is used more during other times of the year. Once littoral temperature exceeds 15 °C, forays into the littoral zone become less frequent and shorter in duration. For example, in Lake 373 (Experimental Lakes Area, Ontario, Canada), lake charr spent an average of 12.8 h day^{-1} in the littoral zone in spring, versus only 0.4 h day^{-1} during summer (Guzzo et al. 2017). Similarly, in Lake Louisa (Algonquin Park, Ontario, Canada), the median duration of summer warm-water forays ranged from 5.6 to 15.7 min and occurred most frequently at dawn when surface temperatures were at their diel minimum (Morbey et al. 2006). Use of lotic habitats follows a similar seasonal trend as occurs in littoral habitats, with greatest use occurring during spring, fall, and winter when temperature is <15 °C (Venard and Scarnecchia 2005; Muhlfeld et al. 2012).

While the magnitude and timing of benthic–littoral habitat coupling in the lake charr is largely a function of water temperature and changes in density of nearshore prey (Muhlfeld et al. 2012; Guzzo et al. 2017), habitat coupling is also influenced by lake morphology. Specifically, the use of a particular nearshore littoral habitat by lake charr is inversely related to the linear distance of epilimnetic water through which the fish must travel to access that habitat. For example, in Lake Louisa (Algonquin Park, Ontario, Canada), lake charr primarily accessed littoral habitats that were adjacent to thermal refuges and were never located over broad areas of littoral habitat (Morbey et al. 2006). Hence, the use of littoral habitat occurs where bathymetry is steepest. Similarly, lake shape was the best predictor of littoral habitat coupling in seven Algonquin Park lakes (Ontario, Canada) (Dolson et al. 2009). In that study, littoral habitat use occurred more frequently in circular lakes than in lakes with complex shorelines, despite the fact that lakes with complex shorelines had a greater abundance of littoral habitat available (Dolson et al. 2009). Together, these observations suggest that accessibility from deep, thermally suitable water was more important than availability for predicting littoral habitat use by lake charr.

Offshore benthic-pelagic coupling (i.e., diel vertical migration) in small and large lakes by both lean and siscowet lake charr appears associated with nocturnal foraging in the epilimnion (Sellers et al. 1998; Hrabik et al. 2006; Stockwell et al. 2010; Ahrenstorff et al. 2011; Cruz-Font et al. 2019), although a reverse migration (descent at night) occurred in Lake Huron (Bergstedt et al. 2016). Diel vertical migration has been observed in Canadian Shield lakes, Lake Superior, and Lake Huron using trawl, hydroacoustic, and acoustic telemetry data, but does not occur consistently among all individuals or by single individuals. Diel vertical migration (DVM), partial DVM, reverse DVM (migration upwards during the day), and individual behavioral variation all occurred in nine acoustically tagged lake charr in Chitty Lake, 426 km south of the Arctic Circle (Gallagher et al. 2018). Lake charr also migrated vertically during periods of 24 h daylight. Overall, their results suggested that light alone was not sufficient to explain DVM. Diel vertical migration may be an opportunistic foraging behavior, associated with movements of coregonine prey (Binder et al. 2021).

In offshore waters, lake charr typically reside within or slightly below the metalimnion (Morbey et al. 2006; Dux et al. 2011; Leander 2015). The bioenergetic thermal optimum for lake charr is assumed to be 10 ± 2 °C (McCauley and Tait 1970; Stewart et al. 1983; Christie and Regier 1988; Magnuson et al. 1990), although field studies have shown that lake charr frequently use habitat at temperatures at or below the lower limit of this range. For example, in Kathleen Lake (Yukon Territory, Canada), 80% of summer detections of fish implanted with temperature-sensitive radio transmitters were in temperatures below 8 °C, with mean temperature occupancy of 5.7 °C (Mackenzie-Grieve and Post 2006). Likewise, mean summer temperature occupancy was 6.9 °C in Alexie Lake (Northwest Territories, Canada; Guzzo et al. 2016) and 5–6 °C in Lake 373 (Experimental Lakes Area, Ontario, Canada; Plumb and Blanchfield 2009). In Lake Huron, mean selected temperatures in summer varied by strain (i.e., stocked lake charr originating from different source lakes), ranging from 8.3 to 9.5 °C for lake charr of Laurentian Great Lakes origin and from 6.4 to 8.2 °C for lake charr of Finger Lakes origin (Bergstedt et al. 2003). In Lake Gautsträsk, northern Sweden, introduced lake charr preferred a summer temperature between 7.5 and 10.5 °C, but swimming activity was at a minimum within this temperature range, which suggested that this thermal habitat was used primarily for refuge and digestion (Leander 2015). Indeed, in a controlled laboratory setting, temperature preference in yearling lake charr was linearly related to ration size, most likely a strategy for maximizing food conversion efficiency (Mac 1985). Together with littoral foraging by lake charr, these observations suggest that time spent in lower and higher than optimum temperatures in the wild may reflect restricted access to food in many lakes.

Light may influence habitat selection in lake charr, although scant evidence supports a direct relationship. More likely, light may influence habitat selection through indirect mechanisms. For example, the magnitude of light penetration influenced the thermal structure of a lake (Schindler and Gunn 2004), and diel changes in habitat use may reflect changes in the distribution. In three small lakes in northwestern Ontario (Canada), lake charr neither avoided bright light nor congregated at a preferred light level (Sellers et al. 1998). In Pedro Lake, Ontario, lake charr used a shallow (< 30 cm) shoreline groundwater refuge site only at night, but avoided the site during the day, not because of light avoidance, but because the fish often moved no more than 100 m offshore, to depths less than 11 m, where they were still exposed to bright light (Snucins and Gunn 1995). Lake charr are visual predators, so light could be a limiting factor in habitat selection. For example, contrary to the prediction that lake charr in Lake 373 (Experimental Lakes Area, Ontario) used littoral habitat more during winter when thermal constraints were absent, home ranges were restricted during winter to the top 3 m of the water column in the center of a small Canadian shield lake (Blanchfield et al. 2009). Low ambient light during the ice-covered period was hypothesized to constrain the spatial and pelagic distribution of lake charr although the shift in habitat use could have reflected a change in the distribution of *Mysis diluviana*, a valuable prey item, during winter (Blanchfield et al. 2009). Lake char spawn on deep (low-light) and shallow (high-light) substrates, even in the same lake, so light does not appear to be a defining characteristic of spawning habitat. However, light appears to affect spawning activity, which occurs primarily at dusk and nightfall or in shadow cast by hills (Martin and Olver 1980; Binder et al. 2021; Goetz et al. 2021).

3 Spawning Habitat

Lake charr, with a few exceptions (Binder et al. 2021; Goetz et al. 2021), spawn from September to early December, though spawning in August occurs in Great Bear and Great Slave lakes and in Lake Superior. Pre-hatch embryos incubate for 4–6 months overwinter in rocky crevices where they are protected from predators and currents.

Free embryos occupy the spawning habitat for several weeks after hatching while they learn to forage and gain size and swimming efficiency. Thus, selection of spawning habitat by adults, and quality of the habitat (i.e., deep interstices with high dissolved oxygen, presence of planktonic prey in spring, and access to deep water) in most cases is critical for lake charr recruitment. Identification of lake charr spawning areas has been a research priority since it became apparent that progress toward restoration was slow in the Laurentian Great Lakes, and impediments to reproduction might exist (Eshenroder et al. 1984, 1999). Description of habitat characteristics that attract spawning lake charr could greatly improve the discovery of spawning sites and evaluation of variables that may affect early life stage survival, such as water quality and predator abundance. Spawning sites were commonly inferred from the presence of aggregations of spawning-ready lake charr caught using gillnets, and such sites have been used for assessment sampling and acquisition of gametes to propagate broodstock from wild sources for hatcheries for decades (e.g., Ellrott and Marsden 2004). By the 1980s, methods were developed to sample and quantify eggs and pre-hatch embryos in the substrate (Stauffer 1981; Peck 1986; Horns et al. 1989; Marsden et al. 1991), and to collect free embryos on spawning reefs (Collins 1975; Stauffer 1981; Chotkowski et al. 2002; Riley et al. 2010), to confirm spawning activity and hatching of free embryos. Development of incubators allowed quantitative in situ assessment of pre-hatch embryo survival and hatching (Manny et al. 1989, 1995; Perkins and Krueger 1994; Casselman 1995). Pre-hatch embryo sampling indicated that spawning was often restricted to smaller areas of habitat than the total areal estimate of a spawning shoal. Early studies used side-scan sonar to survey large areas of substrate for sites that matched characteristics deemed important for embryo incubation (e.g., Edsall and Kennedy 1995; Edsall et al. 1992, 1995; Marsden et al. 2016; Binder et al. 2018), and scuba and remotely operated vehicles were used to visualize substrate and assess the extent to which rocky crevices were infilled with silt and fine materials (Davis et al. 1997; Marsden and Janssen 1997; Simard 2017). More recently, acoustic telemetry has been used to find locations of lake charr aggregations where spawning activity could be inferred (Riley et al. 2014; Landsman et al. 2011; Callaghan et al. 2016; Marsden et al. 2016; Binder et al. 2017, 2018; Farha 2018; Farha et al. 2020).

Basic requirements for lake charr lacustrine spawning sites are the protection of pre-hatch embryos from dislodgement and predation, water temperatures below 12 °C, and high dissolved oxygen. Within these constraints, characteristics of spawning habitats vary with latitude, lake size, bedrock geology, and glacial activity across the range of lake charr, but most sites include a cobble–rubble substrate. Latitude influences the timing and extent of ice formation, temperature regime, precipitation, and wind patterns. Lake size and orientation to prevailing winds affect fetch (the length of open water across which waves impact the shoreline) and the influence of wind forces on lakes, which affect thermocline structure, shoreline erosion, sediment deposition, and physical energy that can dislodge and damage pre-hatch embryos or clean substrates (Schall et al. 2017). Local geology, weathering processes, and glacial history determine the distribution and composition of substrates in lakes.

Thus, substrates available for spawning by lake charr are highly variable among lakes and constrain the selection of spawning habitat.

Early descriptions of lake charr spawning reefs focused on steep slopes, substrate size, and interstitial spaces as essential components of habitat to generate what is now termed the "cobble-contour" model. Cobbles and boulders (200–999 mm, Marsden et al. 1995a) have been thought to create optimum interstitial spaces in which fertilized eggs can settle below the reach of epifaunal predators and wave turbulence (Fig. 2; Jonas et al. 2005; Claramunt et al. 2005; Fitzsimons and Marsden 2014). Steep slopes at many spawning areas are used by lake charr (e.g., Marsden and Krueger 1991; Marsden et al. 1995b; Fitzsimons 1995; Kelso et al. 1995; Janssen et al. 2006; Farha 2018). Steep changes in contour or lakebed relief increase the likelihood that lake currents will create flows through interstitial spaces, reduce sedimentation, and oxygenate pre-hatch embryos (Marsden and Krueger 1991). The upper edge of steep contour breaks may also serve as a physical focal point for aggregating spawning lake charr (Marsden and Krueger 1991; Marsden et al. 1995a, b). Steep lakebed contours are often a result of glacial processes and resultant structures (e.g., drumlins and eskers, Riley et al. 2014, 2017), or are associated with talus slopes near steep shorelines or offshore bedrock escarpments, so slope and spawning substrate frequently co-occur. Searching for cobble-contour spawning sites has benefitted from referring to shoreline topography and geology, where freeze–thaw processes at steep, rocky slopes tend to shed cobbles that form rocky, nearshore reefs (Fig. 2; Sly and Widmer 1984; Ellrott and Marsden 2004). For example, locations of lake charr spawning sites in an Ontario lake were predicted using data on slope, depth, distance to shore, aspect, and fetch (MacLean et al. 1990; Flavelle et al. 2002). Despite limitations (see below), this model provides a practical starting point to identify high potential lake charr spawning sites in new areas or lakes and may also help to predict colonization patterns resulting from a changing environment. Steep bathymetric relief can be identified using charts and sonar surveys, and the presence of cobble piles can often be inferred from local geology (e.g., Ellrott and Marsden 2004).

Recent work has revealed numerous exceptions to the cobble-contour model with lake charr spawning on pea gravel (2–64 mm) in shallow and deep water (Tibbits 2007; Binder et al. 2018; Farha 2018; Farha et al. 2020) and immediately adjacent to and underneath undercuts of large boulders up to 7.3 m in diameter (Binder et al. 2018; Farha et al. 2020; Fig. 2). Introduced populations spawn on macrophytes (Beauchamp et al. 1992), bedrock with no cobbles, and sites without slopes (Fig. 2; Simard 2017; Binder et al. 2018; Farha 2018; Farha et al. 2020). Although the presence of rocky substrate appears to be important for spawning, substrate diameter does not appear to be limited to one size class (Farha et al. 2020). Instead, location, arrangement, and contour of spawning shoals affects interactions between substrates and currents, such that numerous combinations of physical habitat parameters can be suitable for spawning dependent on individual site characteristics. This variability in the relative importance of habitat parameters has confounded the use of the cobble-contour model, which suggests the model should be expanded (see Table 1). The ability of lake charr to find new spawning substrate and to successfully colonize new lakes further emphasizes the need for an expanded model of spawning habitat based

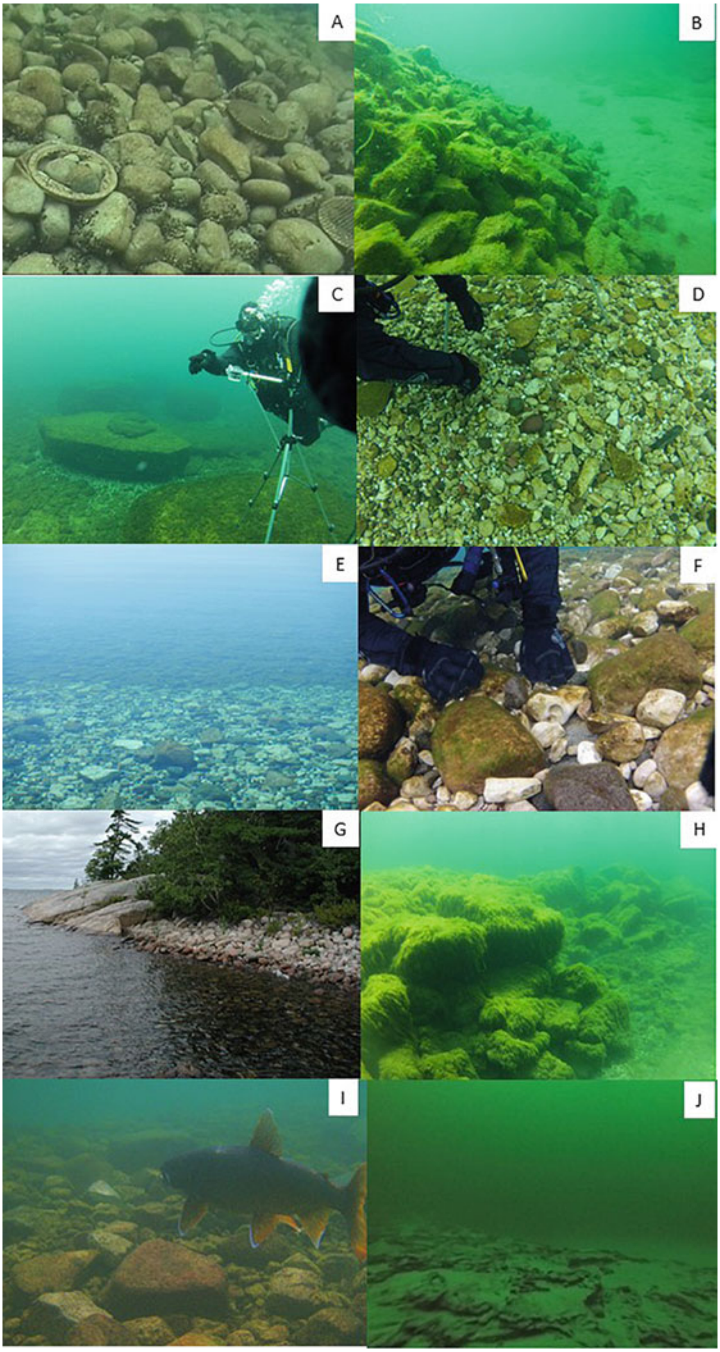

Fig. 2 Lake charr *Salvelinus namaycush* spawning substrates, illustrating the diversity of habitat use in the Laurentian Great Lakes (**a**–**i**) and an invaded lake (**j**). Spawning has been documented at all sites. (**a**) Cobbles on a crib in northern Lake Huron (credit: RM Claramunt, Michigan Dept. of Natural Resources) and (**b**) an artificial reef in Thunder Bay, Lake Huron, illustrating the ‘cobble-

Table 1 A simplified list of lake charr *Salvelinus namaycush* spawning habitat characteristics that extend beyond the "cobble-contour model" to consider additional physical, chemical, and biological variables relevant to early life stages. Constraints that affect the importance of each variable for spawning habitat selection are listed; for example, in lakes that lack embryo predators, physical features of habitat that protect embryos have low importance

Variable	Life stages	Relevant features of habitat	Constrained by
Dissolved oxygen	Pre-hatch embryos	Presence of currents (influenced by fetch, depth, hyporheic flow, local geology) Low sedimentation (influenced by currents, land use, surface turbulence)	Low latitude and shallow lakes with warm water; high productivity that generates biological oxygen demand
Temperature	Pre-hatch embryos	Temperatures below 10 °C	Low latitude, shallow sites
	Post-embryos	Access to deep water	Low latitude, shallow sites
Physical shelter	Pre-hatch embryos	Crevices and interstices for protection from displacement, physical damage	Large lakes with high surface turbulence from wind and fetch
	Free embryos	Protection from predators	Presence of predators
Access to food	Free embryos	Plankton density Scope to forage and seek shelter	Local productivity Presence of physical shelter
	Post-embryos	Access to deep water, *Mysis*	Bathymetry

on individual site characteristics, and general requirements for spawning, embryo incubation, and survival.

Recent progress toward broadening understanding of spawning habitat has integrated a wide range of habitat characteristics (lakebed surface roughness, substrate particle size, current patterns, and hyporheic flow) at multiple spatial scales (lake, site, and patch) to identify potential spawning habitat types (Riley et al. 2019). In particular, physical processes must create structure and flow conditions suitable for embryo incubation. Understanding local geological features such as drumlins, eskers, and moraines, groundwater flow, and lake configuration relative to prevailing winds (i.e., fetch) will guide the identification of spawning areas. Spawning habitats are also characterized by biotic variables including local productivity, predators, and

Fig. 2 (continued) contour' model of spawning reefs (credit: JE Marsden); (**c**) gravel/rubble substrate at the base of 'giant' boulders, Boulder Alley, Drummond Island Refuge, Lake Huron (credit: HT Thompson, U.S. Geological Survey); (**d**) gravel substrate on Scammon Shoal, Drummond Island Refuge, Lake Huron (credit: TR Binder); (**e**) cleaned area (foreground) of rubble/cobble substrate on Horseshoe Reef, Drummond Island Refuge, Lake Huron (credit: TR Binder); (**f**) close-up of unsorted substrate from Horseshoe Reef (credit: HT Thompson); (**g**) cobbles on shoreline indicating presence of cobbles underwater at Mary Island, Parry Sound, Lake Huron, (credit: JE Marsden); (**h**) portion of boulder-strewn spawning habitat in Thunder Bay, Lake Huron (credit: JE Marsden); (**i**) flat substrate with unsorted rocks, Great Bear Lake (credit: CC Krueger); sand/silt substrate, Breeze Channel Hump, Yellowstone Lake (credit: LG Simard, Vermont Dept. of Fisheries and Wildlife) prey. Extensive algal growth, such as *Cladophora*, can occur in the southern portion of the lake charr's distribution and generate low dissolved oxygen in substrate interstices during autumn and winter unless patch-scale currents or groundwater flow is sufficient to remove organic debris. Deep crevices are an important feature of spawning habitat as refuge from predators but may not be an important habitat characteristic in the absence of embryo predators (Simard 2017). Similarly, invasion success of lake charr in Canadian inland lakes was negatively correlated with fish species richness, likely due to predator pressure on free embryos (Evans and Olver 1995). The presence of plankton is also important for first-feeding free embryos. Finally, a complete model of spawning habitat must include adjacency to deep water where age-0 lake charr will have access to cold temperature and prey, such as *Mysis*. By understanding critical features of spawning habitat (dissolved oxygen, temperature, protection from displacement and predators, and access to food), and recognizing the lake charr's flexibility in habitat selection, the search for where lake charr choose to spawn can be broadened to include local lake and habitat characteristics.

3.1 Substrate Size

The relative importance of substrate size is likely related to interstitial volume and stability of the substrate for incubating developing embryos over winter (Fitzsimons 1995; Marsden et al. 1995a). Large and well-sorted substrates are thought to be more permeable to currents, are more stable during high wave energy, and have interstices with more connectivity than small or poorly sorted substrates (Marsden et al. 2005). Consequently, water flow can penetrate deeper into substrates comprised of large than small particles to keep pre-hatch embryos well oxygenated and free of silt. Pre-hatch embryos that settle into deep interconnected interstices of large substrate are less likely to be affected by turbulence or be found by infaunal predators in the maze of interstices (Claramunt et al. 2005). Large interstices may also facilitate foraging by free embryos to increase their ability to seek refuge. Conversely, small particles have more occlusion points that create crevices where pre-hatch embryos can become lodged. In reality, spawning shoals are generally comprised of an intricate mix of many substrate diameters with a patchy distribution. A complex matrix of interstices will separate pre-hatch embryos to reduce mortality from fungus and reduce foraging efficiency of predators. Ultimately, substrate size alone is not an accurate representation of the true interstitial volume, so is likely to be an insufficient predictor of spawning habitat use, particularly in areas with abundant suitable habitat. At reef areas adjacent to Drummond Island, Lake Huron, substrate size was not a predictor of spawning activity (Farha 2018).

Gravel substrates (2–64 mm) have small interstices with limited depth. Unlike most salmonines, lake charr do not bury fertilized eggs by digging redds, and thus gravel has a limited capacity to hold passively deposited eggs. Small particles like gravel that are also less stable than cobbles and boulders can be moved more easily by wave energy in nearshore areas. Thus, gravel substrates may be used more commonly at deep sites where wave energy has low effect, in shallow water in small lakes with limited fetch, or in northern lakes where early ice formation prevents wave action. Observations of lake charr spawning on gravel are limited but support this prediction. Lake charr spawned on gravel in 1 m depth along the shoreline of Otsego Lake where the fetch was less than 1 km, and near Drummond Island, Lake Huron in depths of 4–10 m (Tibbits 2007; Binder et al. 2018; Farha 2018; Farha et al. 2020). Gravel substrates, with less capacity for interstitial flow than large particles, are also more likely to accumulate fine sediments. In shallow water, gravel substrates may be kept clear of silt by wave action, as in Otsego Lake where substrates were heavily silted below 1 m depth but clean above that depth (Tibbits 2007). At Drummond Island, pre-hatch embryos were deposited in gravel substrates under large boulders, where Venturi effects appeared to keep the substrate free of sediment (Binder et al. 2018; Farha et al. 2020; Riley et al. 2019).

3.2 Currents

Understanding currents and their influence on hyporheic exchange may be the largest knowledge gap in our conceptual understanding of lake charr spawning habitat selection (Riley et al. 2019; Farha et al. 2020). Currents, particularly micro-currents in crevices, are challenging to measure in situ, and the presence of currents is generally inferred from wind-fetch models and bathymetric features that produce Venturi effects (Riley et al. 2019). Interactions between substrates, lakebed relief, and currents in natural lakes and their importance for lake charr spawning habitat are not well understood. Currents in lakes are complex, and the interaction of currents with bathymetric features is affected by wind direction and velocity, fetch and morphology of the lakeshore, and depth and distance of a site from shore (Riley et al. 2019). Fetch is related to the orientation of a lake with respect to prevailing wind direction and wind energy so that sites with long fetch tend to have strong currents, although the presence of nearshore islands or bars can moderate or enhance these effects. Nearshore areas exposed to long fetch are high-energy environments and are erosional, whereas deep, offshore areas are low-energy and depositional. Consequently, silt cover on nearshore spawning substrates is inversely related to wind-wave energy, and the quality of spawning sites can be predicted by fetch (Schall et al. 2017). Sites with high fetch can result in higher pre-hatch embryo loss due to displacement than from predation, so large lakes may experience higher pre-hatch embryo mortality than small lakes with short fetch (Fitzsimons et al. 2007). Lake charr appear to choose spawning sites with moderate mechanical energy where currents are strong enough to provide oxygen to pre-hatch embryos but not so strong as to dislodge them (Fitzsimons and Marsden 2014). Most work on lake charr spawning habitat has been conducted at relatively shallow, nearshore sites, where currents and wave energy are major features of the habitat. Nearshore currents and surface turbulence may keep substrates clean by removing fine substrate particles (e.g., Sly 1973). Lake charr can spawn at deep sites (>90 m) in the Laurentian Great

Lakes (Eschmeyer 1955, 1964; Edsall et al. 1995; Janssen et al. 2006), but fieldwork is logistically difficult in these areas due to depth and severe autumn weather, and therefore work at deep sites has been limited (Marsden et al. 1995b, Marsden and Janssen 1997, Fitzsimons et al. 2005, Janssen et al. 2007). Ice cover may also protect incubating embryos from turbulent currents generated by winds, so effects of ice will likely be site-specific but to date are understudied. Currents that occur in deep waters are likely to differ from nearshore currents found at shallow spawning sites, and therefore constraints on the physical properties of deep sites may differ from nearshore sites. Relatively little information is available regarding the physical characteristics of deep spawning sites relative to nearshore sites, particularly with respect to currents. More research is needed to determine how constraints for spawning, such as substrate characteristics and current patterns, differ between deep and shallow sites.

3.3 Temperature

Water temperature and seasonal occurrence of ice also affect the suitability of a site for pre-hatch embryo development. Lake charr embryo development rate is related to water temperature and dissolved oxygen (Goetz et al. 2021), but because incubation occurs overwinter, lethal temperatures are unlikely to be reached in most lake charr lakes except shallow southern lakes where temperatures may be too warm for incubation or shallow northern lakes that freeze to the bottom in winter. However, asynchrony in the rate of pre-hatch embryo development and timing of emergence in spring may negatively affect survival. Warm overwinter temperatures may result in early hatching (Casselman 1995), well before sufficient plankton are available for free embryo foraging. Across their range, lake charr spawn in lakes where embryos hatch under the ice, or in open water. Ice movement, particularly during spring thaw, can scour nearshore substrates (e.g., Sly and Schneider 1984), but the effect on pre-hatch embryos has not been studied.

3.4 Spawning Habitat Selection

Substrate, current, and temperature define broad areas of habitat that are suitable for lake charr pre-hatch embryo incubation and free embryo survival. Within such areas, habitat selection may be based on physical variables at fine spatial scales (Riley et al. 2019). Spawning lake charr appear to select small patches within larger sites of suitable spawning habitat but may not use apparently similar habitats located nearby (Marsden and Krueger 1991; Kelso et al. 1995; Claramunt et al. 2005; Marsden et al. 2016; Binder et al. 2018; Farha 2018; Farha et al. 2020). In Thunder Bay, Lake Huron, lake charr focused activity during the spawning season in a 15,440 m^2 area comprising 28% of total available contiguous habitat, although they also spawned on artificial reefs with an area of 214 m^2 (Marsden et al. 2016). Similarly, spawning lake charr tracked using acoustic telemetry at Drummond Island, Lake Huron, were not distributed evenly over available substrate but aggregated in areas that comprised less than 10% of available habitat on a given reef (Binder et al. 2018).

The size of suitable spawning habitat patches may affect the density of spawning lake charr. The highest densities of fertilized eggs among 30 sites sampled in lakes Michigan, Huron, and Champlain were found on the smallest reefs (18–53 m^2), which suggests that spawners were more tightly aggregated at these sites (Marsden et al. 2005). However, among 29 artificial reefs constructed in Thunder Bay, Lake Huron, lake charr either did not find or did not choose to spawn on the four smallest reefs, 80 m^2 in area (Marsden et al. 2016). The relative importance of protection from predation, protection from dislodgement, and sources of oxygen (atmospheric exchange and photosynthesis) vary locally. For example, deep interstices may be less important at deep sites below the influence of surface turbulence (Janssen et al. 2007; Fitzsimons et al. 2005) or if interstitial predators such as sculpins (*Cottus* spp.) are rare or absent (Fitzsimons et al. 2005). Variables affecting embryo incubation at spawning sites may act at very small spatial scales, so fine-scale assessment of currents and substrates at these sites may be useful to fully understand spawning habitat selection.

In addition to physical habitat characteristics, social cues may also play a role in spawning habitat selection, particularly if spawning substrate is not limiting (Gunn 1995). To find spawning sites, lake charr could return to the site where they were hatched (natal homing) or to a previously used site (repeat homing, or spawning site fidelity), although the success of lake charr at rapidly colonizing new lakes after anthropogenic introductions (Martinez et al. 2009) argues against natal homing as a sole method of finding spawning sites (Binder et al. 2021). However, evidence of olfactory orientation has been inferred based on large aggregations of spawning lake charr seen annually during autumn at a breakwall adjacent to effluent from a salmonid hatchery in Lake Champlain (Ellrott and Marsden 2004; Marsden et al. 2005) and observed near a hatchery outfall draining into the south shore of Lake Superior (Krueger et al. 1986). Individual lake charr return to sites where they spawned previously. For example, 90% of 29 tagged lake charr returned in successive spawning seasons to Thunder Bay, Lake Huron, (Binder et al. 2017) and 61–74% of 93 tagged lake charr returned to spawning reefs in Lake Champlain (Pinheiro et al. 2017; Binder et al. 2021). Spawning site fidelity appears to depend on proximity to other spawning sites, as evident from within-season movements between adjacent spawning locations (Martin 1960; DeRoche 1969; Binder et al. 2017). For example, in Lake Opeongo, Ontario, lake charr moved between spawning sites located approximately 2.5 km apart, with 52% of females and 6% of males moving between sites within a single spawning season (MacLean et al. 1981). Spawning site fidelity or natal homing may influence broad-scale habitat selection with lake charr using olfactory, auditory, or visual-behavioral cues from conspecifics to select fine-scale patches within large sites, thereby resulting in localized aggregations of spawners (e.g., Bett and Hinch 2016). Such aggregations may focus on one or more of several suitable patches, but the importance of having many mates to choose from, especially for females, may outweigh the advantages of spreading eggs across broad areas of habitat (Goetz et al. 2021).

Artificial reefs can be used to test the relative importance of different habitat characteristics for attracting spawners and incubating embryos (Marsden et al. 1995b). Fine-scale tracking of lake charr movements around 29 reefs constructed with different orientations, heights, and sizes in Thunder Bay, Lake Huron, showed that height (1.5 and 3 m) and orientation did not affect spawner density, but lake charr were more likely to aggregate on larger reefs (73 m × 7 m vs. 9 m diameter), and reefs closer to an existing natural spawning site (Marsden et al. 2016). A complete understanding of lake charr selection of spawning habitat will require research that focuses on interactions between lake currents and substrates at shallow and deep sites, and on variables likely to create suitable conditions for embryo incubation.

4 Free Embryo and Juvenile Habitat

The habitat of free embryos is determined by spawning habitat selected by adults that is also suitable for embryo incubation. Free embryos reside in interstitial spaces of rocky habitat for 4–6 weeks until their yolk sac is absorbed (e.g., Marsden et al. 2005). During this period, they make nocturnal vertical forays out of the substrate but return to crevices when in the presence of predators (Baird and Krueger 2000; Strakosh and Krueger 2005; Binder et al. 2021). To date, research on movements at this stage has only been conducted on simulated laboratory substrates comprised of cobbles with interstices larger than the size of free embryos, where movement within the substrate is reasonably unconfined and feeding may occur within interstices (Baird and Krueger 2000; Ladago et al. 2016). Age-0 lake charr in lakes are found on boulder, cobble, rubble, and gravel substrates, less frequently on sand, and rarely on silt (Jude et al. 1981; Nester and Poe 1987; Peck 1982), perhaps because silt and sand do not provide refuge from predators.

Optimal spawning habitats should provide ready access to suitable feeding habitat for juveniles (Marsden et al. 1995a). Relatively little is known about the habitat of small juvenile lake charr (i.e., age-1) and most of what is known is construed from sampling juveniles on trawlable habitat (i.e., sand-silt substrates free of obstructions or rocky areas), and extrapolating habitat use from diet analyses (e.g., Swedberg and Peck 1984; Elrod and Gorman 1991; Marsden et al. 2018). Juvenile lake charr <300 mm TL were observed with a remotely operated vehicle in two small (266 and 1772 ha) lakes in Quebec (Davis et al. (1997). Their observations confirmed results from gillnets that indicated juvenile lake charr were resting or moving along the bottom, concentrated at 15–20 m depth and 5.4–6 °C water during the day and in shallower, warmer water at night (5–10 m, 10–18 °C). Observations in the Laurentian Great Lakes suggest that juveniles rapidly move away from spawning sites to rearing habitats in waters 10–80 m deep (e.g., Royce 1951; Martin 1957; DeRoche 1969; Martin and Olver 1980; Elrod and Schneider 1987; Bronte et al.

1995), where juveniles remain close to the bottom and accessible by bottom trawling (Marsden et al. 2018). In Lake Ontario, lake charr juveniles older than age-0 were found in the warmest water in winter and spring (4 °C), then were found in 6–12 °C water during summer (Elrod and Schneider 1987), again indicating that juveniles sought habitats that optimized temperature requirements for foraging and digestion. Similarly, in Lake Champlain, juvenile lake charr ages 0–3 were concentrated at 35–50 m, within 10 m above and below the lower edge of the thermocline, while the lake was stratified, but were found in shallower depths (25–35 m) when the lake was isothermal (Marsden et al. 2018; J. E. Marsden, unpublished data). Transition into deep water may be a behavior to avoid predation by nearshore species, avoid unfavorably warm nearshore temperatures, or maximize overlap with prey. Habitat near the thermocline may optimize these variables by keeping juveniles in a region where preferred temperatures of juveniles and their prey are readily accessible. The temperature range of age-0 lake charr for maximum power output was at water temperatures from 12 to 20 °C (Evans 2007), considerably warmer than the habitat where they are usually found, which suggests that juveniles may remain in temperatures colder than their temperature optima to avoid cannibalism by large lake charr (Evans and Willox 1991). In large northern lakes, where surface waters do not exceed temperature preferences of lake charr or temperature changes occur less rapidly than in small lakes, age-0 juveniles remained in shallow water longer, which supports the hypothesis that temperature is the factor driving offshore migration (Miller and Kennedy 1948; Peck 1982; Simard et al. 2019; Chavarie et al. 2019). Age-0 lake charr in laboratory tests sought temperatures near 10 °C, a temperature at which they would overlap with predator species (alewife *Alosa pseudoharengus* and rainbow smelt *Osmerus mordax*—two non-native predators in many southern lake charr lakes), although the specific growth rate was highest near 12.5 °C (Edsall and Cleland 2000). Unlike adult lake charr, juveniles do not have the thermal mass to buffer temperature changes and make extended foraging forays into warm water without rapidly reaching sub-lethal body temperatures (Morbey et al. 2006), and do not appear to vertically migrate in the water column (Gorman et al. 2012).

Juvenile lake charr remain close to the substrate until at least age-3 or approximately 300 mm total length, where they are readily captured in bottom trawls but with limited success in small-mesh gillnets (19–38 mm stretch mesh), in which they are caught in the lower 0.3 m of the net (Davis et al. 1997; Marsden et al. 2018). Food of age-0 lake charr tends to be associated with bottom substrates, thus suggesting benthic habitats are important (Vinson et al. 2021). Diet of age-0 lake charr in Lake Superior was chironomids, copepods, and cladocerans (Swedberg and Peck 1984), whereas in Lake Champlain was primarily *Mysis* (J. E. Marsden, unpublished data). Age-1 to age-3 lake charr transition to consumption of small prey fishes (e.g., sculpins, alewife, and smelt at the southern edge of lake charr distribution) and then larger fishes as they grow (Elrod and Gorman 1991; Isaac et al. 2012; Marsden unpublished data). Alewife, smelt, and larval deepwater sculpin (*Myoxocephalus thompsonii*) vertically migrate but are available during the day on the bottom, so small lake charr do not need to expend energy to chase them up into the water column.

A relatively unstudied aspect of juvenile lake charr habitat is the effect of internal seiches. The thermocline is a dynamic feature in most large lakes where strong wind events force downwind downwelling of the metalimnion, with associated upwind upwellings, followed by oscillations of the metalimnion back to a stable level. During extreme oscillations, the metalimnion can tilt to the surface (i.e., a deflection up to 30 m or more), with associated water velocities along the metalimnion up to 32 cm s^{-1} (Manley et al. 2012; Cossu et al. 2017). Juvenile lake charr during these events may remain in place to experience rapid temperature changes, move downwards along the bottom to areas below the extent of seiche activity, or move vertically in the water column to follow the thermocline. Whatever their behavior, seiche events are likely to cause energetic stress for juvenile lake charr. On the other hand, such events also affect benthic communities (Cossu et al. 2017). The energy associated with the moving front of an upwelling may stir up benthos and alter vertical migration patterns of *Mysis* such that food items become more available to lake charr.

5 Anthropogenic Effects on Lake Charr Habitat

Freshwater shorelines have been extensively modified by human activities in many parts of the world, and these activities may disrupt natural physical and ecological processes in nearshore areas (Strayer and Findlay 2010). Therefore, many of the known or suspected lake charr spawning habitats in nearshore areas of the Laurentian Great Lakes (Goodyear et al. 1982; Marsden et al. 1995a) and inland lakes (Martin and Olver 1980) are vulnerable to human development, including dredging, gravel removal, agriculture, road building, timber harvest, mining, shoreline modification and hardening, industrial effluents, residential development, logging and riparian damage that increase erosion and deposition of sediments, and introduction of invasive species. Lake charr foraging habitats are located in deep offshore waters in large volumes of water, particularly in the Laurentian Great Lakes, and are less vulnerable to human impacts than nearshore areas. Except for nearshore spawning habitats (see below), most human activities likely have greater effects on lake charr habitats in small inland lakes than in large lakes. Anthropogenic change can have a variety of direct and indirect effects on lake charr populations throughout their range, but here we focus only on effects on lake charr spawning and foraging habitats.

Changes in sediment distribution in nearshore spawning habitats associated with construction activities, vegetation removal, agriculture, mining, forest harvest, and other anthropogenic activities is perhaps the most pervasive effect of human activity on lake charr spawning habitats. Increased sediment loads from anthropogenic activities have been hypothesized to have contributed to loss of lake charr spawning habitats, and subsequent population declines in lakes Ontario, Erie, Champlain, Cayuga, and Seneca (Martin and Olver 1980; Sly and Widmer 1984, Ellrott and Marsden 2004). Sediments suspended by lake currents that settle on spawning habitats would render them unattractive to spawning lake charr or smother pre-hatch embryos (e.g., Sly 1988). Sedimentation of spawning beds can be an important source of lake charr pre-hatch embryo mortality in the Great Lakes (Manny et al. 1995), and broad-scale sedimentation related to forest harvest may have contributed to the extirpation of wild lake charr populations from Lake Champlain (Ellrott and Marsden 2004) and Cayuga Lake (Webster et al. 1959). Sedimentation from industrial activities, such as erosion of stockpiled cement kiln dust into nearshore waters, degraded lake charr spawning habitats in Thunder Bay, Lake Huron (Marsden et al. 2016), and agriculture and forest harvest resulted in increased nearshore sedimentation in Lake Simcoe, Ontario (Evans et al. 1996). Mining may contribute large volumes of mobile toxic sediments to lakes that may smother spawning habitats and persist for a long time (e.g., Kerfoot et al. 2014).

In addition to landscape alterations that affect inputs of sediment, many areas of Laurentian Great Lakes coastlines, particularly near urban areas, have been subjected to various levels of development that may disrupt nearshore physical processes within lakes that control sediment transport (Meadows et al. 2005). For example, gravel has been extracted from nearshore glacial deposits throughout the Laurentian Great Lakes basin for over a century, but effects of these extractions on fish habitat have rarely been evaluated (Steedman and Regier 1987). In Lake Ontario, gravel and cobble were extracted for construction activities in Toronto for decades (Whillans 1979; Sly 1991). These glacial deposits may have been spawning habitat for lake charr that were permanently altered by dredging. Clear-cut logging around small boreal lakes can alter wind speeds and patterns that influence thermocline stability, with decreased water clarity and increased thermocline depth, although these alterations do not necessarily reduce the volume of suitable foraging habitat for lake charr (Steedman and Kushneriuk 2000).

Eutrophication has long been recognized as an important potential threat to salmonid communities in oligotrophic lakes (e.g., Ryder and Johnson 1972) that may have some direct effects on lake charr spawning habitat. Eutrophication resulting from agriculture or residential development near lakes can increase the accumulation of detritus in nearshore zones (Lambert et al. 2008; Rosenberger et al. 2008) and foul spawning substrates or create localized anaerobic conditions (Colby et al. 1972). In the Laurentian Great Lakes, dense concentrations of the native algae *Cladophora* has fouled substrates in nearshore areas subject to eutrophication (Auer et al. 2010; Marsden et al. 2016). Sloughed, dead *Cladophora* may be transported by lake currents to settle on spawning habitats (e.g., Crowder et al. 1996). Eutrophication may also result in widespread lowered hypolimnetic dissolved oxygen levels that might affect spawning and foraging habitats for lake charr (Colby et al. 1972). However, the effect of summer and autumn deposition of organic debris on winter interstitial oxygen levels is not clear, because currents may scour organic debris from reefs in autumn. East Reef in Thunder Bay, Lake Huron, has a thick coverage of *Cladophora*, yet produces more lake charr free embryos than adjacent newly constructed reefs without *Cladophora* (Marsden et al. 2016). Eutrophication and sedimentation may also increase turbidity, which could affect lake charr visual foraging.

Invasive species have had a variety of effects on fish communities in the Laurentian Great Lakes (e.g., sea lamprey *Petromyzon marinus*; Smith and Tibbles 1980) and inland lakes. In the Great Lakes and Lake Champlain, invasive alewife and rainbow smelt largely replaced native planktivorous coregonines and altered planktonic prey populations and lake charr diets (Cuhel and Aguilar 2013; Simonin et al. 2018). The invasion of dreissenid mussels reduced phytoplankton and increased water clarity, which could affect water temperatures at spawning sites. Bottom substrates in many areas of lakes are now covered by dreissenid mussels (Vanderploeg et al. 2002) that exacerbate effects of eutrophication described above: benthic algal growth in the Great Lakes may have increased in recent years due to effects of nutrient excretion by dreissenids (e.g., Zhang et al. 2008) and dreissenid colonies are often accompanied by large mats of *Cladophora* (Brooks et al. 2015). The resulting shift in nutrient and energy flow from pelagic to benthic and littoral pathways has resulted in re-engineered ecosystems (Higgins and Vander Zanden 2017). Dreissenid mussels have also changed rocky habitats throughout the Great Lakes basin by occluding interstices, creating sharp surfaces that damage fertilized eggs (Marsden and Chotkowski 2001), and reducing entrainment of fertilized eggs into habitat (Ellrott and Marsden 2004). Another recent invader in the Great Lakes, the round goby, is now very abundant at many nearshore spawning sites and preys on all embryo stages of lake charr (Chotkowski and Marsden 1999).

Climate change is predicted to impart significant physical and biological changes in temperate lakes (Adrian et al. 2009) and widespread changes to ice phenology have been observed in temperate lakes in recent decades (e.g., Hewitt et al. 2018). A water temperature increase of just a few degrees in summer could prevent lake charr recruitment in Arctic lakes (McDonald et al. 1996). For example, an entire year class of stocked juvenile lake charr was eliminated in Gullrock Lake by an El Nino warming event, though adult lake charr may have survived by finding cold-water seeps for thermal refuge (Gunn 2002). Climate change is also expected to alter precipitation, wind speed, and wind direction, which would affect lake levels and currents and lead to complex interactions that may affect the volume and distribution of suitable oxythermal habitats for fishes (De Stasio et al. 1996; Schindler 2001). At the southern edge of the species' range, water temperature is likely to be the primary driver of foraging habitat quality for lake charr, and predicted increases in water temperature (IPCC 2014) might alter the availability of suitable oxythermal foraging habitat for lake charr through changes in water temperatures and timing and duration of ice cover (Jansen and Hesslein 2004; Guzzo and Blanchfield 2017; Lester et al. 2021). In lakes where lake charr are constrained by high littoral water temperatures, lake charr may have reduced access to preferred prey in summer and may suffer reduced growth and condition (Guzzo et al. 2017). These effects will vary with lake size, depth, and latitude, with northern lakes likely remaining cold enough in summer to support lake charr foraging habitats lakewide, while small lakes along the southern edge of the range will be most affected (e.g., Johnson 1975). However, suitable thermal habitat for lake charr could increase in Lake Michigan under conditions of climate change due to the large volume of water contained in this lake (Magnuson et al. 1990). Climate change may also alter the timing of spawning if warmer summer temperatures result in delayed cooling to temperatures that stimulate spawning (i.e., 12 °C).

Many authors have suggested that low availability of spawning habitat, or habitat degradation, may limit restoration of lake charr in the Laurentian Great Lakes, although little evidence exists for either possibility (Farha et al. 2020). Degradation of spawning habitat is mostly a consequence of sedimentation and infilling of interstices in small lakes and nearshore areas of large lakes that are susceptible to anthropogenic effects such as dredging and erosion of manipulated landscapes (e.g., Marsden et al. 2016), whereas such effects are likely rare on deep, offshore sites in large lakes. For example, degradation of nearshore habitat in Thunder Bay, Lake Huron was construed to limit restoration of spawning stocks, but recovering populations spawned on extensive but previously unknown areas of rocky habitat slightly farther offshore (Marsden et al. 2016). Because of ease of access for researchers, most work on spawning sites has occurred in shallow, nearshore waters, thereby leading to an unintended presumption that most spawning habitats were in shallow water. However, in the Great Lakes, offshore lake charr spawning habitats may historically have been more productive than nearshore habitats (Dawson et al. 1997). Lake charr are selective in their use of spawning habitat and tend to use the same locations year after year (e.g., Binder et al. 2018). However, lake charr will move to nearby alternative spawning areas if their previously used area becomes unavailable (McAughey and Gunn 1995), so local degradation of a particular habitat patch could result in the use of alternative patches rather than reproductive failure at a degraded patch. In Otsego Lake, severe sedimentation of most substrate below 1 m water depth likely led to lake charr spawning within a few meters of shore on gravel, where spawning sustains the population (Tibbits 2007).

In many lakes, human activities have increased the amount of prime nearshore spawning habitat, including breakwalls, piers, and water intake structures that have large cobbles and steep slopes, (Peck 1981, 1986; Jude et al. 1981; Fitzsimons 1996, Ellrott and Marsden 2004, Marsden et al. 2005; Marsden and Chotkowski 2001). On the other hand, similar to natural reefs, breakwalls and other anthropogenic structures attract embryo predators, are heavily colonized by dreissenid mussels, and may increase the amount of *Cladophora* in nearshore areas (Riley et al. 2015; Marsden et al. 2016). The contribution of artificial reefs to natural recruitment has not been evaluated, because identification of the source of wild recruits is a challenging problem. Unless habitat loss is widespread within a given lake, lake charr populations may be relatively unaffected if they use only a fraction of the available spawning habitat in a given lake or can transition to alternative sites if access to preferred sites are blocked (McAughey and Gunn 1995). The attraction of spawning lake charr to breakwalls and purpose-built reefs may have mixed outcomes if these sites concentrate spawning at sites that also attract predators or draw spawners away from better natural sites. Recently, wind farm developers have begun to advocate for turbine installations that use cobble foundations as artificial reefs. However, the effect of turbine vibrations and site selection relative to local currents and sediment movements should be considered during government permitting.

6 Discussion

In 1995, the RESTORE symposium summarized priorities for research and management of lake charr habitat in the Laurentian Great Lakes based on knowledge at that time (Marsden et al. 1995a). The first two priorities for habitat research focused on the need for better tools to identify spawning sites, particularly deepwater sites, and sample early life stages. These tools would facilitate research on the third priority, to document availability and use of suitable spawning habitat in the Laurentian Great Lakes. Substantial progress has been made on all three priorities. Use of high-resolution sonar has produced more comprehensive maps, particularly of large areas that encompass multiple spawning patches (e.g., the Mid-Lake Reef Complex, Lake Michigan, Warner et al. 2009; Drummond Island, Lake Huron, Binder et al. 2018; southern Lake Michigan, Redman et al. 2017). The development of inexpensive, high-resolution underwater cameras and remotely operated underwater vehicles (ROVs) has greatly expanded visual access to spawning sites, which previously was limited to scuba divers in relatively shallow water (<30 m). Expansion of ROV capabilities to include electroshocking and embryo suction sampling has confirmed spawning activity in deep sites and boulder-associated spawning and rearing habitats (Marsden and Janssen 1997; Janssen et al. 2006; Farha et al. 2020). However, the tool that has most significantly expanded knowledge of lake charr habitat use, including during non-spawning seasons, is acoustic telemetry. Binder et al. (2018) located spawning aggregations within a 19–27 km^2 region near Drummond Island, Lake Huron using fine-scale telemetry, mapped the area using high-resolution multibeam sonar surveys, and confirmed spawning by diver observations of deposited eggs and pre-hatch embryos. Currently, confirmation of spawning still relies on physical evidence of embryos in the substrate or visualization of spawning adults, but as studies continue to accumulate correlations between acoustic telemetry data and activity associated with spawning, physical sampling may no longer be necessary. For example, the effectiveness of lake charr suppression in Yellowstone Lake was substantially increased by the use of acoustic telemetry data to concentrate gillnetting in areas of highest fish concentrations during the spawning season to remove large numbers of spawners (P. Bigelow, National Park Service, personal communication).

Use of acoustic telemetry, and additional studies in systems other than the Laurentian Great Lakes, including Alexie, Whitepine, Tahoe, Otsego, and Yellowstone lakes, have expanded understanding of spawning habitat from the initial, simplistic, cobble-contour conceptual model to a more general model that includes multiple physical, biological, and dynamic (e.g., currents and flow) features (Riley et al. 2019). Geological information can be used to identify broad areas where spawning substrates occur (e.g., many cobble areas created by glacial processes; Riley et al. 2014, 2017), and patches within such areas by using fine-scale telemetry, ROVs, divers, and embryo collections (Gunn et al. 1996). Constructed reefs have been used to examine variables associated with spawning habitat choice, such as height, orientation, size, and proximity to natural reefs (Marsden and Krueger 1991; Marsden et al. 2016).

Since RESTORE, most attention has been paid to describing known spawning habitat and discovering new spawning areas. We need to learn more about habitat use in the non-spawning season, and habitat use by juveniles between departure from spawning reefs at age-0 through ages to first maturity. Advances in acoustic telemetry include tags that record temperature and pressure, so individual fish can be tracked in three dimensions and relative to the thermocline. In small systems, such as Alexie Lake and lakes at the Experimental Lakes Area (Ontario), whole-lake positioning systems can be used to track movement and habitat use by lake charr throughout the year, concurrently with other top predators in the system (e.g., Guzzo et al. 2016). Foraging behavior, identifiable by changes in speed and direction, may be tracked in time and space. Changes in the use of habitat resulting from anthropogenic effects such as climate change can be observed and quantified when detection data are collected over several years.

Research in lakes invaded by lake charr, notably lakes in the western USA, has highlighted the behavioral plasticity of lake charr. Lake charr do not have prior knowledge of spawning sites in newly invaded lakes, and these lakes generally have different biological communities than lakes in the native range of the lake charr. Consequently, the lake charr must be highly adaptive to survive and reproduce in these new habitats. Spawning in western lakes, such as Yellowstone Lake, has emphasized the diversity of habitats that can be used by lake charr (Simard 2017).

7 Future Research

Several key knowledge gaps have been identified in this chapter, and here we propose several recommendations and potential research questions. In particular, identification and protection of high-quality spawning habitats are important to the conservation of native lake charr populations. Expertise in geological process, fluid dynamics, physical limnology, and lake hydrodynamics, and use of new technologies (e.g., instrumentation to measure fine-scale in situ differences in water velocity, pressure, or hydraulic head; autonomous underwater vehicles fitted with acoustic doppler current profilers or other instrumentation; multi-beam sonar; acoustic telemetry) will benefit research on spawning site characteristics. Understanding the role of embryo predators and access to forage (zooplankton and *Mysis*) in the selection of habitat is equally important, and research in newly invaded habitats will continue to provide new insights into behavior in the presence of novel biotic communities. Expanded use of acoustic telemetry, particularly with tags that record depth, temperature, acceleration, and predation events, will expand understanding of vertical habitat use, thermal habitat use, and foraging behavior, particularly by juvenile lake charr.

Expand research on juvenile and adult movements and habitat use

- Develop methods to sample juvenile lake charr on deep and rocky habitats that cannot be sampled with traditional gear such as trawls.
- Expand use of acoustic telemetry in small lakes that can be partially or completely covered with two- and three-dimensional positioning systems to track habitat occupancy during all seasons, particularly winter, and at all stages of thermocline development and breakdown.
- Determine whether early life experience influences adult habitat use. In large lakes, how is habitat located and selected?
- Determine how projected climate change scenarios affect the amount and quality of habitat available to lake charr in various systems and potential effects on distribution and abundance.

Expand research on lake charr adult habitat in the northern portions of their range and in small lakes

- Temperature, physical habitat, and exposure to exotic species in the southern edge of the lake charr range, where most habitat studies have been conducted, are likely different than over the remainder of the range. A comparison between latitudinally different habitats will likely reveal further thermal and morphological adaptations.

Expand research on habitat used by different morphotypes of lake charr

- Most research on lake charr, until relatively recently, has been focused on the lean morphotype. Research in northern lakes and Lake Superior is likely to reveal new morphs and additional differences in habitat use including temperature and depth preferences and different seasonal uses of habitat.
- Determine whether spawning habitat characteristics differ among sites within a lake occupied by sympatric lake charr morphotypes.

Expand research to describe and identify spawning habitat in large lakes

- Examine the relative importance of nearshore and offshore sites for spawning in large lakes. Nearshore sites are vulnerable to anthropogenic degradation. Offshore and deep sites have been neglected due to challenges of access and harsh weather during the spawning season, but acoustic telemetry allows remote identification of spawning aggregations. Identification of offshore spawning areas requires an understanding of geologic processes that may generate habitat with necessary features for lake charr.
- Develop a better understanding of how lake currents interact with substrates to effectively model lake charr spawning habitat.
- Determine whether spawning success and subsequent recruitment is affected by the extent and duration of ice cover.
- Determine viability of pre-hatch embryos and subsequent recruitment generated from clean natural reefs compared to degraded natural reefs and constructed reefs.

- Determine whether currents differ between sites that support lake charr spawning and those that do not. What physical mixing mechanisms are predominant at spawning sites? How do these differ among lakes of different sizes?
- Determine whether the likelihood that lake charr will spawn at a site can be predicted by fetch, aspect, depth, distance from shore, relief, site size, or other variables, and how spawning and these variables change with lake size or shape.

Expand research to describe and identify spawning habitat in northern, small, and invaded lakes

- Determine whether lakes of different size (area and depth) support quantifiably and predictably different habitat types and current regimes that support lake charr spawning.
- Determine the relationship between size, latitude, and geology of lakes and different kinds of spawning habitats available for lake charr. Are lake charr spawning habitats different among lakes with differing amounts of glacial till or bedforms in their lakebeds?
- Examine spawning substrates selected by lake charr in invaded lakes, with different biotic communities and no prior habitat knowledge (e.g., imprinting) by lake charr.

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Movement Ecology and Behavior

Thomas R. Binder, J. Ellen Marsden, Matthew S. Kornis, Frederick W. Goetz, Gustav Hellström, Charles R. Bronte, John M. Gunn, and Charles C. Krueger

Abstract Understanding movement ecology and behavior of lake charr *Salvelinus namaycush* is important for successful conservation and management of populations. The lake charr is a cold-water species that evolved in meltwaters along the margins of retreating glaciers. Lake charr exhibit diverse life history, physiology, and behavior that allowed them to adapt to a variety of ecosystems

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across their native range, and to quickly colonize new lakes, as has occurred recently in the western United States. Movement and behavior of lake charr are motivated by four primary drivers: (1) access to cool, well-oxygenated water, (2) foraging opportunities, (3) predator avoidance, and (4) reproduction. Much has been learned about lake charr movement and behavior over the last several decades since the last major review of lake charr movement ecology and behavior. Increasingly detailed observations of novel behavior, made possible largely through use of advanced technologies that allow repeated observations of individuals over large spatial or temporal scales, suggest that lake charr behavior is more complex than has been previously described. We have incorporated these new observations into revised conceptual models. Our intent is that these revised models be viewed as testable hypotheses that serve as a theoretical framework on which to base future research.

Keywords Behaviour · Foraging · Habitat use · Homing · Migration · Navigation · Partial vertical migration · Spawning behavior

1 Introduction

Understanding movement ecology (i.e., causes, patterns, mechanisms, and consequences of spatial movement) and behavior (i.e., the way animals interact with other organisms and the physical environment) of animals is critical to successful conservation and management of populations. To that end, during the last approximately 70 years, lake charr *Salvelinus namaycush* ecology has been of considerable interest among scientists and managers, particularly in lakes near the southern extent of the species' range. For example, in four of the five Laurentian Great Lakes, near-complete extinction of the species occurred after decimation of stocks by commercial fishing and predation by non-native sea lamprey *Petromyzon marinus* prompted extensive restoration efforts in the basin. Stocking of hatchery-reared fish and post-stocking evaluation highlighted the need to understand the distribution, movement ecology, and behavior of naturally produced and hatchery-reared fish in the wild (e.g., Pycha et al. 1965; Swanson 1973; Krueger et al. 1986; Elrod 1987; Rybicki 1990; Perkins and Krueger 1995). In small inland lakes, studies have focused more on habitat use and environmental interactions, and how lake charr behavior and population dynamics were influenced by changing environmental characteristics such as water chemistry and temperature (e.g., Martin 1952; Beggs and Gunn 1986; Snucins and Gunn 1995; Gunn 2002; Morbey et al. 2006; Blanchfield et al. 2009; Guzzo and Blanchfield 2017; Marsden et al. 2021). Finally, more recent interest has been focused on understanding lake charr behavior from the perspective of species invasions, both in temperate Canadian lakes where native lake charr must compete for resources with introduced populations of smallmouth bass *Micropterus dolomieu* (Vander Zanden et al. 2004; Kaufman et al. 2009; Sharma et al. 2009), and in the western United States, where lake charr are invasive and have had devastating effects on native species (Donald and Alger 1993; Fredenberg 2002; Dux et al. 2011, 2019; Cox et al. 2013; Hansen et al. 2016; Syslo et al. 2016; Simard 2017; Fredenberg et al. 2017; Williams 2019).

The lake charr is a cold-water species that presumably evolved during the Pleistocene Era in meltwater lakes and streams along the margins of retreating glaciers (Wilson and Mandrak 2004, 2021), and, thus, is likely best adapted to thrive in cold oligotrophic habitats with simple fish communities (Gunn and Pitblado 2004; Marsden et al. 2021). This evolutionary history plays an important role in governing the movement ecology and behavior of contemporary populations. Lake charr movement and behavior are derived largely from four separate but interacting drivers: (1) need for access to cool, well-oxygenated water (i.e., habitat requirements), (2) foraging opportunities, (3) predator avoidance, and (4) reproduction. However, lake charr are also highly adaptive and can exhibit diverse life history, physiological, and behavioral traits that allow them to survive across a range of environments (Martin and Olver 1980; Muir et al. 2016). Indeed, in some deep lakes with comparatively few species, this ability to diversify has resulted in development of multiple sympatric morphotypes, each specialized to occupy a different available niche (Muir et al. 2016; Chavarie et al. 2021). For example, at Isle Royale, Lake Superior, at least four distinct morphotypes occur—the widespread lean morphotype and three deep-water morphotypes (siscowet, humpers, and redfins; Muir et al. 2014). Most studies on lake charr movement ecology and behavior in large lakes have focused on the lean morphotype. By comparison, virtually nothing is known about the movement and behavior of deep-water morphotypes. Thus, unless otherwise stated, data and observations presented in this chapter pertain mainly to the lean morphotype, and any generalizations to deep-water morphotypes should be made with caution. Despite the tendency to generalize observed behavior across populations of lean lake charr, constraints on movement and behavior of this morphotype can vary greatly across the species' range. Therefore, highlighting differences in behavior among populations is important because these differences may provide insight into potential mechanisms of behavior and, thereby, expand lake charr conceptual behavior models.

Compared to other salmonines, particularly Pacific salmons *Oncorhynchus* spp., behavior of the lake charr is poorly understood. However, several notable characteristics set the lake charr's behavior and life history apart from that of other salmonines. The most obvious characteristic is that most lake charr populations complete their life cycle completely within freshwater lakes, although a few observations have been made of movement into rivers for foraging or spawning (Loftus 1958; Muhlfeld et al. 2012; Jones et al. 2018), and some populations at the northern extent of the range make partial annual anadromous migrations to brackish coastal waters to feed (Swanson et al. 2010; Harris et al. 2014). Relative to the salmons, lake charr disperse only a short distance during their life. Dispersal distances are largely constrained because most lake charr populations reside in small lakes with limited area, or with physical barriers that limit movement between lakes, but even in the Laurentian Great Lakes, where lake charr are free to migrate hundreds of kilometers, movement distances tend to be small (i.e., rarely >100 km; Schmalz et al. 2002; Kapuscinski et al. 2005; Bronte et al. 2007; Riley et al. 2018) compared to anadromous migrations of salmon in the ocean (e.g., Dittman and Quinn 1996). Spawning behavior of the lake charr also differs from that of other salmonines by the absence of nest building and agonistic interactions (Esteve et al. 2008; Muir et al. 2012). In contrast, such behavior is critical to reproductive success in other salmonine species (Esteve 2005).

Restriction of the lake charr to cold water has been an impediment to investigating and acquiring a complete understanding of lake charr behavior. Most lake charr research has occurred at the southern extent of the species' range, even though the ecology of remote and relatively inaccessible northern lakes is likely more similar to lakes in which the lake charr originally evolved. In southern lakes, lake charr tend to find summer thermal refuge in deep offshore waters, where they are more difficult to study than shallow, nearshore species. Adult lake charr are most accessible in autumn during the spawning season after the thermocline breaks down and fish converge on nearshore spawning sites. However, this period is often marked by stormy weather and unfavorable working conditions, especially in large lakes, that create logistically challenging conditions for studies.

The most comprehensive review of lake charr movement and behavior to date was compiled by Martin and Olver (1980) and was primarily informed by netting surveys, mark-recapture studies, and above-surface or diver observations of behavior at very shallow spawning sites. In recent decades, however, technological advancements have helped improve the quality and quantity of behavior and movement data available for the lake charr. In some cases, these new data corroborate earlier observations, but in other cases, new data have been used to refine current conceptual models of lake charr movement ecology and behavior. In this chapter, we briefly describe technologies currently being used to study lake charr movement ecology and behavior and then review the current state of knowledge regarding these topics, with an emphasis on research conducted since the review by Martin and Olver (1980). By necessity, some of the material presented here overlaps with information from other chapters in this volume; notably habitat (Marsden et al. 2021), trophic ecology (Vinson et al. 2021), and reproductive biology, developmental ontogeny and early life history (Goetz et al. 2021) chapters. We tried to minimize repetition, and in several places, we refer readers to other chapters for more in-depth reviews of specific topics.

2 Methods for Studying Movement and Behavior

Methods used for studying lake charr movement ecology and behavior fall into three general categories based on the research questions being addressed. First, methods that address population or system-scale questions are typically low-resolution, low-cost techniques that can be applied to large numbers of fish (e.g., coded-wire tags, fin clips, chemical, or thermal markers) or to a random sample large enough to adequately represent a population metric (e.g., otolith chemistry, genetic markers, external tags [e.g., dart and jaw] used in mark-recapture studies). These methods offer the ability to test population-scale questions, but typically are limited to a few data points per fish (most often only release location and re-capture location). Second, methods that assess individual movement or behavior (e.g., telemetry) are typically high-resolution, high-cost techniques applied to relatively few fish. These methods provide high-resolution, repeated, or continuous observations of individual fish and are used to answer behavioral questions beyond what is feasible with other techniques. Third, surveillance techniques (e.g., video and sonar) are used to address questions that require direct observation, such as description of spawning behavior. Below we describe specific techniques associated with each of these approaches and provide examples of research questions that have been addressed using each technique, along with their strengths and weaknesses (Table 1).

2.1 Population- or System-Scale Movement and Behavior

Methods for addressing population-scale movement and dynamics questions in lake charr have included mass marking of hatchery fish, external tagging of field-caught fish, and otolith chemistry and stable isotope analysis. Mass marking methods such as fin clips (removal of one or more of the paired or adipose fins at the post-embryo stage), thermal or chemical marking of sagittal otoliths (creation of distinct structural or chemical signature within the otolith, such as with oxytetracycline), and coded-wire tags (subdermally implanted binary-coded or numbered cylindrical wire) are commonly applied to young hatchery-reared lake charr to evaluate large-scale stocking efforts. For example, in the Laurentian Great Lakes of the United States, millions of hatchery-reared lake charr have been marked using these techniques and stocked each year since the mid-1960s to support rehabilitation of collapsed or extirpated populations (Elrod 1987; Eshenroder 1987; Holey et al. 1995; Bronte et al. 2007; Kornis et al. 2019a). Mass-marking can be applied to thousands or millions of fish at low cost per fish, and is suitable for application to early life stages, but movement data obtained from recaptured fish are typically limited to release site and subsequent recapture location. Except for fin clips, mass marking techniques usually require the fish to be lethally sampled to obtain data. One advantage of mass marking long-lived fish such as the lake charr is that, because large numbers of fish are marked, they can be recovered over long periods of time (decades) allowing ontogenetic comparisons of distribution, behavior, and susceptibility to fisheries.

Mass-marking techniques are usually applied as a batch mark and have been used extensively to advance understanding of coarse-scale movement and behavior of lake charr. For example, fin clips have been used to quantify swimming depth and dispersal distances of lake charr after stocking (Pycha et al. 1965), and to document movement related to foraging or spawning aggregations (Hansen et al. 2008). Coded-wire tags can be manufactured with many different codes and used to mark groups of fish (e.g., by stocking source, site, and year). The largest lake charr coded-wire tagging operation in the world has been conducted in the Laurentian Great Lakes, with 4–6 million hatchery-reared fish tagged each year (Bronte et al. 2012;

Table 1 Summary of common methods used to study movement ecology and behavior in lake charr and other fishes, including potential applications and limitations for each technology

Method	Examples	Scale of data	Life stage	Potential applications	Limitations
Mass marking	Coded-wire tags	Population, individual	Juvenile, adult	Population dynamics, age-specific analyses, dispersal, homing, low-resolution horizontal movement	Fish must be recaptured and lethally sampled, movement data limited to release and recapture location, limited ability to assess individual behavior
	Fin clips	Population	Juvenile, adult	Population dynamics, dispersal, homing, low-resolution horizontal movement	Fish must be recaptured, movement data limited to release and recapture location, limited ability to assess individual behavior
	Chemical or thermal otolith marking	Population	Embryo, juvenile, adult	Population dynamics, dispersal, homing, low-resolution horizontal movement	Fish must be recaptured and lethally sampled, movement data limited to release and recapture location, limited ability to assess individual behavior
External tagging	Dart tags	Population, individual	Juvenile, adult	Population dynamics, dispersal, homing, low-resolution horizontal movement	Fish must be recaptured, movement data limited to release and recapture location, limited ability to assess individual behavior, not suitable for early life stages
	Jaw tags	Population, individual	Juvenile, adult	Population dynamics, dispersal, homing, low-resolution horizontal movement	Fish must be recaptured, movement data limited to release and recapture location, limited ability to assess individual behavior, not suitable for early life stages
	Visible implant tags	Population	Juvenile, adult	Population dynamics, dispersal, homing, low-resolution horizontal movement	Fish must be recaptured, movement data limited to release and recapture location, limited ability to assess individual behavior, not suitable for early life stages
Otolith chemistry	Strontium (Sr) concentration	Population, individual	Embryo, juvenile, adult	Low-resolution movement between ecosystems with different chemical signatures, natal origin of individuals, repeatability of behavior	Natural mark (all fish have mark), fish must be lethally sampled, movement can only be inferred if environments have different chemical signatures
Stable isotope ratios	Carbon (δ13C), nitrogen (δ15N), sulfur (δ34S)	Population, individual	Embryo, juvenile, adult	Diet, littoral-pelagic low-resolution movement, and habitat use	Natural mark (all fish have mark), provides a snapshot of recent behavior (months) because signals are lost during tissue turnover

Electronic tagging	Acoustic telemetry	Population, individual	Juvenile, adult	Low- or high-resolution vertical and horizontal movement, homing and navigation, habitat use, spawning behavior, repeatability of behavior	Equipment expensive, low to moderate number of individuals tagged, low efficacy in high noise environments, data only recorded when within detection range of a receiver, suitable for large fish only
	Radio telemetry	Population, individual	Juvenile, adult	Low- or high-resolution vertical and horizontal movement, homing and navigation, habitat use, spawning behavior, repeatability of behavior	Equipment expensive, low to moderate number of individuals tagged, data only recorded when within detection range of a receiver, use limited to shallow lakes (<6 m) or rivers, not suitable for high conductivity environments, suitable for large fish only
	Archival tags	Population, individual	Juvenile, adult	Low-resolution horizontal movement, low- or high-resolution vertical movement, habitat use, repeatability of behavior	Equipment expensive, low to moderate number of individuals tagged, tags must be recovered to obtain data, suitable for large fish only
	Pop-up satellite archival tags	Population, individual	Adult	Low-resolution horizontal movement, low- or high-resolution vertical movement, habitat use, repeatability of behavior	Equipment expensive, low to moderate number of individuals tagged, coarse position accuracy, tag must be recovered to obtain complete data record, tag must be attached to outside of fish, currently suitable for large fish only
Surveillance	Underwater video	Population, individual	Embryo, juvenile, adult	Foraging behavior, spawning behavior, species interactions, habitat use	Limited field of view, limited efficacy in dark or turbid conditions, time-intensive analysis
	Direct observation	Population, individual	Embryo, juvenile, adult	Foraging behavior, spawning behavior, species interactions, habitat use	Limited field of view, limited efficacy in dark or turbid conditions, labor intensive
	Sonar related	Population, individual	Juvenile, adult	Foraging behavior, spawning behavior, species interactions, vertical movement, habitat use	Equipment expensive, time-intensive processing, often requires supplemental sampling to verify accurate species or habitat identification

Webster et al. 2019). Coded-wire tags have been used to investigate basin-wide movement patterns (Adlerstein et al. 2007), relative survival rates (Elrod et al. 1988; Bronte et al. 2006, 2007; Kornis et al. 2019a), spawning and stocking site fidelity, and homing (Elrod et al. 1996; Bronte et al. 2002, 2007). Thermal and chemical markings have shown promise as a batch marking technique in fishes (Weber and Ridgway 1962; Bergstedt et al. 1990; Volk et al. 1994, 1999), but not yet been widely used in lake charr studies (Bergstedt et al. 1990; Negus 1999).

External tagging techniques (e.g., anchor tags, Floy tags, and spaghetti tags) are typically applied to field-captured fish, and their use is largely restricted to late-juvenile and adult individuals. Like mass marking, external tagging requires that tagged (i.e., marked) fish be recaptured, and movement data are usually limited to release and recapture locations. External tags are commonly used for estimating lake charr abundance and population parameters such as survival and growth but have also been used to study large-scale movement patterns and homing rates (Eschmeyer et al. 1953; Rahrer 1968; Swanson 1973; Bronte et al. 2002). Unlike most mass-marking techniques, external tags do not require that fish be lethally sampled to obtain data, thereby allowing multiple observations from a single fish.

Otolith chemistry and stable isotope ratios have been used to determine movement and natal origin of lake charr. Otolith chemistry was used to validate anadromy (Swanson et al. 2010) and brackish-water resident populations (Kissinger et al. 2016) of lake charr in the Arctic, and to determine source and date of introduction of non-native lake charr into Yellowstone Lake, Wyoming (Munro et al. 2005). Stable isotope ratios, such as $\delta^{18}O$, from otoliths, were used to confirm that presumed wild lake charr from southern Lake Michigan were not unmarked hatchery fish or migrants from Lake Huron (Landsman et al. 2017). Additionally, stable isotope ratios of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) have been used to describe lake charr diets and infer movement, habitat use, and niche overlap (Dolson et al. 2009; Syslo et al. 2016; Colborne et al. 2016; Guzzo et al. 2017; Mumby et al. 2018; Kornis et al. 2020).

2.2 *Individual, High-Resolution Movement and Behavior*

Biotelemetry is increasingly being used to obtain high-resolution continuous data on individual fish movement, behavior, habitat use, and survival (Cooke et al. 2013). Electronic tags affixed to fish either transmit coded information to listening stations (e.g., acoustic and radio telemetry), store sensor data such as temperature, pressure (a surrogate for depth), and acceleration on internal memory (e.g., archival tags), or do both (e.g., pop-up satellite archival tags). The relatively high equipment cost of electronic tags and associated equipment can limit the number of fish tagged. However, this limitation may be offset by a much higher sampling rate and greater quantity of data obtained than from traditional mark-recapture studies, and an unparalleled ability to collect high-resolution spatiotemporal data on movement and behavior of individual fish, and environmental data. Each telemetry system has its own set of strengths and weaknesses (Cooke et al. 2013), so selection of an appropriate telemetry system is based on environmental context and research question (Table 1).

Radio telemetry tags transmit information using radio waves detectable by receivers above the water surface over long distances (i.e., several km). These properties, together with frequent transmission rates, make radio tags well suited for real-time tracking. However, radio transmission detection probability decreases rapidly with water depth and conductivity, which limits its use to lotic environments and shallow freshwater lakes. Nonetheless, radio telemetry has been used with lake charr to monitor thermal habitat use (Mackenzie-Grieve and Post 2006), locate nearshore and lotic spawning sites (Scanlon 2010), and monitor movement among connected lakes (Muhlfeld et al. 2012).

Acoustic telemetry tags (transmitters) operate on the ultrasound spectrum, which requires use of underwater hydrophones for tags to be detected. Acoustic telemetry is generally more appropriate than radio telemetry across most lake charr habitats. Thus, acoustic telemetry has been used to address a wide range of lake charr movement ecology and behavior-related questions. For example, mobile tracking of acoustic transmitters was used to study diel and seasonal changes in spatial habitat use of lake charr in small lakes in Montana (USA; Dux et al. 2011; Fredenberg et al. 2017). Whole-lake arrays of stationary receivers with overlapping detection ranges and transmitters with depth sensors have been used to obtain three-dimensional positions of tagged lake charr every couple of minutes for several months (Leander 2015; Guzzo et al. 2016). In the Canadian Arctic, acoustic telemetry was used to quantify rare estuarine-coastal migration of lake charr in brackish water outside the Halokvik River (Harris et al. 2014). In the Laurentian Great Lakes, acoustic telemetry was used to evaluate the use of artificial spawning habitats (Marsden et al. 2016), study fine-scale spawning habitat use within a refuge (Binder et al. 2018), and compare lake-wide movement patterns of different populations (Binder et al. 2017).

Although tracking data can reveal detailed information on movement patterns and habitat use, these data are seldom detailed enough to capture more subtle behavior, such as the act of spawning and foraging. However, miniaturized acoustic telemetry transmitters inserted into female fish through the genital tract and then expelled with eggs at the time of spawning may be useful for accurately and precisely estimating the time and location of spawning of lake charr (Binder et al. 2014). In addition, sensors incorporated into telemetry tags may help further understand such behavior, especially when combined with position data. For example, acoustic tags with accelerometers were used to quantify activity and energy expenditure of lake charr tracked over an entire lake (Callaghan et al. 2016). Energy expenditure and swimming activity, as well as spawning behavior, has also been remotely monitored in lake charr using electromyogram (EMG) telemetry (Kaseloo et al. 1996; Weatherley et al. 1996; Thorstad et al. 2000), and temperature-sensitive acoustic transmitters have been used to study behavioral thermoregulation through occupation of groundwater thermal refuges in some Canadian Shield lakes (Snucins and Gunn 1995). In an innovative study, detailed foraging behavior of lake charr attacking schools of ciscoes *Coregonus artedi* was recorded by combining acoustic telemetry with an advanced multibeam echo sounder system (Dunlop et al. 2010). Approaches that integrate different tracking technologies with biologging sensors represent a promising direction for future lake charr studies beyond simple movement behavior.

Archival tags record data (e.g., pressure and temperature) from environmental sensors within the tag onto internal memory. Tags are either implanted within the peritoneum of the fish or attached externally, and usually require that the tag and thus the fish be recovered to retrieve stored data (but see PSAT tags). Internal archival tags were used to show that rapid warming associated with the 1998 El Nino event led to extreme body temperatures (exceeding 20 °C) and mortality of lake charr in a shallow (max. 13 m) isothermal lake, in contrast to high survival and maintenance of body temperature <10 °C through most of the season in a typical dimictic lake (Gunn 2002). Archival tags in lake charr have also been used to monitor bathythermal habitat use of different strains of stocked lake charr in Lake Huron (Bergstedt et al. 2003, 2012; Mattes 2004). In laboratory studies, archival tags were used to show that lake charr can make short excursions into suboptimal warm temperatures without incurring major changes to internal body temperature (Negus and Bergstedt 2012).

Pop-up satellite archival tags (PSAT) tags overcome the data recovery challenge associated with conventional archival tags by incorporating an antenna for data recovery via satellite. PSATs are tethered externally to fish and continually log data on parameters such as depth, temperature, light, and geolocation (location estimates contain large error bounds unsuitable for small lakes) for a specified duration (weeks to months), after which the tag detaches from the fish, floats to the surface, and transmits archived data and the tag's location to an orbiting satellite of the Argos System (http://www.argos-system.org/) so that the tag can be recovered. Pop-up archival tags without transmitting functionality are a less expensive alternative to PSAT tags, but recovery of data depends on the tags landing on shore and being discovered and returned by members of the public (Raby et al. 2017). PSATs have not yet been widely adopted by lake charr researchers, but they are currently being used to track swimming depth and movement of lake charr in Lake Superior (R. Goetz, unpublished data).

2.3 Direct Surveillance

Direct surveillance techniques are non-invasive and provide highly detailed information on individual and group behavior. They are often expensive or time consuming, so their use is generally confined to studying aspects of behavior that are not possible to study using other methods described above. The most used surveillance techniques include direct observation from the surface, scuba diving or underwater video, and sonar-related methods (e.g., hydroacoustics, side-scan sonar). Direct observation and underwater video have been used to describe lake charr spawning behavior (Royce 1951; Martin 1957; Deroche 1969; Esteve et al. 2008; Muir et al. 2012; Binder et al. 2015), determine reaction distances to prey (Vogel and

Beauchamp 1999), and describe lake charr spawning habitat (Nester and Poe 1984, 1987; Horns et al. 1989; Edsall et al. 1992; Davis et al. 1997; Janssen et al. 2006). Sonar technologies (e.g., hydroacoustics and side-scan sonar) detect underwater objects by emitting sound pulses and measuring their return after reflection. Echo sounders (i.e., hydroacoustics) quantify numbers and sizes of fish targets to locate spawning aggregations of lake charr (Janssen et al. 2006; Warner et al. 2009), estimate abundance (Ruzycki et al. 2003), study vertical migrations of lake charr and their prey (Jensen et al. 2006; Hrabik et al. 2006; Ahrenstorff et al. 2011), connect vertical distribution of lake charr with environmental drivers (Sellers et al. 1998), and describe in situ swimming behavior and prey reaction distances when used in conjunction with acoustic telemetry (Dunlop et al. 2010). In contrast, side-scan sonar creates an image of the lake bottom to map lake charr spawning habitat (Edsall et al. 1989). Advances in sonar technology, including side-scan sonar and dual-frequency identification sonar (DIDSON), have improved resolution of images to identify fish aggregations and potentially fish species (e.g., Able et al. 2014). Sonar technologies are widely used in fishery science, but often require video or some other sampling method to confirm findings (Beauchamp et al. 1992; Janssen et al. 2006).

3 Movement Ecology and Behavior

3.1 Age-0

Lake charr produce large, lipid-filled eggs. Fertilized eggs hatch prior to completion of embryonic development, which continues outside the egg for several weeks after hatching, dependent on water temperature. Newly hatched free embryos have little swimming ability, being constrained by their yolk sac, which constitutes the bulk of their total weight (Balon 1980). In laboratory culture, free embryos at lake temperatures (~4 °C) remain largely motionless on their sides for several days unless supported by habitat structure. In hatchery culture, food pellets are not introduced until yolk-sac adsorption is complete because salmonine free embryos ignore motionless food (Brown and Buck 1939; Dill 1967). This general belief that feeding does not commence until completion of yolk adsorption has strongly influenced past assumptions about lake charr behavioral development. Recently, however, feeding by free embryos has been observed. Within a week of hatching, free embryos begin to visually track moving plankton, and soon thereafter begin to actively forage. In laboratory experiments, free embryos began feeding by 650 degree-days (E. Marsden, unpublished data). Gut contents were documented in wild-caught free embryos as small as 19 mm with most of their yolk sac still intact (Ladago et al. 2016). Lake charr free embryos in Lake Superior had food in their stomachs at a length of 25 mm, with up to 50% of 25–27 mm free embryos having gut contents (Swedberg and Peck 1984). Stomachs of 25–35 mm free embryos caught in June from Gull Island Shoal, Lake Superior, contained *Mysis*, calanoid copepods, and Chironomidae pupae (Hudson et al. 1995).

Once foraging commences, the period of mixed feeding from endogenous (i.e., yolk sac) and exogenous foods allows free embryos to prolong yolk use by saving yolk as a buffer for periods of low food availability (Vinson et al. 2021). For example, yolk sac adsorption in Arctic charr *Salvelinus alpinus* is prolonged if food is available and ingested early in development (Alanärä 1993). Free embryos may forage within interstitial spaces where they are relatively protected from predation, or above the substrate. In the wild, free embryos as small as 18 mm begin to move out of spawning substrate (Ladago et al. 2016) or 1 week after hatching in the laboratory (Stauffer 1981). Free embryos migrate vertically out of spawning substrate at night, while they are still photophobic, and in the laboratory, were caught in traps suspended up to 57 cm above the substrate (Baird and Krueger 2000). These nocturnal movements may be related to feeding when free embryos can avoid visual predators to access zooplankton that also migrate vertically to feed. In fry traps checked weekly, 20% of early-stage free embryos (19–26 mm) and 98% of late-stage free embryos (25–30 mm) contained food (Ladago et al. 2016). Most free embryos were likely caught well prior to trap retrieval, so free embryos must have been feeding within the trap, which supports a hypothesis that feeding occurs within substrate interstices.

Field studies of early free embryo behavior are difficult and challenged by the need to work underwater and by depth of interstices where free embryos are concealed for weeks after hatching. Thus, most information about free embryo behavior has been gained from laboratory observations of free embryos from lean lake charr. Free embryos are photophobic and remain in interstices except for nocturnal forays into the water column. However, the timing of loss of photophobia, completion of yolk sac adsorption under controlled conditions (no feeding), and filling of the gas bladder all appear to be variable. Free embryos were photophobic for 1–2 days after filling the gas bladder between stage $F^2$10 and early $A^1$11 (Baird and Krueger 2000; stages described by Balon 1980), whereas Balon (1980) considered photophobia to end at the termination of the $F^2$10 stage, prior to yolk sac absorbance and filling of the gas bladder.

During their residence in spawning substrate, free embryos are vulnerable to predation by infaunal species that can penetrate interstitial spaces, such as sculpins Cottidae spp. and crayfishes Cambaridae spp. (Stauffer and Wagner 1979; Horns and Magnuson 1981; Savino and Henry 1991; Savino and Miller 1991; Hudson et al. 1995; Fitzsimons et al. 2006). During diel movement out of substrate, free embryos are also vulnerable to epifaunal fishes such as yellow perch *Perca flavescens*, burbot *Lota lota*, rock bass *Ambloplites rupestris*, and basses *Micropterus* spp. (Riley and Marsden 2009). In the Laurentian Great Lakes, invasive predators also include round gobies *Neogobius melanostomus*, alewife *Alosa psuedoharengus*, and white perch *Morone americana* (Krueger et al. 1995, 2014; Riley and Marsden 2009). Free embryos and post-embryos can seek shelter by moving rapidly into interstices in the presence of predators (Savino et al. 1993; Strakosh and Krueger 2005). Thus, presence of predators may impede movement and feeding by free embryos and indirectly cause early mortality by starvation. In the absence of predators, lake charr free embryos may forage for longer periods and at greater distances above the substrate than in the presence of predators, and would therefore have higher growth potential and a prolonged interval before exhaustion of endogenous food resources. For example, invasive lake charr in Yellowstone Lake, a species depauperate lake (two native fish species and three invasive fish species), remained on a spawning reef until much later after yolk sac absorption and were significantly larger at the end of yolk sac adsorption than in the Great Lakes (Simard et al. 2019).

After the yolk sac is mostly absorbed and some remnant yolk remains within the body, post-embryos in tanks spend extended periods swimming freely above the substrate and moving along the bottom, during both day and night (Stauffer 1978; E. Marsden and C. Krueger personal observation). These movements and diel vertical migration may strengthen swimming ability, and eventually contribute to dispersal from spawning reefs by active swimming and passive movement by currents (Baird and Krueger 2000). Free embryos in tanks left simulated spawning substrate over an extended period 1–12 weeks after hatching (Stauffer 1978). Early-stage free embryos did not prefer deep areas of tanks, whereas feeding free embryos (29–48 mm) tended to move to deep water when introduced to experimental raceways with no bottom substrate. Such movement may have been similar to the diel vertical movement seen by Baird and Krueger (2000), wherein free embryos would have returned to the substrate if it had been available in experimental tanks.

The lake charr is physostomous and assumed to fill its gas bladder from the atmosphere around the time of yolk sac absorption (e.g., Tait 1960; Balon 1980). This assumption appears to be drawn from the behavior of adfluvial salmonines that hatch in water less than a few meters deep, where atmospheric air is readily accessible. However, for lake charr that spawn on deep reefs, such as the Lake Michigan Mid-Lake Reef Complex (Janssen et al. 2007), access to atmospheric air would entail a vertical migration of at least 40 m to the surface and would expose fish to a substantial risk of predation. Lake charr may have alternate methods for filling the gas bladder, and the method used could vary among morphotypes. For example, lake charr could either delay filling the gas bladder until buoyancy compensation becomes important as a consequence of increasing size (Tait 1960), or they may fill the gas bladder without access to surface air by increasing partial pressure of gases in the blood, as demonstrated in coregonines (Saunders 1953; Tait 1956) and the Arctic charr *Salvelinus alpinus* (Sundnes and Bratland 1972). Alternatively, lake charr may initially fill their gas bladder by swallowing air bubbles (such as those resulting from decomposition in the benthos or produced by algae via photosynthesis), or by “pirating” gas in their diet, such as from *Chaoboros* larvae (Teraguchi 1975).

Post-embryos leave the spawning reef soon after the yolk sac is absorbed (Royce 1951; Martin 1957; Eschmeyer 1964; Deroche 1969), 4–8 weeks after hatching (Bronte et al. 1995), and move into deep water where they forage on larger prey items than free embryos use (Eschmeyer 1956; Peck 1981; Bronte et al. 1995; Vinson et al. 2021). Departure from the spawning reef is likely motivated by increasing epilimnetic temperature (Marsden et al. 2021). Habitat choice of age-0 lake charr may be a compromise among factors that accelerate growth and those that minimize vulnerability to predation. As post-embryos disperse, their response to predators, and predators to which they are exposed, change. In tank experiments, post-embryos exposed to alewife *Alosa pseudoharengus* fled either toward the substrate or to the surface (Strakosh and Krueger 2005). The former behavior is advantageous only until post-embryos have left rocky shoals. On sandy habitat, post-embryos are exposed on the bottom, and may benefit from their countershading and dispersion in three dimensions by moving upwards. The largest post-embryos caught in fry traps on spawning substrate are 30 mm, have no vestige of internal yolk, and have parr marks (Ladago et al. 2016). The distribution of post-embryos in trawls changes in late summer as the fish disperse from shallow, rocky reefs to deeper sandy "nursery habitat" (Peck 1981; Bronte et al. 1995). At Gull Island Shoal, an offshore site in Lake Superior, age-0 lake charr captured in beam trawls and bottom trawls from June to September appeared to move off the reef to a down-current nursery area (Bronte et al. 1995). At the nursery area, they were most abundant at 15–19 m depth in June and July, but transitioned to deeper water in late August and September, with the highest abundance at 35–39 m, and even deeper in October (>40 m). Near Presque Isle, Lake Superior, 36–45 mm age-0 lake charr remained in the area at the same depth (2–8 m) as a near-shore spawning site until late June to mid-July (Peck 1981).

Age-0 lake charr actively seek and prey on *Mysis diluviana*, chironomid larvae and pupae, calanoids, cladocerans, copepods, and small fishes (Eschmeyer 1956; Swedberg and Peck 1984; Hudson et al. 1995; Holbrook et al. 2013; E. Marsden, unpublished data; Vinson et al. 2021). In the Great Lakes and inland lakes where *Mysis* are present, *Mysis* are the predominant prey throughout the first year, with the highest occurrence and highest biomass among all prey items found in lake charr stomachs (Eschmeyer 1956; Hudson et al. 1995; Roseman et al. 2009; Holbrook et al. 2013; E. Marsden, unpublished data). An interesting exception was in Presque Isle Harbor, Lake Superior, where very few *Mysis* were found in 25–51 mm free embryos and post-embryos, likely because these fish were collected from shallow water, 2–12 m deep where *Mysis* were absent (stomachs in those charr most frequently contained copepods and chironomid larvae and pupae; Swedberg and Peck 1984). By September, age-0 lake charr in the Laurentian Great Lakes are 50–91 mm (Hudson et al. 1995; Marsden et al. 2018) and begin to add small fishes such as sculpins *Cottus* spp. and age-0 non-native rainbow smelt *Osmerus mordax* to their diet. At this stage, foraging likely switches to daylight periods, when lake charr use visual cues for feeding (Vogel and Beauchamp 1999; Cruz-Font et al. 2019).

Access to *Mysis*, an abundant and lipid-rich resource, may be important for overwinter survival and recruitment of age-0 lake charr. In summer, juvenile *Mysis* prefer depths where temperature is 11 °C, whereas adults prefer 6–8 °C (Rudstam et al. 1999), although both stages undergo extensive diel vertical migrations. Small lake charr may have the best opportunity to forage on *Mysis* during the day when *Mysis* are concentrated on the bottom and not up in the water column. Most (up to 91%) age-0 lake charr collected in daytime bottom trawls in Lake Champlain had full stomachs containing mostly *Mysis* (E. Marsden, unpublished data), but few data are available from nighttime trawling. The slimy sculpin *Cottus cognatus*, which also consumes *Mysis,* chironomids, and plankton, is the primary potential food competitor of age-0 lake charr. Diet overlap with lake charr occurs primarily while the two species occupy rocky benthic habitats, whereas the potential for competition decreases after lake charr move to deeper, sandy habitat (Hudson et al. 1995). Lake charr at 30–50 mm total length remain 75–100 mm off the bottom, which could reduce their potential competition with and vulnerability to benthic sculpins (Stauffer 1978). However, Chironomidae larvae and pupae are benthic, and *Mysis* are largely in and on the benthos during daylight hours when lake charr are foraging, so lake charr are likely to also be foraging on the bottom.

3.2 Juvenile

Behavior and distribution of juvenile lake charr (age-1 to ~age-6) have largely been deduced from catches in bottom trawls and diet analyses that indicated where and on what they had been foraging. Age-1 to age-3 juveniles were caught in along-contour bottom trawls in Lake Superior at 35–55 m in spring, summer, and fall, with a maximum abundance at 45 m (Selgeby and Hoff 1996). Similarly, most (92%) age-1 to age-4 lake charr caught in summer bottom trawling in Lake Ontario at temperatures below 12 °C were concentrated near the intersection of the bottom and the lower boundary of the thermocline in lakes Ontario and Champlain, Vermont USA (Elrod and Schneider 1987; Elrod and O'Gorman 1991; Marsden et al. 2018; Wilkins and Marsden 2020). This distribution may facilitate foraging by juveniles at preferred temperatures, while also providing opportunities to briefly forage in warmer water. For example, juveniles up to 300 mm in small Canadian Shield lakes obtained half of their diet from littoral sources (France and Steedman 1996). Juvenile lake charr increasingly feed on small fishes, such as rainbow smelt, sculpins, alewife, and bloater *Coregonus hoyi*, but in the absence of abundant fishes, will continue to consume *Mysis* and *Diporeia* (Elrod and O'Gorman 1991; Madenjian et al. 1998; E. Marsden, unpublished data). Littoral foraging appears to be associated with diel benthic migration (Ray et al. 2007), with higher densities captured in bottom trawls in shallow water (<30 m) at night than during the day (Gorman et al. 2012). Juveniles do not appear to engage in diel vertical migration like adult lake charr (Gorman et al. 2012).

Short-term movement into the littoral zone in summer may cause thermal stress in juvenile lake charr, unlike adults that have sufficient thermal mass to resist rapid body temperature increase (Snucins and Gunn 1995). In laboratory experiments, summer fingerlings preferred 10.8 °C (Peterson et al. 1979), and yearlings preferred 11.7 °C (McCauley and Tait 1970). Juveniles in Lake Ontario were found in temperatures of 4–14 °C, but were concentrated below 10 °C. However, in small lakes (<500 km^2), the thermal niche of lake charr appears much broader (4–21 °C) than in large lakes and may be an adaptation for accessing epilimnetic resources that are closer to deep water than typically occurs in large lakes (Sellers et al. 1998).

Seasonal movement of juvenile lake charr varies among lakes and is likely modulated by vertical temperature changes and location of prey, although the distribution of lake charr predators probably also plays a role (e.g., Chavarie et al. 2019). In Lake Superior, age-1 to age-3 lake charr were mostly caught at 45 m during all seasons, whereas age-4 to age-5 lake charr appeared to move from 35 m in spring to deep water in summer (maximum abundance at 75 m) and back to shallow water (15 m) in autumn (Selgeby and Hoff 1996). In contrast, age-2 lake charr in Lake Ontario moved shoreward from deeper water (35–55 m) in spring to 25–35 m depths in summer, with younger fish (age-2) tending to remain in deeper water than older (age-3–4) fish (Elrod and Schneider 1987). Depth distribution of juvenile lake charr in Lake Ontario largely coincided with the greatest abundance of their primary prey, rainbow smelt and age-1 alewife, but sometimes the lake charr were deeper than their prey (Elrod and O'Gorman 1991). Depth distribution appeared temperature-mediated and varied seasonally among different strains of stocked lake charr at age-1 to age-3 in Lake Ontario, where stocked fish propagated from a lean Lake Superior source occupied deeper waters than a strain from Clearwater, Manitoba, Canada regardless of season (Elrod and Schneider 1987). In subarctic Great Bear Lake (Northwest Territories), where only a weak summer thermocline may occur, juvenile lake charr occupied all depths except surface water and depth occupancy did not shift ontogenetically among juvenile lake charr (Chavarie et al. 2019).

Stocked age-1 lake charr in Lake Superior remained near stocking locations for at least 2 months after release, but dispersed up to 3.2–6.4 km away as time-at-large and age increased to age-3, with little relationship between age or size at time of capture and dispersal distance (Pycha et al. 1965). The direction of movement was associated with lake currents (Pycha et al. 1965), as it was for age-1 lake charr stocked into Lake Ontario (Elrod 1987). Recoveries of coded-wire tagged age-4 to age-6 lake charr from the 2010–2013 year classes in Lake Michigan suggested similar movement patterns and distances as those reported by Pycha et al. (1965; U.S. Fish and Wildlife Service, unpublished data). Eighty percent of recoveries of tagged juvenile and adult lake charr caught in assessment sampling in spring were 100 km or less from their stocking sites (U.S. Fish and Wildlife Service, unpublished data). These dispersal distances were consistent with those observed from other lake charr mark-and-recapture studies in large lakes (Schmalz et al. 2002; Kapuscinski et al. 2005; Bronte et al. 2007).

3.3 Adult

Martin and Olver (1980) provided a detailed review of horizontal and vertical movement of adult lake charr from studies prior to 1980, which mostly focused on lean lake charr at the southern extent of their range. These early studies primarily used mark-recapture tagging or, in the case of assessing vertical movement, the frequency of capture at depth, to infer movement patterns within populations. The maximum distance charr moved depended on lake size (i.e., Laurentian Great Lakes versus inland lakes), but in large lakes, such as Lakes Superior and Michigan, the longer the stocked fish were at liberty after release, the further they dispersed.

Since Martin and Olver's review, technological advancements have provided opportunities to study lake charr movement at temporal and spatial scales that were previously not possible. Research has continued to focus heavily on the lean morphotype in lakes near the southern extent of the species' range. However, a number of more recent studies have focused on other morphotypes, populations in northern lakes, and invasive populations.

3.3.1 Horizontal Movement

Studies in the Laurentian Great Lakes provide the best available information on maximum horizontal movement distances in adult lake charr (typically >age-6). Individual long-distance movement greater than 200 km from release locations have been noted in many Great Lakes populations (Eschmeyer et al. 1953; Schmalz et al. 2002; Kapuscinski et al. 2005; Riley et al. 2018), but most lake charr appear to remain within about 100 km of their spawning or stocking location. For example, in Lake Michigan, analysis of 8905 lake charr recaptures showed a 90% dispersal radius of 68 km for spring-tagged fish and 61 km for fall-tagged fish (Schmalz et al. 2002). Other tagging studies found that dispersal distances varied among stocking locations. For example, 90% of lake charr dispersal radii ranged 24–146 km across eight stocking locations in Lake Michigan (109 km on average; Bronte et al. 2007). Similarly, 90% of lake charr dispersed 54–197 km among six stocking areas in Lake Superior (83 km on average; Kapuscinski et al. 2005). In the latter study, distance moved was positively related to time at liberty for fish tagged in one of six management units, but the relationship may have been due to bias in spatial distribution of recovery effort. Dispersal distance averaged 42 km for fish captured during non-spawning season and only 17 km for fish captured during the spawning season (Kapuscinski et al. 2005). This result is consistent with the notion that lake charr return to previously used spawning sites during autumn (see Sect. 3.3.3.2), but in some populations, many fish appear to remain relatively close to their site of spawning year-round (Schmalz et al. 2002).

Movement distance estimated from recapture data is inherently biased because the capture location is not likely the maximum straight-line distance travelled from the release point for all fish. Therefore, actual movement distances may be greater than reported in the above studies. However, an acoustic telemetry study of two distinct lake charr populations in Lake Huron also found that most lake charr appeared to remain within a radius of about 100 km of their spawning location throughout the year (Binder et al. 2017). Nonetheless, lake charr movement often occurs across jurisdictional management boundaries, which has important implications for implementing regulations, applying stock assessment models used for harvest control (Adlerstein et al. 2007; Binder et al. 2017), and assessing the utility of refuges to protect recovering populations (Akins et al. 2015; Johnson et al. 2015; Binder et al. 2017).

In the Laurentian Great Lakes, lake charr movement tends to follow the shoreline, and evidence to support cross-basin transits across open water appear rare. For example, offshore movements by mature stocked fish were minimal in Lake Superior (Pycha et al. 1965; Krueger et al. 1986) and in Lake Michigan (Bronte et al. 2007), prompting stocking of age-0 lake charr on offshore reefs to encourage colonization of these areas (Holey et al. 1995; Bronte et al. 2007). Only nine lake charr marked with external tags in the Clay Banks reef area of Lake Michigan (located along the western shoreline) were recaptured on the opposite eastern shoreline, a distance of 80 km from the release location, compared to 182 recaptures (>20 times as many) along the western shoreline of Lake Michigan at distances greater than 80 km from the release location (Schmalz et al. 2002). In Lake Huron, lake charr also appeared to disperse from spawning grounds following the shoreline, with lake charr from Drummond Island primarily moving eastward and fish from Thunder Bay primarily moving southward (Binder et al. 2017). Lake charr stocked at offshore locations appear to be an exception, however, as these fish will traverse open waters to reach nearshore habitats. For example, coded-wire tagged lake charr stocked on the Mid-Lake Reef Complex and Julian's Reef, two offshore locations in Lake Michigan, often dispersed both to the east and west shorelines where they contributed significantly to sport fisheries (Kornis et al. 2019b). Movement across open water has also been occasionally detected by other studies (e.g., Schmalz et al. 2002; Riley et al. 2018). Low detection rates on nearshore acoustic telemetry receivers during winter (Binder et al. 2017), combined with evidence that lake charr reside in deeper water in winter than in spring or fall (Bergstedt et al. 2012, 2016), suggests that lake charr may move offshore during winter. The infrequency of observed movements across open water in the Laurentian Great Lakes could be a byproduct of nearshore tagging and release locations, but also could serve to isolate lake charr stocks from each other (Schmalz et al. 2002), although the degree to which movement maintains gene flow among stocks is unknown.

Despite common use of terms such as "dispersal," "random," and "nomadic" to describe lake charr movement between spawning seasons (Martin and Olver 1980), mounting evidence suggests that inter-spawning season movement reflects directed migration to familiar foraging locations. Directional bias has been noted in between-spawning season dispersal of several lake charr populations (Swanson 1973; Schmalz et al. 2002; Binder et al. 2017), but the most convincing evidence of true directed migratory behavior comes from studies with repeat observations of individuals. For example, highly variable littoral and pelagic habitat use was evident among acoustically tagged lake charr in Lake Louisa (Algonquin Park, Ontario, Canada), but individual lake charr showed high interannual fidelity to particular foraging zones (Morbey et al. 2006). Similarly, post-spawning migrations were variable, but individually consistent in 78% of fish with acoustic telemetry transmitters in Lake Huron, with 21% of tagged fish consistently overwintering near or within forage-productive Saginaw Bay, ~100 km from the spawning location (Binder et al. 2017). Long-distance, cross-basin migrations (>200 km), while rare, have also been observed to be repeated annually (Riley et al. 2018). Additional evidence of directed foraging migrations comes from anadromous migrations of lake charr populations in the Arctic. Based on otolith chemistry and stable isotope analysis, 27% of lake charr from four lakes in the West Kitikmeot region of Nunavut (Canada) made annual anadromous migrations to brackish coastal habitats for feeding starting at a mean age of 13 years (Swanson et al. 2010). Although these anadromous migrations were relatively short ($<$3 km), anadromous migrations of at least 50 km have been observed in other populations (Harris et al. 2014).

Studies of horizontal movement of lake charr in small inland lakes have centered on habitat selection and littoral-pelagic food-web coupling (e.g., Morbey et al. 2006; Dolson et al. 2009; Blanchfield et al. 2009; Guzzo et al. 2017). In general, degree and timing of movement between pelagic and littoral habitats depends primarily on water temperature and prey availability, although lake morphology is also important (reviewed by Marsden et al. 2021). Because water temperature varies seasonally within the southern range, lake charr movements into and out of littoral zones also tend to occur seasonally when water temperatures are less than 15 °C, with foraging movement into the littoral zone occurring mostly during spring and movement onto nearshore spawning reefs occurring during autumn (Dux et al. 2011; Guzzo et al. 2017). In lakes where offshore prey fish are absent, lake charr sometimes make short-duration forays into the littoral zone during summer to feed (Morbey et al. 2006; Guzzo et al. 2017). Use of lotic habitats and movement between connected lakes, such as occurs by invasive lake charr in the Flathead River System in northwestern Montana (USA) and between Priest Lake and Upper Priest Lake in northern Idaho (USA), also occurs seasonally and is limited to periods when water temperatures are less than 15 °C (Venard and Scarnecchia 2005; Muhlfeld et al. 2012).

The extent to which factors such as temperature and prey availability influence lake charr movement in large lakes such as the Laurentian Great Lakes is less well understood, mostly due to the geographic scale of movement in those lakes and the complexity of vertical thermal regimes, which are largely influenced by wind-driven currents and upwelling in lakes. In contrast to many small inland lakes near the southern extent of the species' native range, lake charr have abundant nearshore access to cold water in the Laurentian Great Lakes, except Lake Erie, where cold-water refuge is limited to the eastern basin during summer months. We, therefore, hypothesize that horizontal movement of lake charr in large lakes is less influenced by temperature than by prey availability. For example, recent food-web changes in lakes Ontario, Huron, and Michigan have reduced the biomass and use of pelagic prey (i.e., alewife and rainbow smelt) and shifted diets toward more benthic-derived energy sources such as *Mysis*, slimy sculpin *Cottus cognatus*, and non-native round goby *Neogobius melanostomus* (Dietrich et al. 2006; Rush et al. 2012; Roseman et al. 2014; Colborne et al. 2016; Happel et al. 2018; Luo et al. 2019). Additionally, substantially faster growth of lake charr from nearshore waters of Lake Michigan compared to those from offshore Sheboygan Reef has been attributed to lower availability of small prey fishes offshore (Madenjian et al. 1998).

3.3.2 Vertical Movement

Most studies of vertical movement in adult lake charr have focused on seasonal changes in depth occupancy (Martin and Olver 1980), which have been consistently linked to water temperature and movement of prey (Sellers et al. 1998; Morbey et al. 2006; Dux et al. 2011; Ahrenstorff et al. 2011; Bergstedt et al. 2016; Gallagher et al. 2019; Marsden et al. 2021). Variation in light levels may also contribute to daily and seasonal vertical movement of lake charr (Blanchfield et al. 2009; Hansen and Beauchamp 2015). Few studies have directly monitored the vertical movement of individual fish, and in many cases changes in depth occupancy occur concurrently with horizontal movement between foraging habitats, similar to diel benthic migrations observed in juvenile lake charr (see Sect. 3.2). Nonetheless, individuals in some populations make diel vertical migrations upward in the water column, presumably to maximize foraging efficiency by maximizing consumption rates while minimizing the metabolic cost of digestion. For example, based on hydroacoustic survey data, lean lake charr migrated vertically daily in two of three small Canadian Shield lakes in Ontario (Sellers et al. 1998). Lake charr in all three lakes were present in the epilimnion during night, but in two of the lakes, fish moved into deeper and cooler water during day. In Lake Huron, lean lake charr showed the opposite pattern. Data from archival depth tags showed that, in 60% of lake charr of Finger Lakes origin and 30% of lake charr of Great Lakes origin, swimming depth increased abruptly during night (Bergstedt et al. 2016). The frequency of these vertical migrations varied among individuals, occurring more often for some fish, but only sporadically for others. A high degree of individual variation in diel vertical migration was also observed in Chitty Lake (Yellowknife, Northwest Territories, Canada), including during the summer period of 24-h light (Gallagher et al. 2019).

Vertical movement has also been observed in the siscowet lake charr morphotype, a deep-water morphotype that typically inhabits depths >80 m in Lake Superior (Moore and Bronte 2001; Bronte et al. 2003). Based on trawl data and hydroacoustic sampling, siscowets undergo diel vertical migrations that mirror those of coregonines, a primary prey (Hrabik et al. 2006; Stockwell et al. 2010; Ahrenstorff et al. 2011). Individual siscowet lake charr fitted with pop-up satellite archival tags that collected depth data every four minutes typically used depths of 150–200 m, but periodically moved vertically upwards over distances of 150 m or greater (R. Goetz, unpublished data). Similar to observations of lean lake charr in Lake Huron (Bergstedt et al. 2016), diel vertical movement of individual siscowets did not occur every day and, at times, were interspersed with periods during which the fish remained in either deep or shallow water. Thus, vertical movement by lake charr does not appear to fit the traditional definition of "diel vertical migration" and might be better described as "opportunistic vertical migration" or "partial vertical migration" (Harrison et al. 2017; Gallagher et al. 2019). Vertical movement is most likely involved with feeding, as has been previously suggested (Hrabik et al. 2006; Stockwell et al. 2010; Ahrenstorff et al. 2011), but likely occurs in response to a broader range of prey than just coregonines. Vertical movement by adult lake charr could also be related to behavioral regulation of metabolism.

3.3.3 Spawning-Related Behavior

3.3.3.1 Timing and Duration of Activity on Spawning Grounds

Lake charr typically broadcast spawn on rocky reefs and shoals in lakes, rather than build nests (redds) on gravel beds in streams like other salmonids (Fitzsimons 1994; Marsden et al. 1995, 2021). However, lake charr populations also spawn in tributaries to eastern Lake Superior, North America (Loftus 1958; Jones et al. 2018), and stream-spawning populations are suspected to occur in large lakes in northern Canada such as Great Slave Lake (C.C. Krueger, personal observation), and in streams along the Canadian Arctic Ocean coast (semi-anadromous populations; Swanson et al. 2010). Most of what is known about lake charr spawning movement and behavior comes from studies of southern populations of the lean piscivorous shallow-water morphotype. Movement onto spawning grounds in southern lakes usually occurs in September and October, and activity on reefs and shoals can persist for at least several weeks (Royce 1951; Eschmeyer 1955; Dux et al. 2011; Binder et al. 2016; Callaghan et al. 2016; Marsden et al. 2016; Gallagher et al. 2019). The exact seasonal timing of activity on spawning grounds differs among populations and depends largely on latitude, although lake size (Royce 1951; Deroche 1969) and lake charr morphotype may also be important (Goetz et al. 2017). Spawning activity at the southern extent of the geographic range typically occurs between late September and early December (Merriman 1935; Royce 1951; Martin 1957; McCrimmon 1958; Deroche 1969; Fitzsimons et al. 2005; Esteve et al. 2008; Binder et al. 2016; Marsden et al. 2016), while populations in the Northwest Territories of Canada are active on spawning grounds in late July, August, and September (Great Bear Lake, Great Slave Lake, Alexie Lake, Chitty Lake; Miller and Kennedy 1948; Muir et al. 2012; Callaghan et al. 2016; Gallagher et al. 2019). Little is known about variability in the timing of spawning activity of different lake charr morphotypes (Martin and Olver 1980), but anecdotal evidence based on observations from commercial fisheries in the Laurentian Great Lakes suggests that temporal arrival on spawning grounds varied considerably among various morphotypes of lake charr (Brown et al. 1981; Goodier 1981). Examination of gametes from sympatric populations in Lake Superior suggests that the timing of spawning activity for deep-water morphotypes differs from the lean morphotype (Goetz et al. 2021), with the siscowet (or fat trout) spawning during spring and autumn (Bronte 1993; Goetz et al. 2011, 2017) and humper spawning in June (Eschmeyer 1955) and August (Rahrer 1965; Burnham-Curtis and Bronte 1996).

Males arrive on spawning grounds first and remain longer than females (Royce 1951; Eschmeyer 1955; Deroche 1969; Bronte et al. 2007; Muir et al. 2012; Binder et al. 2015; Marsden et al. 2016; Pinheiro et al. 2017). While these trends have been inferred mainly on the basis of seasonal timing of first capture and seasonal changes in sex ratios of fish caught with gill nets on spawning grounds, recent tracking of electronically tagged lake charr with acoustic transmitters confirmed these behavioral differences between males and females. For example, in Alexie Lake, individual males were detected in spawning groups for 4–25 days, while females were detected in spawning groups <9 days, and males spent about 35% longer at spawning sites than females (Callaghan et al. 2016). In Lake Champlain, males generally remained closer to spawning sites than females, spent more days on spawning sites than females, and spent more time on spawning sites on a given day than females, although length of residency on spawning sites between 2014 and 2015 differed by about 16% (19–22 days) for females and by about 46% (24–35 days) for males (Pinheiro et al. 2017).

Within lakes, annual timing of movement onto spawning grounds can vary among years by as much as several weeks (Martin 1957; Binder et al. 2016; Marsden et al. 2016). Interannual variability in timing and duration of activity on spawning grounds appears to be influenced by climatic conditions. Temperature, wind, and light levels have all been proposed as controlling factors (Royce 1951; Martin 1957; McCrimmon 1958; Dux et al. 2011; Fredenberg et al. 2017), although a high degree of correlation among these factors makes it difficult to deduce which is most important, and multiple variables likely interact to influence behavior (Royce 1951). To further complicate matters, little distinction has been made between arrival on spawning grounds and the act of spawning, which can be separated by a period of almost a month (McCrimmon 1958; T. Binder, personal observation). Nonetheless, a general conceptual model has been proposed whereby cool, cloudy, and windy autumn conditions seem to induce accelerated spawning seasons that are short in duration, whereas warm, bright, and calm autumn conditions induce spawning seasons that are delayed and sometimes protracted (Royce 1951; Martin 1957; Martin and Olver 1980).

In lakes that thermally stratify, water temperature plays a primary role in regulating the timing and duration of activity on spawning grounds, with the first fish arriving on spawning grounds when surface temperatures decline to at least 15 °C and more commonly 12 °C (Dux et al. 2011; Callaghan 2016; Fredenberg et al. 2017), and spawning typically begins once surface temperatures drop below ~10 °C (Martin and Olver 1980; Beauchamp et al. 1992; Dux et al. 2011). The role of wind in reproductive behavior, however, is less clear. Lake charr activity often increases on spawning grounds during and immediately after storm events (McCrimmon 1958; Deroche 1969; Esteve et al. 2008; Muir et al. 2012). The prevailing theory among researchers is that high wind during storms destabilizes the thermocline in southern lakes and causes mixing of warm surface waters with cooler waters below that rapidly decreases water temperature on shallow-water spawning sites (Royce 1951; Martin and Olver 1980; Marsden et al. 1995). However, fall turnover was not correlated with spawning activity in several small inland lakes in Algonquin Park, Ontario, Canada (Martin 1957). Similarly, in Seneca Lake, New York, USA, where spawning occurs well below the thermocline in 30–60 m of water, lake charr spawn well in advance of lake turnover (Royce 1951). Moreover, in the far north at Great Bear Lake, Northwest Territories, storm events were associated with higher levels of activity on spawning shoals (Muir et al. 2012). In the latter lake, fish may wait for strong winds to produce currents that clean substrate interstices in advance of gamete deposition (Muir et al. 2012). Rough conditions during storms may also restrict access to and residency on spawning shoals, so a peak in spawning activity observed directly after storms may be a result of a buildup of spawning-ready fish waiting for calm conditions to allow access to spawning sites. Further study is needed to disentangle the relationship among temperature, wind, and waves associated with storm events, and timing of activity on spawning shoals.

Evidence is limited for a relationship between seasonal variation in light levels and timing of movement onto spawning grounds or initiation of spawning. Seasonal variation in light levels could influence the timing of sexual maturation (Goetz et al. 2021). Date of spawning was significantly related to the combination of temperature and number of cloudy days over 3 months preceding spawning (Royce 1951), although the correlation did not hold for the two variables individually and other factors were not considered. Similarly, McCrimmon (1958) suggested that duration of the pre-spawning period (time between first arrival on the spawning grounds and actual spawning) was a function of cumulative number of hours (60–65 h) of clear sky after arrival on spawning grounds, but acknowledged that the relationship may have been coincidental. Whether daily variation in light level controls diel timing of spawning activity is unknown, but release of gametes occurs most frequently under low light immediately after sundown. A rare observation of daytime spawning in Kushog Lake, Ontario, Canada, may have been a result of reduced underwater visibility due to turbidity that followed a period of high winds and rain (Esteve et al. 2008).

3.3.3.2 Homing and Navigation

The term "homing" (a.k.a., "site fidelity") refers to the propensity of individuals to return to spawning sites with which they have had previous experience, either as embryos (natal homing) or as adults (repeat homing). Homing is a widespread reproductive strategy among fishes, and has been particularly well-studied in the Pacific salmonids (Dittman and Quinn 1996; Bett and Hinch 2016). Compared to the salmons, homing in the lake charr is poorly understood. Indeed, several life-history characteristics of the lake charr complicate the study of homing in this species. First, in contrast to the Pacific salmons, which spawn only once before dying (semelparous), the lake charr is long-lived (to more than 60 years; Hansen et al. 2021) and can spawn many times during their lifetime (iteroparous). Therefore, investigation of individual behavior requires years of study. Second, while most salmon species return to their natal streams (i.e., natal homing behavior) during their single spawning season, a strategy that maximizes fitness by helping to ensure that individuals locate habitats that previously supported successful reproduction, a lake charr can choose a different spawning site each spawning season of adult life, or possibly even spawn at or visit multiple sites in a single year (Krueger et al. 1986; Bronte et al. 2002; Pinheiro et al. 2017). Depending on the size and physical geology of the lake, potentially suitable lake charr spawning sites may be discrete and widely distributed. Thus, it would be impractical in many lakes to monitor every possible spawning site to quantify the degree of straying and subsequent spawning in a population. Third, because adult lake charr are highly mobile, the assumption that capture location of a spawning-ready lake charr represents the location of its spawning site could be wrong (Eschmeyer 1955). Fourth, not all lake charr spawn every year (Sitar et al. 2014; Goetz et al. 2021). Skipped spawning (i.e., mature fish that do not spawn that year) in lake charr populations makes it difficult to distinguish an individual that did not spawn from one that chose to spawn elsewhere without resorting to histology. Lastly, no objective, standard definition exists for what spatially constitutes a "spawning site." The issue is largely one of scale because spawning site selection likely occurs at multiple spatial scales (Riley et al. 2019), and the entire areal size of some inland lakes, where much of the spawning behavior research has occurred, are no larger than individual spawning reefs in large systems like the Laurentian Great Lakes.

Decades of traditional mark-recapture studies have shown that lake charr often return to the same location during the spawning season repeatedly over several years (Eschmeyer 1955; Loftus 1958; Martin 1960; Rahrer 1968; Deroche 1969; Swanson 1973; Martin and Olver 1980), with the degree of homing to these sites ranging from ~60% to over 90%. A lower homing rate (41%) was reported in Yellowstone Lake (Montana, USA), where lake charr are invasive, but artificial selection caused by intense fishing pressure on spawning sites to remove lake charr may have been responsible for higher rate of straying in this population than elsewhere (Williams 2019). Quantification of homing by lake charr with mark-recapture methods has relied mainly on two methods. The first is estimation of the proportion of marked fish that return during subsequent spawning seasons to the spawning site where they were marked. This approach provides a minimum estimate of homing that is biased low because not all marked fish present at the site each year are captured, and also does not account for mortality between spawning seasons. The second method addresses the problem from the opposite direction by estimating the degree of straying in the population. For this technique, multiple spawning sites are monitored for marked fish during the spawning season, and degree of homing is the portion of fish that returned to the marking site relative to the number of fish caught at all monitored sites. Based on the latter method, one study found that tagging site fidelity was 74% in autumn and 73% in spring, which suggests such estimates could be driven by low dispersal rather than by homing (Schmalz et al. 2002). Nonetheless, the straying estimation method is less sensitive to low recapture rates and mortality, as long as they can be assumed equal among monitored sites, but estimates of homing rates determined in this manner may be biased high (i.e., degree of straying underestimated) if all possible spawning sites in the system are not monitored.

Recently, a third, more robust method has been used to estimate mortality independent homing rates in lake charr and other iteroparous species using a combination of acoustic telemetry and Cormack-Jolly-Seber (CJS) capture-recapture models (Binder et al. 2016; Hayden et al. 2018) that simultaneously estimate recapture probability and mortality using encounter histories over time (Lebreton et al. 1992). Because acoustic telemetry receivers listen continuously for transmitters implanted into fish and have large detection ranges (often >1 km), true recapture probability (i.e., probability of detecting an individual that is present) of tagged individuals can reasonably be assumed to be close to 1.0. When this assumption is true, estimates of recapture probability returned from CJS models can be interpreted as the probability that an individual returned to the site given that it was still alive (Binder et al. 2016). Using this technique, estimated annual homing rates for fish on a multi-reef complex in northern Lake Huron population over 5 years ranged from 78 to 86%, depending on sex and whether the fish were wild or hatchery origin. However, true homing rates in that population may have been higher than reported because the models could not distinguish straying to other spawning locations from skipped spawning (Sitar et al. 2014).

Individual lake charr often move among discrete spawning sites separated by hundreds of meters to many kilometers within a single spawning season (MacLean et al. 1981; Bronte et al. 2002; Binder et al. 2016; Callaghan 2016; Marsden et al. 2016; Pinheiro et al. 2017; Williams 2019). The probability of movement among sites is related to the degree of spatial proximity of sites and relative spawner density, and therefore would seem to be more likely to occur in small lakes with abundant spawning sites in close proximity to each other than in large lakes with sparse or highly dispersed spawning habitat. Whether lake charr deposit gametes on multiple spawning sites is unknown, but we propose that movement among spawning sites (1) reflects a bet-hedging strategy whereby gametes are deposited at multiple spawning sites, which increases reproductive fitness by reducing the chance of random catastrophic loss of reproductive output at one site; (2) is stimulated by site competition due to high spawner density on primary or highly desirable spawning sites that causes dispersal elsewhere, which presumably increases reproductive fitness by enhancing the probability of pairing with a mate and reducing superimposition of gametes on specific sites where spawning occurs; or (3) represents low-risk exploratory behavior that occurs during the day or outside the peak period of spawning activity, which may increase fitness by allowing individuals to discover alternative high-quality spawning habitat. This latter explanation may be especially important in the Laurentian Great Lakes where large (100 km^2) offshore (50+ km) spawning sites are characterized by small patches of good substrate interspersed with large patches of poor or marginal habitat. Whether propensity to stray from known spawning locations is an innate trait is unknown, but some individuals have a greater tendency to move between spawning sites than others (MacLean et al. 1981; Marsden et al. 2016). The proclivity for exploring new territory in some lake charr likely drives colonization of new spawning sites, and consequently, likely played a key role in successful establishment of spawning populations after glacial recession and in lakes outside their native range (Crossman 1995; Martinez et al. 2009).

Lake charr may home to natal sites as adults to spawn (Eschmeyer 1955; Rahrer 1968; Swanson 1973; Horrall 1981). No direct evidence exists to support this presumption, but several indirect lines of evidence suggest some degree of natal homing in lake charr. For example, lake charr with unique characteristics (e.g., body form, skin, and fin coloration) persisted on the same spawning sites, consistent with natal homing contributing to some degree of reproductive isolation (Horrall 1981). In addition, lake charr stocked as yearlings (13–15 months old) often returned as adults to habitat near stocking locations and hatchery outflows (Krueger et al. 1986; Ellrott and Marsden 2004; Bronte et al. 2007), which suggests imprinting (a process of rapid learning during early life stages to acquire information used later in life) occurs. For example, in Lake Michigan, 40% of more than 2200 yearlings stocked at eight different locations were recaptured as spawning adults 5 or more years later at their stocking site (Bronte et al. 2007). Degree of straying varied by location, but many fish that strayed from their stocking location were recaptured at nearby adjacent spawning sites (Bronte et al. 2007). Additional support for imprinting comes from an experiment on Devils Island Shoal, Lake Superior, where 17 million fertilized eggs were deployed in artificial turf incubators over 15 years (1981–1995) to re-establish a spawning population on the reef (Bronte et al. 2002). Surveys of the adult population between 1985 and 1997 showed a marked increase in wild-reared spawners beginning in 1988, the approximate date of first sexual maturity for the stocked embryos, while the number of hatchery-reared spawners remained consistent and low. Moreover, year-class-specific stock recruitment analysis indicated that variation in recruitment of wild-reared spawners was better explained by the number of fertilized eggs stocked than by the number of spawners present at the site that year (Bronte et al. 2002).

While available evidence suggests some degree of natal homing in lake charr, other mechanisms must exist for locating spawning habitat. For example, stocked and invasive lake charr find suitable nearshore spawning sites and reproduce, despite not having had an opportunity to imprint to those sites during early development (i.e., as embryos or post-embryos). In addition, experimental work in three small inland lakes (Whitepine Lake and Helen Lake in Ontario, Canada and Lake Aux Sables in Quebec, Canada) showed that when traditional shoreline spawning sites were made unsuitable for spawning (by covering them with opaque plastic sheets), lake charr quickly located and colonized new nearby spawning sites (McAughey and Gunn 1995; Gunn and Sein 2000; Benoît and Legault 2002). Distance appears to be a factor in colonization of new spawning sites, as does proximity to shoreline. In the Laurentian Great Lakes, lake charr stocked as juveniles were unable to colonize known historic offshore spawning sites (Krueger et al. 1986), unless they were stocked on offshore sites (Bronte et al. 2007). Moreover, lake charr stocked as adults on offshore spawning sites in Lake Huron emigrated to nearshore sites when the stocking location was not isolated from suitable nearshore sites by either distance or water depth (Eshenroder et al. 1995b). These results suggest that, in the absence of reliable homing cues, lake charr may revert to an evolutionarily derived search strategy designed to locate suitable spawning sites along the shoreline, which is where most spawning habitat occurs in small inland lakes (Eshenroder et al. 1995a).

A three-tiered, hierarchical hypothesis was recently proposed to explain navigation to spawning grounds in salmonids: (1) imprinted olfactory cues, (2) conspecific olfactory cues (i.e., pheromones), and (3) non-olfactory environmental cues (Bett and Hinch 2016). In short, migrants first search for imprinted odors (i.e., natal homing), which act as the principal navigation cue. If imprinted odors are absent or do not lead to suitable spawning sites, migrants will search for odors from conspecifics, and if neither imprinted nor conspecific olfactory cues are available, they will rely on non-olfactory cues (e.g., bathymetry, temperature, and substrate) to lead them to suitable spawning locations. We propose that this hierarchical navigation model may explain navigation to spawning sites in the lake charr. However, we also predict that olfactory cues (either imprinted or derived from conspecifics) could be less precise in their ability to lead fish to spawning sites in open water than they are in rivers where odor signals are embedded in a strong directional current. This difference could partially explain why lake charr appear to home to a region (e.g., reef complex), rather than to a specific spawning site.

Specific navigation cues in lake charr have not yet been identified. Foster (1985) suggested that lake charr may imprint to olfactory cues emanating from feces left in the substrate by free embryos before they vacate spawning sites in late spring and early summer. However, a recent field experiment failed to demonstrate attraction to spawning substrate seeded with free embryo feces, and concurrent chemical, physiological, and behavioral studies in the laboratory suggested that odors emitted from feces of free embryos most likely dissipate or degrade well in advance of the spawning season (Buchinger et al. 2017). Adult lake charr may be attracted to substrate from known spawning sites where spawners are already present, although odors may not persist between spawning seasons (Wasylenko et al. 2013). Similarly, two-choice behavioral experiments in the laboratory have demonstrated that adult males and females are attracted to odors from conspecific males (Buchinger et al. 2015). Neither adult males nor females were strongly attracted to odors from conspecific females, but adult males were attracted to odor from juveniles (Buchinger et al. 2015). This pattern of conspecific attraction to male odor is consistent with the observation that male lake charr arrive first on the spawning grounds and supports the existence of a male attractant pheromone for drawing females and late-arriving males to spawning sites. The specific chemical (or chemicals) that attracts lake charr remains to be identified, but lake charr can detect bile acids produced and released by conspecifics at nanomolar concentrations, thereby making these substances ideal candidates as aggregating pheromones (Zhang et al. 2001). Possible non-olfactory navigation cues include sound produced by conspecifics on spawning grounds (Johnson et al. 2018), environmental noise (e.g., waves crashing on shallow reefs), substrate type and particle size (e.g., Marsden et al. 2016), hydrodynamic cues (e.g., distortion of water flow patterns across reefs), and lakebed bathymetry such as steep drop-offs associated with reefs. Such cues could aid navigation over distances up to a few kilometers, but the observation that some lake charr make repeated migrations of up to several hundred kilometers between spawning seasons (Binder et al. 2017; Riley et al. 2018) suggests other non-olfactory cues may be involved (e.g., solar cues or geomagnetic orientation; Binder et al. 2011; Putman et al. 2013). Alternatively, lake charr may be capable of remembering the landscape and location of sites on which they have previously spawned or encountered spawners. In iteroparous species, the importance of external navigation cues may diminish with age as individuals gain more spawning experience. Thus, learning and memory could play a critical role in navigation to, and selection of, suitable spawning habitats in the lake charr, a possibility that warrants further investigation.

3.3.3.3 Pre-spawning Behavior

Males arrive on spawning grounds first and form loose aggregations 1–3 weeks before the spawning period (Fig. 1; Royce 1951; McCrimmon 1958; Deroche 1969; Peck 1986; Marsden and Krueger 1991; Muir et al. 2012). During daytime, shallow shoreline shoal spawners (including river spawners in Lake Superior) may move offshore, away from spawning sites into deeper water (Merriman 1935; Royce 1951; Loftus 1958; Esteve et al. 2008), while offshore reef-spawners tend to aggregate near popular spawning sites (Marsden and Krueger 1991; Muir et al. 2012; Binder et al. 2015). At night, males move back onto spawning grounds, and are sometimes observed swimming near the substrate without an obvious pattern (Fig. 1; Deroche 1969; Esteve et al. 2008). Females are seen less frequently on spawning sites during the pre-spawning period and presumably remain in deep water, possibly to avoid harassment by males. Little is known about the behavior of females during this period, but we speculate that they may make short visits to multiple spawning sites to evaluate spawning options for that year (Pinheiro et al. 2017).

Males may arrive early on spawning grounds to minimize missed spawning opportunities. However, three possible alternate explanations have been proposed for early arrival of males on spawning sites: territorial establishment, substrate cleaning, and female attraction (Muir et al. 2012). No evidence exists for territoriality in this species (Muir et al. 2012), but the latter two hypotheses are supported. During the pre-spawning period, spawning sites often become visibly cleaner than surrounding sites not used for spawning. Occasional occurrences of rubbing behavior reminiscent of nest digging in other salmonids (i.e., forward acceleration accompanied by turning to the side and vigorous tail beating; Fig. 2a) have been reported (Martin 1957; Binder et al. 2015). However, most cleaning is thought to be due to large numbers of fish making contact with the substrate while swimming across spawning grounds (Merriman 1935; Royce 1951; Deroche 1969; Foster 1985; Esteve et al. 2008). Whether cleaning is purposeful or incidental is debatable. In addition to substrate cleaning, swimming close to substrate may serve multiple purposes. First, contact with substrate may allow the fish to evaluate rocky substrate quality in terms of size, shape, and presence of silt and organic material in interstices. For example, sweeping motions by the tail over the substrate could suspend silt and other debris to indicate the degree of interstitial infilling (Marsden and Krueger 1991). Another possibility is that fish use their lateral lines to detect currents within the substrate (Montgomery et al. 1995) to indicate the presence of clean, well-irrigated interstices suitable for protecting and aerating pre-hatch embryos during incubation. Second, males may mark substrate with scents that attract females to sites of good quality incubation substrate (Foster 1985; Buchinger et al. 2015). For

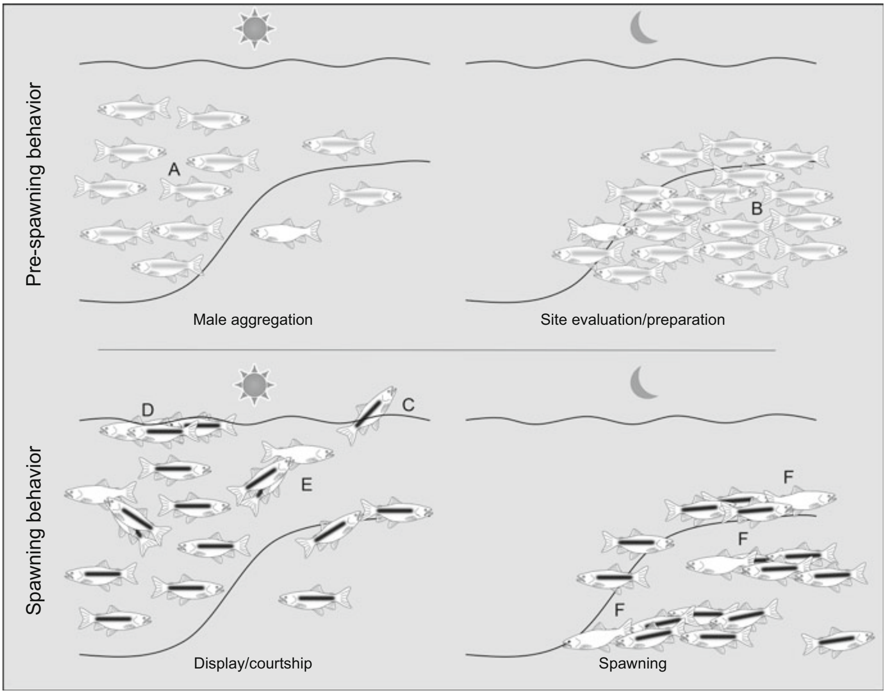

Fig. 1 Proposed lake charr *Salvelinus namaycush* spawning behavior model. Fish with horizontal bands are males, and those without bands are females. Males arrive on the spawning grounds in advance of the spawning period and form loose aggregations. During the pre-spawning period, males reside offsite during day (A), and then move up onto spawning grounds at night where they swim apparently randomly in close proximity to the substrate (B), possibly to evaluate habitat quality and clean the substrate of infill, or to mark the substrate with scents to attract females. Once the females arrive on the spawning grounds, males develop dark bands along their sides and begin courtship behavior (e.g., jumping—C; finning—D; hovering—E), which appear to occur primarily at the margin of the spawning grounds during daytime, but could also occur at night. After male suitors are selected by the female, she moves to the spawning grounds; spawning occurs almost exclusively during night. Lake charr spawn in roving groups consisting of one female and up to nine males (F). The female travels over the spawning grounds with males in tow, periodically sinking to deposit eggs in the substrate. While travelling, males attend the female and jockey with one another for one of two positions immediately adjacent to the female. Only the three to four closest males to the female sink with her to fertilize the eggs

example, capture rates of adult lake charr and white sucker *Catostomus commersoni* were higher in trap nets containing substrate from a spawning reef than in trap nets containing substrate from a non-spawning reef (Wasylenko et al. 2013). Therefore, spawning substrate may contain chemosensory cues that are attractive to both adult lake charr and to lake charr egg and pre-hatch embryo predators, although specific odorant(s) involved in behavioral responses are not known (Wasylenko et al. 2013).

Fig. 2 Images of lake charr *Salvelinus namaycush* spawning-related behaviors. (**a**) Substrate rubbing behavior—reminiscent of redd digging in other salmonines. The purpose of this behavior is unknown, given that lake charr do not build redds, but it has been hypothesized that substrate rubbing may mark the substrate with odorants that attract conspecifics. (**b**) Finning—a courtship

3.3.3.4 Courtship and Spawning Behavior

Most observations of lake charr spawning behavior have come from small inland lakes and from spawning sites less than 2 m deep (Merriman 1935; Royce 1951; Martin 1957; Gunn 1995; Esteve et al. 2008). Early descriptions of spawning behavior led to a conceptual model that differed greatly from that of other salmonines and seemed inconsistent with evolutionary theory, given that sex ratios on the spawning grounds are heavily skewed toward males. Lake charr do not build redds or defend territory, but rather display an itinerate spawning behavior whereby spawning groups led by females travel widely over spawning grounds, while stopping multiple times to deposit gametes into the substrate (Esteve et al. 2008; Muir et al. 2012; Binder et al. 2015). Prior to the late 2000s, lake charr spawning was described as promiscuous and indiscriminate, with no obvious mate selection or intra-sex competition (Merriman 1935; Royce 1951; Esteve et al. 2008). Of particular note was the near-complete absence of agonistic behavior among males (Royce 1951; Gunn 1995; Esteve et al. 2008), a prominent feature of spawning behavior in other salmonines (Esteve 2005). However, evolutionary theory suggests that females with high reproductive investment (i.e., relatively few, large, and lipid-filled eggs) should be selective about mates. Recent studies have suggested that understanding of lake charr spawning behavior is incomplete, and observations of previously undescribed behaviors have expanded the spawning conceptual model to include possible forms of female mate selection (Muir et al. 2012; Binder et al. 2015) and male–male competition (Binder et al. 2015). In this section, we synthesize available literature on lake charr courtship and spawning behavior and propose an updated lake charr spawning behavior model for the shallow-water lean morphotype (Fig. 1).

During late autumn, activity on spawning sites is mainly nocturnal. Isolated spawning events have been observed during daytime (Esteve et al. 2008; Binder et al. 2015), but these events are rare, and likely occur only at peak spawning. Arrival of ripe females on spawning grounds is accompanied by marked changes in behavior and appearance of males. Many authors have described dark banding along the

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Fig. 2 (continued) behavior observed at Great Bear Lake, Northwest Territories, Canada. Groups of two or more lake charr hold station or moving slowly just beneath the water surface with a partially erect dorsal fin, adipose fin, and only occasionally the dorsal lobe of the caudal fin, breaking the water surface. (**c**) Hovering—a courtship behavior observed at Drummond Island, Lake Huron. The female hangs stationary in the water column while being attended by one or more males who move slowly along her sides and ventral surface while rubbing, quivering, and nipping her. (**d** and **e**) Travelling—a single female swims in large circles over the spawning grounds flanked by one or more males following in tight formation. Males attend the female and jockey with one another for the two positions immediately adjacent to the female. (**f**) Gamete release—the travelling female stops swimming and the group slowly sink to the substrate, where they arch slightly upward with vents aligned and quiver vigorously while thrusting forward and releasing gametes into the substrate. Photos of the spawning act (**d**, **e**, and **f**) were taken during a rare observation of daytime spawning. Most spawning in lake charr occurs during the night. Photo credit: **a** and **c**—T. Binder; **b**—C. Krueger; **d**–**f**—H. Thompson lateral lines of males during the spawning period (Royce 1951; Martin 1957; Muir et al. 2012; Binder et al. 2015), which appears to be caused by contraction of chromatophores on the back that cause the back to lighten in color (Royce 1951). However, the degree to which banding develops appears to vary among populations. For example, the color change in males was "striking" in two Great Bear Lake morphotypes (Muir et al. 2012), but more subtle in Lake Huron (Binder et al. 2015), Lake Champlain (Muir et al. 2012), and Lake Superior (C.R. Bronte personal observations on ROV), and was not always observed in Kushog Lake (Esteve et al. 2008). The purpose of male banding is unknown, but given that it coincides with the arrival of ripe females on the spawning ground, and that it accentuates sexual dimorphism, banding may play a role in mate recognition and selection (Muir et al. 2012).

Early descriptions of lake charr spawning behavior lacked evidence of mate selection, but recent observation of two previously undescribed behaviors, "finning" (Muir et al. 2012) and "hovering" (Binder et al. 2015), suggest that female mate selection may occur. Finning occurred in two Great Bear Lake morphotypes, and was characterized by groups of two or more lake charr "stationary or moving slowly just beneath the water surface with a partially erect dorsal fin, adipose fin, and only occasionally the dorsal lobe of the caudal fin, breaking the water surface" (Fig. 2b; Muir et al. 2012). Observations of this behavior from the surface did not allow sex determination, but was inferred to represent display courtship by males to females. "Hovering" was observed in Lake Huron and appeared to be a largely tactile courtship behavior that may be analogous to "finning" in Great Bear Lake. In hovering, a solitary female hung stationary in the water column while being attended by one or more males who took up position below at a 40–60° angle to her long axis, and slowly moved along her sides and ventral surface while rubbing, quivering, and nipping her (Fig. 2c; Binder et al. 2015). Finning and hovering were both observed during daylight hours and along the margin of the spawning reef, which suggests that courtship and mate selection may be separated spatially and temporally from nocturnal spawning (i.e., lekking; Foster 1985; Fig. 1). Courtship could also occur at night, but is challenging to observe. The possibility that courtship is separate from spawning is further supported by the fact that courtship behavior of this nature has not been observed at shallow onshore spawning shoals, where fish must travel farther from spawning grounds than reef spawners to reach deep water (e.g., >5–10 m). Other presumed courtship behaviors such as splashing, jumping, and "porpoising" (i.e., swimming while partially emerged from the water) have been commonly observed from the surface (Merriman 1935; Royce 1951; Muir et al. 2012), but their functions are unclear. For example, three instances of jumping were observed on underwater video recordings on a spawning reef in Lake Huron, but in each case the action was performed by a solitary individual and did not appear to elicit a response from surrounding fish (Binder et al. 2015). We suggest that future studies should focus on documenting behavior of lake charr while they are adjacent to but off spawning sites, because these observations appear to hold the greatest potential for making progress toward a more complete understanding of lake charr courtship and spawning behavior.

Descriptions of the spawning act have been consistent across populations, although studies are limited to shallow-spawning populations (e.g., spawning behavior has not been observed in deepwater siscowet or humper morphotypes in Lake Superior). Shallow-spawning lake charr spawn in groups of one female and up to nine males (Fig. 1; Royce 1951; Deroche 1969; Esteve et al. 2008; Muir et al. 2012). Spawning includes at least three distinct behaviors: travelling, sinking, and gamete release (Esteve et al. 2008; Muir et al. 2012; Binder et al. 2015). Travelling appears to be initiated by females and consists of a single female swimming in large circles over the spawning grounds flanked by one or more males following in tight formation (Fig. 2d, e). As the female leads the group over the spawning grounds, males nibble, nudge, and quiver against her, while jockeying with one another for prime locations immediately adjacent to her on either side. Behavior of travelling males has been interpreted as courtship behavior (Esteve et al. 2008), but travelling probably occurs after mate selection and may represent a novel form of male–male competition (Binder et al. 2015). Reproductive success of an individual male in multi-male spawning groups is inversely related to time and distance for sperm to reach eggs, relative to other males in the group (Mjølnerød et al. 1998). Therefore, in roving spawning groups, selection should favor males that successfully maintain proximity with a female as she travels over spawning grounds (Esteve et al. 2008).

While travelling over spawning grounds, the female periodically stops swimming and sinks to the substrate. The three or four males closest to the female sink with her, while those farther back in the group swim slowly around and above the spawning group (Esteve et al. 2008), apparently waiting for the female to resume travelling. Sinking is often associated with gamete release. Nine of 16 observed instances of sinking at a spawning site in Lake Huron resulted in gamete release (Binder et al. 2015). In most cases, the reason for resuming travelling without releasing gametes was not clear, but in one case spawning was disrupted by a male swimming beneath the female while she was sinking to the substrate. Gamete release lasts about 2 s (Esteve et al. 2008; Binder et al. 2015) and appears similar to gamete release in other salmonines (Esteve 2005). The fish arch slightly upward with vents aligned, pelvic and pectoral fins splayed, and dorsal fins erect. Males and the female quiver vigorously and simultaneously release gametes into the substrate as they accelerate forward and slightly upward, often with gaping mouths (Fig. 2f; Esteve et al. 2008; Binder et al. 2015). Milt is emitted in a cloud around the female. A female distributes her eggs among several locations on a single spawning site over a period of several minutes (Esteve et al. 2008; Binder et al. 2015), but whether females deposit eggs on multiple discrete spawning sites in a single season is unknown (Pinheiro et al. 2017). Both sexes presumably can spawn with more than one spawning group and at more than one location during a single spawning season, but this behavior has never been documented, and remains unknown in our understanding of lake charr reproductive ecology.

4 Summary and Conclusions

Much has been learned about movement and behavior of the lake charr over the last several decades, and this new information has prompted us to revisit and refine current conceptual models, many of which have persisted for nearly a century. Increasingly detailed observations of behavior made possible largely through use of advanced technologies, such as acoustic telemetry, that allow repeated observations of individuals over large spatial or temporal scales, suggest that lake charr behavior is more complex than has been previously described. In addition, the lake charr displays considerable behavioral plasticity, which has contributed to its ability to thrive in a wide variety of ecosystems, from Arctic and sub-Arctic lakes in northern Canada, to lakes and reservoirs in the western United States where the lake charr is not native, to the Canadian and Laurentian Great Lakes of North America. Throughout this chapter, we have attempted to incorporate some of this behavioral complexity into revised conceptual models (Table 2 and Fig. 1). Our intention is for these revised models to serve as testable hypotheses within a theoretical framework on which to base future research.

Movement ecology of the lake charr changes over the life cycle and is tightly linked to habitat availability (Marsden et al. 2021) and trophic ecology (Vinson et al. 2021), and is, therefore, location- and population-specific. Within populations, a high degree of individual variation occurs in movement behavior, but individual movement patterns tend to be repeated among years (Morbey et al. 2006; Binder et al. 2017; Gallagher et al. 2019). Between spawning seasons, adults appear to migrate to known foraging locations. Whether individual variation in migration patterns (i.e., distance and direction of migration) is genetically controlled is not known, but lake currents appear to play a role in determining the initial direction of dispersal of young lake charr as they leave spawning grounds where they began life (Pycha et al. 1965; Elrod 1987; Bronte et al. 1995). Given the long life of the lake charr, we suggest that experiential learning may be important in determining migration patterns of individual lake charr, and therefore, we predict that individuals will adjust and adapt migration patterns to ecological changes that occur in the system. Maximum migration distance is limited by basin size and degree of inter-lake connectivity, but is generally less than 100 km. When unconfined, some lake charr individuals migrate long distances (200+ km) between spawning seasons (Schmalz et al. 2002; Kapuscinski et al. 2005; Riley et al. 2018), and, where marine access is available, will push their physiological limits by migrating into brackish water (Swanson et al. 2010; Harris et al. 2014), which suggests that the individual fitness benefit of long-distance migrations may be access to higher quality prey. Therefore, the probability and occurrence of long-distance migrations may depend on predator and prey densities and may be more acute when local prey are scarce. At a population level, these more exploratory individuals may facilitate rapid expansion into new habitats, such as occurred after the last ice age (Wilson and Mandrak 2004), and in the western United States where lake charr were widely introduced (Martinez et al. 2009).

Table 2 Summary of movement and behavior conceptual models for each stage of the lean (shallow water) lake charr life cycle, derived largely from studies near the southern extent of the species range. The movement and behavior of deepwater morphotypes are less well described

Life stage	Behaviors exhibited	Vertical movements	Horizontal movements
Free embryo Hatch to 4 weeks 	• Light avoidance (photophobia) • Refuge seeking from predators • Foraging on plankton to supplement endogenous food supply • Filling of gas bladder	• Refuge seeking in substrate during daytime • Nocturnal vertical migration out of substrate to forage and fill gas bladder	• Limited ability to perform horizontal movement due to presence of yolk sac
Post-embryo 4–8 weeks 	• Light avoidance (photophobia) ends • Migration from natal sites to deep water • Predator avoidance • Foraging on plankton	• Vertical movement toward the substrate or toward the water surface to avoid predation, depending on the type of substrate present	• Down-current migration offshore from natal sites into nearby deepwater nursery areas
Age-0 8 weeks to 1 year 	• Predator avoidance • Foraging on plankton, small benthic invertebrates, and small fishes	• Primarily benthic foraging • Vertical habitat use a trade-off between predation risk and food availability	• Extent of horizontal movement unknown, but appear to remain nearby to natal/stocking site
Juvenile 1–6 years 	• Dispersal from nursery habitat • Behavior changes throughout juvenile development • Predator avoidance during early juvenile stage, but decreases with age • Foraging shifts from age-0 diet to adult diet as fish increase in size	• Younger fish reside deeper than older fish • Depth occupancy dictated by seasonal changes in temperature, dissolved oxygen, and prey distribution (see Fig. 1 in Wellband et al. 2021) • Reside below the thermocline; short forays into the epilimnion for foraging	• Age-1 lake charr disperse down-current from natal/stocking sites, usually following the shoreline • Maximum dispersal distance typically less than 100 km from natal/stocking site • Seasonal movement between pelagic and littoral habitats

(continued)

Table 2 (continued)

Life stage	Behaviors exhibited	Vertical movements	Horizontal movements
		• May occupy all depths in lakes with no thermocline • Opportunistic vertical migration for foraging	
Adult 6 to >60 years 	• Opportunistic foraging; primary prey items include fishes and benthic invertebrates • Seasonal migration to and from spawning sites • Homing, possibly to a region rather than a specific spawning site • High fidelity to foraging locations between spawning seasons • Courtship and spawning behavior (see Fig. 1 in Marsden et al. 2021)	• Depth occupancy dictated by seasonal changes in temperature, dissolved oxygen, and prey distribution (see Fig. 1 in Wellband et al. 2021) • Reside below the thermocline; short forays into the epilimnion for foraging • May occupy all depths in lakes with no thermocline • Opportunistic vertical migration for foraging	• Individually variable, annual repeated migration between known foraging and spawning locations • Maximum migration distance typically less than 100 km • Seasonal movement between pelagic and littoral habitats • Partial anadromy to brackish water when provided access to marine ecosystem

Individual lake charr show high annual fidelity (repeat homing) to specific spawning locations, although movement among adjacent spawning sites is common (Krueger et al. 1986; Bronte et al. 2002). Natal homing appears to occur to some extent but is likely not as precise a navigation tool for the lake charr as it is for river-spawning salmonids. Lake charr spend a relatively short period of time on spawning grounds after hatching. Therefore, imprinting to natal spawning sites would have to occur very early in development, as in pink salmon *Oncorhynchus gorbuscha* (Bett et al. 2016). Imprinting at later stages of development, as in many salmonines (Keefer and Caudill 2014), could result in homing cues that bring fish close to natal spawning locations, but could not be used to identify specific natal spawning sites. Furthermore, lack of consistent unidirectional flow in lakes could make pinpointing the specific source of natal cues more difficult than in streams and rivers. Other olfactory and non-olfactory cues could be important for navigation to spawning sites, but identification of specific cues and confirmation of their contribution to navigation to spawning sites is needed. For example, mature males and females are attracted to olfactory cues from conspecific males (Buchinger et al. 2015), which suggests pheromone communication could play a role in aggregating lake charr on spawning sites. However, when traditional spawning sites are no longer available (McAughey and Gunn 1995) or when naïve lake charr are introduced or invade an adjoining lake, they appear to default to an evolutionarily derived search strategy designed to locate suitable spawning sites located along a shoreline, rather than historically important and productive offshore spawning sites (Eshenroder et al. 1995a). We propose a three-tiered, hierarchical navigation model (Bett and Hinch 2016), whereby fish navigate via (1) imprinted olfactory cues, (2) conspecific olfactory cues, and (3) non-olfactory environmental cues (e.g., bathymetry, temperature, and substrate), may best explain navigation to spawning sites in the lake charr. Cues in all three tiers are probably used to locate suitable spawning sites, with each playing a role at different spatial scales (i.e., macro- vs microhabitat selection).

Spawning behavior of the lake charr remains somewhat of an enigma. Spawning has only rarely been observed for this species, with the most detailed observations during relatively rare instances of daytime spawning that are limited to the shallow-water lean lake charr morphotype (Esteve et al. 2008; Binder et al. 2015). Whether spawning behavior observed during the day represent spawning behavior at night, when the ability to use visual cues would be diminished and the density of fish on spawning sites is much greater, remains unknown. Until recently, lake charr spawning was viewed as indiscriminate, with little evidence of female mate selection or intraspecific competition among males. However, recent observations of previously undescribed behaviors inferred to represent courtship (Muir et al. 2012; Binder et al. 2015) suggest that understanding of lake charr spawning behavior is incomplete. Unlike other salmonines, lake charr do not build redds, but rather spawn in roving groups comprised of one female and several males (Esteve et al. 2008; Binder et al. 2015). The spatially wide-ranging nature of lake charr spawning behavior poses a significant challenge to gaining a full understanding of spawning behavior because of the logistical difficulty of viewing the entire sequence of behavior within the frame of a single stationary underwater camera. Moreover, observations of courtship behavior occurring along the border of spawning reefs suggest that mate selection may occur spatially or temporally isolated from the spawning act (Muir et al. 2012; Binder et al. 2015). We propose that detailed observations of the behavior of individuals at night, and in spawning aggregations just off spawning reefs, both before and during the spawning period, are needed to gain a more complete understanding of the lake charr mating system.

5 Future Research Directions

Throughout this chapter, we have identified several key knowledge gaps, and have proposed conceptual models (summarized in Table 2 and Fig. 1) that require rigorous testing, and where necessary, adaptation and modification to fit new observations. These proposed conceptual models pertain mainly to the lean lake charr morphotypes because understanding of movement ecology and behavior is virtually non-existent for other morphotypes and remains a major gap in understanding of the species. Filling existing knowledge gaps will likely depend heavily on technologies that allow for repeated observations of many individuals over large spatial scales for an extended time period and those that allow for monitoring of early life stages. Increased use of surveillance methods (e.g., direct visual observations, or video recordings of behavior) will also be necessary to fully characterize fine-scale behavior. In the case of spawning behavior, use of advanced low-light cameras for capturing nighttime behavior, and use of camera systems that can track individuals over relatively large areas (e.g., remotely operated vehicles, or multi-camera video systems) will be key to furthering understanding of lake charr reproductive behavior. Increased use of experimental study designs (as opposed to descriptive study designs), and explicit behavioral comparisons among populations in disparate ecosystems (i.e., small vs. large lake, southern vs. northern lake) will be helpful for achieving a broader mechanistic understanding than currently exists of lake charr behavior, including how behavior varies across systems. Lastly, incorporating traditional ecological knowledge may provide insight into movement ecology and behavior of lake charr in remote lakes, where conducting scientific research is logistically difficult and expensive (Marin et al. 2017). Below we propose some future research directions based on knowledge gaps we identified while compiling this review chapter.

5.1 Research Needs to Fill Lake Charr Movement Ecology Knowledge Gaps

- Determine whether age-0 movement ecology in the wild corresponds with observations in the laboratory.
- Determine whether movement ecology of age-0 and juvenile lake charr differs between ecosystems with abundant predators and those with few predators.
- Determine whether age-0 lake charr swim to the surface to fill their swim bladders, as in other salmonid species, or by other means that reduce risk of predation.
- Determine mechanisms by which individual foraging sites are selected.
- Determine whether size of an individual's home range is heritable.
- Determine if movement ecology contributes to the maintenance or degradation of morphotype diversity in large lakes.

- Determine how movement patterns (horizontal and vertical) and habitat use vary seasonally and with lake size.
- Determine how quickly lake charr alter movement patterns in response to physiochemical or biological ecosystem change.
- Determine how projected climate change could affect movement ecology of populations (including different morphotypes) in various ecosystems.
- Determine what ecological drivers influence partial anadromy in Arctic populations.
- Determine what variables limit lake charr invasion and colonization of new lakes.

5.2 Research Needs to Fill Lake Charr Homing and Navigation Knowledge Gaps

- Determine at what stage(s) of development olfactory imprinting might occur in lake charr.
- Determine the extent to which lake charr home to natal spawning sites. Do wild-hatched lake charr return to the spawning site where they were hatched, or does homing only bring them to the reef, or general region of their natal spawning site?
- Determine which cues are used by lake charr to navigate long distances travelled to and from foraging sites between spawning seasons. Presumably, olfactory cues would not be effective over such long distances. Do lake charr exhibit celestial or magnetic orientation?
- Identify the role of conspecific chemical (pheromone) communication in navigation to spawning sites.
- Determine whether spawning site use by individual lake charr changes over time. For semelparous species, which only have one chance to spawn, natal homing is likely the best way to maximize reproductive success, but in long-lived species that can spawn multiple times throughout their life, reproductive success may be maximized by spawning at better quality sites than where they were hatched. If lake charr switch spawning sites, what process is used to identify alternative sites?

5.3 Research Needs to Fill Lake Charr Spawning Behavior Knowledge Gaps

- Determine whether nighttime and daytime spawning behavior is similar.
- Elucidate the mechanism by which mates are selected. Determine if females select mates and if males compete prior to the spawning period when males aggregate on the spawning reefs without females. If female mate selection occurs, what are the characteristics used by females to select her mate(s)?

- Determine whether individual lake charr spawn more than once and at multiple sites within a spawning season. Presumably, males are capable of spawning multiple times in a single season, but do females spread their eggs among multiple spawning sites to minimize the likelihood of catastrophic reproductive failure?
- Determine whether multiple reproductive strategies exist in lake charr (e.g., do "sneaker males" occur?), and if so, what is the relative success rate of alternative reproductive tactics?
- Determine how projected climate change scenarios could affect timing of spawning and reproductive success of populations in various ecosystems.
- Determine what mechanisms are responsible for the development and maintenance of multiple sympatric morphotypes. Do different morphotypes exhibit spatial, temporal, or behavioral reproductive isolation?
- Identify cues used to synchronize spawning in deepwater lake charr morphotypes. Surface temperature is a significant factor in determining timing of spawning in lean lake charr that spawn on shallow water shoals at the southern border of the species range, but deepwater morphotypes likely experience little temperature variation throughout the year.

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Life History and Population Dynamics

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Abstract Lake charr *Salvelinus namaycush* life history and population dynamics metrics were reviewed to evaluate populations inside ($n = 462$) and outside ($n = 24$) the native range. Our goals were to create a database of metrics useful for evaluating population status and to test for large-scale patterns between metrics and latitude and lake size. An average lake charr grew from a 69-mm length at age-0 (L_0) at 89 mm/year early growth rate (ω) to 50% maturity at 420 mm (L_{50}) at age 8 (t_{50}), and then continued to grow toward a 717-mm asymptotic length (L_∞). L_{50} was positively correlated to ω, whereas t_{50} was inversely correlated to ω. Lake charr grew slower toward larger size and older age in northern latitudes and larger lakes than in southern latitudes and smaller lakes. Population density (number/ha) and yield density (kg/ha) decreased with lake size, and yield and total annual mortality (A) decreased with latitude. Native populations grew slower (ω), were heavier at

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500 mm (W_{500}), matured at shorter L_{50}, grew to a shorter L_∞, and suffered lower annual mortality A than non-native populations. Our review and database should be useful to managers and researchers for quantifying lake charr population status across the species range.

Keywords Age: at 50% maturity, t_{50} (see maturity), at length-0, $t_{0,}$ maximum, $t_{\max,}$ mean, t_{ave} · Density, N/ha · Dynamics · Fecundity, eggs/kg · Growth: early growth rate, ω, instantaneous growth coefficient, K · Lake size · Latitude · Length: at 50% maturity, L_{50} (see maturity), at age-0, $L_{0,}$ mean, $L_{\text{ave},}$ asymptotic, $L_{\infty,}$ maximum, $L_{\max}$ · Life history: invariants, metrics · Maturity: age at 50% maturity, t_{50}, length at 50% maturity, L_{50} · Mortality: annual, A, instantaneous, Z · Native · Non-native · Population: abundance, dynamics · Weight: weight at length-500 mm, W_{500}, weight-length relationship, $\log_{10}(\alpha)$ and β · Yield, kg/ha

1 Introduction

The life history of the lake charr *Salvelinus namaycush* makes its populations vulnerable to collapse from exploitation and environmental change, while also making it highly successful at colonizing new systems (Hansen et al. 2019a). Paradoxically, the lake charr is a species that is simultaneously difficult to restore when native populations are depleted and difficult to deplete when non-native populations are established (Hansen et al. 2019a). For example, the largest lake charr populations in the world, in the Laurentian Great Lakes, declined from over-fishing for decades before sea lamprey *Petromyzon marinus* arrived and drove most populations to near extinction (Hansen 1999; Krueger and Ebener 2004; Muir et al. 2012). Similarly, the lake charr population in the western arm of Great Slave Lake, Northwest Territories, Canada, declined to extinction after only 10 years of commercial fishing (Keleher 1972; Healey 1978). These native populations have been extraordinarily resistant to recovery (Hansen 1999; Krueger and Ebener 2004; Muir et al. 2012). Coincidentally, lake charr established self-sustaining populations throughout western North America from widespread stocking in the late 1800s and early 1900s (Crossman 1995) and subsequently interacted negatively with native species (Donald and Alger 1993). For example, lake charr were introduced intentionally and unintentionally into large lakes and reservoirs in eight states of the western USA (Martinez et al. 2009), where they became well established and negatively affected native salmonid populations (Donald and Alger 1993; Fredenberg 2002; Koel et al. 2005) and subsequently altered ecosystem structure and function (Tronstad et al. 2010; Ellis et al. 2011; Syslo et al. 2016). These non-native populations have been extraordinarily resistant to efforts to suppress their abundance, despite relatively intensive long-term fishing (Hansen et al. 2019a).

To provide a reference for those researching or managing native and non-native populations, we updated the classic review of lake charr life history and population dynamics by Martin & Olver (1980) from the book on the *Salvelinus* genus by Balon (1980). Specifically, we reviewed published information about lake charr life history and populations metrics, including growth metrics estimated from the von Bertalanffy (VBM) length–age model (t_0 = age in years at length-0; L_0 = length in mm at age-0; ω = growth rate near t_0 in mm/year; K = instantaneous growth coefficient in year^{-1}; and L_∞ = average asymptotic length in mm), maturity metrics estimated from logistic regression or logit models (L_{50} = length at 50% maturity and t_{50} = age at 50% maturity), body condition metrics estimated from weight–length models ($\log_{10}(\alpha)$, β, and W_{500} in kg, where 500 mm is quality length for proportional size distribution indices; Neumann et al. 2012), population structure metrics estimated from samples (L_{ave} = mean length in mm, t_{ave} = mean age in year, $L_{\max}$ = maximum length in mm, $t_{\max}$ = maximum age in years), and population metrics (fecundity = egg/kg, density = number/ha, yield density = kg/ha, and A = total annual mortality). We also compared life-history metrics between native and non-native lake charr populations in North America, as a basis for understanding why introduced populations have been difficult to suppress using traditional fishing methods, while native populations have been relatively easy to deplete using similar methods and intensive long-term fishing (Hansen et al. 2019a). This part of our review was enabled by many studies of non-native lake charr populations that were not available to Martin and Olver (1980). Last, we tested associations between life-history metrics and environmental drivers at broad (latitude) and local (lake size) scales, as recent studies have shown (e.g., McDermid et al. 2010a).

Estimates of life-history and population-dynamics metrics were assembled from published accounts, beginning with summaries by Martin and Olver (1980), and other studies through internet searches using Web of Science and Google Scholar. Original published sources were examined whenever possible, whereas unpublished sources were referenced to original published sources (e.g., Martin and Olver 1980). We used Tukey's fences as an objective method to identify outliers for further examination: lower fence = $Q_1 - k \times (Q_3 - Q_1)$; upper fence = $Q_3 + k \times (Q_3 - Q_1)$; Q_1 = 25th percentile; Q_3 = 75th percentile; and $Q_3 - Q_1$ = interquartile range (Tukey 1977). To be conservative, outliers were limited to far-outside values exceeding three times the interquartile range ($k = 3$; Tukey 1977). Each outlying estimate was examined to determine if it was transcribed correctly. Values transcribed from the original source were assumed to be correct, except when biologically implausible (e.g., weight–length parameters, $\log_{10}(\alpha)$ and β, for Arctic Lake, British Columbia, from Piccolo et al. 1993). Tukey's fences and quantiles were calculated using R (R Core Team 2018), and descriptive statistics, skewness, kurtosis, and plots were generated using the psych package for R (Revelle 2018).

Length–age summaries tabulated by Healey (1978) and Martin and Olver (1980) were converted into growth metrics by fitting the VBM length–age model with nonlinear regression and multiplicative errors (Quinn and Deriso 1999), except when growth parameters were biologically implausible because age was underestimated from scales (e.g., Wollaston Lake, Saskatchewan, from Healey 1978). Length-based metrics originally reported in fork length (FL) were converted into total length (TL) using the length-conversion equation developed by Hansen et al. (2020).

Sample sizes were increased greatly from tabulated summaries in Martin and Olver (1980): growth estimates (t_0, L_0, ω, K, and L_∞) from 31 (Table 7, Martin and Olver 1980) to 264 (Table 1, this study), maturity estimates (L_{50} and t_{50}) from 55 (Table 2, Martin and Olver 1980) to 203, weight–length estimates ($\log_{10}(\alpha)$, β, and W_{500}) from 25 (Table 9, Martin and Olver 1980) to 97, maximum length and age ($L_{\max}$ and $t_{\max}$) from 7–9 (Table 8, Martin and Olver 1980) to 272, fecundity estimates (eggs/kg) from 12 (Table 3, Martin and Olver 1980) to 23, density estimates (number/ha) from 17 (Table 14, Martin and Olver 1980) to 45, yield density estimates (kg/ha) from 75 (Table 16, Martin and Olver 1980) to 145, and mortality estimates (A and Z) from 45 (Table 17, Martin and Olver 1980) to 248.

All life history metrics were estimated for a set of lake charr populations that were part of a life history variation study across the native range of the species. Life history metrics were previously published for populations in Lake Mistassini, Quebec (Hansen et al. 2012), Great Slave Lake, Northwest Territories (Hansen et al. 2016a), Isle Royale, Lake Superior (Hansen et al. 2016b), Rush Lake, Michigan (Chavarie et al. 2017), and Great Bear Lake, Northwest Territories (Chavarie et al. 2018, 2019). Methods of analysis were previously described in those publications, so we provide a short summary of methods used for estimating life-history parameters of samples not previously published from Great Bear Lake, Northwest Territories (McTavish Arm in 2004 and 2012, Dease Arm in 2012), Naknek Lake, Alaska (2001), Skilak Lake, Alaska (2006), and five locations across Lake Superior (Big Reef in 2006 and 2014; Grand Marais in 2002 and 2003; Klondike Reef in 2004; Stannard Rock in 2013 and 2014; Superior Shoal in 2013). Samples were collected using graded-mesh gillnets set within three depth strata (0–50 m, 50–100 m, and 100–150 m). Gillnets were 183-m long by 1.8-m high, and made of multifilament nylon twine, with 30.5-m panels of stretch-mesh sizes ranging from 50.8 to 114.3 mm, in 12.7-mm increments. Nets were set on bottom for 24 h. Data collected from each fish included total length ($TL = mm$), weight ($W = g$), sex (male or female), and maturity status (immature or mature). Growth parameters for the VBM length–age model (t_0, L_0, ω, K, and L_∞) were estimated using nonlinear mixed-effects models (Vigliola and Meekan 2009) from increment measurements on epoxy-embedded, thin-sectioned otoliths (Campana et al. 2008), and back-calculated growth histories (Campana 1990). Length and age at 50% maturity (L_{50} and t_{50}) were estimated using logistic regression (Hosmer and Lemeshow 2000). Weight–length metrics ($\log_{10}(\alpha)$, β, and W_{500}) were estimated from the linear regression of $\log_{10}(W)$ against $\log_{10}(TL)$. Total annual mortality (A) was estimated for each morph from the number of fish in mature age classes caught during gillnet sampling using the Robson–Chapman estimator (Robson and Chapman 1961). We did not differentiate among morphs because nearly all life history estimates from other published sources were for the lean morph (See Chavarie et al. 2021, for morph description).

One or more life history or population dynamics metrics was estimated for 487 lake charr populations distributed across the species native and introduced range in North America (Fig. 1, data available online as CSV file). Populations were distributed broadly, south to north, from 36.3226 N (South Holston Lake, Tennessee) to 71.8333 N (Capron Lake, Northwest Territories), with 50% of

Table 1 Distributional statistics for lake charr life history metrics from North American lakes

Metric	n	0%	2.5%	25%	50%	75%	97.5%	100%
Latitude	487	36.32	42.61	46.22	47.42	54.29	63.75	71.83
Longitude	487	–158.98	–146.06	–106.41	–83.52	–78.38	–68.65	–63.70
Elevation (m)	487	0	79	267	358	467	1879	2806
Area (ha)	448	8	33	192	573	3012	363,156	8,210,262
Depth (m)	348	12	15	30	43	73	248	614
t_0	45	–3.62	–2.62	–1.36	–0.95	–0.50	0.43	0.50
t_{50}	204	2.9	4.0	6.4	8.0	10.0	16.3	27.0
t_{ave}	268	1.9	4.1	6.3	8.0	12.0	22.4	28.7
t_{max}	272	4	8	16	23	32	49	68
L_0	45	5	10	50	69	120	255	276
L_{50}	203	208	273	357	420	480	598	660
L_{ave}	270	225	327	405	475	544	704	824
L_∞	293	343	457	605	717	880	1396	1687
L_{max}	272	372	506	700	851	949	1120	1200
$\log_{10}(\alpha)$	97	–6.754	–6.485	–5.834	–5.589	–5.173	–4.413	–3.425
β	97	2.400	2.794	3.080	3.210	3.307	3.538	3.640
W_{500}	97	0.838	0.944	1.070	1.162	1.366	1.643	1.674
K	264	0.020	0.045	0.099	0.130	0.171	0.277	0.450
ω	264	33	43	70	89	107	165	237
Eggs/kg	23	883	1032	1244	1396	1599	2031	2226
N/ha	45	0.11	0.302	1.507	7.087	13.100	25.028	28.953
kg/ha	145	0.004	0.072	0.280	0.570	0.980	3.418	5.860
A	248	0.026	0.071	0.130	0.205	0.296	0.660	0.792

t_0, age at length zero; t_{50}, age at 50% maturity; t_{ave}, mean age of fish sampled; t_{max}, maximum age of fish sampled; L_0, length at age zero; L_{50}, length at 50% maturity; L_{mean}, mean length of fish sampled; L_∞, asymptotic length; L_{max}, maximum length of fish sampled; $\log_{10}(\alpha)$, intercept of weight–length relationship; β, slope of weight–length relationship; W_{500}, weight of a 500-mm lake charr estimated from the weight–length relationship; K, instantaneous rate at which an average fish grew toward L_∞; ω, early annual growth rate; Eggs/kg, fecundity per kg of body weight; N/ha, population density; kg/ha, yield density of lake charr; A, total annual mortality

Fig. 1 Locations of native (black circles) and non-native (gray circles) populations of lake charr *Salvelinus namaycush* in North America for which one or more life history or population metric were estimated. Map borders are 83°N (top edge), 25°N (bottom edge), 170°W (left edge), and 50°W (right edge)

populations occurring between 46.22 and 54.31 N, and 95% occurring between 42.61 and 63.77 N (Fig. 1; Table 1). Populations were also distributed broadly, east to west, from 63.6956 W (Norman Lake, Quebec) to 158.9790 W (Chikuminuk Lake, Alaska), with 50% of populations occurring between 78.38 W and 106.24 W, and 95% occurring between 68.64 and 146.06 W (Table 1). Lakes averaged 574 ha in surface area, and varied from 16 ha (Lake 442, Experimental Lakes Area, Ontario) to 8,210,262 ha (Lake Superior), with 50% varying from 193 to 3031 ha and 95% varying from 34 to 366,037 ha (Table 1). Lakes averaged 43 m in maximum depth, and varied from 12 m (Swan Lake, Alberta) to 614 m (Great Slave Lake, Northwest Territories), with 50% varying from 30 to 73 m and 95% varying from 15 to 248 m (Table 1). Lakes averaged 358 m elevation and varied from 0 m (Albert Edward Bay and Fish Trap Lake, Nunavut) to 2806 m (Twin Lake, Colorado), with 50% varying from 266 to 459 m and 95% varying from 79 to 1851 m (Table 1).

2 Early Life History

2.1 Age at Length-0 (t_0)

Lake charr populations averaged −0.95 year in model-based estimates of t_0 among 45 populations. The distribution of t_0 was moderately skewed left (skew = −0.80) and platykurtic (kurtosis = 0.99). Estimates of t_0 varied from a minimum of −3.62 years in Landlocked Tangle Lake, Alaska, to a maximum of 0.50 year in Round

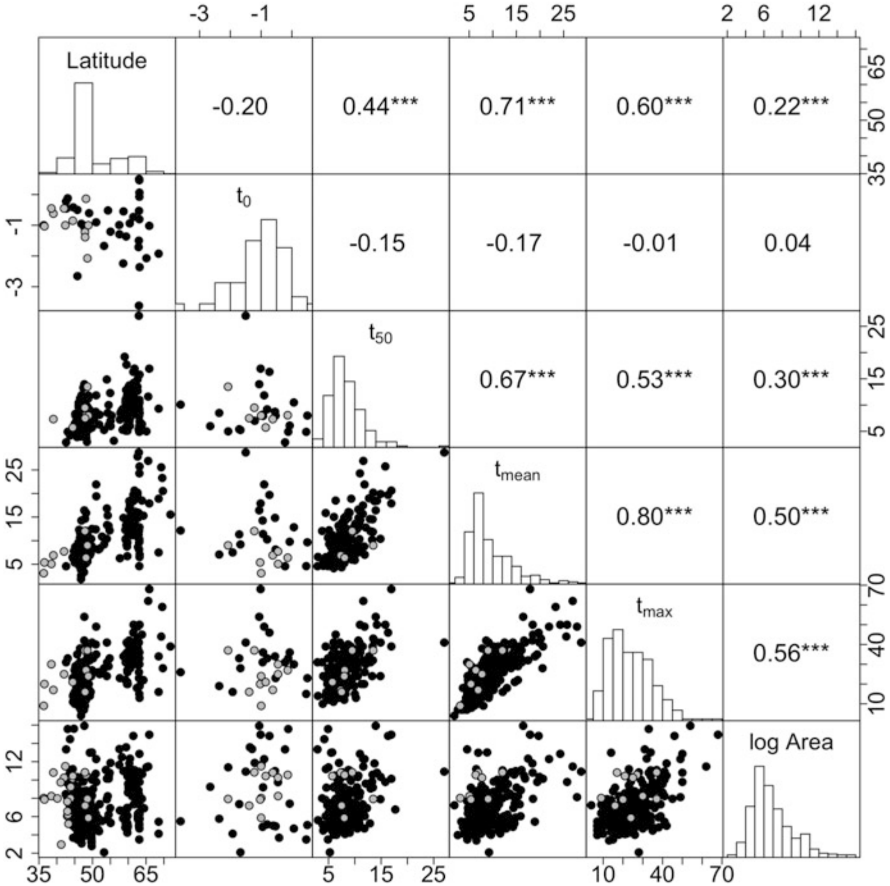

Fig. 2 Scatter-plot matrix of age-based life history metrics (t_0 = age at length zero; t_{50} = age at 50% maturity; t_{ave} = mean age of sampled fish; $t_{\max}$ = maximum age of sampled fish) for native (black circles) and non-native (gray circles) lake charr *Salvelinus namaycush* populations in relation to latitude and surface area of lakes sampled in North America

Tangle Lake, Alaska, with 50% of populations varying between −1.36 and −0.50 year and 95% varying between −2.62 and 0.43 year (Table 1). Estimates of t_0 were not significantly related to either latitude or lake size (Fig. 2). Mean t_0 did not differ significantly between native (−1.01 year, SE = 0.145, n = 32) and non-native (−0.99 year, SE = 0.227, n = 13) populations ($F_{1,\ 43} = 0.004$; $P = 0.95$).

Model-based estimates of t_0 in our review were generally higher than direct estimates of incubation time from field and laboratory studies (t_0 is an analog of incubation time for a species like the lake charr, where hatching and annulus formation are at nearly the same time of year). For example, incubation times of populations measured in the field ranged 4–6 months in most lakes (Hacker 1957; DeRoche 1969; Bronte et al. 1995) and only 1–3 months in rivers and some lakes

(Royce 1951; Loftus 1958; Paterson 1968). In a hatchery, embryos incubated at a relatively warm temperature of 5.1 °C hatched after only 3.4–3.6 months (104–109 days, McDermid et al. 2010b), whereas embryos reared under ambient lake-water temperatures of 0.8–2.0 °C hatched after 5.2–5.6 months, much closer to field measurements (157.3–169.6 days, Pakkasmaa and Jones 2002). Differences in t_0 between indirect model-based estimates and direct field estimates are likely caused by size-selective sampling of the largest individuals from young age classes that biases model-based t_0 downward and L_0 upward (Sect. 2.2). Because of this problem, t_0 is sometimes set to $t_0 = 0$ for growth analyses (e.g., especially for lake charr populations in Canada; Payne et al. 1990; Shuter et al. 1998). In addition, relatively large variation in model-based estimates of t_0 in our review may have been caused by wide variation in spawning depth and time, and overwinter incubation water temperatures that can vary from 15 to 1 °C between egg deposition and hatching (Bronte et al. 1995) among and within lake charr populations.

2.2 Length at Age-0 (L_0)

Lake charr populations averaged 69 mm in model-based estimates of L_0 among 45 populations. The distribution of L_0 was skewed right (skew = 1.27) and platykurtic (kurtosis = 1.50). Estimates of L_0 varied from 5 mm in Two Bit Lake, Alaska, to 276 mm in Lake Manitou, Ontario, with 50% of populations varying between 50 and 120 mm and 95% varying between 10 and 255 mm (Table 1). Estimates of L_0 were not significantly correlated with latitude or lake size (Fig. 3). Mean L_0 did not differ significantly between native (86 mm, SE = 10.6, $n = 32$) and non-native (95 mm, SE = 16.6, $n = 13$) populations ($F_{1,\,43} = 0.22$; $P = 0.64$).

Lake charr typically hatch at about 22 mm, which is shorter than we found in our review of model-based estimates of L_0. As with t_0, size-selective sampling of the largest individuals from young age classes likely explains the apparent upward bias in model-based estimates of L_0. In Lake Champlain, direct field estimates of L_0 varied from 18 to 26 mm (Ladago et al. 2016). In a hatchery, mean L_0 differed slightly between two groups (17.95 and 18.69 mm) because of differences in egg size (maternal effect) and hatching time (environmental effect, Pakkasmaa and Jones 2002). Based on the relationship between fish length and otolith radius for juvenile lake charr during their first few months of life after hatching from Gull Island Shoal in western Lake Superior (Bronte et al. 1995), the biological intercept for lake charr was estimated as $L_0 = 21.7$ mm (fish size at hatching) and $O_0 = 0.137$ mm (otolith size at hatching; Hansen et al. 2012), for use in the biological-intercept back-calculation model (Campana 1990). Temperature variation during pre-hatch embryo development can affect L_0 by affecting incubation time t_0 (Pakkasmaa and Jones 2002). Surprisingly, we did not detect a correlation between L_0 and latitude (which we expected to be correlated to incubation time), which suggests either (1) variation in local conditions may be greater than a latitudinal trend in temperature as an influence on L_0, or (2) the incubation environment is relatively constant across latitude.

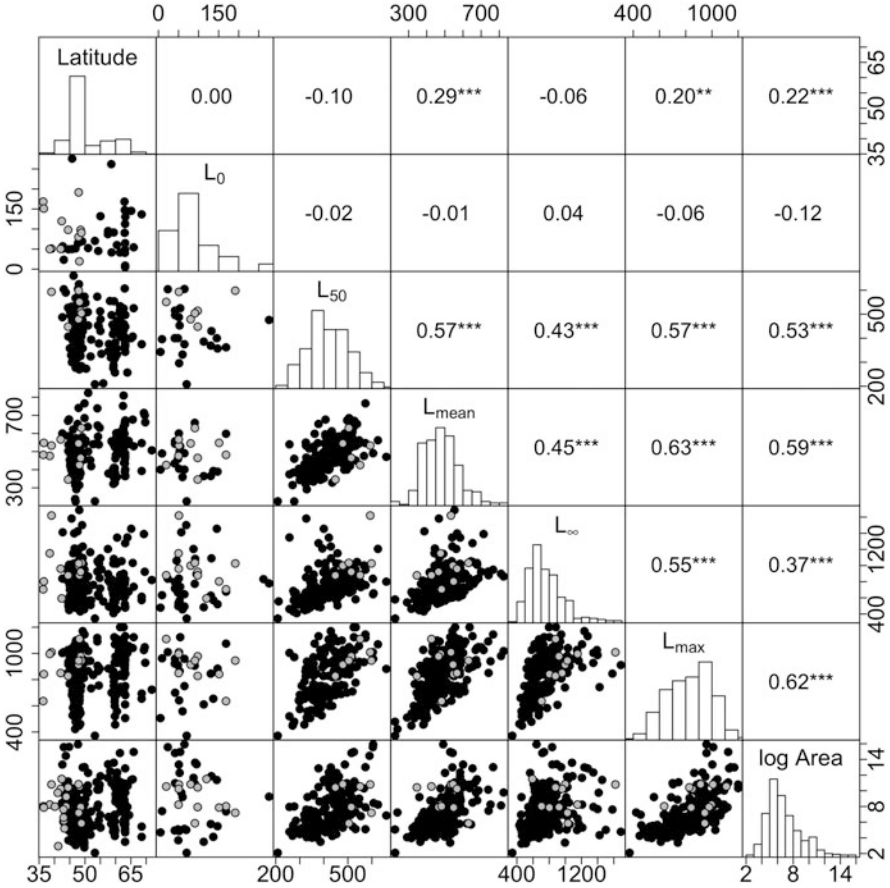

Fig. 3 Scatter-plot matrix of length-based life history metrics (L_0 = length at age zero; L_{50} = length at 50% maturity; L_{ave} = mean length of sampled fish; L_∞ = asymptotic length; $L_{\max}$ = maximum length of sampled fish) for native (black circles) and non-native (gray circles) lake charr *Salvelinus namaycush* populations in relation to latitude and surface area of lakes sampled in North America

3 Growth

3.1 Early Growth Rate (ω)

Lake charr populations averaged 89 mm/year in ω for 264 populations. The distribution of ω was skewed right (skew = 1.18) and platykurtic (kurtosis = 2.56). Estimates of ω varied from a minimum of 33 mm/year in Wrigley Lake, Northwest Territories, to a maximum of 237 mm/year in Lake Erie, with 50% of populations varying between 70 and 107 mm/year and 95% varying between 43 and 165 mm/year (Table 1). Estimates of ω were negatively correlated with latitude, but not with lake size (Fig. 4). Mean ω was significantly lower for native (91 mm/year,

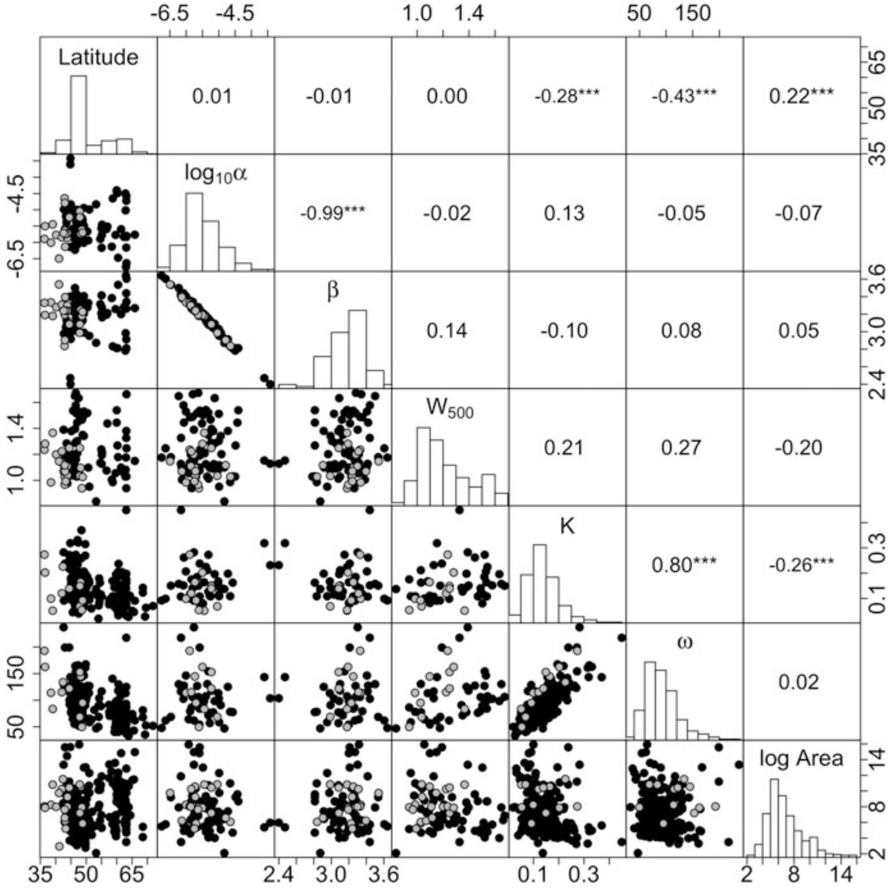

Fig. 4 Scatter-plot matrix of growth-based life history metrics ($\log_{10}\alpha$ = intercept of weight–length relationship; β = slope of weight–length relationship; W_{500} = weight of a 500-mm lake charr *Salvelinus namaycush* estimated from the weight–length relationship; K = instantaneous rate at which an average fish grew toward the asymptotic length L_∞; ω = annual growth rate at which lake charr grew) for native (black circles) and non-native (gray circles) lake charr *Salvelinus namaycush* populations in relation to latitude and surface area of lakes sampled in North America

SE = 1.98, $n = 251$) than non-native (114 mm/year, SE = 8.69, $n = 13$) populations ($F_{1,\,262} = 6.78$; $P = 0.010$).

Omega ($\omega = K \times L_\infty$) was proposed by Gallucci and Quinn (1979) to describe growth near t_0 as a statistically robust growth rate estimate for comparing populations. Shuter et al. (1998) found that ω was positively related to total dissolved solids (TDS) and not related to lake size (as in this study), thereby suggesting lake productivity influenced ω. Although we did not include TDS in our analyses, our findings also suggest that ω was higher in more productive lakes with warmer water temperatures and longer growing seasons, albeit using latitude as a surrogate for productivity and water temperature. McDermid et al. (2010a) used an index of pre-maturation growth (h; mm/year, mean length divided by age of immature fish within 3 years of t_{50}), which is like ω in representing early growth. Like our findings and those of Shuter et al. (1998) for ω, low h values were associated with cold temperature, whereas higher h values were associated with high productivity (i.e., higher TDS values; McDermid et al. 2010a; Wilson et al. 2019). Rate traits, like ω, are often associated with climate variables, because fish are ectotherms (McDermid et al. 2010a; Wilson et al. 2019).

3.2 *Instantaneous Growth Coefficient (***K***)*

Lake charr populations averaged 0.130/year in K for 264 populations. The distribution of K was skewed right (skew = 1.15) and platykurtic (kurtosis = 2.58). Estimates of K varied from a minimum of 0.020/year in Tagetochlain Lake, British Columbia, to a maximum of 0.450/year in Sevenmile Lake, Alaska, with 50% of populations varying between 0.099 and 0.171/year and 95% varying between 0.045 and 0.277/year (Table 1). Estimates of K were negatively correlated with both latitude and lake size (Fig. 4). Mean K did not differ significantly between native (0.139/year, SE = 0.004, $n = 251$) and non-native (0.137/year, SE = 0.017, $n = 13$) populations ($F_{1,\,262} = 0.015$; $P = 0.90$).

Like ω, K was negatively correlated with latitude, which was not surprising because ω includes K and the two metrics are correlated ($r = 0.800$, $n = 263$, $P < 0.001$). The relationship is likely explained because water temperature covaries with latitude. Interestingly, K was not correlated with latitude for lake charr populations outside their native range ($r = 0.350$, $n = 12$, $P = 0.14$), which is most likely a function of low variation in water temperature and low sample size. Estimates of K were also negatively correlated with the lake area. A higher percentage of the variation in K was explained by $\log_{10}$ surface area for 47 populations in Ontario ($r^2 = 0.02$, Payne et al. 1990) than for 253 populations in our review ($r^2 = 0.07$, this study). The decline in K with lake area may also be an artifact of the strong negative correlation between K and L_∞, rather than a function of slow growth in large lakes (Payne et al. 1990).

4 Body Condition

4.1 *Weight at Length = 500 mm (***W***$_{500}$)*

Lake charr populations averaged 1.16 kg in W_{500} for 97 populations. The distribution of W_{500} was skewed right (skew = 0.59) and leptokurtic (kurtosis = −0.67). Estimated W_{500} varied from a minimum of 0.84 kg in Sassenach Lake, Alberta, to a maximum of 1.67 in Flack Lake, Ontario, with 50% of the populations varying between 1.07 and 1.37 kg and 95% varying between 0.944 and 1.643 kg (Table 1).

Estimated W_{500} was not correlated with either latitude or lake size (Fig. 4). Mean W_{500} was significantly heavier for native (1.25 kg, SE = 0.02, $n = 75$) than for non-native (1.10 kg, SE = 0.04, $n = 22$) populations ($F_{1,\ 95} = 10.86$; $P = 0.001$).

The difference in W_{500} between native and non-native populations could be a result of non-native lake charr populations being dominated by the lean morph, despite lakes with non-native populations being deeper on average (mean = 124 m, SE = 23.8) than lakes with native populations (mean = 62 m, SE = 3.5). Large variation in maximum depth of lakes with non-native populations was caused by two large lakes, Tahoe, Nevada (501 m) and Pend Oreille, Idaho (351 m). The lean (slender) morph typically lives in depths <50 m, whereas the siscowet (fat) morph lives in depths >80 m (Hansen et al. 2016a; Chavarie et al. 2021). The fat morph in Great Slave Lake Northwest Territories, Canada was much heavier than the lean morph at 500 mm (fat morph = 1.183 kg, lean morph = 0.978 kg; Hansen et al. 2016a). Where lake charr are non-native, they are typically sampled in depths < 80 m, which suggests the lean morph predominates in these systems. For example, most lake charr are caught at depths < 60 m in Yellowstone Lake, Wyoming (Syslo et al. 2016).

4.2 *Weight–Length Parameters (log$_{10}$(α) and β)*

Lake charr weight-at-length was described by an average intercept of $\log_{10}(\alpha) = -5.589$ and an average slope of $\beta = 3.210$ among 97 populations. The distribution of $\log_{10}(\alpha)$ was skewed right (skew = 0.81) and platykurtic (kurtosis = 1.45), whereas the distribution of β was skewed left (skew = −0.83) and platykurtic (kurtosis = 1.48). Estimates of $\log_{10}(\alpha)$ varied from a minimum of −6.754 in Landlocked Tangle Lake, Alaska, to a maximum of −3.425 in Wollaston Lake, Ontario, with 50% of populations varying between −5.834 and −5.173 and 95% varying between −6.485 and −4.413 (Table 1). Estimates of β varied from a minimum of 2.400 in Wollaston Lake, Ontario, to a maximum of 3.640 in Landlocked Triangle, Alaska, with 50% of populations varying between 3.080 and 3.307 and 95% varying between 2.794 and 3.538 (Table 1). Estimates of $\log_{10}(\alpha)$ and β were both not correlated to latitude or lake size (Fig. 4). Mean $\log_{10}(\alpha)$ did not differ significantly between native (−5.458, SE = 0.066, $n = 75$) and non-native (−5.572, SE = 0.122, $n = 22$) populations ($F_{1,\ 95} = 0.672$; $P = 0.41$). Similarly, mean β did not differ significantly between native (3.168, SE = 0.025, $n = 75$) and non-native (3.191, SE = 0.046, $n = 22$) populations ($F_{1,\ 95} = 0.19$; $P = 0.66$).

The average weight–length model from our review, $\log_{10}(g) = -5.589 + 3.210 \log_{10}(\text{mm})$, predicted weights that are slightly higher for small-sized (1.2 g higher at 200 mm), slightly lower for medium-sized (16 g lower for 500 mm), and much lower for large-sized lake charr (164 g lower for 800 mm) than predicted from the standard-weight model developed from 75th percentile weights at length, $\log_{10}(g) = -5.681 + 3.2462 \log_{10}(\text{mm})$ (Piccolo et al. 1993). The average weight–length model reported here can be used to estimate relative condition, $K_n = (W/W')$, where W is the measured weight of an individual fish, and W' is the predicted weight of a fish of the same length using our weight–length equation (Neumann et al. 2012). Our average weight–length model may be useful for judging how the mean length-specific body condition of a population compares to the 96 populations tabulated from across native and non-native ranges.

5 Length and Age at 50% Maturity (L_{50} and t_{50})

Lake charr populations matured at an average L_{50} of 420 mm and an average t_{50} of 8.0 years among 203 populations. The distribution of L_{50} was skewed right (skew = 0.16) and leptokurtic (kurtosis = −0.33), whereas the distribution of t_{50} was skewed right (skew = 1.67) and platykurtic (kurtosis = 5.58). Estimates of L_{50} varied from a minimum of 208 mm in Sassenach Lake, Alberta, to a maximum of 660 mm in Tremblant Lake, Quebec, with 50% of populations varying between 357 and 480 mm and 95% varying between 273 and 598 mm (Table 1). Estimates of t_{50} varied from a minimum of 2.9 years in Lake Erie to a maximum of 27 years in Qamanirjuaq Lake, Nunavut, with 50% of populations varying between 6.4 and 10.0 years and 95% varying between 4.0 and 16.3 years (Table 1). Estimates of L_{50} were unrelated to latitude and positively related to lake size (Fig. 3), whereas estimates of t_{50} were positively related to both latitude and lake size (Fig. 2). Mean L_{50} was significantly shorter for native (418 mm, SE = 6.08, $n = 195$) than for non-native (487 mm, SE = 30.0, $n = 8$) populations ($F_{1,\ 201} = 5.04$; $P = 0.025$). In contrast, mean t_{50} did not differ significantly between native (8.5 years, SE = 0.227, $n = 196$) and non-native (8.1 years, SE = 1.12, $n = 8$) populations ($F_{1,\ 202} = 0.102$; $P = 0.75$).

Patterns of L_{50} and t_{50} were generally inconsistent with patterns of growth described above. First, the lack of a relationship between L_{50} and latitude was surprising, because we found that ω was negatively correlated to latitude, which should have led to shorter L_{50} at high latitudes (Healey 1978; McDermid et al. 2010a; Wilson et al. 2019). In contrast, our findings of a positive correlation between t_{50} and latitude and a negative correlation between ω and latitude were expected (McDermid et al. 2010a; Wilson et al. 2019). Positive correlations we found between lake size and both L_{50} and t_{50} were surprising, because ω was not correlated with lake size (consistent with Shuter et al. 1998). We did not differentiate between L_{50} and t_{50} of males and females, because L_{50} and t_{50} often do not differ (e.g., Hansen et al. 2016a). For populations with separate maturity estimates for males and females, we found that males and females did not differ significantly in t_{50} (< 1.0 year):

GM functional regression; $L_{50\ \mathrm{sex\ =\ F}} = 0.8621 + 1.0107 \times L_{50\ \mathrm{sex\ =\ M}}$, $R^2 = 0.884$

H_0 = intercept $b_0 \neq 0$, $t_{1,\ 29} = 0.98$; $P = 0.34$;
H_0 = slope $b1 \neq 1$, $t_{1,\ 29} = 0.13$; $P = 0.91$.

In contrast, males matured at a significantly shorter L_{50} (86-mm) than females: GM functional regression; $t_{50\ \mathrm{sex}\,=\,\mathrm{F}} = 86.132 + 0.9379 \times t_{50\ \mathrm{sex}\,=\,\mathrm{M}}$, $R^2 = 0.777$

H_0 = intercept $\neq 0$, $t_{1,\ 25} = 97.9$; $P < 0.001$;
H_0 = slope $\neq 1$, $t_{1,\ 25} = 0.72$; $P = 0.48$.

Such a small difference in t_{50} may not be statistically detectable for many sample sizes, whereas large differences in L_{50} seem more likely to be statistically detectable. Martin and Olver (1980) also suggested that males matured 1-year younger than females. After reaching maturity, lake charr females do not always spawn every year (i.e., resting = mature, but with eggs not ready for spawning). For example, L_{50} increased from 443 to 614 mm, and t_{50} increased from 11.4 to 21.4 years for siscowet lake charr in Lake Superior, when mature resting females were treated as immature (Sitar et al. 2014). Larger L_{50}, but similar t_{50}, for non-native populations, compared to native populations, was likely caused by faster ω that enabled non-native populations to reach mature age at a larger size.

6 Fecundity (eggs/kg)

Lake charr fecundity averaged 1396 eggs/kg for 23 populations (see also Goetz et al. 2021). The distribution of estimated fecundity was skewed right (skew = 0.70) and platykurtic (kurtosis = 0.24). Fecundity varied from a minimum of 883 eggs/kg in Greenwich Lake, Ontario, to a maximum of 2226 eggs/kg in Burnt Island, Ontario, with 50% of the populations varying between 1244 and 1599 eggs/kg and 95% varying between 1032 and 2031 eggs/kg (Table 1). Fecundity was not correlated with latitude or lake size (Fig. 5). Fecundity did not differ significantly between native (1445 eggs/kg, SE = 73.7, $n = 17$) and non-native (1419 eggs/kg, SE = 124, $n = 6$) populations ($F_{1,\ 21} = 0.032$; $P = 0.86$).

Fecundity increased with the body size of lake charr in Lake Superior (Eschmeyer 1955; Peck 1988), although a similar pattern was not evident for all populations (Martin and Olver 1980). If fecundity generally increases with body size, average fecundity would vary with size distribution of fish sampled, and thereby explain some variation in fecundity among populations. Healey (1978) found that fecundity was not lower for northern populations, as we found, although his review included only seven populations. Fecundity may not be sensitive to variation in growth or maturity, because fecundity–length relationships were similar among five of six lakes in northwestern Ontario, despite slower ω and older t_{50} in three lakes of lower conductivity (Trippel 1993).

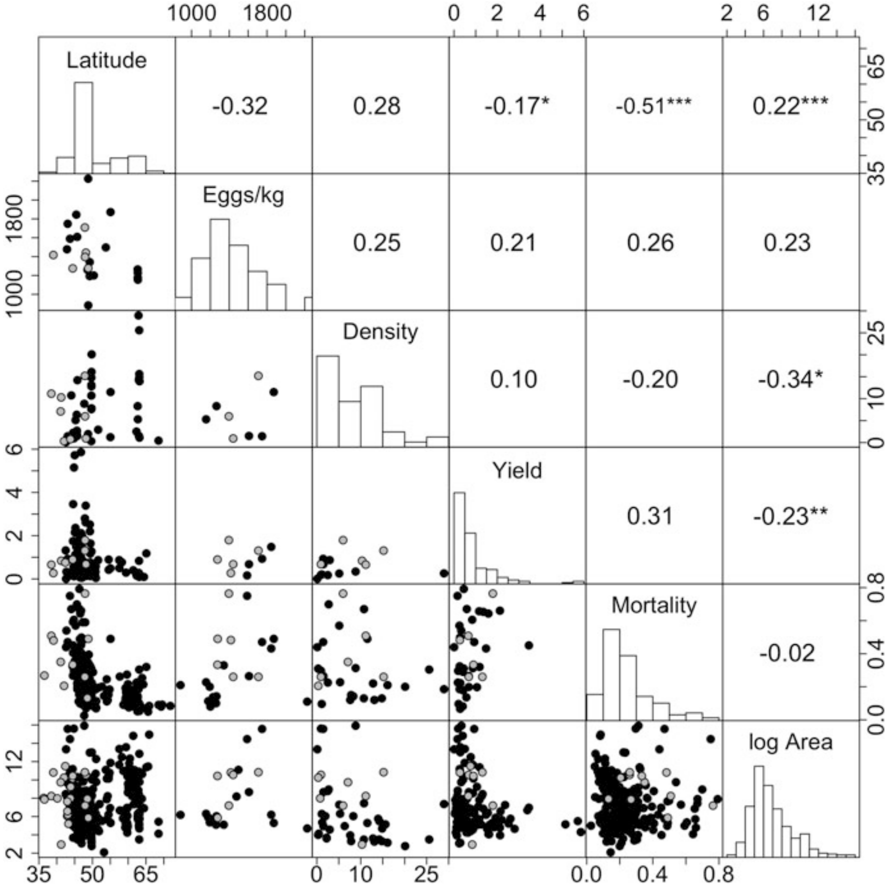

Fig. 5 Scatter-plot matrix of population metrics (Eggs/kg = fecundity per kg of body weight; Density = number per ha of the lake charr *Salvelinus namaycush* population; Yield = kg per ha of lake charr harvested; Mortality = total annual mortality) for native (black circles) and non-native (gray circles) lake charr populations in relation to latitude and surface area of lakes sampled in North America

7 Maximum Size and Age

7.1 Asymptotic Length (L_∞)

Lake charr populations averaged 717 mm in L_∞ among 293 populations. The distribution of L_∞ was skewed right (skew = 1.28) and platykurtic (kurtosis = 2.11). Estimated L_∞ varied from a low of 343 mm in Sassenach Lake, Alberta, to a high of 1687 mm in Cote Lake, Quebec, with 50% of populations varying between 605 and 880 mm and 95% varying between 457 and 1396 mm (Table 1). Estimated L_∞ was unrelated to latitude and positively related to lake size (Fig. 3), opposite from ω

(negatively correlated with latitude and not correlated with lake size). Mean L_∞ was significantly shorter for native (756 mm, SE = 13.3, $n = 280$) than non-native (916 mm, SE = 62.3, $n = 13$) populations ($F_{1,\ 291} = 6.34$; $P = 0.012$).

As in our review, McDermid et al. (2010a) found that L_∞ was not correlated with latitude, and Payne et al. (1990) and Shuter et al. (1998) found that L_∞ was positively correlated with lake surface area. Population mean L_∞ is difficult to estimate accurately because large old fishes are inherently rare, so L_∞ is informed by very few fish, regardless of their size in relation to the true population mean L_∞. Furthermore, the age of old fish is underestimated from scales (Dubois and Lagueux 1968; Burnham-Curtis and Bronte 1996), which was the structure used for many historical studies (Healey 1978; Martin and Olver 1980) that often causes biologically unreasonable estimates of L_∞ (in addition to all other growth parameters). Consequently, L_∞ is sometimes estimated indirectly, if available sampling data does not permit accurate estimation as a parameter of a length–age model. Such indirect methods usually rely on setting L_∞ equal to the mean length of a subset of large individuals in the sample. For example, L_∞ of lake charr sampled from lakes used to develop the lake charr management model in Lester et al. (2021) was indirectly estimated as the mean length of the largest 10% of fish sampled, excluding fish shorter than 300 mm. Native populations likely grew to a shorter L_∞ than non-native populations because they grew slower (lower ω), which thereby led to a shorter L_{50} and L_∞ for native populations than non-native populations.

7.2 Maximum Length ($\mathbf{L}_{max}$) and Age ($\mathbf{t}_{max}$)

Lake charr populations averaged 851 mm in $L_{\max}$ and 23 years in $t_{\max}$ among 272 populations. The distribution of $L_{\max}$ was skewed left (skew = −0.21) and leptokurtic (kurtosis = −0.64), whereas the distribution of $t_{\max}$ was skewed right (skew = 0.77) and platykurtic (kurtosis = 0.66). Estimates of $L_{\max}$ varied from a low of 372 mm in Sassenach Lake, Alberta, to a high of 1200 mm in Snowbird Lake, Nunavut, and Mosquito Lake, Northwest Territories, with 50% of populations varying between 700 and 949 mm and 95% varying between 506 and 1120 mm (Table 1). Estimates of $t_{\max}$ varied from a low of 4 years in Matagamasi Lake, Ontario, to a maximum of 68 years in Great Bear Lake, Northwest Territories, with 50% of populations varying between 16 and 32 years and 95% varying between 8 and 49 years (Table 1). Estimated $L_{\max}$ and $t_{\max}$ were both positively related to latitude and lake size (Figs. 2 and 3). Mean $L_{\max}$ did not differ significantly between native (826 mm, SE = 10.45, $n = 260$) and non-native (869 mm, SE = 48.7, $n = 12$) populations ($F_{1,\ 270} = 0.75$; $P = 0.39$). Similarly, mean $t_{\max}$ did not differ significantly between native (24.4 years, SE = 0.681, $n = 260$) and non-native (24.2 years, SE = 3.17, $n = 12$) populations ($F_{1,\ 269} = 0.003$; $P = 0.95$).

A positive relationship between $L_{\max}$ and latitude was somewhat surprising, because McDermid et al. (2010a) found no such relationship for lake charr populations across the range. In contrast, our findings of positive relationships between lake size and estimated $L_{\max}$ and $t_{\max}$ were confirmed by McDermid et al. (2010a). Estimates of $L_{\max}$ and $t_{\max}$ of lake charr are subject to the same biases of size-selective sampling and age estimation described above in relation to L_{∞}. The heaviest known lake charr (46.3 kg), not nearly the longest (126.0 cm), was caught by gillnetting in Lake Athabaska, Saskatchewan, on 8 August 1961 (Scott and Crossman 1973). The two longest lake charr known (157.5 cm), not nearly the heaviest, were caught by angling from Bennett Lake, Yukon, in 1906 (39.5 kg) and Lake Huron in 1888 (36.3 kg, Martin and Olver 1980). Maximum ages of 62 years were reported from Contwoyto Lake, Nunavut, Qamanirjuaq Lake, Nunavut (formerly Kaminuriak Lake, Northwest Territories, Bond 1975, cited by Martin and Olver 1980), and Zeta Lake, Nunavut (Campana et al. 2008). The latter fish was part of the definitive age validation study of lake charr based on bomb-radiocarbon signatures in otoliths of fish hatched before the period of nuclear bomb testing, which showed that thin-sectioned otoliths accurately recorded interpretable ages to at least 50 years (Campana et al. 2008).

8 Mean Length (L_{ave}) and Age (t_{ave})

Lake charr populations averaged 475 mm in L_{ave} among 270 populations and 8.0 years in t_{ave} among 268 populations. The distribution of L_{ave} was skewed right (skew = 0.51) and platykurtic (kurtosis = 0.59), and the distribution of t_{ave} was also skewed right (skew = 1.51) and platykurtic (kurtosis = 2.47). Estimates of L_{ave} varied from a minimum of 225 mm in Rawson Lake, Ontario, to a maximum of 824 mm in Red Lake, Ontario, with 50% of populations varying between 405 and 544 mm and 95% varying between 327 and 704 mm (Table 1). Similarly, estimates of t_{ave} varied from a minimum of 1.9 years in Matagamasi Lake, Ontario, to a maximum of 28.7 years in Qamanirjuaq Lake, Nunavut, with 50% of populations varying between 6.3 and 12.0 years and 95% varying between 4.1 and 22.4 years (Table 1). Estimates of L_{ave} and t_{ave} were both positively related to latitude and lake size (Figs. 2 and 3). Mean L_{ave} did not differ significantly between native (483 mm, SE = 6.18, $n = 259$) and non-native (477 mm, SE = 30.0, $n = 11$) populations ($F_{1, 268} = 0.038$; $P = 0.84$). Mean t_{ave} did not differ significantly between native (9.6 years, SE = 0.30, $n = 259$) and non-native (7.2 years, SE = 1.59, $n = 9$) populations ($F_{1, 266} = 2.27$; $P = 0.13$).

Lack of correlations between L_{ave} and t_{ave} and latitude and area, along with lack of differences between native and non-native populations, may be an artifact of relatively large variation in size selectivity among sampling methods that reduced power to detect such patterns and differences. Accurate estimation of L_{ave} and t_{ave} requires relatively random samples of all sizes and ages of fish from the population, which can only be obtained by using sampling methods that subject all sizes of fish to an equal vulnerability to capture. However, sampling methods used for populations in our review varied among agencies, with angling or gillnetting (fishery-dependent or fishery-independent) being most common. Size selectivity can differ between angling and gillnetting (e.g., Hansen et al. 2010, 2019b) but can also be similar (e.g., Sitar et al. 1999; Linton et al. 2007), depending on gillnetting mesh sizes (Hansen et al. 1997). Such differences in size selectivity among samples in our review would thus induce variation in L_{ave} and t_{ave} when comparing among populations sampled by different methods. Nonetheless, the effect of gear selectivity on our estimates of L_{ave} and t_{ave} is likely to be similar across sampling programs, so our summaries of these metrics will still be useful benchmarks.

9 Population Indices

9.1 Population Density (N/ha)

Lake charr population density averaged 7.1 fish/ha among 45 populations. The distribution of population density was skewed right (skew = 0.87) and platykurtic (kurtosis = 0.29). Population density varied from a low of 0.11 fish/ha in Lake Erie to a high of 28.9 fish/ha in Paxson Lake, Alaska, with 50% of populations varying between 1.5 and 13.1 fish/ha and 95% varying between 0.3 and 25.0 fish/ha (Table 1). Population density was unrelated to latitude and negatively related to lake size (Fig. 5). Population density did not differ significantly between native (8.4 fish/ha, SE = 1.2, $n = 37$) and non-native (6.5 fish/ha, SE = 2.5, $n = 8$) populations ($F_{1,\ 43} = 0.474$; $P = 0.50$).

Our review expanded greatly on earlier reviews by Healey (1978; 6 estimates) and Martin and Olver (1980; 15 estimates) and thereby increased the range of population density. Consistent with the lake-size pattern we observed, Healey (1978) alluded to an inverse relationship between population density and lake size, because the highest densities in his review were from the smallest lakes. This result may be related to reduced habitat area for lake charr in large, deep lakes. For example, habitat area for the lean (shallow-water) form of lake charr in the upper Laurentian Great Lakes is defined as surface area shallower than 80 m (Lake Michigan, Holey et al. 1995; Lake Superior, Hansen 1996; Lake Huron, Ebener 1998). Lake surface area was directly related to maximum depth for lake charr lakes in our review ($\log_e(\text{depth}) = 2.469 + 0.204 \times \log_e(\text{area})$; $F_{1,\ 345} = 286.5$; $P < 0.001$), so the proportion of total surface area that lays above 80 m declines with area and depth, thereby causing population density to decline with area. A lack of difference in population density between native and non-native populations was somewhat surprising, because fish assemblages in western lakes outside the native range generally have fewer species than in lakes within the native range, although fish community structure may have little effect on lake charr abundance, indexed by yield (Goddard et al. 1987). In contrast, the relative abundance of native lake charr populations appeared to decline rapidly after other species such as bass were introduced (Kaufman et al. 2009).

9.2 *Abundance Dynamics*

Temporal variation in lake charr abundance has been quantified for relatively few populations, but several long-term studies suggest that abundance may be more variable for exploited than unexploited populations. Notable long-term studies of abundance dynamics include: (1) native populations in the Laurentian Great Lakes, where populations collapsed from over-fishing and harvest is now intensively regulated to facilitate recovery; (2) non-native populations in several western lakes, where populations are presently subjected to intensive suppression programs; and (3) a small number of unexploited native populations in research lakes of Canada, where pristine populations were protected from harvest. In eight Michigan management areas of Lake Superior, exploited population abundance varied somewhat less among years before collapse (20–48% in 1929–1943) than during recovery (26–73% in 1984–1998), perhaps because of the contribution of stocked fish to reproduction during the period of recovery (Wilberg et al. 2003; Richards et al. 2004). In Lake Pend Oreille, Idaho, abundance varied among years as in Lake Superior, while declining exponentially in response to intentional and intensive exploitation (38% in 2006–2016, Dux et al. 2019). In contrast, unexploited populations varied only 8–18% among years for eight populations within the Experimental Lakes Area of northwestern Ontario (9–24 years per lake during 1975–1999; Mills et al. 2002).

9.3 *Yield Density (kg/ha)*

The yield density of lake charr populations averaged 0.57 kg/ha among 145 populations. The distribution of yield density was skewed right (skew = 2.82) and platykurtic (kurtosis = 10.01). Yield density varied from a low of 0.004 kg/ha in Lake Erie to a high of 5.86 kg/ha in Cut Lake, Ontario, with 50% of populations varying between 0.28 and 0.98 kg/ha and 95% varying between 0.07 and 3.42 kg/ha (Table 1). Yield density was negatively correlated to both latitude and lake size (Fig. 5). Mean yield density did not differ significantly between native (0.86 kg/ha, SE = 0.083, $n = 137$) and non-native (0.90 kg/ha, SE = 0.344, $n = 8$) populations ($F_{1,\ 143} = 0.015$; $P = 0.90$).

Based on an often-cited earlier review of lake charr populations across the species' range, Healey (1978) predicted that yield density higher than 0.5 kg/ha would cause over-fishing, which was exceeded by more than half (52%) of 145 populations in our review across the species' range. Even lake charr populations that experience only angling can collapse quickly (< 4 months) if harvest approaches 4.0 kg/ha (Gunn and Sein 2000). The negative correlation between yield density and latitude we found was likely caused by the inverse relationship between ω and latitude, whereas the negative correlation between yield density and lake surface area may be related to reduced habitat area for lake charr in very large, often very deep, lakes. Similarly, relationships between annual yield (kg/year) or yield density and lake size have often been studied as possible indirect predictors of sustainable yield (Goddard et al. 1987; Christie and Regier 1988; Payne et al. 1990; Marshall 1996; Shuter et al. 1998). Most earlier studies also found that yield density declined with lake surface area, because the slope of the relationship between $\log_{10}$(kg/year) and $\log_{10}$(ha) was significantly less than 1.0 (slope = 0.435, Goddard et al. 1987; slope = 0.706, Christie and Regier 1988; slope = 0.844, Marshall 1996; slope = 0.83, Payne et al. 1990, Shuter et al. 1998). Our spatial coverage of this topic is the most expansive to date, so we provide the predictive relationship here: $\log_{10}(\text{kg/year}) = -0.00463 + 0.912 \times \log_{10}(\text{ha})$ ($r^2 = 0.850$; $F_{1,\ 143} = 808.9$; $P < 0.001$). The lack of a difference between yield density of native and non-native populations was surprising because some non-native populations are being subjected to intensive long-term exploitation (e.g., Lake Pend Oreille, Idaho, Yellowstone Lake, Wyoming; Hansen et al. 2019a, b).

9.4 Total Annual Mortality (A)

Lake charr populations averaged 0.205 in A among 248 populations. The distribution of A was skewed right (skew = 1.41) and platykurtic (kurtosis = 1.82). Estimates of A varied from a low of 0.026 in Touridi Lake, Quebec, to a high of 0.792 in Wakwekobi Lake, Ontario, with 50% of populations varying between 0.130 and 0.296 and 95% varying between 0.071 and 0.660 (Table 1). Estimates of A were negatively correlated to latitude but unrelated to lake size (Fig. 5). Mean A was significantly lower for native (0.237, SE = 0.0097, $n = 235$) than for non-native (0.360, SE = 0.041, $n = 13$) populations ($F_{1,\ 246} = 8.46$; $P = 0.004$).

As with yield density, Healey (1978) suggested that A should not exceed 50% to avoid over-fishing. Contrary to the result we found for yield density, we found that A of only 7% of 245 populations exceeded 50%, which suggests that most lake charr populations were not over-exploited, based on Healey's recommended biological reference point. This observation was somewhat surprising, because exploitation is the single most critical stress affecting lake charr populations in Precambrian Shield lakes of eastern Canada and northeastern United States (Olver et al. 2004). Not surprisingly, we found a negative correlation between A and latitude, likely because ω was inversely related to latitude (this study) and directly related to natural mortality (Pauly 1980). In contrast, the lack of correlation to lake size we found was somewhat surprising, because L_∞ was positively related to lake size (Shuter et al. 1998; this study) and negatively related to natural mortality (Pauly 1980; Shuter et al. 1998). Last, higher A for non-native populations we found may reflect intensive suppression programs aimed at non-native populations in some western lakes (e.g., Lake Pend Oreille, Idaho, Yellowstone Lake, Wyoming; Hansen et al. 2019a, b).

10 Summary and Synthesis

10.1 Lake Charr Life History and Population Dynamics

An average lake charr in an average population grew from an L_0 of 69 mm at an ω of 89 mm/year to an L_{50} of 420 mm and t_{50} of age 8 and then continued to grow toward an L_∞ of 717 mm (Fig. 6). L_{50} was positively correlated to ω ($r = 0.272$; df $= 168$; $P < 0.001$) and t_{50} was inversely correlated to ω ($r = 0.516$; df $= 169$; $P < 0.001$). Lake charr grew slower toward larger sizes and older ages in northern latitudes than in southern latitudes and in larger lakes than in smaller lakes (Figs. 2, 3, and 4). Lake charr populations averaged 7.1 fish/ha in density, 0.57 kg/ha in yield density, and 20.5% in A. Population and yield density decreased with lake size, and yield density and A decreased with latitude. Many patterns we observed in life history and population metrics were also observed by Healey (1978), Martin and Olver (1980), Shuter et al. (1998); and McDermid et al. (2010a), which attests to the robustness of these patterns for lake charr populations. Most metrics did not differ between native and non-native populations, although native populations grew

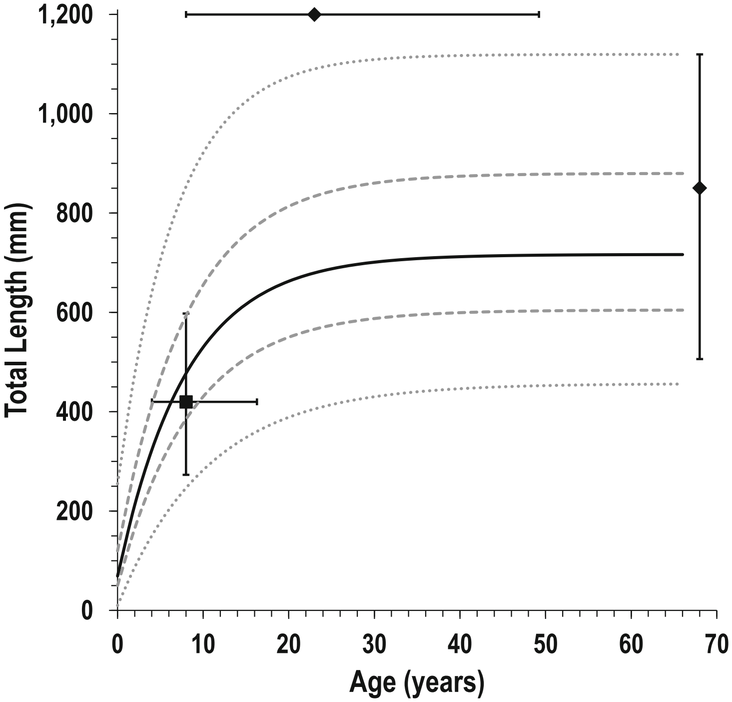

Fig. 6 Length at age for an average (solid black line) lake charr *Salvelinus namaycush* population in North America (gray dashed lines = 50% of populations; gray dotted lines = 95% of populations), along with length and age at 50% maturity (black square ± 95% confidence limits) and maximum length and age (black diamonds ± 95% confidence limits)

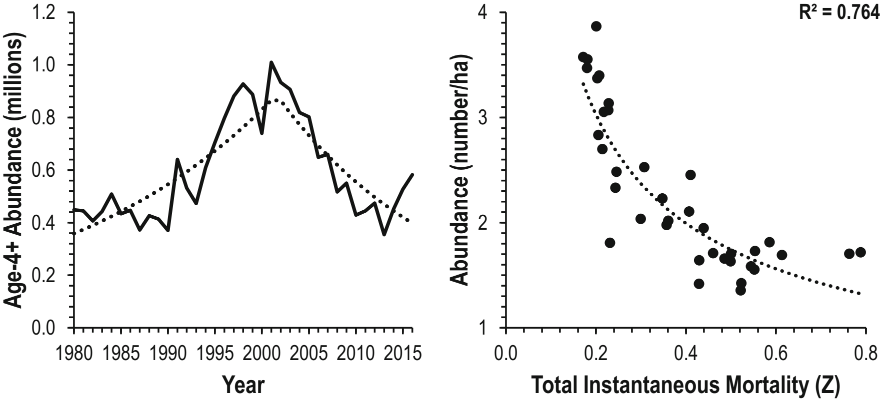

Fig. 7 Abundance of age-4+ lake charr (left panel; thick black line = annual estimates, dotted line = exponential function) and the relationship between population density of age-4+ lake charr and total instantaneous mortality (right panel; blackened circles = annual estimates, dotted line = power function) estimated by statistical catch-age analysis of stock-assessment statistics for western Lake Superior during 1980–2017

23 mm/year slower in ω, were 0.15 kg heavier in W_{500}, matured at 69-mm shorter L_{50}, grew to a 160-mm shorter L_{∞}, and suffered 12% lower A than non-native populations.

The lake charr population residing in western Lake Superior provides an interesting case study of the vulnerability of the lake charr, as a species, to fishing mortality. Lake charr stocks famously collapsed in the first half of the twentieth century, initially because of intensive fishery exploitation, and later because of added mortality caused by sea lamprey predation (Hansen 1999). Lake-wide controls on fisheries, combined with intensive stocking and sea lamprey control, enabled stocks to recover to the point that stocking was stopped in the 1990s (Hansen and Bronte 2019). In Wisconsin waters of western Lake Superior, population density of wild (non-stocked) lake charr increased through 2000 but subsequently declined because of increased fishing mortality, which greatly exceeded natural sources of mortality (including sea lamprey) that were relatively stable throughout the period (WSTTC 2017). From 1980 through 2001, abundance of age-4+ lake charr estimated with a stock-assessment model increased exponentially ($\lambda = 1.04$), more than doubling in size, while fishing mortality declined from as much as 83% to less than 25% of total mortality (Fig. 7). In contrast, from 2001 through 2017, abundance of age-4+ lake charr declined exponentially ($\lambda = 0.95$), halving in size, as fishing mortality increased from less than 25% to as much as 80% of total mortality (Fig. 7). The inverse relationship between stock size (number/ha) and total instantaneous mortality, $Z = -\log_e(1 - A)$, is a striking illustration of the susceptibility of the lake charr to fishing mortality.

10.2 Lake Charr Life History in Relation to Theory

Life history metrics of lake charr generally conformed to theoretical expectations (Jensen 1996, 1997) and empirical observations (Charnov 1993) of life-history invariants. First, the relationship between Z and K for lake charr populations ($Z/K = 1.876$; 95% CI = 0.494–8.351) was 25% higher than that based on life history theory (Fig. 8; $M/K = 1.5$; Jensen 1996) but was within the range of teleosts (Charnov 1993, $M/K = 1.7$, range = 1.6–2.1, for 175 fish stocks compiled by Pauly 1980). Among 29 estimators of the instantaneous natural mortality rate M reviewed by Kenchington (2014), 17 required an estimate of K, which attests to the strong relationship between these two life history metrics. Furthermore, K was

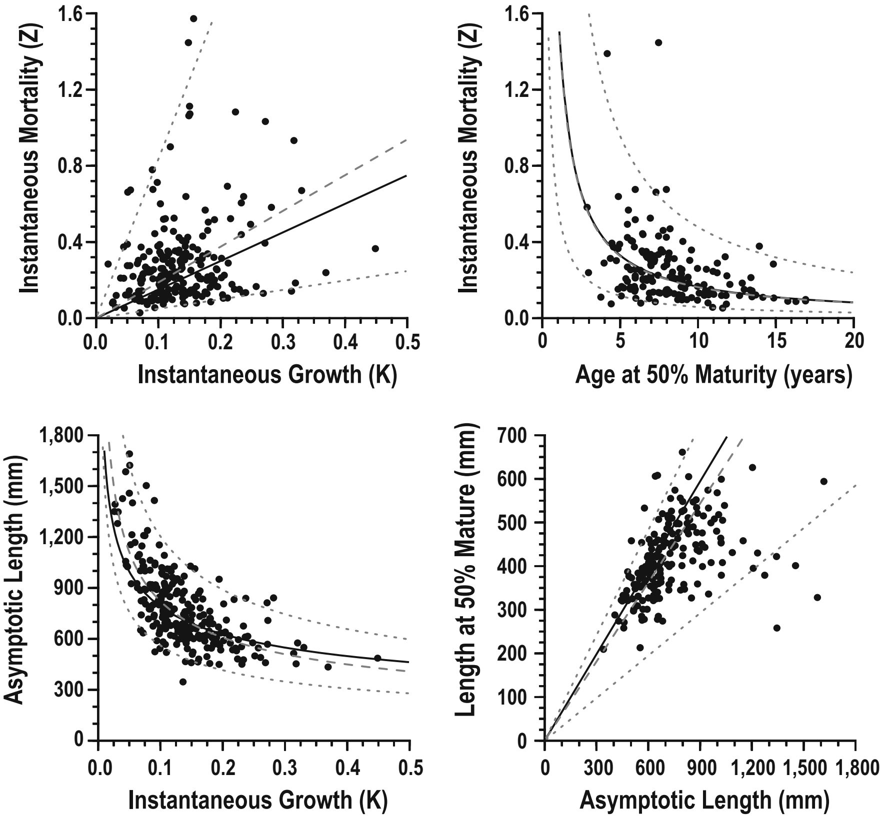

Fig. 8 Life-history invariants (solid black lines) compared to empirical relationships (median = dashed gray lines, 95% prediction interval = dotted gray lines) between instantaneous total mortality (Z = 1/year) and instantaneous growth (K = 1/year, upper left panel); instantaneous total mortality (Z = 1/year) and age at 50% maturity (t_{50} = years, upper right panel); asymptotic length (L_∞ = mm) and instantaneous growth (K; lower left panel); and length at 50% maturity and asymptotic length (mm) (K; lower right panel) for lake charr populations in North America

the dominant predictor of M in the multiple-regression model developed by Pauly (1980) that also includes size (W_∞ or L_∞) and temperature (Griffiths and Harrod 2007). Relative to what we found for lake charr ($Z/K = 1.876$), the ratio between Z and K was 5% higher for Arctic charr *Salvelinus alpinus* ($Z/K = 1.969$, SD = 0.171, $N = 26$ populations, Vøllestad and L'Abée-Lund 1994) but 38% lower for brown trout *Salmo trutta* ($Z/K = 1.155$; SD = 0.313; $N = 55$ populations, Vøllestad et al. 1993).

Second, the relationship between Z and t_{50} for lake charr populations ($Z \times t_{50} = 1.63$; 95% CI = 0.59–4.78) was nearly the same as expected based on life history theory (Fig. 8; $M \times t_{50} = 1.65$; Jensen 1996), and within the range of empirical values for fish in general (2.00; Charnov and Berrigan 1990), Gadiformes (1.54), Pleuronectiformes (1.54), and brown trout (3.33; Beverton and Holt 1959). Total mortality Z is inversely related to $t_{\max}$ (Hoenig 1980), so $Z \times t_{50}$ is analogous to an invariant that relates t_{50} to $t_{\max}$ ($M \times t_{50} \propto t_{50}/t_{\max}$; Beverton 1992). For the lake charr, the negative association between $\log_e(Z)$ and $\log_e(t_{\max})$ ($r^2 = 0.464$, $n = 208$, intercept = 1.841, SE = 0.254; slope = −1.049, SE = 0.0786) did not differ significantly from that of 53 other fish species ($r^2 = 0.68$, $n = 84$ stocks, intercept = 1.46; slope = −1.01, Hoenig 1980). Therefore, $t_{50}/t_{\max}$ for lake charr (median = 0.313; 95% CI = 0.151–0.614) did not differ significantly from the average or range of values for other species (median = 0.267; range = 0.16–0.39, Beverton 1992).

Third, the negative relationship between L_∞ and K for lake charr populations ($L_\infty = C \times K^h$, $h = -0.434$, 95% CI = −0.484 to −0.385; $C = 303$, 95% CI = 273–337) was steeper than expected from life history theory (Fig. 8; $h = -0.333$; Jensen 1997), but within the range observed for a wide range of species (Charnov and Berrigan 1991). In contrast, the estimated slope (h) of the relationship for lake charr was close to the overall value among populations of closely related species and among species ($h = -0.5$; Pauly 1980) and for multiple populations ($n = 13$–91 populations within species) of 11 species of Gadidae, Clupeidae, and Engraulidae ($h = -0.447$, SD = −0.129; Charnov and Berrigan 1991). Similarity of the relationship between L_∞ and K for lake charr populations to numerous other species, but steeper than expected from theory, may partly be explained by age-estimation error that would coincidentally overestimate L_∞ and underestimate K (Healey 1978; Payne et al. 1990).

Last, the relationship between L_{50} and L_∞ for lake charr populations ($L_{50}/L_\infty = 0.604$; 95% CI = 0.325–0.804) was less than 10% lower than that based on life history theory (Fig. 8; $L_{50}/L_\infty = 0.66$; Jensen 1996) and was only 2% higher than the average of 69 fish taxa ($L_{50}/L_\infty = 0.608$; SD = 0.17) tabulated by Beverton and Holt (1959). Similarly, the relationship between L_{50} and L_∞ we found for lake charr populations was within the range (0.47–0.79) of other taxa surveyed by Beverton (1992). Relative to what we found for lake charr, the ratio between L_{50} and L_∞ was only 2% higher for brown trout ($L_{50}/L_\infty = 0.617$; SD = 0.176; N = 55 populations, Vøllestad et al. 1993) and 21% higher for Arctic charr ($L_{50}/L_\infty = 0.728$, SD = 0.171, N = 30 populations, Vøllestad and L'Abée-Lund 1994). Based on the relationship between length at first maturity and L_∞ developed from 265 species in 88 families and 27 orders (Froese and Binohlan 2000), the length at first maturity for lake charr would be only 0.473 of the median L_∞ among all 292 populations compiled for our review.

10.3 Management Implications

For lake charr biologists and managers of both native and non-native populations, our summary provides a useful range-wide view of life history and population metrics that can serve as benchmarks for judging population status. For managers of native populations, the growth and maturity of typical populations (Fig. 6) can serve as benchmarks for judging the current status of populations being managed for harvest or progress toward restoration from a depleted state. For example, past assessments of the status of recovery of lake charr stocks in the Great Lakes could have been better informed and therefore managed with more realistic expectations if more complete knowledge of life-history characteristics had been available. For managers attempting to suppress lake charr for the benefit of other (often native) species, our summary suggests that the life history features of native and non-native populations are similar and therefore native and non-native populations are equally susceptible to fishery exploitation and collapse. For example, strategies that led to collapses of native populations could be employed for suppressing undesirable non-native populations.

10.4 Future Research Needs

Future research needs of lake charr life history and population dynamics fall under two categories:

Improving analytical approaches to estimating well-studied metrics;

Initiating studies of metrics that have only been rarely quantified. First, sampling programs across the range should rely on otoliths for age estimation and a standardized method of otolith preparation that matches the validated method (i.e., epoxy-embedded thin sections, Campana et al. 2008). Not surprisingly, results of many studies of lake charr life history and population dynamics were rendered useless because they relied on age-estimation structures such as scales that underestimate age with bias that increases with age (Dubois and Lagueux 1968; Burnham-Curtis and Bronte 1996). However, otoliths must also be prepared using a method that does not disturb or remove information, usually on the outer margin of the structure where many annuli reside (e.g., hand sanding, rather than embedding and thin-sectioning). Last, back-calculation can overcome sampling selectivity that often excludes small young fish, but also, the absence of large old fish that are rare in populations (Vigliola and Meekan 2009). To overcome these issues, back-calculated growth histories should be analyzed using nonlinear mixed-effects models that account for within-group correlation of longitudinal, autocorrelated, and unbalanced data (Vigliola and Meekan 2009). Choice of back-calculation model is also crucial, and we recommend either the linear biological-intercept model (Campana 1990) or the nonlinear biological-intercept model (Vigliola et al. 2000), whichever is appropriate for the sample (Vigliola and Meekan 2009).

Second, our review highlighted, by their omission, several life history metrics that would benefit from more study. Natural mortality is perhaps the most difficult life history metric to estimate directly, except for unexploited populations, which are increasingly scarce. For example, Shuter et al. (1998) found only six populations in all of Ontario where fishing mortality could be assumed to be zero. For most lake charr populations, indirect methods must be used to estimate natural mortality, such as models that rely on other life-history metrics (reviewed by Kenchington 2014) or by subtracting an estimate of fishing mortality from an estimate of total mortality (Ricker 1975). Like natural mortality, survival from pre-hatch embryo to age 1 (S_0) is extraordinarily difficult to measure, but unlike natural mortality, this metric is difficult to estimate because of logistical issues related to sampling early life stages in nature during the first year of life. For example, Bronte et al. (1995) quantified density, hatching dates, and movement of age-0 lake charr at Gull Island Shoal, in western Lake Superior, but were unable to estimate survival because of relatively continual recruitment in the nursery area. Nonetheless, Bronte et al. (1995) concluded that natural mortality was likely low during the first four months of life because: (1) mean density did not differ among sampling dates (should decline through time if mortality is relatively high); and (2) back-calculated hatch dates were relatively stable among successive sampling dates (should increase with sample date because earlier hatching individuals suffer greater accumulative mortality than later hatching individuals). In contrast, Ferreri et al. (1995) used a matrix model to estimate that age-0 lake charr survival was lower in 1988–1993 (current period) than either before the appearance of sea lamprey (1929–1950) or during the period of peak sea lamprey abundance (1951–1962). Relatively low survival from pre-hatch embryo to age-1 (Ferreri et al. (1995), but relatively high survival from pre-hatch embryo to 4-months of age (Bronte et al. 1995) suggests that most mortality in the first year of lake charr life occurs during the last 8 months of the first year. Early mortality can also be location-specific due to the presence of predators on early life history stages (e.g., Krueger et al. 1995). Nonetheless, we conclude that more such studies are needed to estimate this crucial life history metric.

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Trophic Ecology

Mark R. Vinson, Louise Chavarie, Caroline L. Rosinski, and Heidi K. Swanson

Abstract The trophic ecology of lake charr *Salvelinus namaycush* morphotypes from small and large lakes within their native and introduced ranges is reviewed over the past 50 years. The lake charr is an apex predator in most habitats it occupies, where it plays a significant role in defining food webs. While often considered piscivores, lake charr feed on a range of aquatic prey throughout their life history, including zooplankton, benthic invertebrates, and fish, as well as terrestrial insects, mammals, birds, amphibians, and reptiles. Lake charr diets that vary within morphotypes among lakes and among sympatric morphotypes reflect differences in habitat use, prey availability, and individual preferences. Temporal variability in diet can result from seasonal prey pulses, thermal barriers, and long-term prey dynamics. Lake charr adapt quickly to consume invasive prey fishes, and often decimate native prey fishes and other piscivores in lakes into which they are introduced. Salient research topics in lake charr trophic ecology include: (1) how best to quantify spatial and temporal trophic niche space; and, (2) how changing environmental conditions, such as invasive species and lake warming, will influence lake charr feeding and broader lake food-web dynamics.

Keywords Anadromy · Cannibalism · Consumption · Diet analysis · Methods · Energy · Fatty acids · Food · Feeding · Habitat · Habits · Movements · Food web · Structure · Feeding · Food habits · Foraging · Habitat coupling · Invasive species · Isotopes · Carbon · Nitrogen · Lake charr · Humper · Lean · Redfin · Siscowet ·

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Morphs · Niche · Non-native species · Nutrients · Ontogeny · Predation · Prey · Exotic · Production · Stable isotopes · Temporal variation · Trophic · Ecology · Levels · Niche · Position

1 Introduction

Trophic ecology, the study of animals' diets, benefits our understanding of predator–prey dynamics and movement of energy through ecosystems. The lake charr *Salvelinus namaycush* is a salmonid with multiple morphotypes that occupy a variety of habitats. Though known mostly as a piscivore, lake charr feed on a range of prey. The degree of dietary specialization of morphotypes that varies among and within populations reflects prey availability, lake charr size, water temperature, fishing pressure, and other variables. Differences in methods used to collect and interpret lake charr diet data, including season(s) sampled, habitats sampled, and tracers used (e.g., stomach contents, stable isotope ratios, fatty acids, DNA barcoding [deoxyribonucleic acid]), influence the ability to synthesize results and infer the trophic ecology, particularly over gradients of space and time.

Lake charr are usually the top fish predator in habitats they occupy. As such, they play a predominant role in structuring lower trophic levels and transferring energy between shallow littoral and deep limnetic and profundal habitats (i.e., habitat coupling). Effects of lake charr on the trophic structure of lakes have been attributed to their voracious and adaptable appetite, large body size, longevity, and the ability of individuals to survive periods of low prey abundance. Lake charr readily adapt to consuming new invasive prey fishes and novel native fishes in lakes into which they are introduced. These traits benefitted lake charr restoration efforts in places like Lake Superior but led to extirpation of native fishes and altered food webs in some lakes into which they were introduced.

Martin and Olver (1980) previously reviewed lake charr ecology, including feeding, and shared a wealth of information from early Canadian government reports that were previously difficult to access. A decade later, the Ontario Ministry of Natural Resources Lake Trout Physiology and Ecology Working Group reviewed the feeding ecology of lean lake charr in relation to population management (MacLean et al. 1990). In this chapter, we review the trophic ecology of the well-described lean lake charr and various lesser-studied intraspecific morphotypes of lake charr across North America, with an emphasis on siscowet, humper, redfin, and anadromous lake charr. Information is drawn principally from studies published in the primary literature over the past 50 years. We also examine how the trophic ecology of lake charr influences food-web structure of habitats into which they are introduced. We review traditional and emerging methods used to quantify trophic ecology and niche overlap, and how complementary techniques, such as telemetry, can contribute to understanding of the trophic ecology.

2 Methods

We used Google Scholar to search the keywords "lake trout, lake char(r), diet, *Salvelinus namaycush,* trophic ecology, feeding, stomach content, isotope, fatty acid" and manually searched the reference lists of publications we reviewed. This yielded ~200 published papers and government reports. Studies were categorized by lake charr morphotype: *lean,* a widespread slender littoral morphotype; *siscowet or fat,* a deep-bodied, deepwater morphotype; *humper* and *redfin*, less common shoal-associated morphotypes, and *anadromous* lake charr from the Arctic (see Chavarie et al. 2021 and plates 1–14 for morphotype descriptions). Studies were also categorized according to whether the population was native or introduced. For each study, we attempted to extract data on sampling years and season, sample size, diet tracer method, percent of fish stomachs collected that were empty (for studies that conducted stomach content analysis), occurrence of cannibalism, and the estimated fish length when transitioning from feeding primarily on invertebrates to becoming primarily piscivorous (i.e., ontogenetic shift). These data were collected to identify broad-scale patterns and begin to characterize the degree of variability in lake charr food habits. We also incorporated data from the U.S. Geological Survey Lake Superior Biological Station's unpublished data set of lake charr stomach contents obtained from lake charr collected throughout Lake Superior from April to November 2012–2018 following standard stomach content analysis methods (e.g., Bowen 1996; Ray et al. 2007; Scharf et al. 2000). These data were used to explore lake charr ontogenetic changes and prey size–predator size relationships, as these types of analyses have not been extensively published for lake charr (cf. Frantz and Cordone 1970; Madenjian et al. 1998; Ruzycki et al. 2003).

3 History of Lake Charr Trophic Ecology Studies

The earliest studies of lake charr trophic ecology focused on stomach content descriptions. Milner (1874) and Bean (1903) provided anecdotal information on diets of a few Lake Michigan lake charr that included mostly bloater *Coregonus hoyi*. Stomachs of 10 lake charr from Lake Michigan contained 21% sculpin (Cottidae), 23% bloater, 46% other fish, and 10% terrestrial insects (Pearse 1921). Lake charr in Lake Nipigon, Ontario, fed almost exclusively on cisco *Coregonus artedi* (Clemens et al. 1923, 1924) whereas lake charr in Lake Ontario fed almost entirely on alewife *Alosa pseudoharengus* (Dymond 1928). In small lakes (<500 km^2), diets of adult lake charr were dominated by the most abundant prey (Fry and Kennedy 1937; Cooper and Fuller 1945; Leonard and Leonard 1949; Martin 1952, 1966). Though based on few specimens, these early accounts showed lake charr were opportunistic predators that fed on native and exotic fishes, benthic and terrestrial invertebrates, zooplankton, and terrestrial animals, findings that would be extensively corroborated over the coming decades.

During 1930–1932, stomachs from nearly 5000 adult nearshore lean lake charr from Lake Michigan contained primarily *Coregonus* fishes (principally cisco and bloater) and sculpin (Van Oosten and Deason 1938). These native prey species were replaced in Lake Michigan lake charr diets by exotic rainbow smelt *Osmerus mordax* and alewife in subsequent decades. Eschmeyer (1956) documented the importance of invertebrates to juvenile lake charr in Lake Superior during their first 3 years of life.

The geographic scope of lake charr trophic studies expanded beyond the Laurentian Great Lakes in the 1940s. In Great Bear and Great Slave Lakes (Mackenzie Basin Great Lakes, Canada), lake charr diets contrasted with contemporaneous reports from the Laurentian Great Lakes (Miller and Kennedy 1948; Rawson 1951). In Great Bear Lake, fish occurred less than half as frequently in adult lake charr stomachs as plankton, benthic invertebrates, and terrestrial insects (Miller and Kennedy 1948). In comparison, fish typically accounted for >90% of prey consumed by adult lake charr in the Laurentian Great Lakes (Van Oosten and Deason 1938). Studies within small inland lakes of the Canadian Shield—led primarily by Nigel Martin in Algonquin Park, Ontario—resulted in numerous published accounts of lake charr life history and often unique diets from the 1940s through the 1970s (e.g., Martin 1952, 1954, 1966, 1970).

In the 1980s, central questions in lake charr trophic ecology were motivated by interest in the management of piscivorous sportfish stocks. In the Laurentian Great Lakes, prey fish communities that were formerly comprised of native *Coregonus* spp. and sculpins were now dominated by non-native alewife and rainbow smelt that fluctuated dramatically in abundance. Stocking of lake charr and Pacific salmonines in the Laurentian Great Lakes was simultaneously occurring at unprecedented high levels. Lake charr were also being widely introduced into lakes and reservoirs, principally in the western United States, to create trophy fisheries. While these introductions initially supported thriving fisheries, lake charr often quickly depleted native prey fish populations and competed with (often out-competing) native piscivores (Crossman 1995; Martinez et al. 2009). These scenarios led managers to ask, “what are the forage requirements of lake charr and other salmonines?” (e.g., Stewart et al. 1983; Ruzycki et al. 2001). Subsequent work led to a better understanding of the implications of stocking policies and provided foundational knowledge on the bioenergetics of lake charr (Hansen et al. 1993).

In the 1990s to the early 2000s, foraging behavior studies were initiated to improve bioenergetic models and enhance understanding of energy transfer pathways among species and between benthic and pelagic habitats. Descriptions of lake charr prey-acquisition behavior was an important outcome of this work (e.g., Beauchamp et al. 1999; Vogel and Beauchamp 1999; Dunlop et al. 2010; Holbrook et al. 2013; Keyler et al. 2015). Habitat work included descriptions of both horizontal (littoral-pelagic; e.g., Morbey et al. 2006; Dolson et al. 2009) and vertical habitat coupling (epilimnetic-hypolimnetic; Hrabik et al. 2006; Jensen et al. 2006; Marsden et al. 2021). More recent studies on habitat coupling have been driven by a desire to better estimate the effect of current and predicted lake warming (Woolway and

Merchant 2018) on lake charr feeding ecology and food-web dynamics (Dolson et al. 2009; Tunney et al. 2014; Guzzo et al. 2017).

Most recently, researchers have renewed interest in "old-school" lake charr trophic ecology descriptions with an eye toward better understanding how morphological and genetic diversity shapes life history strategies of lake charr morphotypes (see Chavarie et al. 2021). Understanding diversity of all aspects of lake charr biology and ecology is essential to meet conservation and restoration goals (Blackie et al. 2003; Swanson et al. 2010; Chavarie et al. 2016a; Vinson et al. 2020), and to reduce effects of lake charr in introduced habitats (e.g., Hansen et al. 2010; Stapp and Hayward 2002; Meeuwig and Peacock 2017).

4 Trophic Ecology Assessment Methods

Understanding the trophic ecology of lake charr requires information on what, where, and when fish are feeding. Stomach content analysis was the primary method for investigating diets from the 1800s through the end of the twentieth century and persists when the taxonomic composition of prey and short-term variability in diet is of interest. Studies of stomach contents report prey species counts, frequency of occurrence, weight, size, or volume of prey types, as well as occurrence of empty stomachs (e.g., Cortés 1997). Identification of prey in stomach contents has been historically based on morphology, but DNA barcoding has been available since 2003 (Hebert et al. 2003). A shortcoming of stomach content analysis is that it only provides information on recent consumption (hours). Stomach content analysis is also subject to biases due to regurgitation during capture, variable rates of digestion of food items, and disparities in the accuracy of identification of partially digested material. To partly compensate for these issues, stomach content studies often aggregate data across days, months, and years to reduce variability within individual sampling events that are associated with fish size, digestion, time of capture, weather, lunar activity, and occurrence of novel prey items. In studies we reviewed, the number of stomachs analyzed ranged from as few as two to more than 28,000. Measures of central tendency indicated large sample sizes are generally employed in stomach content studies (average = 1545, median = 148 individual fish per study).

DNA barcoding is a method used to identify an organism to species by comparing a short-standardized DNA sequence to a molecular reference library (Hebert et al. 2003). This approach has been shown to improve the ability to identify prey collected in stomach contents that lack distinct morphological characteristics, such as larval fish or partially digested items (Carreon-Martinez et al. 2011; Bartley et al. 2015; Jo et al. 2016). In a study of predatory fish diets in Canadian boreal shield lakes, more than 80% of stomach content items were identifiable to a lower taxonomic level with barcoding than with morphology (Bartley et al. 2015). Moreover, barcoding indicated that lean lake charr fed in both nearshore and offshore habitats whereas morphological stomach content analyses indicated that lean lake charr fed only in nearshore habitats (Bartley et al. 2015).

Beginning in the 1990s, stable isotope analyses were added to the "toolkit" used for studying trophic ecology. From an isotopic perspective, fish (tissues) "are what they eat" (*sensu* Boecklen et al. 2011). White muscle tissue has been the most frequently evaluated tissue of lake charr, but liver, blood plasma, fins, scales, otoliths, mucus, and eggs have also been evaluated. Isotopic turnover rate varies among tissue types and analyzing different tissues can thus provide insights into trophic ecology over multiple temporal scales (Vander Zanden et al. 2015). For adult rainbow trout *Oncoryhnchus mykiss*, $\delta^{13}C$ retention time was 154 (95% CI: 106–224) days for liver tissue and 292 (95% CI: 257–763) days for white muscle, and $\delta^{15}N$ retention time was 186 (95% CI: 114–329) days for both white muscle and liver (Skinner et al. 2017). Isotopic turnover in ectotherm tissues is also generally correlated with body mass (Vander Zanden et al. 2015).

Stable isotope analyses ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) of lake charr have been used to infer trophic level ($\delta^{15}N$), basal production sources ($\delta^{13}C$; benthic vs. pelagic [e.g., Hoffmann 2017]), trophic linkages (Harvey and Kitchell 2000), migrations (including anadromy, $\delta^{34}S$, e.g., Swanson et al. 2011), and habitat use (e.g., Chavarie et al. 2016a). Two- and three-isotope Bayesian mixing models were used to infer feeding patterns and distinguish hatchery-reared yearlings from similarly sized wild lake charr in Lake Ontario (Colborne et al. 2016). Sample sizes across isotopic studies we evaluated ranged from 8 to 575 fish. Measures of central tendency indicated much smaller sample sizes were used in isotopic studies than stomach content studies (average = 128, median = 60 individual fish per study). Many studies used both stable isotope analyses and stomach content analyses on the same individual, as complementary methods (e.g., Hulsman et al. 2016).

Over the past decade, analysis of fatty acids in muscle tissue has been increasingly used to examine lake charr diets. This technique provides insight into diet at a temporal perspective that is intermediate between stomach content and stable isotopic analyses (several weeks to months; e.g., Happel et al. 2016). Most vertebrates are unable to synthesize omega-3 fatty acids longer than 15 carbons (e.g., Lança et al. 2011), so these essential fatty acids are often used as diet tracers. Fatty acid signature studies have been used to evaluate differences in diet among lake charr morphotypes in Great Bear Lake (Chavarie et al. 2014) and Lake Superior (Hoffmann 2017), describe spatial variability in lean lake charr diets in Lakes Huron and Michigan (Happel et al. 2017a), and describe differences between lean lake charr and Pacific salmon diets in the Lake Ontario (Happel et al. 2017b). Sample sizes across studies ranged from 30–339 (average = 132, median = 76 individual fish per study). In these studies, both fatty acids and stomach contents were examined. Fatty acid signatures indicated greater diet specialization among lake charr morphotypes (Chavarie et al. 2014; Hoffmann 2017) and less overlap among Lake Ontario piscivores (Happel et al. 2017b) than stomach content analyses.

Fish tracking technology, such as acoustic (e.g., Hussey et al. 2015) and satellite (e.g., Block et al. 1998) telemetry, can be useful for assessing spatial-temporal dynamics in trophic resource use, particularly when movement data are combined with dietary tracers from sympatric individuals. Remotely collected data can include individual location, depth, temperature, dissolved oxygen concentration, and activity levels, which can be used to infer daily and seasonal feeding behavior patterns. Acoustic telemetry over an 11-year period was used to assess how annual variability in spring-summer water temperature altered access of lean lake charr to littoral habitats that supported preferred prey (Guzzo et al. 2017).

The most complete understanding of lake charr trophic ecology will come from integration of results from multiple methods (McMeans et al. 2016), and by explicitly accounting for different temporal scales represented by each method. For example, rates at which diet tracers were incorporated into tissues varied with prey quality and predator growth, and among tissues (e.g., O'Reilly et al. 2002; Martínez del Rio and Carleton 2012; Vander Zanden et al. 2015). Researchers need to be cognizant of these rates and qualify their inferences accordingly. The integration of diverse techniques is particularly important for discerning trophic ecology of lake charr, which have opportunistic feeding behaviors and which occupy high-latitude and often deep and remote lakes that are difficult to study year-round.

5 Trophic Ecology

5.1 Changes Through Ontogeny

Lake charr diets change through ontogeny. In Lake Superior, fry (i.e., free-embryos per Marsden et al. 2021) <25 mm did not have food in their digestive tracts, free-embryos 25–30 mm contained food and still had large yolk sacs, and all free-embryos >30 mm had food in their digestive tracts and no yolk sac (Swedberg and Peck 1984). Small Chironomidae were the primary prey consumed by lake charr free- and post-embryos, along with zooplankton and *Mysis* in the smallest fish, but some lake charr >30 mm also contained small sculpin and rainbow smelt. In Lake Champlain, 19% of lake charr free-embryos captured 2 weeks after hatching contained food, and by the time of yolk sac absorption, 98% of post-embryo stomachs contained a mix of cladoceran, calanoid, and cyclopoid zooplankton, and terrestrial insects (Ladago et al. 2016). In the Laurentian Great Lakes, age-0 lake charr consumed primarily *Mysis*, followed by zooplankton and aquatic insects (Eschmeyer 1956; Hudson et al. 1995; Roseman et al. 2009). Similar young-of-year feeding ontogeny, from small to progressively larger invertebrates, has also been observed in lakes in which lake charr were introduced, e.g., Lake Tahoe (Frantz and Cordone 1970).

An ontogenetic shift from near-total invertivory to near-total piscivory (in lakes where prey fish are available and abundant) in lake charr has been documented at lengths of 130–500 mm. Diets shifted from juvenile to adult (across all studies we examined with size-specific data) at 300 mm, including 292 mm for lean lake charr (11 studies) and 400 mm for siscowet (one study). Lean lake charr from the Laurentian Great Lakes underwent an ontogenetic shift from benthic to pelagic

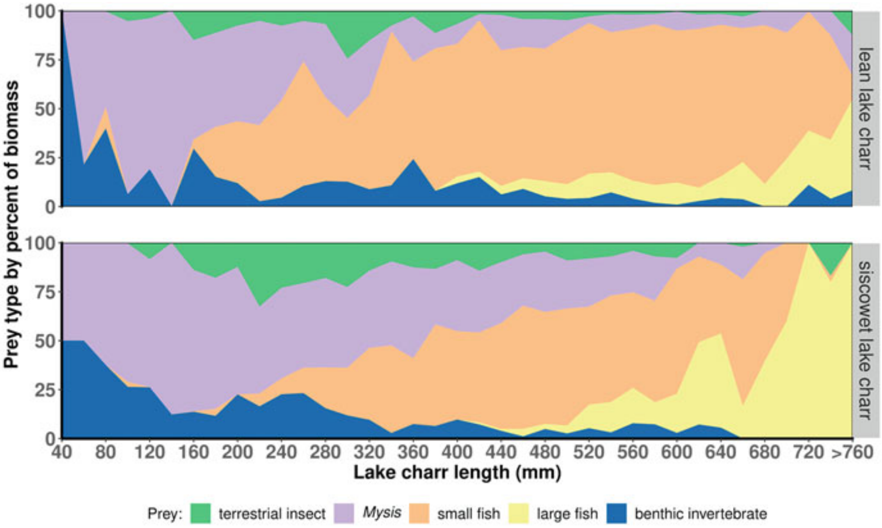

Fig. 1 Diet proportions by major prey type for lean and siscowet lake charr *Salvelinus namaycush* from Lake Superior. Data were calculated as prey biomass averages for individual lake charr within 20 mm total length bins. Fish were collected from April to October 2012–2018 by the Wisconsin Department of Natural Resources and U.S. Geological Survey using gill nets and bottom trawls. Small fish were <150 mm and large fish were >150 mm. Sample sizes were 3838 individual lean and 3577 individual siscowet lake trout

feeding at 400–490 mm (Muir et al. 2015) whereas shallow-water (lean-like) and deepwater (humper- and siscowet-like) morphotypes of lake charr from Great Slave Lake and Lake Mistassini (Quebec, Canada) underwent the same ontogenetic shift at ~430 mm (Zimmerman et al. 2006, 2009). Sculpin are often the first fish consumed by young lake charr (Eschmeyer 1956; Stewart et al. 1981; Eck and Wells 1986; Elrod 1983; Madenjian et al. 1998) in the Laurentian Great Lakes, presumably due to their availability to gape-limited predators. Similarly, juvenile lake charr consume age-0 alewife and rainbow smelt where they occur (Stewart et al. 1981; Elrod 1983; Eck and Wells 1986; Ray et al. 2007). In small Canadian Shield lakes, littoral prey fish species such as suckers *Catostomus spp.*, yellow perch *Perca flavescens*, johnny darter *Etheostoma nigrum*, and shiners *Notropis spp.* are often the first fish consumed by young lake charr (Martin 1952, 1970).

Data from Lake Superior (2012–2018) shows lean lake charr begin consuming primarily benthic invertebrates to mostly *Mysis* at ~50 mm, small fishes (<150 mm) at ~160 mm, and large fishes (>150 mm) at ~400 mm (Fig. 1). Prevalence of small fish consumption throughout life is due to eating rainbow smelt, a prey that is both abundant in nearshore habitats and typically <150 mm. Compared to leans, Lake Superior siscowet lake charr transition to consuming fish at a larger size, ~200 mm, and continue to eat a relatively high (~25% or more) proportion of *Mysis* until they reach a very large size (>660 mm). Siscowet lake charr transition from primarily consuming small fish to large fish at ~440 mm and large fish by the time they reach 700 mm.

Lake charr consume increasingly larger prey as they grow in both small and large lakes and for both native and introduced populations (Martin and Olver 1980; Frantz and Cordone 1970; Ruzycki et al. 2003). In Lake Michigan, invertebrates (principally *Mysis*) were consumed by lake charr <200 mm, slimy sculpin *Cottus cognatus* and deepwater sculpin *Myoxocephalus thompsonii* formed almost half of the diet of 200–400 mm lake charr, rainbow smelt dominated the diets of 400–600 mm lake charr, and alewife was the most important prey of the largest (>600 mm) lake charr (Madenjian et al. 1998). Lake charr in the Arctic consume conspecifics that were up to 50% of their own length (Swanson 2010). In Lake Tahoe, Nevada/California, introduced lake charr commonly ate prey up to 53% of their length (Frantz and Cordone 1970). In Yellowstone Lake, Wyoming, introduced lake charr began feeding on native Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* at 320 mm, consumed cutthroat trout that were 11–57% of their body length, and 90% of cutthroat trout prey were 20–45% of their length (Ruzycki et al. 2003). Conversely, the length of invasive alewife and rainbow smelt consumed by lean lake charr in Lake Huron was not significantly related to lake charr size, perhaps because maximum length of these exotic prey fishes was not as large as the length range of native prey fishes (Diana 1990).

In Lake Superior, prey fish length range increased with lake charr length, but many prey fish sizes were consumed by any given lake charr size class (Fig. 2). Maximum prey length was 60% of lean lake charr length and 65% of siscowet lake charr length. Lean lake charr consumed rainbow smelt throughout life, which did not generally exceed 200 mm, so the average increase in prey length with lake charr length was less than for siscowet lake charr. Siscowet lake charr consumed relatively larger native *Coregonus* spp. and burbot *Lota lota* with age, but also continued to eat relatively small deepwater sculpin throughout life. Maximum prey length consumed by Lake Superior lake charr was larger than for other northern lake fishes (Gaeta et al. 2018), but less than some saltwater fish that consumed prey fish up to 80% of their length (Scharf et al. 2000). Mouth size is the main factor limiting prey size consumption (Mihalitsis and Bellwood 2017), but prey size availability, behavior, handling time, capture success, and competition all play a role in prey size selection (Gaeta et al. 2018). Higher relative abundance and capture probability for small prey relative to large prey may lead to high predation rates on small prey fishes, and also because search, capture, and handling costs are lower for small prey (Scharf et al. 2000; Juanes et al. 2002). Continued consumption of small prey by large fish may result in a competitive disadvantage for smaller predators (Wilson 1975) and also cause large and small lake charr to be in the same habitat to increase cannibalism.

Lake charr trophic position indicated by $\delta^{15}N$ did not increase with body size, but the relationship between $\delta^{15}N$ and body size varied significantly among populations in Canadian Shield lakes (Vander Zanden et al. 2000). In these and other lakes, an increase in prey size did not necessarily correspond with an increase in $\delta^{15}N$ because large planktivorous *Coregonus* spp. do not typically occupy a higher trophic position than small invertivore sculpins.

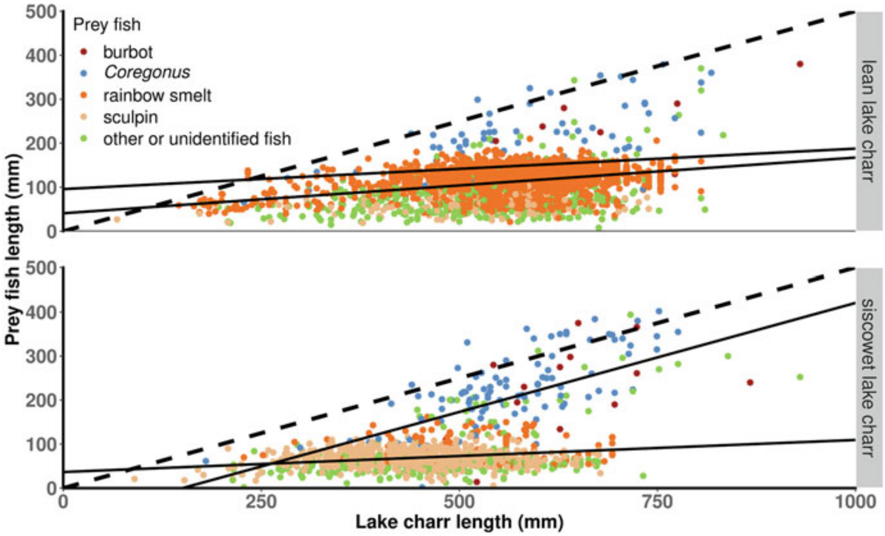

Fig. 2 Predator size–prey fish size scatter diagrams for lean and siscowet lake charr *Salvelinus namaycush* from Lake Superior. Fish were collected from April to October 2012–2018 by the Wisconsin Department of Natural Resources and U.S. Geological Survey using gill nets and bottom trawls. Each data point represents a single prey fish species consumed by a lake charr. Coregonus includes cisco *C. artedi*, bloater *C. hoyi*, and kiyi *C. kiyi*. Sculpin includes slimy *Cottus cognatus*, spoonhead *Cottus ricei*, and deepwater *Myoxocephalus thompsonii*. The dashed line denotes 50% of the lake charr length. Solid lines are 0.5 and 0.9 quantile regression lines. Lean 0.5: $y = 0.12685x + 40.64482$; 0.9: $y = 0.09254x + 95.38806$. Siscowet 0.5: $y = 0.07277x + 35.00127$; 0.9: $y = 0.49540x - 74$. Sample sizes were 3838 individual lean and 3577 individual siscowet lake trout

Foraging habitat can vary through ontogeny. Increasing depth of occupation with size is a common phenomenon of fishes, a.k.a., Heincke's Law (Heincke 1913), and lake charr generally conform to this law (Sitar et al. 2008). In addition to size-mediated shallow to deep foraging patterns, large lake charr fed at the surface more often than small lake charr in both large and small lakes ([large fish were ~ > 350 mm or ~ > 2 kg] Miller and Kennedy 1948; Martin 1952; Martin and Olver 1980). Perhaps surface feeding was more common in large fish because large fish are more mobile than small fish (Martin and Olver 1980). Larger fish also face a lower risk of predation when leaving benthic habitats. In Great Bear Lake, juvenile lake charr overlapped with adult lake charr in their distribution across and within depth zones, except for surface-water habitat, where juveniles were absent, perhaps because juvenile lake charr avoided avian predation (Chavarie et al. 2019).

5.2 Seasonality

Studies of the seasonality of lake charr diets are limited, perhaps because field research in many systems that support lake charr is arduous in seasons other than summer. Of the studies we reviewed, 49 were in summer, 25 were in spring, 19 were in fall, and only four were in winter. Much of our understanding of seasonal trophic patterns comes from early work in Algonquin Park, Ontario (e.g., Martin 1952, 1954, 1970), where seasonality of lake charr diets was a function of both prey availability and temperature-mediated habitat availability.

The most common response to seasonal changes in prey abundance by lake charr is consumption of terrestrial insects in summer. This response to a primarily summer prey pulse by all sizes of fish has been observed in small Canadian Shield Lakes (Martin 1952, 1954, 1970; Martin and Olver 1980; France and Steedman 1996), the Laurentian Great Lakes (Fig. 1; Hoffmann 2017), and Mackenzie Basin Great Lakes (Zimmerman et al. 2007, 2009; Chavarie et al. 2016a). Consumption of novel prey, such as terrestrial mammals (mice, voles), amphibians, snakes, and birds, also peaks in summer (Martin and Olver 1980, M. Vinson, unpublished data).

Aggregations of adult spawners, eggs, and age-0 fish also provide seasonal prey pulses for lake charr. In the Laurentian Great Lakes, predation by lake charr on rainbow smelt is highest during spring, when rainbow smelt congregate in shallow areas to spawn (Ray et al. 2007; Gamble et al. 2011a). In small Canadian lakes, cyprinids are most commonly consumed in spring (Martin and Olver 1980), when the lack of a thermal barrier allows lake charr to forage in littoral habitats (Fry 1939; Martin 1954; Dolson et al. 2009; Tunney et al. 2014; Guzzo et al. 2017).

Age-0 lake charr diets varied little among years but varied monthly in Lake Superior (Hudson et al. 1995). Benthic microcrustacea (Harpacticoida) and Cladocera were eaten mostly in June, Chironomidae pupae and calanoid copepods were eaten mostly in June and July, and planktonic cladocerans and *Mysis* were eaten mostly in August and September (Hudson et al. 1995).

In autumn, lake charr switch their focus from foraging to reproduction, so mature, spawning fish feed less (Miller and Kennedy 1948; Frantz and Cordone 1970; Martin 1970; Eschmeyer 1955). With cooling water temperatures in autumn, shallow littoral habitats become available, with concurrent increases in the consumption of cyprinids (Martin and Olver 1980).

Despite the lure of high adventure for investigators, winter diet studies are exceedingly rare. Our literature search revealed only two studies (Martin 1954; Eck and Wells 1986). Winter lake charr diets in small Canadian Shield lakes from December to April during 1948–1952 varied less than in other seasons and were associated with habitat (Martin 1954). Winter stomach contents contained more littoral-oriented fishes, such as yellow perch and cyprinids, and fewer less littoral-oriented lake whitefish *Coregonus clupeaformis*), benthic invertebrate, and plankton than in other seasons (Martin 1954). Few empty stomachs of lake charr in December and March from Lake Michigan (~15%) indicated active feeding during winter (Eck and Wells 1986). Primary prey were age-0 alewives in December and slimy sculpins in March, along with rainbow smelt and deepwater sculpin in deep water (>55 m; Eck and Wells 1986). Bloater were eaten only sparingly, although they were abundant in both sampling periods (Eck and Wells 1986). In winter, thermal barriers that limit lake charr access to littoral habitats in other seasons are absent (Guzzo et al. 2017).

5.3 Empty Stomachs

A simple measure available from stomach content analyses is the percentage of fish sampled with empty stomachs. The frequency of empty stomachs varies with autecological factors, such as gastric evacuation rates, diet and feeding habits, fish health, and environmental conditions (e.g., prey encounter rate and temperature). Sampling may also result in empty stomachs, when contents are regurgitated upon capture or digested after capture before stomach content collection (Vinson and Angradi 2011). In studies we reviewed, 32% of fish had empty stomachs, across all morphotypes, fish sizes, and seasons, similar to the 30% average (range 24–35%, $n = 57$ data sets) reported previously for lake charr (Vinson and Angradi 2011). The percentage of lake charr with empty stomachs increased with fish age, from 4% at age-0, to 6% at age-1, and 17% at age-2 (Eschmeyer 1956). In many studies, more than 40% of adult stomachs were empty. Occurrence of empty stomachs is typically greater in autumn than spring or summer (e.g., Miller and Kennedy 1948; Eschmeyer 1955; Frantz and Cordone 1970; Martin 1970; Fisher and Swanson 1996), presumably because fish are focused on spawning rather than feeding. In small Algonquin Park lakes, the percentage of empty lake charr stomachs was 55% in winter, 49% in fall, 17% in spring, and 11% in summer (Martin 1954). We found no studies that examined changes in the occurrence of empty stomachs through time in lakes that underwent large changes in prey fish abundance or composition.

5.4 Cannibalism

Martin and Olver (1980) suggested that lake charr cannibalism was generally insignificant, except perhaps in Arctic lakes with limited prey. Swanson (2010) hypothesized that differences in food chain length among coastal Arctic lakes could reflect variability in the frequency of lake charr cannibalism. In her study, cannibal lake charr were larger and older than non-cannibals. Loss of deepwater habitat in winter through hypoxia or loss of littoral habitat in summer through warming could decrease habitat segregation between adult and juvenile lake charr and thereby increase cannibalism. Cannibalism was found in only 9 of 41 studies we reviewed with sufficient stomach content data. For example, lake charr cannibalism was observed in only two of 228 Canadian Shield populations (Vander Zanden et al. 2000). Cannibalism has also been observed in large lakes, including Great Bear Lake

(Chavarie et al. 2014, 2016a), Lake Michigan (Miller and Holey 1992; Madenjian et al. 1998), Lake Ontario (Dietrich et al. 2006), and Lake Superior (Fisher and Swanson 1996; Gamble et al. 2011a), and in the introduced population in Flathead Lake, Montana, USA (Stafford et al. 2013). In support of the contention that cannibalism was likely a response to low prey abundance, the cannibalism rate (number of lake charr stomachs that contained lake charr/total number of stomachs examined) decreased from 0.0036 to 0.00063 after the introduction of cisco into Lake Opeongo, Ontario (Matuszek et al. 1990). Adult lake charr cannibalized newly released (stocked) age-1 lake charr (103–174 mm) in Lake Michigan during May and June (Madenjian et al. 1998) and in Lake Ontario (Dietrich et al. (2006).

5.5 Habitat Coupling

Habitat coupling occurs when distinct but connected habitats are linked through physical and chemical processes and movement of organisms (Polis et al. 1997; Schindler and Scheuerell 2002.) Habitat coupling by lake charr has been defined as deriving energy (prey) in one habitat and occupying another habitat. Lake charr coupled littoral and pelagic habitats (Morbey et al. 2006; Dolson et al. 2009; Guzzo et al. 2017), profundal and limnetic habitats (Hrabik et al. 2006; Jensen et al. 2006), and freshwater, brackish, and marine habitats (Swanson et al. 2010, 2011; Kissinger et al. 2016). The degree of littoral-pelagic coupling driven by lake charr appears to be a function of lake size (McCann et al. 2005) and shape (Dolson et al. 2009), with circular lakes providing greater opportunities for lake charr to forage in littoral habitats, particularly during periods of thermal restriction (Dolson et al. 2009). Littoral-pelagic coupling by lake charr also appears to be more prevalent in small lakes, particularly those that lack cisco (Kennedy et al. 2018). In large lakes, siscowet and other deepwater forms of lake charr track vertically migrating *Coregonus* prey (Eshenroder and Burnham-Curtis 1999; Hrabik et al. 2006). Siscowet lake charr that moved vertically to follow prey have higher foraging and growth rates than if they had remained in one or the other habitats (Jensen et al. 2006; Hrabik et al. 2006). Anadromy in Arctic lake charr may increase productivity and fecundity, enhance colonization of new habitats, and allow persistence in extreme and highly variable environments (Swanson et al. 2010).

5.6 Native Lake Charr Consumption of Exotic Prey

Studies from the Laurentian Great Lakes highlight the ability of native lake charr to adapt to feeding on whatever prey is abundant, whether native or exotic, such as rainbow smelt, alewife, and round goby *Neogobius melanostomus*. Rainbow smelt were first detected in Lake Michigan in 1924, Lake Huron in 1925, and Superior in 1930. Prior to the arrival of rainbow smelt, adult lake charr diets in Lake Superior were comprised of >90% *Coregonus* species (Dryer et al. 1965). *Coregonus* populations began to decline in the 1950s (Selgeby 1982), while rainbow smelt populations increased rapidly (Bailey 1964). By the mid-1960s and continuing to present, the rainbow smelt was the predominant prey of lean lake charr in Lake Superior (Fig. 1; Dryer et al. 1965; Conner et al. 1993; Fisher and Swanson 1996; Ray et al. 2007; Gamble et al. 2011a). Offshore siscowet lake charr in Lake Superior continued to primarily consume *Coregonus* spp., because rainbow smelt are generally restricted to (Gorman et al. 2012) and consumed by lean lake charr in nearshore habitats (Fig. 2; Ray et al. 2007; Gamble et al. 2011a).

Prior to arrival of alewife in Lake Michigan in 1949, lake charr fed primarily on sculpins in the southern basin, *Coregonus* spp. in the northern basin, and lake shiner *Notropis atherinoides* in Green Bay. Alewife populations increased dramatically during the late 1950s in Lake Michigan (Smith 1968), and lean lake charr predation tracked this abundant prey (Stewart et al. 1983). Alewife became a predominant prey of adult lean lake charr in nearshore habitats of Lake Michigan, whereas the primary prey was rainbow smelt at shallow reefs and bloater at deep offshore reefs (Eck and Wells 1986; Jude et al. 1987; Stewart and Ibarra 1991; Miller and Holey 1992; Madenjian et al. 1998). The round goby was first observed in Lake Michigan in 2000, when it appeared in one lean lake charr stomach, but was relatively common in lean lake charr stomachs by 2004 (Brey 2006). Alewife and rainbow smelt were the predominant prey of Lake Huron lake charr during 1983–1986 (Diana 1990). More recently (2009–2011) in Lake Huron, with reduced alewife populations, lake charr diets were dominated by rainbow smelt, round goby, and native prey fishes (Roseman et al. 2014; Happel et al. 2017a).

In Lake Ontario, lake charr switched from eating native to invasive prey fish after the loss of native *Coregonus* spp. and the arrival of alewife, rainbow smelt, and round goby (Brandt 1986; Olson et al. 1988; Dietrich et al. 2006; Rush et al. 2012; Yuille et al. 2015). The round goby was first observed in Lake Ontario in 1999, but increased to the second-most consumed prey species of lean lake charr after alewife by 2003–2004 (Dietrich et al. 2006). More recently, the round goby has overtaken alewife as the primary prey of lake charr in Lake Ontario (Colborne et al. 2016; Rush et al. 2012). This dietary switch from alewife, a pelagic planktivore, to round goby, a littoral benthivore, implies a switch from consuming primarily offshore-derived energy to nearshore-derived energy, at least during periods, typically summer, when round goby occupy nearshore waters.

5.7 Introduced Lake Charr

Lake charr were widely introduced into lakes beginning in the late 1800s (Crossman 1995), and in the western United States, were stocked in >200 lakes and reservoirs (Martinez et al. 2009). While creating high-quality fisheries, especially initially, introduced lake charr have been voracious and adaptable predators that can decimate populations of native fishes. Introduced lake charr can affect native species through both predation and competition. Their foraging habits have led to introductions of other exotic species, such as *Mysis* and kokanee *Oncorhynchus nerka,* to satiate their hunger, and hampered restoration efforts for native piscivores, such as bull charr *Salvelinus confluentus* and cutthroat trout *Oncorhynchus clarkii* (Martinez et al. 2009). Large bodies and mouths, longevity, adaptable feeding habits, and ability to forage across large areas on diverse prey items convey a competitive advantage to lake charr in new ecosystems. Ecological effects of both intentional and accidental introductions and subsequent invasions of lake charr, including extirpations of native species and effects on food-web structure, are illustrated by what occurred in Yellowstone Lake and Lake Tahoe (Hansen et al. 2021).

Lean lake charr colonized Yellowstone Lake in the 1980s from nearby introductions, but were first reported in 1994 (Kaeding et al. 1996). Following introduction, their population quickly expanded (Kaeding et al. 1996; Munro et al. 2005) at the primary expense of Yellowstone cutthroat trout. In 1996 alone, lake charr consumed 15 metric tons of Yellowstone cutthroat trout (522,000 fish, Ruzycki et al. 2003). By 2003, Yellowstone cutthroat trout, the native piscivore, had declined in abundance by 60% in the Yellowstone Lake and 99% in a major spawning tributary (Koel et al. 2005). The addition of lake charr and loss of Yellowstone cutthroat trout led to a four-level aquatic trophic cascade in Yellowstone Lake (Tronstad et al. 2010) that ultimately affected terrestrial populations of black bear *Ursos americanus,* grizzly bear *U. arctos,* Rocky Mountain elk *Cervus elaphus* (Middleton et al. 2013), and North American river otter *Lontra canadensis* (Crait et al. 2015). The illegal introduction of lake charr into Yellowstone Lake has led to an unanticipated disruption of natural aquatic–terrestrial linkages that could permanently affect many native species in Yellowstone National Park (Middleton et al. 2013).

Intentional introductions of lake charr to create recreational fisheries have also led to unintended consequences to native aquatic species. For example, lake charr were intentionally introduced into Lake Tahoe in 1888. By 1938, a combination of fishing and lake charr predation resulted in extirpation of the native pelagic Lahontan cutthroat trout *Oncorhynchus clarki henshawi* (Frantz and Cordone 1970). An attempt to reestablish Lahontan cutthroat trout failed due to lake charr predation. The first major lake charr diet study in Lake Tahoe in 1962–1964 showed that large lake charr consumed benthic-oriented Piute sculpin *Cottus beldingii* and Tahoe sucker *Catostomus tahoensis*, whereas small lake charr consumed zooplankton (Frantz and Cordone 1970). Lack of *Mysis* was viewed as an impediment to lake charr growth in many systems, so *Mysis* were stocked in Lake Tahoe in ~1964. Establishment of *Mysis* increased lake charr production and growth but led to the disappearance of two cladoceran zooplankton taxa, *Daphnia* and *Bosmina* (Vander Zanden et al. 2003). In Flathead Lake, a population of introduced lake charr increased 14-fold after the establishment of *Mysis*, and the expanded lake charr population resulted in extirpation of an earlier introduced prey fish, kokanee, which precipitated a decline in bull charr, the native piscivore (Stafford et al. 2002).

In northern Finland, where native Arctic charr *Salvelinus alpinus*, interact trophically with introduced lake charr, lake charr consumed littoral prey fishes whereas Arctic charr consumed pelagic *Coregonus* spp. (Eloranta et al. 2015). Lake charr appeared to have only a minor (if any) impact on native fishes and food-web structure (Eloranta et al. 2015).

6 Morphotype Specific Patterns

6.1 Lean Lake Charr

Lean lake charr have a fusiform body with a large head, long snout, small eyes, long and narrow caudal peduncle, and short paired fins (Eschmeyer and Phillips 1965; Moore and Bronte 2001; Muir et al. 2014; Chavarie et al. 2021). They occur over a large geographic range in a wide variety of lake types, from small lakes with no prey fish to large lakes with diverse prey fish assemblages. Occurrence in a diversity of habitats has led to a high degree of trophic specialization and genetic differentiation among lean lake charr populations (Bernatchez et al. 2016; Wellband et al. 2021). High among-lake variation in diets of lean lake charr reflects differences in prey abundance and composition, co-occurrence with other piscivores, and access to littoral habitats. Littoral feeding has been related to lake morphometry, with lean lake charr in circular lakes deriving more energy from littoral zones than lean lake charr in reticulate lakes, despite reticulate lakes having greater littoral areas and presumably higher production (Dolson et al. 2009). Littoral foraging by the lean lake charr may be regulated by thermal conditions rather than prey production (Dolson et al. 2009; Guzzo et al. 2017).

6.2 Lean Lake Charr in Small Lakes

Small lakes with lake charr occur across the species range, but in high density throughout the Canadian Laurentian Shield and Northwest Territories Barrenlands. Across the range, small lakes vary greatly in morphometry, community composition, and physical–chemical composition. In response to this diversity, lean lake charr diets vary, but in a generally predictable pattern that appears related to lake size and shape and coexistence with other fishes (Rawson 1961; Vander Zanden and Vadeboncoeur 2002; Dolson et al. 2009; Hulsman et al. 2016; Kennedy et al. 2018). As lake size increases, prey communities become more diverse and lake charr become more piscivorous. Adult lean lake charr from lakes >10 km^2 do not readily consume zoobenthos, whereas lean lake charr from lakes ≤ 10 km^2 consume primarily invertebrates (Vander Zanden and Vadeboncoeur 2002), with some populations feeding exclusively on zooplankton (Vander Zanden et al. 2000; Houde and Scrosati 2003). Feeding patterns are not all easily explained by prey relative abundance, which may reflect food quality. In Lake Louisa, Ontario, copepods were ~ 87% and cladocerans were ~ 13% of the zooplankton community, yet stomachs of lake charr contained ~2% copepods and ~ 98% cladocerans (Martin and

Olver 1980). From a life history standpoint, planktivorous lean lake charr have slimmer bodies and more gill rakers (Bernatchez et al. 2016), reach smaller adult sizes, and mature at earlier ages than piscivorous lean lake charr (Martin 1952, 1966; Konkle and Sprules 1986; Pazzia et al. 2002).

Presence of other piscivores can influence lean lake charr feeding. In the Canadian Barrenlands (Northwest Territories), lean lake charr consumed primarily pelagic zooplankton when coexisting with burbot, but fed primarily on littoral fishes when coexisting with cisco, longnose sucker *Catostomus catostomus*, and round whitefish *Prosopium cylindraceum* (Hulsman et al. 2016). In a small lake in New York, USA, lake charr were largely non-piscivorous in the presence of introduced smallmouth bass *Micropterus dolomieu*, whereas lake charr became piscivorous within 2 years of the initiation of smallmouth bass removal (Lepak et al. 2006). The studies reviewed above suggest that lake charr diet and position in the food web reflect both principal prey sources and fish community composition.

6.3 Lean Lake Charr in Large Lakes

The trophic ecology of lean lake charr in large lakes (>500 km^2) has been most intensively studied in the Laurentian Great Lakes. Prior to the establishment of alewife and rainbow smelt, native planktivores (*Coregonus* spp.) were the main prey for lean lake charr in the Laurentian Great Lakes. For example, in Lake Michigan, lean lake charr diets were historically dominated by bloater and cisco, with some contributions from sculpin species (*Cottus* spp.) and lake shiner (Van Oosten and Deason 1938 and papers cited therein). In Lake Superior in the 1950s, the diet of adult lean lake charr was comprised of >90% *Coregonus* spp. (Dryer et al. 1965).

Concurrent with a decline in abundance of native *Coregonus* spp., lean lake charr began exploiting abundant populations of introduced alewife and rainbow smelt in the Laurentian Great Lakes. In the 1950s, cisco populations in Lake Superior began to decline (Selgeby 1982) while rainbow smelt populations increased rapidly (Bailey 1964). Rainbow smelt made up <2% of Lake Superior lean lake charr diets in 1950, and 66% of diets by 1963 (Dryer et al. 1965). During 1981–2005, lean lake charr diets in Lake Superior were dominated by rainbow smelt (60–80%), with lesser contributions from *Coregonus* spp. (9–15%), and sculpins (~4%) (Conner et al. 1993; Fisher and Swanson 1996; Ray et al. 2007; Gamble et al. 2011b). In Lake Michigan in the 1980s, lean lake charr ate mainly alewife, rainbow smelt, and sculpins (Eck and Wells 1986). The native planktivore, bloater, was abundant but rarely eaten. The bloater may have been more elusive than either alewife or rainbow smelt, so the bloater may become a major forage species if prey species that are easier to catch become scarce (Eck and Wells 1986). During this same period (1980s), alewife and rainbow smelt were also the primary prey of adult lean lake charr in Lake Ontario (Brandt 1986; Olson et al. 1988).

In the Mackenzie Basin Great Lakes in northwestern Canada, shallow-water lake charr are more trophically diverse than elsewhere (Blackie et al. 2003; Chavarie et al. 2014, 2016a, 2016b, 2021). For example, lake charr in Great Bear Lake consumed considerably more benthic invertebrates than lake charr in the Laurentian Great Lakes (Miller and Kennedy 1948). Similarly, in Great Slave Lake, fish were the predominant prey in the main lake, whereas crustaceans, insects, molluscs, and fewer fish were predominant prey in the east arm of the lake (Rawson 1951). In Great Bear Lake during the summers of 1963–1965, "[diets] in general reflect more the site of capture than any specific food preference" (Johnson 1975). Forty years later, stomach contents overlapped greatly between two morphotypes of lake charr, piscivores and insectivores (Blackie et al. 2003). A decade later, four shallow-water morphotypes described using a combination of stomach, isotope, and fatty acid techniques suggested that three generalists and one pelagic specialist coexisted in shallow-water (<30 m) habitats (Chavarie et al. 2013, 2016a). Fatty acids corroborated isotope findings, but also identified a benthic–pelagic dietary gradient among morphotypes (Chavarie et al. 2014). Terrestrial insects were an important summer prey (Chavarie et al. 2016b) and cannibalism was common (Chavarie et al. 2014, 2016a). Resource use also varied among lake regions within morphotypes, illustrating the roles of prey availability and habitat differences in lake charr diets (Chavarie et al. 2014).

6.4 Siscowet Lake Charr

Siscowet lake charr are deep-bodied "fat" fish with large eyes located high on a broad short head, long maxilla, short and deep caudle peduncle, and moderately long paired fins (Eschmeyer and Phillips 1965; Moore and Bronte 2001; Muir et al. 2014), features that make them well suited for striking prey from below in low light environments. High fat levels in muscle make it energetically profitable for siscowet lake charr to move vertically through the water column to track prey items, such as *Mysis* and deepwater *Coregonus* spp., that undergo regular vertical movements (Henderson and Anderson 2002; Hrabik et al. 2006).

Although siscowet-like lake charr occur throughout the geographic range of the species (Muir et al. 2015), their trophic ecology is less well studied. The relative paucity of information likely reflects the fact that siscowet are not targeted by commercial and recreational fisheries. In Lake Superior, siscowet diets have been described for nearshore and offshore populations from stomach contents (Fisher and Swanson 1996; Ray et al. 2007; Sitar et al. 2008; Gamble et al. 2011a, b; Sitar et al. 2020; Vinson et al. 2020), stable isotopes (Harvey et al. 2003), and a combination of stomach contents, fatty acid profiles, and stable isotopes (Hoffmann 2017). Small (<500 mm) siscowet eat primarily macroinvertebrates (Fig. 1; fingernail clams [Pisidiidae], *Mysis,* and aquatic insects), sculpins, and *Coregonus* spp. (Fisher and Swanson 1996; Sitar et al. 2008; Gamble et al. 2011b). Large (>500 mm) siscowet eat fewer invertebrates and more fish, including rainbow smelt, burbot, sculpins, lake charr, and *Coregonus* spp. (Figs. 1 and 2; Fisher and Swanson 1996; Ray et al. 2007; Sitar et al. 2008; Gamble et al. 2011b; Sitar et al. 2020; Vinson et al. 2020). Feeding forays to the surface to consume terrestrial invertebrates in Lake Superior by siscowet lake charr occur at even the deepest bathymetric depths (~400 m, Sitar et al. 2008). Siscowet stomach contents varied little among years in nearshore Lake Superior during 1990–2001 (Ray et al. 2007). On the basis of stomach contents and $\delta^{15}N$ and $\delta^{13}C$, siscowet-like lake charr in Great Slave Lake primarily ate sculpins and *Coregonus* spp. (Zimmerman et al. 2009).

In Lake Superior, diet overlap between lean and siscowet lake charr can be high (Dryer et al. 1965; Fisher and Swanson 1996) or low (Harvey and Kitchell 2000; Kitchell et al. 2000; Ray et al. 2007). Differences in diet overlap likely reflect variation in prey composition and abundance among years and locations. Based on $\delta^{15}N$ and $\delta^{13}C$ isotope ratios, younger siscowet lake charr were isotopically similar to lean lake charr, but diets diverged as siscowet lake charr aged (Harvey et al. 2003), which likely reflected greater use of nearshore habitat by young siscowet lake charr. Based on stable isotope and fatty acid data, siscowet and lean lake charr diet overlap differed between two offshore, seamount sites (Stannard Rock and Superior Shoal) in Lake Superior, with higher overlap at Stannard Rock than Superior Shoal (Hoffmann 2017). A $\delta^{15}N$ and $\delta^{13}C$ isotope study in Lake Superior suggested that nearshore siscowet lake charr consumed mostly rainbow smelt and cisco (Harvey et al. 2003), like lean lake charr, whereas offshore siscowet lake charr consumed mostly deepwater ciscoes, presumably *C. kiyi*, and deepwater sculpin (Kitchell et al. 2000). Diet overlap between the two morphotypes appears to be lessened by different habitat preferences.

6.5 Humper Lake Charr

Humper lake charr have a small head, short snout, short maxilla, large eyes, and short and narrow caudal peduncle (Moore and Bronte 2001; Muir et al. 2014), and occur in both small and large lakes. Humpers are considered an offshore, shoal-associated morphotype that occupies intermediate depths compared to lean and siscowet lake charr (Hansen et al. 2016). Little has been published on the trophic ecology of humper lake charr. At two offshore shoals in Lake Superior, humper lake charr consumed less fish and more *Mysis* than lean, siscowet, or redfin lake charr (Hoffmann 2017). In contrast to other morphotypes at these shoals, deepwater sculpin were the only fish identified from stomach contents of humper lake charr from Lake Superior (Hoffmann 2017). Epibenthic feeding by humper lake charr in Lake Superior was also indicated by the common occurrence of fish eggs and rocks in stomachs, unlike any other morphotypes (Hoffmann 2017). In Rush Lake, Michigan, a humper-like morph, *S. namaycush huronicus,* consumed *Mysis,* benthic invertebrates, and rainbow smelt and had a more pelagic offshore trophic signal based on $\delta^{13}C$ data than the sympatric lean lake charr morphotype (Chavarie et al. 2016c). An introduced humper-like, deepwater lake charr in Flathead Lake, consumed mostly *Mysis* at lengths <600 mm and a variety of fishes, including pygmy whitefish *Prosopium coulterii*, lake charr, and lake whitefish, at lengths >600 mm (Stafford et al. 2013).

Diets of humper and other lake charr morphotypes overlapped little in Lake Superior based on stomach content analysis (Vinson et al. 2020) and fatty acid profiles (Hoffmann 2017). Fatty acid profiles suggested that humper lake charr diets were least similar to lean lake charr, most similar to siscowet, and less similar than between lean and siscowet lake charr. Stable isotope analysis indicated humper lake charr relied more on profundal than pelagic resources (Hoffmann 2017). In Rush Lake, a lean morphotype occupied a slightly higher trophic position than a huronicus (humper-like) morph, with an average $\delta^{15}N$ of 9.1 per mil for the lean morphotype and 8.8 per mil for the humper-like morph, and stomach contents indicated greater piscivory by lean lake charr and higher *Mysis* consumption by the humper-like lake charr (Chavarie et al. 2016c).

6.6 Redfin Lake Charr

The colloquial name “redfin” has been used to describe lake charr from both Great Bear Lake (Alfonso 2004) and Lake Superior (Rakestraw 1968; Goodier 1981; Muir et al. 2014). In Lake Superior, the redfin is a robust morph, with the largest head, snout, eyes, longest and deepest caudal peduncle, and longer pelvic and pectoral fins than other morphotypes (Muir et al. 2014). Based on stomach contents, stable isotopes, and fatty acid profiles of 60 adult redfins from Superior Shoal, Lake Superior in summer 2013, stomachs contained mostly *Mysis*, while biomass was predominantly fish (*Coregonus* spp., burbot, and sculpins; Sitar et al. 2020; Vinson et al. 2020). Fatty acid profiles and $\delta^{34}S$ ratios indicated a diet of profundal origin, and $\delta^{13}C$ and $\delta^{15}N$ ratios indicated a similar trophic position and carbon source to that of sympatric humper lake charr (Hoffmann 2017). Diet overlap based on stable isotope and fatty acid analysis indicated more overlap with humper and siscowet than with lean lake charr (Hoffmann 2017).

6.7 Anadromous and Brackish Water Lake Charr

Based on otolith microchemistry and muscle-derived $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ data, anadromous populations of lake charr exist in a coastal region of Nunavut, Canada (Swanson et al. 2010). Stable carbon, nitrogen, and sulfur isotope ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) data indicated that semi-anadromous lake charr collected from 3 lakes in the Canadian Arctic relied on ~60–65% marine-derived food sources and ~35–40% freshwater benthic food sources, whereas freshwater pelagic food sources were relatively unimportant (Swanson et al. 2011). Stomach contents from semi-anadromous lake charr included capelin *Mallotus villosus* and saffron cod *Eleginus* *gracilis*), two saltwater species (Swanson et al. 2010). A brackish-water life history type of lake charr also occurs in the Canadian Arctic (Kissinger et al. 2016), although no data are available on diets or trophic ecology of brackish-water lake charr.

7 Future

As a long-lived, cold-water stenotherm with broad latitudinal distribution, the lake charr may be an ideal organism to study when assessing effects of changing thermal regimes. Will lake charr be as successful adapting to new thermal regimes as they have been at adapting to new habitats? Will they continue to be as dominant in introduced habitats at the lower latitudinal distribution of their natural range?

Over the past several decades, northern hemisphere lakes have warmed (O'Reilly et al. 2015). The effect of this warming on thermal habitat varies with lake morphometry, but the deepest areas of large lakes are generally characterized by a later onset of thermal stratification, shorter stratified warming season, and higher warming rates than shallow areas (Woolway and Merchant 2018). Early on, lake charr were observed to adjust their feeding in response to interannual variation in thermal conditions. For example, in Lake Opeongo, shallow-water yellow perch, an important food for lake charr, was much less abundant in lake charr stomachs in warmer water years when the thermocline was particularly sharp (Fry 1939). More recently, climate-mediated habitat occupation responses by lake charr have been observed in small Canadian boreal lakes (Tunney et al. 2014; Guzzo et al. 2017). In warmer water years with shorter springs and longer summers, lean lake charr reduced their use of littoral habitat and increased their use of deep pelagic habitat during summer (Tunney et al. 2014; Guzzo et al. 2017). This resulted in less energy acquisition from littoral habitats, and a shift from consuming larger littoral prey to smaller pelagic prey (Guzzo et al. 2017). While the inferred temperature-induced shift from littoral to pelagic feeding resulted in reduced growth and condition, lean lake charr adapted their foraging behavior to maintain thermal preference. This type of response may allow lake charr to persist in lakes where surface water temperature models would predict otherwise (Cline et al. 2013), but further study of trade-offs between temperature preference and food quality, and concomitant effects on fitness and food-web stability, is required.

Much has been learned about the trophic ecology of lake charr in the past century and the incredible plasticity and diversity in food habits of this species. Further quantification of variability in diet among morphotypes, lakes, habitats, life history types, seasons, and years will allow more informed predictions of how lake charr will respond to changes in aquatic thermal regimes, productivity, and prey. Research that incorporates multiple contemporary tools, such as compound-specific stable isotope analysis, quantitative fatty acid signature analysis, and data on movement and habitat occupation, along with new analytical techniques for modeling trophic niche space (e.g., Swanson et al. 2015), will enhance understanding of lake charr trophic ecology to enable better management of this iconic species in both pristine and disturbed ecosystems (McMeans et al. 2016).

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Reproduction

Frederick W. Goetz, J. Ellen Marsden, Catherine A. Richter, Donald E. Tillitt, Shawn P. Sitar, Stephen C. Riley, and Charles C. Krueger

Abstract Lake charr *Salvelinus namaycush* are typically fall spawners although one ecotype has populations that spawn during spring and fall (siscowets in Lake Superior). Lake charr are iteroparous (reproduce more than once in a lifetime) with group-synchronous ovarian development and typically spawn once per year. However, lake charr may not reproduce every year, a phenomenon known as skipped spawning. Free embryos are active on spawning reefs, make diurnal vertical movements from spawning substrate, and feed exogenously much earlier than previously assumed. The abundance of food and predators strongly affects the rate of

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Stephen C. Riley is retired at the time of publication.

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development, yolk sac absorption, and duration of residence on spawning sites. The necessity for, and timing of, gas bladder inflation, and mechanisms for inflation without access to the surface, need further study. The low survival of free embryos due to thiamine deficiency has likely contributed to the lack of recruitment of lake charr in the Laurentian Great Lakes for decades. Thiaminase, a thiamine-degrading enzyme, appears to be the causal agent for thiamine deficiency in Great Lakes lake charr.

Keywords Development · Early mortality syndrome · Embryo · Fecundity · Gas bladder inflation · Hatching · Reproductive timing · Skipped spawning · Swim-up syndrome · Thiamine deficiency complex

1 Introduction

Most lake charr *Salvelinus namaycush* are primarily lacustrine, living and spawning in lakes, with some adfluvial populations (Jones et al. 2018; Loftus 1958), even fewer known semi-anadromous populations in the Canadian Arctic (Swanson et al. 2010, 2011), and yet others completing their life history in brackish waters (Kissinger et al. 2016). A general strategy of reproduction in lentic habitats differs from adfluvial and anadromous life histories of most other salmonines that result in differences in spawning behavior, early embryonic and postembryonic development, and possibly natal homing.

The lake charr is long-lived with ages commonly exceeding 20 years and can be as much as 60 years or more (Campana et al. 2008; Hansen et al. 2021). Mean age at first maturity can be as early as 4.5 years in southern lakes such as Lake Erie (Markham et al. 2008) or as late as 13–15 years or more in Lake Mistassini in Quebec (Hansen et al. 2012) and Lake Superior (Hansen et al. 2012). In North America, many lakes contain sympatric populations of lake charr ecotypes that inhabit shallow and deep-water habitats (see Chavarie et al. 2021 Throughout the Laurentian Great Lakes, many forms of lake charr occurred historically (Agassiz 1850; Brown et al. 1981; Goodier 1981), although multiple forms now only occur in Lake Superior (Muir et al. 2016). The reported forms include the lean, siscowet, humper, and redfin (Moore and Bronte 2001; Muir et al. 2014), but based on collections of lake charr around complex bathymetric environments such as Isle Royale (northern Lake Superior), more ecotypes likely exist, some of which were described anecdotally (Rakestraw 1968). These ecotypes were differentiated based on osteology, morphometry, physiology (Burnham-Curtis 1993; Burnham-Curtis and Smith 1994; Goetz et al. 2010; Goetz et al. 2014; Khan and Qadri 1970; Moore and Bronte 2001) and, to some extent, the depth at which they are captured. Siscowets are considered deep-water forms (>80 m), (Bronte et al. 2003; Sitar et al. 2008), leans and redfins are shallower (<80 m) (Bronte et al. 2003; Muir et al. 2014), and humpers are found at intermediate depths on "humps" or sea mountlike structures (Eschmeyer and Phillips 1965; Lawrie and Rahrer 1973; Rahrer 1965). Given the importance of temperature on rates of growth, maturation, and embryonic development, depth differences among forms is of interest in the study of lake charr reproduction.

This chapter reviews the biology of the reproductive period of lake charr life history, including adult reproduction (timing, spawning omission, fecundity), fertilization and pre-hatch embryo development, embryo mortality factors, and post-hatching development and behavior. Several unique aspects of the lake charr's reproductive ecology are highlighted in this chapter while others are covered in greater detail by Marsden et al. (2021a, b) and Binder et al. (2021). A separate section at the end of our chapter is devoted to the thiamine deficiency complex (TDC), which has been a perplexing problem in the Laurentian Great Lakes impeding population restoration. Finally, because many uncertainties remain and little is known about differences in reproductive ecology, developmental ontogeny, or early life history among lake charr ecotypes, each section concludes with recommendations for future research.

2 Adult Reproduction

Lake charr are iteroparous (reproduce more than once in a lifetime) with group-synchronous ovarian development and typically spawn once per year. Martin and Olver (1980) summarized findings up until 1980 on reproduction in lake charr including the timing of reproduction, spawning omission, and fecundity. Here we focus primarily on synthesizing new information since Martin and Olver's review.

2.1 Reproductive Timing

Similar to other charr species, most lake charr are fall spawners with spawning periods ranging from August in northerly locations (e.g., Alaska and Northwest Territories) to early December in lakes in Ontario, Wisconsin, New Hampshire, and New York (Martin and Olver 1980). In most fish species, including salmonines, photoperiod is believed to be the primary environmental cue synchronizing gonadal maturation to a given time of the year (Bromage et al. 2001). While water temperature affects gonadal maturation and the time of spawning (release of eggs and sperm from the body), temperature is usually considered to modulate rather than dictate the timing of reproduction (Davies and Bromage 2002). Even at depths inhabited by some lake charr ecotypes such as the siscowet, photoperiod is probably still an important cue that governs overall seasonal synchronization of gonadal development. Photoperiod also affects the reproductive timing of other charrs such as the brook charr *Salvelinus fontinalis* (Holcombe et al. 2000) and the Arctic charr *Salvelinus alpinus* (Gillet 1994). Water temperature is also related to the time of spawning in brook charr populations that spawn in lakes (Blanchfield and Ridgway 1997; Warren et al. 2012). To our knowledge, no studies have specifically determined the effects of photoperiod or temperature on the seasonal timing of reproduction in the lake charr. Changes in temperature do not appear obligatory for spawning because three lean lake charr strains still spawned when held in the laboratory under constant temperature year-round (Foster et al. 1993). However, changes in water temperature may alter specific spawning times within a reproductive season (see Binder et al. 2021).

Seasonal reproduction in fish requires several sequential processes including gonadal maturation, oocyte final maturation (meiosis), ovulation (release of oocytes from follicles), spermiation (release of sperm to sperm ducts), and spawning. Though temporally connected, these processes are controlled by different hormones and are also likely to be influenced or controlled by different environmental cues. Because of the number of processes involved, initiation of gonadal maturation occurs well in advance of actual spawning. In southern Lake Superior, female and male gonadosomatic indices (GSI—gonad weight relative to body weight) began to increase significantly in August (females—Fig. 1), but the initiation of oogenesis (oocyte development) and spermatogenesis (sperm development) actually began in June, as evident by significant histological changes in gonadal maturation stage (Fig. 1). Timing of gonadal maturation and changes in GSI were the same in both lean and siscowet lake charr ecotypes from two separate populations east and west of the Keweenaw Peninsula in southern Lake Superior (Goetz et al. 2011). Increases in circulating estradiol 17B (primary female estrogen) directly coincided with changes in ovarian GSI and were probably linked to stimulation of vitellogenesis (yolk protein production and deposition in the oocyte). In contrast, the primary male androgen, 11-ketotestosterone, was correlated with the latter stages of spermatogenesis, as in other salmonines (Goetz et al. 2011).

While most studies of the timing of lake charr reproduction indicate fall spawning, siscowet lake charr reproduction can occur earlier in Lake Superior. For example, ripe (eggs and milt flowing freely) male and female siscowets were collected in late April from deep water northeast of the Apostle Islands in Lake Superior (Bronte 1993). Similarly, one "nearly ripe" and one "nearly spent" siscowet lake charr were collected in early June off eastern Isle Royale National Park, Lake Superior (Eschmeyer 1955). Further, historical accounts of lake charr in Lake Superior consistently indicated that siscowets reproduced either earlier than leans (Milner 1874) or at various times of year (Goode 1888; Sweeny 1890). In waters surrounding Isle Royale National Park, GSIs and gonadal staging indicated siscowets spawned during spring and fall, while leans, redfins, and humpers appeared to reproduce only during fall (Goetz et al. 2017). Siscowet lake charr are deep-water ecotypes while leans are shallow-water ecotypes (Bronte et al. 2003; Krueger and Ihssen 1995; Krueger et al. 1995a; Moore and Bronte 2001; Muir et al. 2012). The importance of spring and fall spawning in siscowets is unknown, although the deep-water form of Arctic charr in sympatric populations of deep-water and shallow-water ecotypes also spawns in both spring and fall (Elliot and

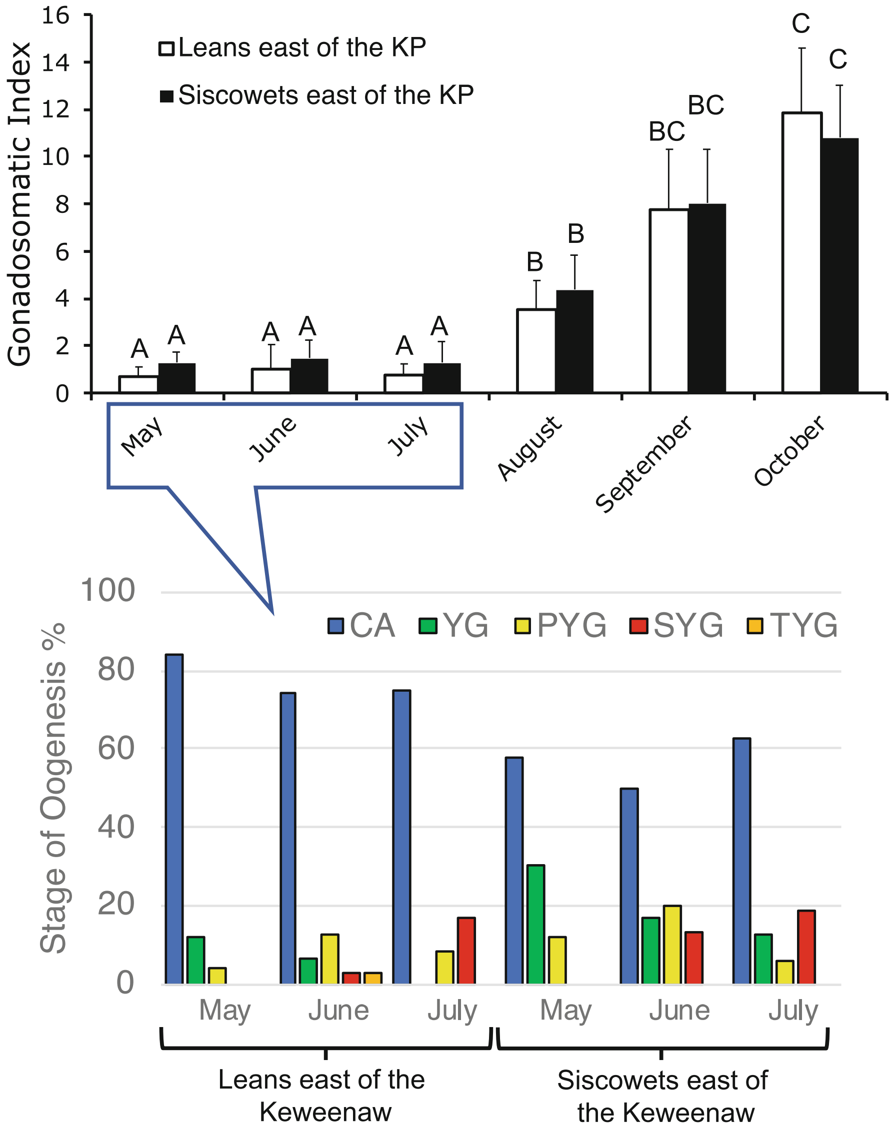

Fig. 1 Timing of gonadal maturation in female lean and siscowet lake charr *Salvelinus namaycush* in Lake Superior. *Upper panel*: Mean gonadosomatic index (GSI) + standard deviation of female lean (white bars) and siscowet (black bars) lake charr sampled east of the Keweenaw Peninsula (KP), Michigan, USA in Lake Superior from May to October. Bars not sharing the same letter designations represent significantly ($p < 0.05$) different means within an ecotype. Note that GSIs do not increase significantly until August. *Lower panel*: Percent of ovaries in various stages of oogenesis in female lean and siscowet lake charr sampled east of the KP, Michigan, USA in Lake Superior from May to July. *CA* cortical alveolus, *YG* yolk granule, *PYG* primary yolk globule, *SYG* secondary yolk globule, *TYG* tertiary yolk globule. See Fig. 4 in Goetz et al. (2011) for examples of each oocyte stage. Staging was not conducted on females with maturing ovaries (GSI > 3.0) from August to October because the ovaries could not be processed for histology because of the large amount of yolk. Note that even while GSIs do not increase from May to July (upper panel), changes in the stage of oogenesis are still occurring as evidenced only by histological analysis. Figure modified from Goetz et al. (2011)

Baroudy 1995; Klemetsen et al. 1997; Telnes and Saegrov 2004). Therefore, maintaining alternative spawning times in deep-water charr ecotypes may be an adaptive strategy to maintain an altered time of departure from spawning reefs, decreased competition with free embryos of fall-spawning fish, or avoidance of adverse conditions or predation during a long winter of incubation.

2.2 Skipped Spawning

Lake charr may not reproduce every year once they attain puberty (development of reproductive competency), a phenomenon previously referred to as "intermittent spawning" (Martin and Olver 1980) or as "infertile" fish (Fry 1949), but now commonly as "skipped spawning" (Rideout et al. 2005). In lake charr populations in several Canadian lakes, 8–87% of females in a population skipped spawning in a given year (Cuerrier and Schultz 1957; Johnson 1972, 1973; Kennedy 1954; Miller and Kennedy 1948; Rawson 1961). Although skipped spawning is prevalent in high-latitude lakes (Martin and Olver 1980), skipped spawning also occurs in both lean (12.2%) and siscowet (58%) lake charr ecotypes in southern Lake Superior, an oligotrophic lake at the southern edge of the lake charr range (Sitar et al. 2014). Further, 48% of 93 females were not maturing at the time of reproduction in the Waterton Lakes (Alberta, Canada), also at the southern edge of the range (Cuerrier and Schultz 1957).

Skipped spawning takes several forms, including retention of fully mature oocytes or ovulated eggs, resorption of oocytes that began vitellogenesis, and cessation of oocyte development prior to vitellogenesis (Rideout et al. 2005). Based on histological examination of ovaries, female lake charr that skipped spawning in southern Lake Superior began to undergo gonadal maturation, but the maturation process then stopped and the largest oocytes began to degenerate and resorb (Goetz et al. 2011). Because oocytes of lean lake charr in southern Lake Superior that develop normally attain a diameter of about 2.0 mm at the yolk globule stage in August, the mechanism that activates degeneration and resorption probably occurs in July or August.

The underlying mechanism(s) controlling skipped spawning in fish has been related to the availability of adequate energy resources necessary for reproductive output. The fact that skipped spawning in males is less prevalent than in females (Morbey and Shuter 2013; Sitar et al. 2014) supports the energy allocation hypothesis because energy investment in male reproduction is less than in females. Further, a high frequency of skipped spawning in lake charr appears related to high lake charr density and low prey density (Chavarie et al. 2016; Morbey and Shuter 2013; Sitar et al. 2014). Similar to Atlantic cod *Gadus morhua* (Skjaeraasen et al. 2012), the hepatosomatic index (weight of liver related to body weight) was significantly lower in siscowets that skipped spawning (Sitar et al. 2014), further indicating that energy reserves are involved in this phenomenon. However, circumstances initiating skipped spawning probably act well in advance of the initiation of gonadogenesis and could involve factors during the prior year, such as attack and parasitism by invasive sea lamprey *Petromyzon marinus* that alter energy reserves of the host (Sitar et al. 2014). Whether skipped spawning is a requisite part of the life history of lake charr ecotypes or just a response to fish density, prey availability, or other environmental variables is unknown. Siscowets in Lake Superior attain puberty at substantially shorter length and much later age than leans. Further, skipped spawning in siscowets extends across a wide range of lengths and ages (Sitar et al. 2014). In contrast, leans reach puberty and skip spawning over a narrower range of lengths and ages. The higher frequency of skipped spawning in siscowets may also be related to their greater longevity than leans. Based on differences in age and size at puberty, skipped spawning of some frequency may be inherent in the siscowet reproductive life history, with the precise frequency further modulated by other factors, such as food availability, density, and lamprey wounding.

For stock assessments that estimate spawning stock biomass as biological reference points to establish total allowable catch limits, the presence and amount of skipped spawning in the population should be considered. In populations where skipped spawning does not occur or is negligible, a maturity ogive (probability of being mature) can be considered equivalent to the reproduction ogive (estimate of fish spawning). However, for populations in which skipped, spawning occurs, maturity and reproductive schedules should be distinguished and applied properly to ensure long-term sustainability of populations. The standing stock biomass of spawning fish can be overestimated when skip-spawners are assumed to be a part of the mature reproductive population (maturity ogive) (Rideout and Tomkiewicz 2011; Sitar et al. 2014; Skjaeraasen et al. 2012). An inflated reproductive potential of the population could then allow excessive fishing mortality if quotas are developed based on over-estimates of standing stock biomass.

2.3 Fecundity

Fecundity is a measure of the number of mature eggs in a reproductively active female during a spawning season. Absolute fecundity is the number of mature eggs per individual female and relative fecundity is the number of mature eggs per unit weight (Bagenal 1978). Fecundity provides a measure of the reproductive capacity of an individual fish and, when summed across all fish in the population, the reproductive potential of a population for use in fishery management decisions (e.g., population fecundity or egg production). In terms of life-history strategy, fecundity can be considered an investment in the quantity of potential individuals for the next generation, which is related to tradeoffs in energy allocated between gonadal and somatic tissue in the context of growth rates mediated by the environment (Koops et al. 2004; Winemiller and Rose 1992). Key environmental variables that affect fecundity include the availability of quality food, temperature, and mortality rates (e.g., Hutchings 1991). For example, the humper lake charr in Lake

Superior is the smallest ecotype, is slow growing, but has a higher relative fecundity (i.e., eggs/kg) than other sympatric ecotypes in a low-mortality environment (Goetz et al. 2017). Tradeoffs in reaction norms such as maturation are also strongly related to fecundity in lake charr. Fecundity can be a compensatory response of populations to high mortality, as when lake charr and lake whitefish fecundity increased after fishery exploitation increased (Healey 1978). Based on a qualitative assignment of relative exploitation or mortality rates, relative fecundity of lake charr was generally higher in lakes categorized as having relatively high exploitation or mortality rates (Table 1; see also Hansen et al. 2021).

Absolute fecundity increases with body size and age of lake charr (Fitzsimons and O'Gorman 1996; Goetz et al. 2017; Peck 1988). However, the relation between absolute fecundity and age in some lake charr populations can be more variable due to confounding variables of age measurement error and variability in growth yielding differences in size-age relations (e.g., O'Gorman et al. 1998). Reported values for lake charr absolute fecundity ranged between 274 and 19,671 eggs and relative mean fecundity ranged from 718 to 2226 eggs/kg (Table 1; see also Hansen et al. 2021). Fecundity was lower for Arctic charr populations in northern compared to southern latitudes due to lower productivity (Power et al. 2005), but a similar pattern was not apparent in lake charr (Table 1; Hansen et al. 2021). However, lake charr populations in lower conductivity lakes had lower fecundity than in high-conductivity lakes (Trippel 1993). Siscowets appear to have lower relative fecundity than leans, albeit in only two time periods (Eschmeyer 1955; Goetz et al. 2011, 2017). In wild leans and siscowets, follicle-stimulating hormone (pituitary gonadotropin that stimulates oogenesis) transcript levels that were significantly lower in parasitized than in nonparasitized individuals indicated an effect of sea lamprey parasitism on reproduction (Smith et al. 2015). Because sea lamprey parasitism rates are higher in siscowets (Moody et al. 2011), an effect of parasitism on the reproductive endocrine axis might explain the lower fecundity of siscowets given their high rates of wounding. Fecundity did not differ significantly between sympatric wild and hatchery lean lake charr populations in southern Lake Superior (Peck 1988). Limited estimates of lake charr fecundity from across the species' range limit inferences about geographical and ecological patterns. Future studies measuring lake charr fecundity across a broad range of lakes and ecotypes would increase understanding of selection pressures that dictate egg production.

2.4 Summary

One of the most interesting findings on lake charr reproduction since Martin and Olver's (1980) review is that certain populations of siscowet lake charr spawn in spring while other ecotypes reproduce in fall. Spring spawning of charrs that inhabit deep water and not shallow water, may confer an advantage to deep-water ecotypes. Advantages of spring spawning could be an altered time of departure from spawning

Table 1 Fecundity of lake charr *Salvelinus namaycush* in North America

Lake	Location	Ecotype	Absolute fecundity (eggs/female)		RE	Relative fecundity (eggs/kg)		Range or mean		Age	Author(s)
			Mean	Range		Mean	Range or 95% CL*	Length (mm)	Weight (kg)		
Susitna	Alaska		7600					698–990			Burr (1987), William (1966)
Old John	Alaska		6633	1230–13,000				345–770			Burr (1987), Craig and Wells (1975)
Itkillik	Alaska		2514	1011–10,623				423–821			Burr (1987), McCart et al. (1972)
Campsite	Alaska		1710	274–10,824				353–753			Burr (1987), McCart et al. (1972)
Chandler	Alaska		3117	1088–6371				420–748			Burr (1987), Furniss (1974)
Alexie	Yellowknife, Northwest Territories		1960					513	1.55		Healey (1978)
Baptiste	Yellowknife, Northwest Territories		2060					522	1.75		Healey (1978)
Chitty	Yellowknife, Northwest Territories		2370					543	1.93		Healey (1978)
Drygeese	Yellowknife, Northwest Territories		2020					516	1.75		Healey (1978)
Squeers	Northwestern Ontario	Lean	2894	664–19,671	H	1500	880–2439	324–905	0.42–11.4	7–36	Ball (1988)
Greenwich	Northwestern Ontario	Lean			LM	883					Trippel (1993); model estimate
Burnt Island	Northwestern Ontario	Lean			LM	2226					Trippel (1993); model estimate

(continued)

Table 1 (continued)

Lake	Location	Ecotype	Absolute fecundity (eggs/female)		RE	Relative fecundity (eggs/kg)		Range or mean		Age	Author(s)
			Mean	Range		Mean	Range or 95% CL*	Length (mm)	Weight (kg)		
Little Joe	Northwestern Ontario	Lean			LM	1200					Trippel (1993); model estimate
Loch Erne	Northwestern Ontario	Lean			LM	1260					Trippel (1993); model estimate
South Otterskin	Northwestern Ontario	Lean		7445	LM	1193					Trippel (1993); model estimate
Superior	Western	Lean	6455	3350–11,823	H	1456	368–2259	640–932	2281-8626	6–17	Schram (1993)
Superior	Southern	Lean-hatchery	6477	1798–12,662	H	1508	1234-1782*	623–889	1.9–5.8		Peck (1988)
Superior	Southern	Lean	5561	1726–12,650	H	1431	1170-1694	623–892	2.2–6.4		Peck (1988)
Superior	Isle Royale, northwestern	Lean	3182	1301–8002	L	1236	437–2820	555–848	1.35–6.09	8–32	Goetz et al. (2017)
Superior	Isle Royale, northwestern	Siscowet	3101	989–7810	L	1194	485–2304	495–858	1.13–8.38	10–44	Goetz et al. (2017)
Superior	Isle Royale, northwestern	Humper	1290	469–2177	L	1313	771–2507	400–548	0.53–1.53	10–30	Goetz et al. (2017)
Superior	Isle Royale, northwestern	Redfin	2685	1396–5168	L	1299	864–2180	505–755	1.09–4.5	12–39	Goetz et al. (2017)
Sudbury Lakes	South-Central Ontario	Lean	2674	604–5375	H	1556	823–2207	323–652	0.38–4.8	4–9	Polkinghorne and Gunn (1981)
Simcoe	Central Ontario	Lean-hatchery			H	2145		1627-2663		4–19	Dolson (2012)

Superior	Southern	Lean			H	1404	598–1742	603–891	1.9–6.1		Goetz et al. (2011)
Superior	Southern	Siscowet			L	1167	700–1647	536–797	1.2–5.8		Goetz et al. (2011)
Ontario	Southwestern	Lean-hatchery	5751	3077–9230	H	1592	1007-2677	617–800	2.36–5.62		Fitzsimons and O’Gorman (1996)
Yellowstone	Wyoming	Lean		798–16,834		718	551–885	468–906			Syslo (2010)
Yellowstone	Wyoming	Lean				1556	777–2335				Syslo (2010)

Relative exploitation (RE) was assigned by us based on reported exploitation or mortality. *L* light to no fishing and low total mortality, *LM* light to modest levels of exploitation and mortality, *M* modest exploitation and mortality, *H* high levels of exploitation and mortality, *blank* no data. Asterisk indicates that value is a 95% CI. If no asterisk value is the range reefs, decreased competition with free embryos of fall-spawning fish, or avoidance of adverse conditions or predation during a long winter of incubation. Alternate spawning times and deep-water spawning (e.g., siscowets) also raises interesting questions related to the relative timing of hatching, first feeding, and yolk sac absorption between spring and fall spawners. Although skipped spawning of lake charr has been known for many years and was reported extensively by Martin and Olver (1980), more recent research has quantified rates of skipped spawning that differ between ecotypes. However, whether skipped spawning is a requisite part of the reproductive life history of some ecotypes, or rather is caused by increased population density, low food availability, or stresses, such as lamprey wounding, is unknown.

2.5 Future Research Needs

Determine the environmental variables controlling seasonal timing of reproduction in lake charr.

- Can changes in photoperiod alter the timing of reproduction in lake charr and does the effect of photoperiod differ among ecotypes?
- What is the effect of temperature on spawning time?

Investigate advantages of spring spawning by deep-water ecotypes

- Does hatching in late summer or fall improve access to prey for free embryos?
- When and how do deep-water spawned free embryos fill their gas bladder?
- Does spring spawning decrease competition for food with free embryos from fall spawners?
- Does spring spawning reduce predation on eggs and pre-hatch embryos by predators that have access to alternative prey during summer?

Describe the developmental timing of embryos spawned in deep water.

- When do deep-water embryos from spring and fall-spawning ecotypes hatch?
- What is the rate of development of deep-water embryos from spring and fall spawning, relative to shallow-water, fall-spawned embryos? How do thermal environments for incubation differ among ecotypes? At what season do they hatch, begin first feeding, and complete yolk sac absorption?

Investigate the frequency and variables that affect skipped spawning in lake charr

- Is skipped spawning an obligatory part of the reproductive life history of some ecotypes (e.g., siscowet lake charr)?
- What is the frequency of skipped spawning?

- Is skipped spawning initiated or modulated (if obligatory) by environmental parameters such as population density, food availability, or perturbations such as sea lamprey parasitism?

Compare fecundity of lake charr across a broad range of lakes and sympatric ecotypes

- What are the differences in fecundity for lake charr ecotypes that live and spawn at different depths?
- Is latitude or productivity related to lake charr fecundity?
- Does relative fecundity differ between ecotypes and is it genetically determined?

3 Developmental and Early Life History

Most knowledge of lake charr development, growth rates, and post-hatching behavior has been informed by laboratory studies and hatchery observations. Such studies provide an understanding of growth and development under controlled conditions at static temperatures, but do not represent events and behavior under typically varying natural environmental conditions. For example, lake charr embryos in hatcheries are generally incubated at a constant temperature (usually 10 °C) so that the hatching date is predictable, occurs within a short interval, and all embryos are ready to begin exogenous feeding at a similar same time. In the wild, lake charr that reproduce in fall in shallow water typically spawn at water temperatures around 9–12 °C along the southern edge of their range, and development is initially rapid as lakes cool prior to winter. Pre-hatch embryo development then slows or stops for four or more months as temperatures approach 0 °C in midwinter and resumes with rising temperatures in spring. Spawning can occur over several weeks, dependent on temperature, female age (Casselman 1995), strain (Horns 1985), and individual variability, so pre-hatch embryos from early and late spawners are exposed to different temperature regimes, and hatching occurs over a considerable period of a month or more. Here, we expand the description of the development and early life history to include data on development, behavior, and sources of mortality from lake charr embryos in the wild.

The most detailed early work on lake charr development was presented by Balon (1980), and we have borrowed heavily from his pioneering work (Table 2). Subsequently, Allen et al. (2005) updated Balon's work with detailed descriptions of developmental stages and morphology of lake charr. Balon defined somewhat discrete intervals (periods, phases, and stages) in development that correspond to the appearance of or changes in physical or developmental characteristics (Table 2). However, these stages impose break-points and categories on what is actually a continuous process. For example, the most obvious change in state in early development is hatching, but hatching "is a fairly artificial character as a boundary between phases" Balon (1975), because the embryo can free itself from the chorion at a range of developmental stages that are influenced by temperature and oxygen.

Table 2 Developmental intervals in lake charr *Salvelinus namaycush* defined by Balon (1975, 1980)

Interval	Developmental changes[a]	Temperature units[b]	Duration[b]	TL[b]
Embryonic period (fertilization to internalization of the yolk sac)		651, 779	82, 149 days	
Cleavage phase—Fertilization to organogenesis (82–82 TU)				
	C^1 formation of perivitelline space and blastodisc, bipolar differentiation			
	$C^2$2 first multiplication of cells, cleavage, formation of morula	3.8	9, 24 h	
	$C^3$3 blastula, gastrula, beginning of epiboly, formation of germ ring and embryonic shield		8, 18 days	
Embryonic phase—Organogenesis to hatching				
	$E^1$4 gradual closure of germ ring, parallel development of neural plate anlage	103, 133	11, 17 days	3.8
	$E^2$5 formation of the first somites, brain ventricles, and optic anlagen, separation of the tail tip; first muscular contractions	150 at 4.4 °C	35 days at 4.4 °C	5.5
	$E^3$6 beginning of trunk movements, heart beats, first type of blood circulation; eyes become pigmented and visible through the chorion (“eye-up stage”)	212 at 6.6 °C	32 days at 6.6 °C	
	$E^4$7 rapid expansion of sub-intestinal vitelline plexus, the addition of hepatic-vitelline circulation and decrease in trunk-tail movements; first chromatophores appear on the head	299, 291	31, 68 days	
	$E^5$8 hepatic-vitelline yolk respiratory system, anlagen of branchial arterioles, and first movement of pectoral fins	330, 427	45, 75 days	
Eleutheroembryo phase—Hatching to internalization or exhaustion of the yolk[c]				
	$F^1$9 head separation from yolk sac, pelvic fin anlagen, jaw and gill cover movements, gradual differentiation of the embryonic fin fold, and development of the first cartilaginous skeletal structures; iridocytes appear in eyes	497, 570	See text	21.9, 19.9
	$F^2$10 onset and duration of strong photophobia, calcification of first skeletal structures	1089 at 6.6 °C, 779 at 9.5 °C		25.1, 26.2
Post-Embryo period (parr marks appear, photophobia ends, gas bladder is filled)				
Protopterygiolarval phase—Entirely exogenous feeding to commencement of differentiation of median fin fold				
	$A^1$11 mixed endogenous and exogenous feeding, separation of median fins, the disappearance of remnants of preanal embryonic fin fold	1353 at 6.6 °C		28.2
	$A^2$12 gas bladder filled, axial skeleton calcifies, exogenous feeding improves, rapid growth	1596 at 9.5 °C		50

(continued)

Table 2 (continued)

Interval	Developmental changes[a]	Temperature units[b]	Duration[b]	TL[b]
Juvenile period (fin fold vestiges absorbed, advanced calcification of skeleton, scale formation begins)				
Adult period (onset of maturity; 4–7 years or longer)				
Senescent period				

[a] Codes for each interval comprise a letter for the phase (Cleavage, Embryonic, and Free embryo (eleutheroembryo)), a superscript number for the sequence within the phase, and a numeral for the overall sequence, i.e., 1 to 10 of 10 overall ontogenetic intervals

[b] Temperature units (TU; the number of degrees above 0 ¯C for each day of incubation), duration (in hours or days), and embryo size (total length, in mm) at which each interval ends were measured from two sets of fertilized eggs (pre-hatch embryos) reared at 9.5 and 4.4 ¯C, respectively, or at other temperatures as noted (Balon 1980)

[c] Balon (1975) also defines this stage as ending when feeding begins, but in lake charr feeding commences prior to yolk sac adsorption. (see Marsden et al. 2021b). Note: Balon's terminology is specific to developmental biology and does not align completely with the terms recommended for field practitioners and publications recommended by Marsden et al. (2021b).

Here, we use a simplified terminology that reflects the correct identification of developmental stages (Marsden et al. 2021b).

3.1 *Fertilization and Pre-Hatch Embryo Development*

Egg size varies among and within female lake charr and averages about 5 mm diameter, with young females tending to produce smaller eggs than older females (Casselman 1995). Prior to spawning, ripe eggs are soft with a malleable shape and weigh 0.067 g on average (Balon 1980). In hatchery propagation, eggs are stripped from females by applying pressure along the belly towards the vent, and milt is added to "dry" eggs (i.e., eggs that have only been exposed to ovarian fluid). Once in contact with water, lake charr eggs begin to adsorb water and become turgid, a water-hardening process that takes 30–90 min (Balon 1980; Piper et al. 1986). Water-hardened eggs increase in weight (0.086–0.105 g for 5.4 mm eggs), but do not change in diameter (Balon 1980). Water-hardened eggs range from 4.4 to 6.8 mm and average 4.5 to 5.0 mm (Martin and Olver 1980). Unfertilized and fertilized eggs settle into interstices in stony substrates after spawning, while those that remain on the surface of the substrate are available to be consumed by epibenthic predators (see below). Fertilized eggs are semi-buoyant and can be resuspended by turbulence or physical disturbance of the substrate. Many fertilized eggs become lodged or wedged in crevices during water hardening, which likely reduces the probability of damage and predation. Laboratory studies have indicated that pre-hatch embryos are highly sensitive to physical shock (e.g., jarring in a container), particularly prior to epiboly (Fitzsimons 1994). Fish culturists avoid handling pre-hatch embryos prior to eye-up (eye pigment visible through the chorion), which is readily identified in live embryos (Piper et al. 1986).

Incubation time varies among parents and among embryos from the same parents and is considerably extended at low temperatures. For example, embryos from two families incubated at 9.5 °C hatched over a range of 45–53 days after fertilization, whereas embryos incubated at 4.4 °C hatched over a range of 69–105 days after fertilization (Balon 1980). Development can also be measured in accumulated temperature units, expressed as either degree-days (DD) or temperature units (TU = the number of degrees above 0 °C for each day of incubation). If the temperature is held constant throughout incubation, the temperature is linearly related to developmental points (e.g., Fig. 23 in Balon 1980). However, the number of temperature units to reach any developmental milestone varies with incubation temperature, so there is not a constant relationship between TU and developmental stage. Therefore, time to hatching in the wild, where embryos are exposed to varying temperatures, is difficult to predict. Hatching time is longer at low temperature than high temperature, although fewer temperature units are required to reach each stage. Embryos hatched at 303–462 TU at 4.4 °C and 356–414 TU at 9.5 °C (Balon 1980). Similarly, embryos hatched after 196 days and 352 TU at 1.8 °C, 90 days, and 572 TU at 6.4 °C, and 58 days and 570 TU at 9.8 °C (Dwyer 1987). Low oxygen increases the number of temperature units and decreases the number of days to hatching. Early hatching in the presence of low oxygen may be an adaptation to enable hatched embryos mobility to access areas with higher oxygen. Overall, incubation time is negatively related to temperature, while temperature units are positively related to temperature and negatively related to oxygen content (Balon 1980). Small changes in date (and therefore temperature) of spawning and overwinter temperatures result in substantial variation in hatching date (Casselman 1995). Based on a model of development in relation to temperature, hatching could extend from early December to early May in Lake Superior (Allen et al. 2005). Hatching can occur under ice or when potential predators move inshore to feed and reproduce (Krueger et al. 1995b; Riley and Marsden 2009). Survival of free embryos may increase with later hatching dates (Casselman 1995), but variability in hatching time presumably provides access to a breadth of temperature regimes that affect vulnerability to predators and availability of forage for free embryos.

3.2 Pre-Hatch Embryo Mortality: Predators

Lake charr eggs and pre-hatch embryos are vulnerable to epifaunal predators until they have settled into crevices, and to infaunal predators throughout winter.

Epifaunal predators, identified by examining stomach contents of fish sampled during the fall-spawning season, include yellow perch *Perca flavescens*, burbot *Lota lota*, white sucker *Catostomus commersonii*, catfishes (Ictaluridae), common carp *Cyprinus carpio*, lake charr, brook charr, lake whitefish *Coregonus clupeaformis*, cisco *Coregonus artedi*, round whitefish *Prosopium cylindraceum*, fallfish *Semotilus corporalis*, and mudpuppies *Necturus maculosus* (Fitzsimons 1990; Marsden 1997; Martin and Olver 1980). The period of vulnerability to these predators is short (i.e., minutes to hours), but fertilized eggs that fail to entrain into the substrate are likely all consumed (Marsden et al. 2005). Infaunal predators are limited to species that are small enough to maneuver through interstitial spaces and large enough to engulf a fertilized egg and break the chorion. Primary infaunal predators are sculpins (Cottidae) and crayfishes (Decapoda), and in the Laurentian Great Lakes basin, the invasive round goby *Neogobius melanostomus* (Chotkowski and Marsden 1999; Claramunt et al. 2005; Fitzsimons et al. 2002; Jonas et al. 2005; Martin and Olver 1980). Macroinvertebrates, oligochaetes, and leeches may also be predators, although such interactions with pre-hatch embryos have not been observed. However, egg incubators (see below) retrieved in spring often have empty compartments with no trace of remnants or fungus that might indicate dead embryo degradation or consumption.

3.3 Pre-Hatch Embryo Mortality: Other Factors

Overwinter pre-hatch embryo mortality may also result from physical displacement, physical damage, freezing, fungus (*Saprolegnia*), low dissolved oxygen, or siltation. Severe storms that scour pre-hatch embryos from interstices may cause mortality from physical shock or predation (Fitzsimons et al. 2007a). Fouling of shoals in the southern portion of the range by invasive dreissenid mussels can inhibit entrainment of fertilized eggs into the substrate (Marsden et al. 2005) or physically damage fertilized eggs by movement over sharp shells (Marsden and Chotkowski 2001). The effect of ice on overwintering pre-hatch embryos is unknown, but freezing or ice scour could physically damage pre-hatch embryos, particularly in lakes where water draw-downs occur during winter or when spawning occurs at very shallow depths. In Otsego Lake, New York, sedimentation has covered all substrate deeper than 2 m, so lake charr now spawn on gravel along the shoreline in 1–2 m depths kept clean by wave action, and hatching occurs at this depth despite ice or ice scour that may extend below 1 m (Tibbits 2007). *Saprolegnia* initially infects dead pre-hatch embryos but can spread rapidly among closely-packed pre-hatch embryos and kill live embryos. In hatcheries, frequent removal of dead pre-hatch embryos or treatment with formalin is used to reduce fungal spread. High (up to 80%) infections by *Saprolegnia* on eggs occurs at spawning sites, but the overall prevalence of this source of mortality is not known (Ellrott and Marsden 2004; Martin and Olver 1980).

Mortality of pre-hatch embryos from sources other than predation, physical shock, or sediments has been evaluated using egg incubators (Kennedy 1980, variously modified by Gunn and Keller 1984 and others) and egg bags (Perkins and Krueger 1995). Egg incubators are plastic or plexiglass grids in which pre-hatch embryos are held in individual flow-through compartments, so the fate of each embryo can be assessed, and embryos are protected from predation and cross-contamination by *Saprolegnia*. Incubators are placed within spawning substrate by divers, oriented vertically so that sediments do not accumulate in compartments and pre-hatch embryos are exposed to ambient water flow and temperature. Sources of mortality within egg incubators can only be inferred, because dead eggs are usually decayed when incubators are retrieved in spring. Egg bags are buried in the substrate, a known number of fertilized eggs are introduced into each bag in fall, and bags are covered. Incubators and egg bags are retrieved in spring prior to or soon after hatching to assess mortality. Mortality was higher in incubators (3.6–14.7%) and bags (0–3.2%) deployed in 8-m depths on a spawning reef than those deployed in shallower depths ~4 m (29–39%, 6.8–15.6%; Perkins and Krueger 1995). For uncovered egg bags at 1, 3, and 9 m depths seeded with lake charr fertilized eggs, recovery was highest in the shallowest bags, likely due to lower abundance of sculpin and crayfish predators (Claramunt et al. 2005).

Dissolved oxygen (DO) is critical for lake charr pre-hatch embryo development and survival: development is negatively affected when DO is below 10.5 mg/L, and mortality occurs prior to hatching when DO is 4.5 mg/L (Garside 1959). Dissolved oxygen lower than 50% saturation causes significant mortality (Carlson and Siefert 1974). Degradation of organic debris, such as algae (particularly *Cladophora* in the Great Lakes) and other periphyton, in autumn, can reduce oxygen levels in substrate interstices. Overwinter DO on lake charr spawning reefs rarely reaches lethal levels. DO was critically low a few centimeters below the substrate surface at sites in the Finger Lakes, New York, Lake Ontario, and lakes Louisa and Opeongo, Ontario in autumn (Sly 1988), but free embryos were collected at one of the sites in Lake Ontario a few years later (Marsden et al. 1988). DO may have increased later in autumn as organic breakdown products were washed out of interstices by water currents generated by autumn storms. DO remained near saturation throughout most of the incubation period near the surface of the spawning substrate (Perkins and Krueger 1995). DO levels were not lower than 6.2 mg/L in the vertical center and base of 3-m high constructed cobble reefs (E. Marsden, unpublished data). Even in areas with high DO, pre-hatch embryos can suffocate if sediment deposition is high, although the measurement of sediment deposition is challenging. Long-term accumulation of sediments can cause highly infilled substrate and an absence of interstices, although lake charr do not spawn on infilled substrate (Marsden et al. 1988; Marsden and Krueger 1991; Perkins and Krueger 1995). More work is needed to evaluate the effect of overwinter sediment deposition on lake charr pre-hatch embryo survival.

Overall, the mortality of pre-hatch embryos may limit the abundance of lake charr populations only when other variables are involved. These factors include the presence of non-native predators, such as round goby, environmental degradation that results in spawning on sub-optimal habitat (Martin 1957), and low density of spawners, which reduces the density of egg deposition relative to a high abundance of predators (Marsden et al. 2005).

3.4 Post-Hatching Development and Behavior

Hatching occurs through the production of proteolytic enzymes from hatching gland cells that break down the chorion, and energetic movements of the embryo that appear to facilitate exit from the chorion (Balon 1980). In *Salvelinus* species and most salmonines, embryos are still undeveloped at hatching and carry up to 75% of the original yolk sac volume (Alanara 1993). At hatching, embryos are 13–22 mm in total length, with the smallest free embryos incubated at low oxygen (Balon 1980). Development continues for several weeks during which the head separates from the yolk sac, jaw, and opercle movements commence, and the first cartilaginous skeletal structures develop (Table 2). In hatcheries, newly hatched embryos (free embryos) initially rest on their sides, then on the yolk sac, with orientation maintained by active movement of the tail and body. In natural substrates, free embryos held upright in crevices may expend less energy to maintain position. Within a few weeks, the skeleton begins to calcify and free embryos exhibit strongly photophobic movement (Balon 1980). During the period that follows, lake charr begin to swim actively to make nocturnal vertical movements out of the substrate, presumably to seek food (Baird and Krueger 2000). Within a week, free embryos begin to respond visually to moving prey and exogenous feeding begins (Ladago et al. 2016; Simard 2017). This stage is followed by a period of mixed feeding that continues until the remaining yolk sac is internalized and eventually absorbed when they become post-embryos (see Marsden et al. 2021b). Embryos as small as 22.5 mm can have over 40 items in their stomachs (Ladago et al. 2016; Simard 2017), and free embryos captured in traps on spawning reefs have food in their stomachs after several days in the trap. Therefore, free embryos must have been able to forage within the confines of a trap and within reef crevices. Access to food appears to delay the exhaustion of the yolk, so free embryos with access to plentiful, nutrient-rich prey are larger at complete yolk sac absorption than those that do not feed exogenously. Consequently, the total length of free embryos does not reflect their age since hatching. Alternatively, measurement of the ratio between yolk sac length and the total length, and length at the internalization of the yolk sac, can be used as a metric to assess relative developmental stage (Ladago et al. 2016; Simard 2017).

The end of the embryonic period in fishes is defined by the end of dependence on maternal food resources (i.e., the yolk), when lake charr are ~28 mm total length (Balon 1975). At this stage of lake charr development (post-yolk sac age-0), parr marks develop along the sides of the fish, the median fins separate, remnants of the preanal embryonic fin fold disappear, and calcification of the axial skeleton is completed (Balon 1980; Table 2). However, because of the potential for mixed feeding that delays yolk sac absorption, this point in development, similar to hatching, may be quite variable and consistent with the term “post-embryo”

(Marsden et al. 2021b). In the presence of predators, which include a wide range of fish species that move inshore during spring (Krueger et al. 1995b; Riley and Marsden 2009), lake charr free embryos may avoid extended foraging bouts, remain within substrate crevices, and exhaust yolk sac resources rapidly. Brook charr respond to the odor of predators (e.g., slimy sculpins *Cottus cognatus*) by emerging early from redds (Mirza et al. 2001). Lake charr that also detect predators would likely seek refuge in spawning substrate (Strakosh and Krueger 2005) or leave the spawning reef, either of which would reduce foraging opportunities and growth for lake charr post-embryos. Invasive lake charr in Yellowstone Lake, Montana, and Wyoming, have access to abundant food resources without competitor or predator interference (this lake contains only six fish species, of which the longnose sucker *Catostomus catostomus* is the largest species found on spawning reefs, but is not known to consume lake charr embryos). Consequently, in Yellowstone Lake, free embryos feed extensively during early development and are fully developed juveniles when the yolk finally disappears (free embryos with an external yolk sac were up to 38 mm in length; Simard 2019). The post-embryo stage (defined as the larval period $A^1$11-$A^2$12 by Balon, Table 2) appeared to be absent and the lake charr completed calcification of the axial skeleton and fin formation while the yolk sac was still present (Simard 2019).

The filling of the gas bladder in lake charr is not completely understood. In many fishes, filling of the gas bladder is accomplished by swallowing air, presumably at the surface, just prior to final departure from the spawning site, which is assumed to be an essential developmental step providing buoyancy regulation to improve swimming and survival (Friedmann and Shutty 1999; Tait 1960). Lake charr that hatch on deep reefs (>30 m) would need to make an extended vertical migration to access air at the water surface to fill their gas bladder. Lake charr in laboratory experiments could swim at least 270 m vertically to fill the gas bladder (Tait 1960). In the wild, lake charr making such a journey would be exposed to predators, temperature gradients, and pressure gradients that may all contribute to stress or mortality. However, the ability to fill the gas bladder is not lost as early development continues (Tait 1960), so the pneumatic duct may remain open to allow late filling of the gas bladder (Blaxter 1988). Lake charr are physostomous and lack the gas gland (*rete mirable*) used by physoclistous fish to exchange gases between the bloodstream and gas bladder (Fahlen 1971). However, in physostomous fishes, gases must be pumped by some means from the bloodstream into the gas bladder to equilibrate buoyancy after fish are at depth (Saunders 1953). Adult Arctic charr fill the gas bladder without access to the surface, although the mechanism was unclear (Sundnes and Bratlund 1967; Sundnes and Sand 1975). Thus, charrs can likely fill their gas bladder even if they do not have access to the surface. Lake charr could obtain gas by ingesting chironomid larvae that contain gas (Janssen et al. 2007; Tait 1959; Teraguchi 1975), or ingest bubbles in the substrate produced by decaying material, as in zebrafish *Danio rerio*, (Goolish and Okutake 1999) or generated by photosynthesis. Alternatively, age-0 lake charr ~30 mm when they leave spawning reefs, may not be inhibited by the absence of gas in the gas bladder because their buoyancy is likely not substantially negative. Juvenile lake charr may remain close to the substrate for the first year to fill their bladders later. In short, the requirement for access to the surface to initially fill the gas bladder, or indeed filling the gas bladder at all until later in the first year, may not be an essential developmental stage of lake charr (Janssen et al. 2007).

3.5 Summary

In the four decades since Balon's detailed description of lake charr development (Balon 1980), substantial work on development, behavior, and variables affecting mortality highlighted differences between early life stages in controlled settings and wild populations. Pre-hatch embryos are vulnerable to epibenthic predators unless they settle into substrate crevices, where access by predators is restricted to small, infaunal species. During overwinter incubation, low DO stimulates early hatching, or kills pre-hatch embryos, although DO levels appear to be sufficient for pre-hatch embryo development even in areas with substantial periphyton in summer. Free embryos in the wild make diurnal vertical migrations from spawning substrate and feed much earlier than previously assumed. The abundance of food and predators strongly affects the rate of development, yolk sac absorption, and duration of residence on spawning sites. The necessity for and timing of first filling of the gas bladder are not well understood, and alternatives to using surface air for filling the bladder need further study, particularly for deep-water spawning populations that lack easy access to the surface.

3.6 Future Research Needs

Quantify sources of pre-hatch embryo mortality in lake charr.

- How do ice or late fall-early winter storms affect pre-hatch embryos in shallow water?
- Do macroinvertebrates damage or consume lake charr pre-hatch embryos? Does the mortality caused by this source substantially affect year-class recruitment?

Determine how access to zooplankton affects growth and survival of free embryos.

- Do free embryos hatched in deep water typically feed prior to yolk sac absorption?
- How rapidly do free embryos in deep water grow and complete yolk sac absorption compared to shallow-water free embryos?

- Do embryos that hatch prior to ice breakup experience high mortality due to the absence of zooplankton prey?
- Can free embryos acquire sufficient thiamine during early feeding to offset thiamine deficiency signs (see TDC below)?

Investigate behavior, timing, and physiology related to the first filling of the gas bladder.

- Is gas bladder inflation without access to the surface a common occurrence? At what depths can and does this occur?
- What mechanisms are used for sub-surface gas bladder inflation (e.g., ingestion of bubbles, scavenging gases from prey)?
- How late in development can lake charr fill the gas bladder without access to the surface?
- Does a relation exist between the timing of gas bladder inflation and lake charr growth or depth distribution?
- What differences occur in the timing and mechanisms of gas bladder inflation among ecotypes?

4 Thiamine Deficiency Complex as an Impediment to Post-Hatch Survival

4.1 Background

Lake charr were virtually extirpated from the lower Laurentian Great Lakes by the 1950s, largely due to over harvest from commercial fishing and predation by sea lamprey (Fig. 2). Rehabilitation efforts for this species have been underway since the 1960s, with little success outside of Lake Superior (Eshenroder and Burnham-Curtis 1999; Krueger and Ihssen 1995; Krueger and Ebener 2004; Muir et al. 2012). In particular, very little natural recruitment of lake charr was observed in the lower Great Lakes until recently (e.g., Hanson et al. 2013; Riley et al. 2007). Various theories regarding the cause of this recruitment failure have been entertained, and chief among them was the possibility that poor survival of lake charr at early life stages was limiting reproduction (Eshenroder et al. 1984).

Low survival of lake charr pre-hatch embryos from some sites in the Great Lakes was observed in rearing experiments during the 1970s and 1980s (Mac et al. 1985), and many free embryos died as a result of blue sac disease (e.g., Symula et al. 1990) or a mysterious fatal "swim-up syndrome" that was characterized by loss of equilibrium, excitability, lethargy, hemorrhage, and anorexia (Fitzsimons 1995a). For decades, concentrations of polychlorinated biphenyls, polychlorinated dibenzo-p-dioxins, and polychlorinated dibenzofurans, collectively referred to as dioxin-like toxic equivalents (TEQs), were high enough to cause low survival in free embryos from Lake Michigan (e.g., Mac and Edsall 1991; Mac and Schwartz 1992) and Lake Ontario (Cook et al. 2003; Tillitt et al. 2008) (Fig. 2; see also Muir et al. 2021).

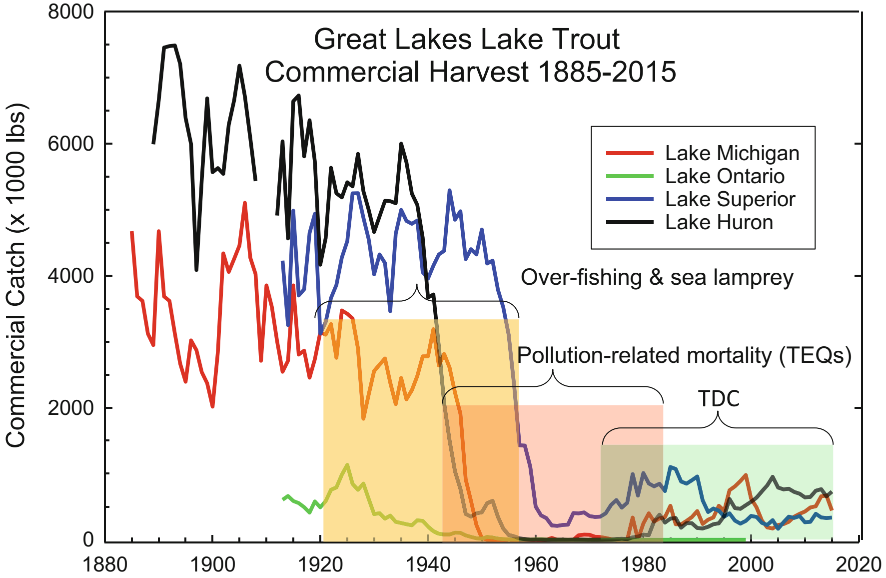

Fig. 2 Great Lakes lake charr *Salvelinus namaycush* historical commercial harvest (number × 1000 lbs./year). Adapted from Tillitt et al. 2008; data from Great Lakes Fishery Commission: Baldwin et al. 2018. Shaded areas correspond to time periods when the various stressors were thought to be a dominant factor in the lack of natural recruitment of lake charr in the lower Great Lakes. Major stressors include: commercial fishing overharvest and sea lamprey predation (approximately 1920–1955); polychlorinated dibenzo-*p*-dioxins and related chemicals, collectively referred to as dioxin-like toxic equivalents (TEQs) (approximately 1943–1983, Cook et al. 2003); and thiamine deficiency complex (TDC; approximately, 1970-present). Naturalization of alewives occurred approximately over the period represented by TEQs

Polychlorinated biphenyls, polychlorinated dibenzo-p-dioxins, and polychlorinated dibenzofurans, collectively referred to as dioxin-like toxic equivalents (TEQs) were at great enough concentrations in lake charr from Lakes Ontario and Michigan to be responsible for the lack of recruitment over several decades (Cook et al. 2003; Tillitt et al. 2008). However, lack of natural recruitment and free embryo mortality remained high as contaminant levels in lake charr declined dramatically through the 1980s (Fitzsimons 1995b; Muir et al. 2021). A breakthrough in the diagnosis of swim-up syndrome was achieved in the early 1990s when symptoms were alleviated by treating lake charr free embryos with thiamine (Vitamin B_1), which indicated the syndrome was related to low thiamine levels (Fitzsimons 1995a). Concurrently, evidence for the role of thiamine deficiency was when early life stage mortality of landlocked Atlantic salmon *Salmo salar* in the Finger Lakes was prevented by thiamine treatment (Fisher et al. 1995). These cases were among the first demonstrations that thiamine deficiency could be responsible for the complete reproductive failure of natural fish populations (Fisher and Swanson 1996).

In North America, salmonine thiamine deficiency was first referred to as “Swim-up Syndrome,” “Cayuga Syndrome” (Fisher and Swanson 1996) or “Early Mortality

Syndrome" (Honeyfield et al. 1998), and a similar syndrome in Atlantic salmon from the Baltic Sea was known as "M74" (Johansson et al. 1995). More recently, these disorders have become known collectively as "Thiamine Deficiency Complex" (TDC) to recognize the role of thiamine deficiency and reflect the fact that symptoms have been observed in adult salmonines, in addition to early life stages (Brown et al. 2005b; Riley and Evans 2008). In the Laurentian Great Lakes, TDC has been documented in the lake charr, Chinook salmon *Oncorhynchus tshawytscha*, coho salmon *O. kisutch*, rainbow trout *O. mykiss*, and Atlantic salmon (Fitzsimons et al. 2005a; Ketola et al. 2009; Marcquenski and Brown 1997; Werner et al. 2006). Immersion of salmonine fertilized eggs and free embryos from feral broodstock in a thiamine solution or injection of feral broodstock with thiamine are both now common in Great Lakes hatcheries as proven effective treatments for TDC (Brown et al. 2005a; Faisal et al. 2013).

4.2 Physiological and Behavioral Effects of TDC

Thiamine is an essential vitamin for all vertebrates that is primarily acquired through the diet. Thiamine is an important cofactor for key enzymes involved in carbohydrate metabolism, the Krebs Cycle (energy production), and ribonucleotide production (RNA synthesis) that plays a key role in nervous system function (Fattal-Valevski 2011; Mulholland 2006). Symptoms of TDC in lake charr free embryos include lethargy, loss of equilibrium, hyperexcitability, spiral "corkscrew" swimming, and failure to feed (Honeyfield et al. 1998). Nervous system disorders are a common outcome of thiamine deficiency across vertebrates because neural tissues are among the most sensitive tissues to loss of functions of thiamine from key metabolic pathways (Bettendorff 2013).

TDC occurs when thiamine levels in adults, pre-hatch embryos, or free embryos are below species-specific thresholds (Brown et al. 2005c; Fitzsimons et al. 2007b; Johansson et al. 1995). An egg thiamine concentration of 2.63 nmol/g was associated with 20% lake charr free embryo mortality (Fitzsimons et al. 2007b) and 3–8 nmol/g was associated with neurological and behavioral effects on lake charr free embryos (Carvalho et al. 2009; Fitzsimons et al. 2009). For management purposes, 4 nmol/g is the minimum recommended thiamine level for lake charr pre-hatch embryos in the Great Lakes (Bronte et al. 2008). This value was based on independent thresholds for survival, growth, prey capture, and predator avoidance. However, when these impairments were evaluated jointly within an individual-based population dynamics model, lake charr median threshold concentrations required for cohort survival were 7.4–10 nmol/g for freshly fertilized eggs (Ivan et al. 2018). This analysis indicated current lake charr populations in the Great Lakes have been under greater threat from TDC than previously estimated.

A wide spectrum of adverse effects potentially leading to indirect mortality can occur in lake charr free embryos at low thiamine concentrations that are above the threshold associated with early mortality before complete yolk sac absorption. Adverse effects associated with TDC in lake charr free embryos with insufficient thiamine include impaired growth, visual acuity, foraging success, predator avoidance, and immune function (Carvalho et al. 2009; Fitzsimons et al. 2009; Ottinger et al. 2012; Ottinger et al. 2014). Symptoms of TDC, including reduced swimming ability and loss of equilibrium, also occur in adult steelhead (rainbow trout) and coho and Chinook salmon during migration runs in the Great Lakes (Fitzsimons et al. 2005a; Futia et al. 2017; Ketola et al. 2005, 2009). To our knowledge, similar adult symptoms of TDC have not been found in wild populations of lake charr. Symptoms of TDC observed in other adult feral animals include reduced growth and condition, abnormal behavior, brain histopathological anomalies, altered blood chemistry, and parasite infestations (Balk et al. 2016; Morner et al. 2017).

4.3 Proximate Causes of TDC

TDC in lake charr and other North American salmonines is not due to low levels of dietary thiamine (Fitzsimons et al. 1998, 2005b; Tillitt et al. 2005), but rather is caused by the presence of thiaminase (a thiaminolytic, or thiamine-degrading enzyme) in their diets (Fisher et al. 1995; Fitzsimons and Brown 1998; Honeyfield et al. 1998; Ji and Adelman 1998). Dietary thiaminase is known to induce thiamine deficiency in a variety of vertebrate species, including humans. Indeed, thiaminase present in some forage fish (e.g., alewife *Alosa pseudoharengus*, rainbow smelt *Osmerus mordax*, Atlantic herring *Clupea harengus*, and common carp) induced TDC in other fish-eating vertebrates such as mink and fox (Green et al. 1941; Petrova et al. 2003). Evidence for thiaminase as the proximate cause of TDC in Great Lakes salmonines is supported by several lines of evidence (Brown et al. 2005b). In contrast, low levels of thiamine in the diet or presence of thiamine antagonists were thought to have caused widespread thiamine deficiency in a variety of wildlife populations in Europe (Balk et al. 2016).

Multiple lines of evidence support thiaminase as the causative agent for TDC in salmonines of the Great Lakes (Brown et al. 2005c). First, lake charr populations with eggs low in thiamine were found in lakes containing high proportions of thiaminase-containing prey, such as invasive alewife and smelt (Fitzsimons and Brown 1998). Additionally, in Lake Michigan, where multiple populations of salmonines including lake charr exhibit TDC, prey fish species in the lake contained thiamine concentrations greater than the presumed dietary requirement (Tillitt et al. 2005). Importantly, TDC can be experimentally induced by feeding lake charr a diet high in artificially added thiaminase or a diet containing prey fish species such as alewife with high thiaminase activity (Honeyfield et al. 2005). When female lake charr were fed a diet of 100% alewife, 60% produced free embryos with TDC, but females fed a diet of 100% bloater (a native species without thiaminase activity) produced no free embryos with TDC (Honeyfield et al. 2005). Alewife contain high concentrations of thiamine (Tillitt et al. 2005), yet still induced TDC in offspring of charr on diets containing 100% or 60% alewife (Honeyfield et al. 2005). This underscores the importance of thiaminase in the diet or prey items as the causative agent for TDC, even when diets have apparently ample amounts of thiamine (alewife thiamine is generally >8 nmol/g; Tillitt et al. 2005). Why high levels of thiaminase can co-occur in prey fish with high levels of thiamine is unknown; however, it is presumed that subcellular compartmentalization of thiaminase protects cells containing thiaminase from thiamine depletion. Thiaminase occurs in lysosomes of kidney and spleen cells in carp (Sato et al. 1994), and other tissues associated with gastrointestinal tracts of other fishes (Niimi et al. 1997).

Ecological evidence came from studies on Lakes Huron and Michigan that the lack of natural recruitment by lake charr and other salmonines may be a result of TDC caused by dietary thiaminase brought about by consuming certain forage fishes. In these lakes, thiamine levels in lake charr eggs increased after the decline of alewife populations (Fitzsimons et al. 2010; Riley et al. 2011). In Lake Huron, lake charr reproduced widely (Riley et al. 2007) and wild adults recruited to fisheries (He et al. 2012) immediately after the alewife population declined from 30 kg/ha to <5 kg/ha in the late 1990s, consistent with the hypothesis that thiaminase activity in alewife led to TDC and lack of recruitment. Similarly, thiamine concentrations in Atlantic salmon eggs from the St. Marys River, a tributary to northern Lake Huron, increased after alewife populations crashed in Lake Huron (Werner et al. 2011), and natural reproduction of Atlantic salmon was subsequently observed (Tucker et al. 2014). More recently, alewife populations in Lake Michigan declined severely (from ~8 kg/ha to <1 kg/ha; Clark et al. 2017) and concentrations of thiamine in lake charr eggs increased (most populations have thiamine concentrations >4 nmol/g; Riley et al. 2011). Subsequently, the natural reproduction of lake charr in Lake Michigan was observed for the first time in over six decades (Hanson et al. 2013). Similarly, the prevalence of TDC in Atlantic salmon in the Baltic Sea is related to the abundance of a thiaminase-containing prey fish, the sprat *Sprattus sprattus* (Karlsson et al. 1999). An alternative explanation for the negative relation between alewife abundance and lake charr recruitment is predation by alewife on lake charr free embryos and post-yolk sac age-0 fish (Krueger et al. 1995b, 2014). The resurgence of reproduction by lake charr was more likely due to a decline in alewife predation on lake charr free embryos than TDC, according to Madenjian et al. (2008). Importantly, hypotheses of predation by alewife and TDC from adult consumption of alewife could work together to prevent natural recruitment. Additionally, the relation between the introduction of alewife and the appearance of TDC in lake charr does not hold for all lakes. For example, high, sustained natural recruitment of lake charr in Lake Champlain after 45 years of stocking occurred *after* the invasion of alewife (Marsden et al. 2018). To date, multiple lines of evidence from field and laboratory work, albeit correlational, indicate that consumption of a thiaminase-rich diet is directly linked to lake-wide recruitment failure, and further work is needed to evaluate a causal relation in wild populations (Harder et al. 2018). Evidence of causality requires identifying causes of mortality of age-0 lake charr from hatching to the end of the first winter, the stage at which recruitment is established, in the wild (Harder et al. 2018). Early foraging by lake charr free embryos indicates that access to thiamine-rich zooplankton could mitigate TDC before signs appear (Ladago et al. 2016; Simard 2017). Quantitative assessment of age-0 lake charr losses directly attributable to predation or TDC across any of the Great Lakes are lacking.

4.4 Potential Sources of Thiaminase Impacting Lake Charr Reproduction

Several species that are common prey of lake charr in the Great Lakes, including the invasive alewife and rainbow smelt, contain high levels of thiaminase in their tissues, but the ultimate source(s) of thiaminase in Great Lakes biota are unknown. Thiaminase has been reported to be produced by bacteria (Abe et al. 1987; Boyd and Walton 1977; Fujita 1954) and has been found in the tissues of some species of zooplankton (Zajicek et al. 2005), fish and shellfish (Greig and Gnaedinger 1971; Hilker and Peter 1966; Hirn and Pekkanen 1975; Tillitt et al. 2005, 2009), insects (Nishimune et al. 2000), and plants (Parker and McCreg 1965). Thiaminases in plant and animal tissues could be produced by these organisms or associated microorganisms, or acquired from environmental or dietary sources.

Potential sources of thiaminase in prey fishes include de novo production by prey fish, in situ production by gut microflora, and dietary acquisition of the enzyme from lower trophic levels of food webs, sources that are not mutually exclusive. The bacteria *Paenibacillus* spp. was hypothesized to be the source of thiaminase in alewife (Fitzsimons et al. 1999; Honeyfield et al. 1998, 2002; Tillitt et al. 2005). Cultured *P. thiaminolyticus* from the gut of 25% of thiaminase-positive alewife indicated that some alewife harbor *P. thiaminolyticus* in their gut (Honeyfield et al. 2002), although thiaminase activity in alewife was unrelated to the abundance of *P. thiaminolyticus* cells or the *P. thiaminolyticus* thiaminase enzyme, which indicates that *P. thiaminolyticus* is not the primary source of thiaminase activity in alewife (Richter et al. 2012). Cyanobacteria are another hypothesized source of thiaminase (Honeyfield et al. 2002; Tillitt et al. 2005) that may be associated with high thiaminase levels in fish (Arsan and Malyarevskaya 1969; Birger et al. 1973), although evidence is equivocal.

Some ecological evidence does not support a relation between diet and thiaminase activity in fishes. For example, thiaminase activity in 39 Great Lakes fish species indicates that taxonomy is the most significant predictor of thiaminase activity (Riley and Evans 2008). Specifically, high thiaminase activity was significantly more frequently observed in basal teleosts, such as Anguilliformes, Clupeiformes, Cypriniformes, and Siluriformes, than in protacanthopterygiians and neoteleosts, such as Salmoniformes and Centrarchiformes (Riley and Evans 2008). Thus, thiaminase may be produced de novo by one or more fish species within food webs.

4.5 Ecological Conditions Under which TDC Is Likely To Occur

In addition to the Baltic Sea and Great Lakes salmonines, thiamine deficiencies have also been observed in rainbow smelt (Chalupnicki et al. 2010), walleye *Sander vitreus* (Rinchard et al. 2011), American and European eels *Anguilla spp.* (Balk et al. 2016; Fitzsimons et al. 2013), American alligator *Alligator mississippiensis* (Honeyfield et al. 2008), hooded seal *Cystophora cristata* (Dagleish et al. 2006), herring gull *Larus argentatus* (Balk et al. 2009), common starling *Sturnus vulgaris* (Balk et al. 2009), blue mussel *Mytilus sp.* (Balk et al. 2016), and common eider *Somateria mollissima* (Balk et al. 2016; Morner et al. 2017). Many examples of TDC in fish populations have been in stressed systems (i.e., Baltic Sea, Laurentian Great Lakes), so TDC may be more likely in systems that underwent changes from anthropogenic or other stressors. In the Great Lakes and the Baltic Sea, food-web changes due to invasive species and other stressors may be responsible for TDC in salmonines (Ahlgren et al. 2005; Brown et al. 2005c; Hansson et al. 2001; Riley et al. 2011). Some species may be more likely to suffer from altered or restricted diets under conditions of poor ecosystem health and thereby lead to TDC. Ecosystem stressors can also reduce the production of thiamine by phytoplankton to reduce thiamine availability (Sylvander et al. 2013). The complex ecological interactions of bacteria, plants, and animals that govern thiamine synthesis, thiamine degradation, thiamine utilization, and salvage of molecular building blocks of thiamine within natural ecosystems remain to be elucidated, even after a century of research since the discovery of thiamine (Kraft and Angert 2017).

4.6 Summary

Thiamine deficiency likely contributed to the lack of lake charr recruitment in the Laurentian Great Lakes for several decades due to severely reduced survival of free embryos (Fig. 2). Other factors, including predation on free embryos by invasive alewife, may have also played a role in recruitment failure. Recruitment has been observed in Lake Huron since 2005 (Riley et al. 2007) and since the 2010s in lakes Ontario (Lantry 2015), Michigan (Hanson et al. 2013), and Champlain (Marsden et al. 2018). The cause of TDC appears related to disrupted food webs, primarily where predominant prey for lake charr have changed from native species to non-native species rich in thiaminase, such as alewives or smelt. Laboratory and field data support the role of thiaminase as the causal agent for TDC in lake charr within the Great Lakes. Treatment of fertilized eggs and free embryos with thiamine rescues deficient lake charr in hatcheries and is routine practice for all salmonine species. Thus, fishery managers have the knowledge and tools to prevent TDC in lake charr, which allows for successful stocking. However, the ecological consequences of TDC within wild lake charr populations have not been fully understood.

More information and tools are required to understand the spectrum of consequences of TDC on the health of the entire life cycle of lake charr in the Great Lakes and other affected populations.

4.7 Future Research Needs

TDC impacts on adult lake charr.

- What physiological and behavioral adverse outcomes of TDC on adult lake charr impair reproduction?
- What clinical measures, such as thiamine-dependent enzymes, would serve as markers of TDC health status?
- What are the thresholds for thiamine tissue concentrations and thiamine health biomarkers related to the reproductive health of lake charr?
- What are the data gaps identified by population models to understand interactions of sublethal effects of TDC on lake charr recruitment?

Determine whether de novo synthesis of thiaminase occurs within prey fish species.

- Is thiaminase produced naturally by certain species of fishes?
- What controls the production of thiaminase in fish?
- What is the purpose of thiaminase in prey species of fishes?

Describe thiamine and thiamine antagonists in natural waters.

- What methods are available, or need to be developed, for measurement of thiamine vitamers in natural waters?
- What is the importance of waterborne thiamine for embryo development?
- What natural or anthropogenic chemicals may be acting as thiamine antagonists to developing lake charr or other species affected by TDC?

Determine sublethal impacts of TDC on developing lake charr and nutritional provisioning of the yolk sac.

- What latent (delayed) effects on free embryos or juvenile lake charr occur under low thiamine stress?
- What are the effects of low thiamine stress on lake charr recruitment?
- What clinical indicators in free embryos and juvenile lake charr are indicative of thiamine stress during development?
- What is the relation between female nutritional resources and the thiamine content of eggs?
- What is the relation between female age and thiamine content of eggs?
- Does early feeding by free embryos ameliorate the effects of TDC?

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Contaminants and Ecotoxicology

Derek C. G. Muir, Marlene S. Evans, Elizabeth W. Murphy, and Daryl J. McGoldrick

Abstract The lake charr *Salvelinus namaycush* is a sentinel of chemical pollution in North America due to its broad distribution and trophic position as an apex predator. We reviewed the extensive literature on contaminants in lake charr, as well as the more limited information on their biological effects. Strong evidence for PCBs and chlorinated dioxins/furans causing reduced hatchability of Great Lakes lake charr embryos emerged in the 1980s. Other stressors, such as thiamine deficiency and parasitism by sea lamprey *Petromyzon marinus* are now thought to be important factors. Measurements of persistent organic pollutants (POPs) and mercury (Hg) in lake charr began in the 1970s. Long-term trends showed major declines in concentrations of PCBs and dioxins/furans in lake charr in the Great Lakes. New contaminants, such as perfluoroalkyl substances and polybrominated diphenyl ethers increased until the early 2000s but are now declining. Similar trends occurred for many of the same POPs in northern large lakes in Canada. Extensive monitoring of Hg in lake charr showed small annual increases from the mid-2000s to 2015 in the Great Lakes and many inland lakes. Understanding future contaminant trends in lake

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charr will require strong ancillary data and information on lake thermal regimes and other climate indicators.

Keywords PCBs · Bioaccumulation · Biomagnification · Climate change · Dioxins/furans · Guidelines · Mercury · Spatial trends · Temporal trends · Toxicity · Toxic equivalents (TEQs) · Toxaphene · Trophic level

1 Introduction

The lake charr *Salvelinus namaycush* has a long history as a sentinel of chemical pollution in North America due to its broad distribution and position as an apex predator in aquatic food webs. Following the discovery during the 1960s of the bioaccumulation of mercury (Hg) in freshwater fishes (Ishikura and Shibuya 1968; Johnels et al. 1968), Hg in lake charr was first measured in the early 1970s (Bache et al. 1971). The lake charr was the first species of fish in which dichlorodiphenyltrichloroethane (DDT)-related compounds were detected as a result of a detailed study of the cause of hatchery losses of lake charr free-embryos (Burdick et al. 1964). Subsequently, DDT was detected in all species of Laurentian Great Lakes (hereafter Great Lakes) fish with lake charr having the highest concentrations (Reinert 1970). Baseline studies for DDT and newly discovered polychlorinated biphenyls (PCBs) started in Lake Michigan in the early 1970s with a focus on lake charr due to their high tissue concentrations (Veith 1975). Lake charr are valuable in recreational, commercial, and sustenance fisheries across their range, so the lake charr was used to monitor contaminant levels and trends in the Great Lakes and many smaller lakes in the USA and Canada over the past 45 years. In addition, adverse effects of contaminants in wild lake charr have been studied to understand population-level effects related to exposure. Tillitt et al. (2008) extensively reviewed toxicological studies related to effects of dioxin-like chemicals on lake charr and synthesized evidence from field studies in the Great Lakes. The purpose of this chapter is to review historical, recent, and ongoing studies of contaminants in lake charr (n.b., almost all contaminants papers use the common name lake trout rather than lake charr). We review research and assessment of a wide range of chemical pollutants or contaminants from Hg, toxic heavy metals such as cadmium, to halogenated organic compounds such as PCBs, DDT, polychlorinated dibenzo-p-dioxins (PCDDs) and –dibenzofurans (PCDFs), polybrominated diphenyl ethers (PBDEs), and poly/perfluoro alkyl substances (PFASs). Generally, our review is focused on a group or total levels rather than individual contaminant congeners, isomers, or isotopes. We also reviewed studies on biological effects of these contaminants on whole ecosystems with lake charr as the top predator, such as those at the Experimental Lakes Area in northwestern Ontario, Canada (Schindler 1990, 2009).

The term “contaminants” is used in the chapter in relation to the presence of chemicals of concern in lake charr. Although the term “pollutants” is often used, contamination is the presence of a substance where it should not be or at concentrations above background, whereas pollution is contamination that results in adverse biological effects (Chapman 2007). Furthermore, chemicals may be more or less bioavailable depending on their chemical form (dissolved, particle bound, ionized, neutral) and on the environmental compartment in which they reside. Appendix 1 provides definitions of acronyms used in the chapter.

An important aspect of contaminant research is the evolution of analytical technology and laboratory methodology for detecting chemical residues in biological samples. Methods will not be reviewed herein, but are important because their evolution was required to advance the field of ecotoxicology. The invention and commercialization of the electron-capture detector for gas chromatography (GC) in the early 1960s (Lovelock 1974) enabled DDT, other chlorinated pesticides, and PCBs to be quantified in fish at part per billion (ng/g) concentrations and set off a huge expansion of measurements worldwide in the late 1960s and early 1970s. Similarly, the use of GC coupled with high-resolution mass spectrometry enabled determination of PCDD/PCDFs and other "dioxin-like" contaminants (polychloronaphthalenes, non-ortho, or mono-ortho substituted PCBs) in biological samples at picogram per gram concentrations. Since the early 2000s, liquid chromatography-tandem mass spectrometry has enabled detection of many relatively water-soluble and ionizable substances, such as PFASs and pharmaceuticals and personal care products (PPCPs) in fish. The development of the automated Hg analyzer (Salvato and Pirola 1996; U.S. EPA 2007) greatly increased the capacity for total Hg analysis in biological samples. The availability of validated, analytical methodology, particularly those promulgated by the U.S. EPA (https://www.epa.gov/measurements/collection-methods) for contaminants in environmental media including fish tissues also facilitated comparison of results among studies. Use of certified reference materials for organic contaminants and trace metals in fish from the National Institute for Standards and Technology (NIST) (Schantz et al. 2009) and the National Research Council of Canada (NRCC 2018) served to check accuracy and precision of data over time. Interlaboratory studies such as those by the U.S. Fish and Wildlife Service (Schmitt et al. 1981), NIST (Reiner et al. 2012), and the Northern Contaminants Program (Tkatcheva et al. 2013) also helped to ensure that results were comparable among labs analyzing contaminants in lake charr.

2 Ecotoxicology Studies

More than 50 substances have been tested for toxicity to lake charr (Table 1; Appendix 1) compared to 239 for rainbow trout *Oncorhynchus mykiss* (see Acute Toxicity Database (Mayer and Ellersieck 1986); https://www.cerc.usgs.gov/data/acute/acute.html). The disparity in testing reflects the commercial availability and wide use of various life stages of rainbow trout for aquatic toxicity testing relative to lake charr. Thus, much less is known about relative sensitivity to chemical exposures of lake charr than rainbow trout. By far the most toxic substance in static acute

Table 1 Aqueous, dietary, intraperitoneal dosing, and exposure studies of lake charr *Salvelinus namaycush* to toxicants based on peer-reviewed studies

Contaminant	Regime	Lowest observable effects[a]	References
Inorganics			
Aluminum	2-day-old eggs static water exposure	200 μg/L Al increased survival at pH 4.2–88% at 6 days	Hutchinson et al. (1989)
Aluminum	sac fry and swim-up fry (i.e., free embryo and post-embryos per Marsden et al. 2021)	>97% survival at pH ≥ 5.1with 200 μg/L Al	Hutchinson et al. (1989)
Arsenic	Adult (2 year) 20 day dietary 0, 100, 1000 μg As/g	Feed refusal, lipid peroxides ↑ at 1000 μg/g, MT induction not observed	Pedlar et al. (2002)
Copper	Embryos and early juveniles exposure at 3–450 μg/L	Embryo mortality at 555 μg/L. Post-hatch early juvenile mortality at >43.5 μg/L	McKim et al. (1978)
Mercury	Fertilized eggs	0.06–14 mg/L produced mortality 0.005–0.014 mg/L did not decrease median hatch time (MHT)	Klaverkamp et al. (1983)
Nickel	Adult (2 year) 18 day dietary	Significant ↑ MT at 1000 μg/g Ni	Ptashynski et al. (2001)
Selenium	Fertilized eggs	200 mg/L Se decreased MHT and delayed mercury-induced morality	Klaverkamp et al. (1983)
H+ ion	2-day-old eggs static water exposure	<50% survival after 4–6 day exposure to pH 4.2	Hutchinson et al. (1989)
H+ ion	Sac fry and swim-up fry	<30% survival after 6 d exposure to pH 4.2	Hutchinson et al. (1989)
Organics			
2,3,7,8-TCDD	Fertilized eggs (48 h static renewal water exposure)	>50% mortality of fertilized eggs at hatching at 100 pg/L or 400 pg/g in eggs. Smaller but significant effect at 40 pg/g in eggs	Spitsbergen et al. (1991)
2,3,7,8-TCDD	Fertilized eggs (48 h static renewal water exposure)	LD50 = 85 (36–210) pg/g egg	Zabel et al. (1995)
2,3,7,8-TCDD	Eggs were injected at 24–50 h post-fertilization with TCDD	CYP1A ↑ expression at TCDD > 88 pg/g egg. Lowest observable effect at 22 pg/g	Guiney et al. (1997)
2,3,7,8-TCDD	Fertilized eggs static-renewal water exposure	Lowest observable effect on sac fry mortality at 51 pg/g in eggs; TCDD at 253 pg/g in eggs induced CYP1A mRNA levels	Guiney et al. (2000)
2,3,7,8-TCDD	Maternally derived TCDD to oocytes	Nonviable oocytes at 233–387 pg/g egg; dose-related sac fry mortality at 50–152 pg/g. No effect of dietary exposure on adults	Walker et al. (1994)

(continued)

Table 1 (continued)

Contaminant	Regime	Lowest observable effects[a]	References
PCB-126	Fertilized eggs (48 h static renewal water exposure)	LD50 = 29,000 (18,000–34,000) pg/g egg	Zabel et al. (1995)
PCB-126	Juvenile ip-injection or dietary gavage (0.7–40 ng/g whole body)	40 ng/g exposure increased thyroid epithelial cell height, plasma T4 dynamics, and T4-glucuronidation. T3 status and fish growth were unaffected	Brown et al. (2004)
PCB-126	Juvenile ip-injection (0.6–25 ng/g whole body)	Hepatic mixed-function oxidase activity (EROD) and oxidative stress indicator (TBARS) significantly ↑ at 6 ng/g and 25 ng/g	Palace et al. (1996)
Toxaphene	Wild adult—5 year after IP injection at 7 μg/g or 3.5 μg/g	Decreased survival 1 year and failure to spawn in the first year following 7 μg/g injection	Delorme et al. (1999)
Erythromycin	Adult water and food exposure	96 h LC50 = 410 mg/L, no effect on growth at 24 mg/g	Marking et al. (1988)
Oxytetracycline	Adult water and food exposure	96 h LC50 <200 mg/L, no effect on growth at 5.5 mg/g	Marking et al. (1988)
Tetracycline	Adult water and food exposure	96 h LC50 = 220 mg/L, no effect on growth at 5.5 mg/g	Marking et al. (1988)
Polyelectrolyte “Superfloc 330”	Juvenile flowing water exposure	LC50 = 0.31 mg/L (11-day exposure)	Biesinger et al. (1976)
Polyelectrolyte “Calgon M-500”	Juvenile static water exposure	LC50 = 2.90 mg/L (2-day exposure)	Biesinger et al. (1976)
Pydraul 50E (organophosphate esters)	Adult flowing water exposure	Survival reduced at 16 μg/L after 90 days, growth and cataracts affected at 5.3 μg/L	Mayer et al. (1993)
Dinoseb	96 h flow-through exposure	96 h LC50 = 79 (67–93) μg/L	Woodward (1976)
Picloram	96 h flow-through exposure	96 h LC50 = 1850 (1630–2100) μg/L	Woodward (1976)

Note that the life stage terminology from the original studies was retained in the table and maybe inconsistent with Marsden et al. (2021)

[a] *MT* metallothionein

toxicity testing of juvenile lake charr was antimycin A, an antifungal antibiotic, with a 24-h LC-50 of 0.053 μg/L. Antimycin A is very toxic and was tested in the 1960s for use to remove fish from lakes (Walker and Lennon 1964). Synthetic pyrethroids (resmethrin and bioethanomethrin) also had LC-50s in static and flow-through testing at or below 1.2 μg/L (Appendix 1). For most other organic and inorganic substances, 96 h LC50s from acute (typically static) or chronic (usually flow through) exposures of juvenile or adult lake charr were in the 100s of μg/L to 100s of mg/L (Table 1 and Appendix 1) and thus at levels unlikely to be reached from typical use in pesticide applications or from emissions due to industrial uses, apart from accidental spills. However, post-hatch age-0, juvenile mortality is a more sensitive indicator of chemical toxicity to lake charr than tests with adult fish. For example, larvae (i.e., post embryos in lake charr) and age-0 juvenile stages of lake charr, and other fish species, were more sensitive to copper than pre-hatch embryos or adults (Table 1; McKim et al. 1978). Little information is available on toxicity of most chemicals to early life stages of lake charr with the important exception of 2,3,7,8-tetrachlorodibenzo-p-dioxin (TCDD) and related compounds (reviewed by Tillitt et al. 2008 and King-Heiden et al. 2012).

Early life stages of vertebrates were known to be the most sensitive to toxicity of TCDD and related planar chlorinated aromatic compounds from results of mammalian and avian research (Gilbertson 1982; McConnell 1980). Thus, the focus of studies of developmental toxicity of TCDD in lake charr and other fishes used fertilized eggs. For example, TCDD toxicity in lake charr (LD-50 = 40–85 pg/g) was quantified for TCDD-injected pre-hatch embryos (fertilized eggs) (Spitsbergen et al. 1991). Induced early life stage mortality in rainbow trout embryos facilitated development of fish-specific TCDD toxic equivalent factors (TEFs) for PCDD/Fs and selected PCB congeners (Walker and Peterson 1991). Subsequent work using a mixture of 2,3,7,8-substituted PCDDs, PCDFs, and non-ortho substituted PCBs showed that these compounds acted via a common mechanism of aryl hydrocarbon receptor (AhR) mediated toxicity to cause lake charr free embryo mortality although their toxicity was not strictly additive (Walker et al. 1996). Of 11 species tested, lake charr was the most sensitive to TCDD, with pre-hatch embryo TCDD LD50s (40–85 pg/g) about threefold less than brook charr *Salvelinus fontinalis* (138–200 pg/g) and fivefold less than rainbow trout (230–488 pg/g) (Tillitt et al. 2008).

Cook et al. (2003) used the TEFs developed from work with individual PCDD/Fs and PCBs on early-life-stage mortality in rainbow trout to estimate 2,3,7,8-TCDD toxicity equivalence in their retrospective risk analysis of dioxin-like compounds in Lake Ontario lake charr. Tillitt et al. (2008) also reviewed the evidence for the extirpation of lake charr in the lower Great Lakes by PCDD/Fs and related dioxin-like chemicals and concluded that a strong case existed for reproductive failure from the mid-1970s to 1980s (Table 2).

Strong evidence for maternally derived PCBs causing reduced hatchability in embryos from southeastern Lake Michigan was available prior to most of the detailed information on the mechanism of AhR mediated toxicity of TCDD (Mac and Edsall 1991). By the early 1990s, TCDD and related compound levels in lake charr pre-hatch embryos in the Great Lakes decreased below levels expected to cause mortality and could not explain observed rates of juvenile lake charr mortality (Harder et al. 2018). In a review of work on early life stage mortality in lake charr, Fitzsimons (1995) concluded that reduced hatching, blue sac disease, and swim-up

Table 2 Criteria and evidence described by Tillitt et al. (2008) to support the relationship between PCDD/Fs and related dioxin-like chemicals and the extirpation of lake charr *Salvelinus namaycush* in the lower Great Lakes (i.e., Erie and Ontario)

Criteria	Evidences
Probability	Lake charr were exposed to elevated concentrations from the initial production and release of these chemicals in the 1930s into the Great Lakes ecosystem until after they were banned in the late 1970s. Concentrations of dioxin toxic equivalents in fertilized eggs of Great Lakes lake charr exceeded these thresholds for toxicity.
Timing	Temporal coincidence of rises in dioxin-like contaminant concentration and increases in reproductive failure.
Strength of association	Geographic distribution of dioxin-like pathologies including blue-sac-related mortality. The term blue sac related mortality or syndrome, was used by Spitsbergen et al. (1991) and in subsequent articles (Walker et al. 1996; Walker and Peterson 1994) to describe the effects produced by TCDD and other dioxin-like chemicals which they concluded were identical to "blue-sac disease," a condition which commonly observed in hatchery-reared salmonines.
Specificity	Presence of blue sac disease in Great Lakes lake charr from the mid-1970s to 1980s was consistent with aryl hydrocarbon receptor (AhR)-related toxicity.
Consistency of association	Geographic distribution of symptoms of dioxin-like toxicity in lake charr was consistent with the relative degree of contamination in the Great Lakes. Signs of toxicity were observed in different species at the same locations.
Predictive performance	Cook et al. (2003) found that sediment core profiles of TCDD and dioxin-like PCBs in Lake Ontario were predictive of the population abundance of lake charr, the signs of sac-fry mortality, and reductions in post-hatch embryo survival. Extracts of lake charr from Lake Michigan produced graded, dose-dependent symptoms of blue sac syndrome in hatchery-raised lake charr embryos (Tillitt and Wright 1997).
Coherence	Lake charr have been found to be the most sensitive species of fish toward dioxin (Spitsbergen et al. 1991; Walker and Peterson 1991). Lake Superior lake charr had significantly lower concentrations of PCBs and PCDD/Fs, were not observed to have symptoms of TCDD-related toxicity, and were not suffering from a lack of recruitment.

syndrome mortality in lake charr eggs were not solely related to the TCDD and other contaminants, and identified pre-hatch embryo rearing conditions, nutrition, poor egg quality, and altered physiology as alternative explanations for early life stage mortality. Subsequent research pointed to the role of thiamine deficiency as a contributing or causal factor in the reproductive problems of lake charr in the Great Lakes from the 1980s onward (Brown et al. 2005; Fisher et al. 1996; Fitzsimons et al. 1995). Tillitt et al. (2008) concluded that thiamine deficiency, parasitism by sea lamprey, and predation on lake charr free embryos by alewife *Alosa pseudoharengus* (an invasive species in the Great Lakes), could be important factors in addition to impacts of contaminants. Clearly, multiple stressors impinged on lake charr populations in the Great Lakes, with the importance of other factors revealed as one stressor was reduced (D. Tillitt, U.S. Geological Survey, personal communication).

2.1 Field-Based Studies of Toxicity to Lake Charr

Early studies suggested that DDT was associated with reproductive failure in lake charr. Elevated DDT-related compounds were correlated with reduced survival of post-hatch embryos in upstate New York lakes with no survival in lake charr post-hatch embryos that contained DDT over 2950 ng/g wet weight (ww) (Burdick et al. 1964). However, Burdick et al.'s methodology did not enable measurements of PCBs, PCDD/Fs, or other chlorinated pesticides. A subsequent study showed that adult lake charr fed diets with 6000 ng DDT per g feed produced 100% mortality in the lake charr post-hatch embryos (Burdick et al. 1972). DDT concentrations in lake charr in Lakes Ontario and Michigan in the 1970s were high enough (means ranging from 5000 to 20,000 ng/g ww) to have contributed to lake charr pre-hatch embryo mortality (Zint et al. 1995).

A series of field experiments involving exposure to toxic contaminants have provided insights into contaminant effects on adult lake charr under natural conditions. Lake charr were treated with a single intraperitoneal injection of toxaphene in Lake 260 in the Experimental Lakes Area (ELA) over a two-year period at nominal doses of 3.5–7 μg/g ww (Delorme et al. 1993, 1999). These doses were similar to concentrations in Great Lakes fishes. Toxaphene is a major organochlorine pesticide contaminant in Great Lakes fishes (Muir et al. 2006; Xia et al. 2012) and its toxicity to fish is well known (Eisler and Jacknow 1985). No threshold has been formally established for adverse effects of toxaphene in lake charr, but treated adult lake charr survival was lower than controls and they apparently failed to spawn in the first year following injection (Delorme et al. 1993, 1999). The percentage of lake charr eggs successfully fertilized from toxaphene-treated female lake charr did not differ from controls and no major changes in growth were evident. Delorme et al. (1993, 1999) concluded that cumulative effects of toxaphene exposure conducted under a multiple stressor environment of a natural lake had the potential to alter lake charr population dynamics.

The biomass of lake charr in Lake 260 at the ELA declined 23–42% during and after addition of 17α-ethynylestradiol (EE2) to the lake, likely an indirect effect from loss of its prey, the fathead minnow *Pimephales promelas*, pearl dace *Margariscus margarita*, and slimy sculpin *Cottus cognatus* (Kidd et al. 2014). Vitellogenin (VTG) was induced up to 18,700 fold in male lake charr compared to reference lakes (Table 3); however, intersex and effects on gonadal development were not detected (Palace et al. 2009). Because EE2 was added only to the epilimnion during summer, EE2 exposure to lake charr occurred after lake turnover during autumn. Exposure of lake charr to EE2 could also have occurred via the diet given the high exposure of lake charr prey, the fathead minnow, and pearl dace, to EE2 in L260.

Table 3 Mean vitellogenin induction in male fathead minnow *Pimephales promelas*, pearl dace *Margariscus margarita*, lake charr *Salvelinus namaycush*, and white sucker *Catostomus commersonii* in Lake 260 of the Experimental Lakes Area of Ontario treated with 17a-ethynyloestradiol (EE2) compared to reference lakes (Palace et al. 2009)

Year	Season	Fathead minnow (homogenate)	Pearl dace (homogenate)	Lake charr (plasma)	White sucker (plasma)
2001	Fall	22200	5900	1900	22
2002	Spring	3800	3000	11500	24
	Fall	8700	3800	2100	62
2003	Spring	6500	15900	18700	94
	Fall	24200	2300	4600	118

Food-web collapse during a lake acidification experiment resulted in lower lake charr survival over a 7-year period in which the epilimnetic pH was lowered from 6.49 to 5.13 (Mills et al. 1987; Schindler et al. 1985). Condition factor ($CF = 100 \times weight/length^3$) of lake charr in Lake 223, ELA gradually declined from 1977 (pH 6.13) to 1983 (pH 5.13; Mills et al. (1987). In 1983, lake charr condition in Lake 223 was less than at any time in any reference lake. By 1983, lake charr were emaciated due to losses of prey organisms. The threshold for lake charr recruitment failure in Lake 223 was pH 5.59, similar to observations for lake charr populations in New York State Adirondack lakes and in a central Ontario survey (Beggs et al. 1985; Schofield 1982).

A whole-lake experimental addition of cadmium (Cd) to ELA Lake 382 did not result in observable effects on lake charr. The study investigated the fate and effects of low concentrations of Cd, not exceeding the Canadian Water Quality Guideline (CWQG) at the time of 200 ng/L (Malley 1996). Over a 6-year period of addition of $CdCl_2$ to the epilimnion, Cd concentrations in water ranged 20–240 ng/L (Lawrence et al. 1996). Cd concentrations in the posterior kidney of lake charr reached 9.5 µg/g ww, a sixfold increase above background. After five years of Cd additions, concentrations in lake charr skeletal muscle remained at background levels of 4 to 8 ng/g ww (Malley, 1996).

Whole lake studies at the ELA illustrate the need to study effects of contaminants at the whole ecosystem level (Blanchfield et al. 2009). While not practical for all chemical contaminant issues due to the need to restore altered habitat to its original state (as required at ELA), ELA experiments yielded unique insights into effects of environmental contaminants on lake charr.

2.2 Bioaccumulation Studies of Organic Contaminants

Early studies of PCBs and DDT-related compounds in lake charr, forage fishes, zooplankton, and water from western Lake Superior demonstrated biomagnification of these contaminants in the food web (Veith et al. 1977) and led to the question of the relative importance of water versus dietary uptake pathways for contaminants.

Juvenile lake charr had a bioconcentration factor (BCF) of 53000 for the uptake of p,p′-DDT from water, which was exceeded by p,p′-DDT uptake from food during a 90-day exposure (Reinert et al. 1974). Both water and dietary uptake routes were important for dieldrin, which was eliminated more rapidly following transfer of fish to uncontaminated water (Reinert et al. 1974). Lake charr exposed to p,p′-DDT, p,p′-DDE (100 ng/L), and PCBs as Aroclor 1254 (100 and 500 ng/L) in a flow-through system over a 12-week period, increased tenfold in concentration for both DDT and PCB related compounds, but did not reach equilibrium (Hesselberg and Nicholson 1981). Laboratory exposures by Reinert et al. and Hesselberg and Nicholson represent the only bioconcentration studies (i.e., uptake) from water only, for organic contaminants in lake charr. However, the question of the importance of waterborne vs. dietary exposure was addressed by many other studies with closely related species, especially rainbow trout. In a long-term (96 days) exposure of rainbow trout to 34 organohalogen compounds, BCFs were much lower than field-derived bioaccumulation factors (BAFs) particularly for chemicals with long half-lives in fish (Niimi and Oliver 1985).

Simultaneous measurements of concentrations in lake charr, water, and sediment demonstrated very high BAFs for persistent and bioaccumulative substances in lake charr. Using data from Metcalfe and Metcalfe (1997), who measured PCB congeners in lake charr and water from north-central Lake Ontario, BAFs (concentration in fish lipid normalized; C_F) divided by concentration in water (dissolved) ranged $0.13–4.07 \times 10^6$ for PCB congeners based on lipid weight (Arnot and Gobas 2006). Based on dissolved PCBs and PBDEs in Lake Michigan, BAFs ranged $0.316–316 \times 10^6$ for PCBs and $0.501–31 \times 10^6$ for PBDE congeners 47, 66, 99, and 100 (Streets et al. 2006). BAFs were correlated with log octanol–water partition coefficient (log K_{ow}) (Fig. 1) and therefore could be predicted relatively accurately from basic physical–chemical properties of the compounds (Streets et al. 2006). Thus, selected congeners could be used for monitoring these contaminants in lake charr and dissolved concentrations in water could be inferred.

BAFs for lake charr in the Great Lakes have also been reported for perfluoro alkyl substances (PFASs) (Furdui et al. 2007), toxaphene (Muir et al. 2004), and Hg (Raymond and Rossmann 2009). While BAFs illustrate the tremendous bioaccumulation potential of persistent organic pollutants (POPs) and could be used to compare lakes and food webs assuming that lake charr were at the same trophic level (Streets et al. 2006), they do not provide information on pathways of bioaccumulation.

Biota–sediment accumulation factors (BSAFs) have been used to assess exposure of invertebrates and fishes, including lake charr, to sediment-associated organic contaminants (Burkhard et al. 2012). BSAFs are calculated by dividing the contaminant concentration (lipid normalized) in whole fish by the concentration in sediment (organic carbon normalized). For fishes, especially those not in direct contact with sediments, BSAFs incorporate a range of pathways and processes including biomagnification, sediment-water column chemical exchange, food-web characteristics, the fish's home range, and transformation of the chemical within the fish and its food web. Burkhard et al. (2004) developed a BSAF data set for PCBs, PCDDs,

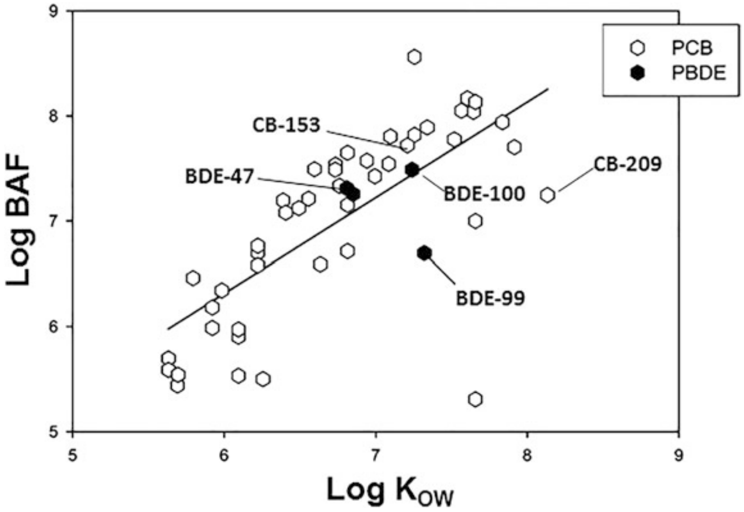

Fig. 1 Bioaccumulation factors versus octanol–water partition coefficients (log BAF vs log K_{ow}) for PCB (open hexagons) and PBDE (closed hexagons) congeners for lake charr *Salvelinus namaycush* in Lake Michigan (Streets et al. 2006)

and PCDFs in southeastern Lake Michigan lake charr. The top 1–2 cm layer was used for determining concentrations in sediment on the basis that it would best represent the exposure history of the lake charr. BSAFs for PCBs and PCDD/Fs for year classes 2–9 were remarkably similar despite known differences in diet. Differences in lipid fraction helped explain a similar range from 5% in 2-year-old lake charr to 18.5% in 9-year-old fish. Variation of BSAFs with log K_{ow} (Fig. 2) for the 6-year-old age class was lower than predicted BSAF based on the Gobas food chain model (described below). The authors concluded that the generally lower observed than predicted BSAFs for PCBs were mainly due to metabolism of some congeners by lake charr. This conclusion was also apparent from the fact that PCDD/Fs had very low BSAFs (0.001–0.2) compared to PCBs (0.1–11), which was consistent with much more rapid elimination and metabolism.

BSAFs were used to relate measurements of PCDD, PCDF, and PCB congeners in Lake Ontario sediments to lipid-normalized concentrations in lake charr unfertilized eggs (Cook et al. 2003). BSAFs for lake charr female and pre-hatch embryos ranged range from >10 to 0.3 for PCBs and from 0.27 to <0.001 for PCDD/Fs. This range was almost identical to BSAF values in southern Lake Michigan lake charr (Burkhard et al. 2004). BSAFs for PCBs in lake charr from Lake Michigan were also strongly correlated with BSAFs for other species, such as adult alewife and walleye in Green Bay ($P<0.003$), and smallmouth bass *Micropterus dolomieu* and yellow perch *Perca flavescens* ($P<0.0001$) in the Hudson River, although absolute values differed (Burkhard et al. 2005). Nevertheless, the relative values of BSAFs for a wide range of PCBs were similar for lake charr and

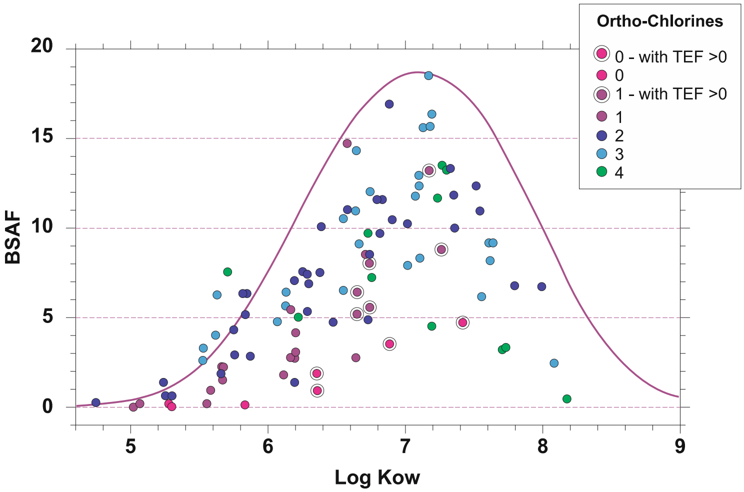

Fig. 2 Biota-sediment accumulation factors (BSAFs) for PCBs in Lake Michigan lake charr *Salvelinus namaycush* (redrawn from Burkhard et al. 2004). Red, purple, blue, turquoise, and green circles represent PCB congeners with 0, 1, 2, 3, and 4 ortho-chlorines, respectively. Double circles are congeners with toxic equivalent factors (TEFs)>0. The curved line illustrates the expected relationship of BSAFs with K_{ow} predicted by use of the Gobas food-web model (Gobas 1993) assuming no metabolism

other fishes across ecosystems. Thus, prevailing concentrations of bioaccumulative chemicals in sediments could be inferred from monitoring of lake charr.

Almost all dietary absorption, uptake rates, and elimination half-lives ($t_{1/2}$) of chemicals in salmonids have been developed using rainbow trout in the 1970s and 1980s (Niimi 1987). However, dietary absorption, or net trophic transfer efficiency (γ), of 75 PCB congeners by lake charr in a laboratory experiment using bloater *Coregonus hoyi* (fed ad libitum) as the source of dietary PCBs was defined as (Madenjian et al. 2012b, 2014):

$$\gamma = \Delta\text{PCB body burden (ng)} \div \text{amount of PCB ingested (ng)}$$

where ΔPCB body burden is the increase during the experiment (determined using average weight of the lake charr × average concentration in whole fish). Increasing the feeding rate caused γ to decrease, whereas the degree of chlorination of the PCB congeners was unrelated to γ, which averaged 0.66 across all congeners (Madenjian et al. 2012b, 2014). However, γ decreased significantly as log K_{ow} increased from 6.0 to 8.2 (Fig. 3), which suggested lower bioavailability of more hydrophobic, highly chlorinated, congeners (Madenjian et al. 2012b, 2014). Activity level did not have a significant effect on γ (Madenjian et al. 2012b, 2014). In a review of dietary bioaccumulation studies of organic contaminants, one (Tomy et al. 2004) of 98 dietary exposure studies on 477 discrete organic chemicals used lake charr (Arnot and

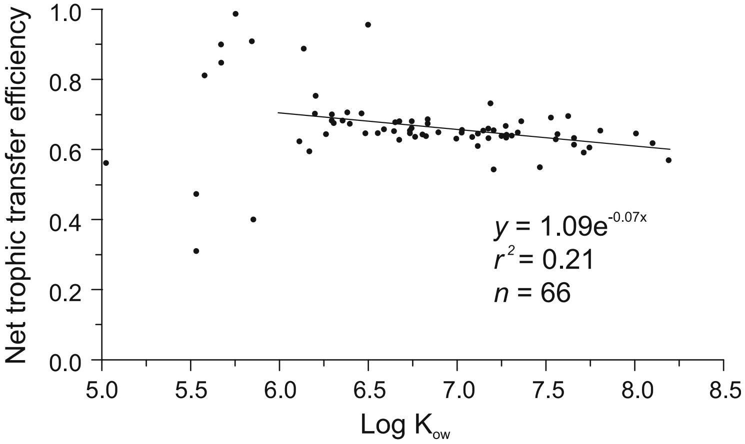

Fig. 3 Estimate of net trophic transfer efficiency (γ) of PCB congeners to lake charr *Salvelinus namaycush* from its prey as a function of the log K_{ow}. Estimates were based on a laboratory experiment, during which lake charr were fed bloater *Coregonus hoyi*. Fitted regression line for congeners with log K_{ow} greater than 6 is also displayed (Madenjian et al. 2012b)

Quinn 2015). Tomy et al. (2004) examined dietary update of polybrominated diphenyl ethers (PBDEs) in juvenile lake charr during a 56-day feeding phase and a 112-day depuration phase (on clean food), along with effects on cytochrome P450 (CYP 1A) enzyme activity, measured as EROD, and free tri-iodothyronine (T3). Half-lives of four PBDE congeners (47, 99, 100, 183) in a low dose exposure (1.1–2.1 ng/g dw food) ranged from 39 to 87 days (Tomy et al. 2004). A higher dose exposure with the same four PBDE congeners were distinctly greater $t_{1/2}$ (173–346 days). Two other BDEs (28, a tribromo-congener and 209, decabromo-) had shorter $t_{1/2}$ (58 and 26 days, respectively; Tomy et al. 2004). The absorption efficiency of very hydrophobic and high molecular weight congener BDE209 in lake charr was much lower (5%) than tribromo- to heptabromo (23–53%) (Tomy et al. 2004). Dietary bioaccumulations of several other BDE congeners (e.g., BDE-66, -77, -153, and -154) by lake charr were much longer than anticipated, likely because these congeners were formed via debromination of other congeners, in addition to being accumulated from food (Tomy et al. 2004). Debromination of PBDE congeners by carp *Cyprinus carpio* (Stapleton et al. 2004) and common sole *Solea solea L.* (Munschy et al. 2011) has also been reported.

Half-lives and absorption efficiencies reported for PBDEs in lake charr can be compared to other species (Appendix 2) for which results of studies of similar design (feeding rates, exposure times, and depuration times) were available from the database for dietary bioaccumulation (Arnot and Quinn 2015). However, concentrations of food varied greatly among studies. Whole-body $t_{1/2}$ of BDE 47 (a tetrabromo congener) were similar in lake charr, carp, and sole (39, 30, and

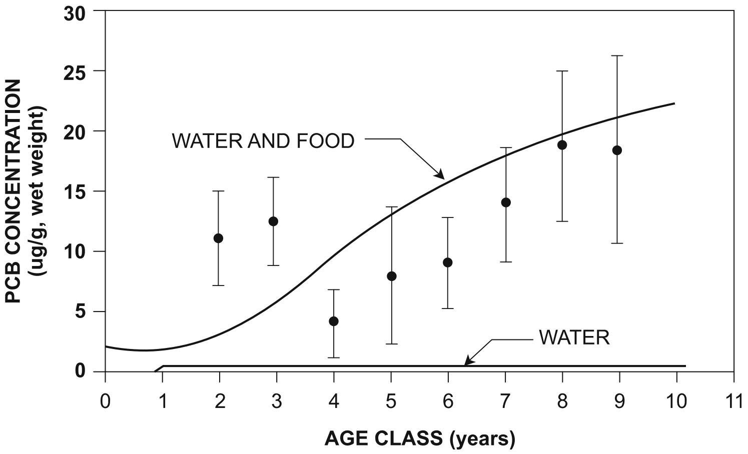

Fig. 4 Predicted versus observed concentrations of PCBs in various lake charr *Salvelinus namaycush* age classes from Lake Michigan from the Thomann and Connally (1984) food chain model. Estimated concentrations from water only exposure and water + food exposure are shown. *Reprinted with permission*

37 days). Half-lives of BDE 28, 100, and 209 in lake charr were within a factor of two of those for sole. Zebrafish had much shorter $t_{1/2}$ for BDE 28, 183, and 209 than lake charr. Fish size and exposure temperature likely influenced some differences (e.g., zebrafish were held at 26 °C versus 12 °C for lake charr). Biotransformation of PCBs to hydroxy-PCBs was positively related to water temperature in rainbow trout (Buckman et al. 2007), although applicability to rates of debromination of PBDEs is uncertain. In vitro studies using liver microsomal incubations showed that debromination rates of PBDE congeners were generally 10–100 times faster in carp than in rainbow trout and Chinook salmon *Oncorhynchus tshawytscha* (Roberts et al. 2011). Further studies of the biotransformation capacity of lake charr for organic contaminants would be useful.

During the 1970s, considerable debate occurred over whether chemicals in fish could be estimated simply from water concentrations using a BCF or log K_{ow} (Hamelink and Spacie 1977). Simple correlative approaches worked well for a wide range of chemicals based on laboratory studies with the fathead minnow (Mackay 1982; Veith et al. 1979), but the approach failed for top predators like the lake charr. Simple empirical correlations between laboratory-derived log K_{ow} and BCFs for PCBs failed to reproduce observed concentrations in lake charr or alewife, even after accounting for fraction of lipid (Thomann and Connolly 1984); Connolly and Pedersen 1988; Thomann 1989). The first food-chain model for PCBs that included 13 age classes of lake charr and predator–prey bioenergetic information for each age class was able to reproduce age-dependent trends and levels of PCB in Lake Michigan lake charr (Thomann and Connolly 1984; Fig. 4). The bioenergetics component accounted for respiration and body weight, metabolic rate, and food assimilation efficiency, based on earlier modelling of PCB accumulation by yellow perch (Norstrom et al. 1976). Connolly and Pedersen (1988) hypothesized that biomagnification occurred due to the development of a chemical gradient in the gut of the fish from preferential lipid breakdown. This concept was subsequently supported by fundamental physical chemistry principles based on diffusion of chemicals from compartments of high fugacity (GI tract) to lipid pools of lower fugacity within the organism (Campfens and Mackay 1997; Gobas et al. 1999).

A bioenergetics model evaluation of PCB accumulation in Lake Michigan lake charr based on knowledge of PCB concentration in lake charr prey consumption (Stewart et al. 1983) indicated that PCB accumulation in lake charr was driven by food consumption, whereas direct uptake of PCBs from the water was negligible (Weininger 1978). Further, lake charr PCB concentration was functionally independent of its lipid content (Weininger 1978). Similarly, a modeling comparison of direct uptake of PCBs by lake charr in Lake Michigan versus uptake of PCBs from food consumption suggested that PCB accumulation was independent of lipid content of the lake charr (Madenjian et al. 1993). In the latter study, bioenergetic dietary accumulation further accounted for individual variation of PCBs in lake charr using a predator–prey encounter submodel that assigned a prey encounter rate that varied with lake charr age and foraging season (Madenjian et al. 1993).

A simplified approach to evaluating PCB dynamics in food webs used a spreadsheet model that incorporated multiple feeding interactions within benthic and pelagic food chains (Fig. 5; Gobas 1993). The Gobas model was validated using concentrations of PCBs in the most important invertebrates and fish species in Lake Ontario from a study of 90 individual chlorinated organics in lake charr and three other species of salmonids (coho salmon *Oncorhynchus kisutch*, brown trout *Salmo trutta*, and rainbow trout) in water, sediment, forage fish, amphipods, oligochaetes, and plankton in Lake Ontario (Oliver and Niimi 1988). Unfortunately, results for lake charr were not reported separately, so no species-specific BAFs or biomagnification factors (BMFs) could be developed. Nevertheless, data were useful for validating the Gobas model, which included a generic salmonid compartment (Fig. 5). The Gobas model was later revised to include aquatic plants and non-lipid organic matter fractions in the diet (Arnot and Gobas 2003, 2004). Later, quantitative structure–activity relationships (QSAR) were developed for predicting biotransformation rates in fish (Arnot et al. 2009). Prediction of BAF and biotransformation rates was included in the U.S. Environmental Protection Agency EPISuite software package (U.S. EPA 2011) and is now widely used to predict organic contaminant concentrations in top predator fishes including lake charr. However, bioaccumulation parameters for dietary assimilation efficiency, uptake from water, biotransformation, and elimination rates in these models do not include data for lake charr, but rather are generally based on data for rainbow trout or other salmonids. Adult lake charr are difficult to work with because of their large size, long time to maturity, and restrictive water quality requirements (Mac and Edsall 1991). These challenges have limited the number of studies and ultimately impacted the accuracy of modeled predictions of lake charr exposure to contaminants.

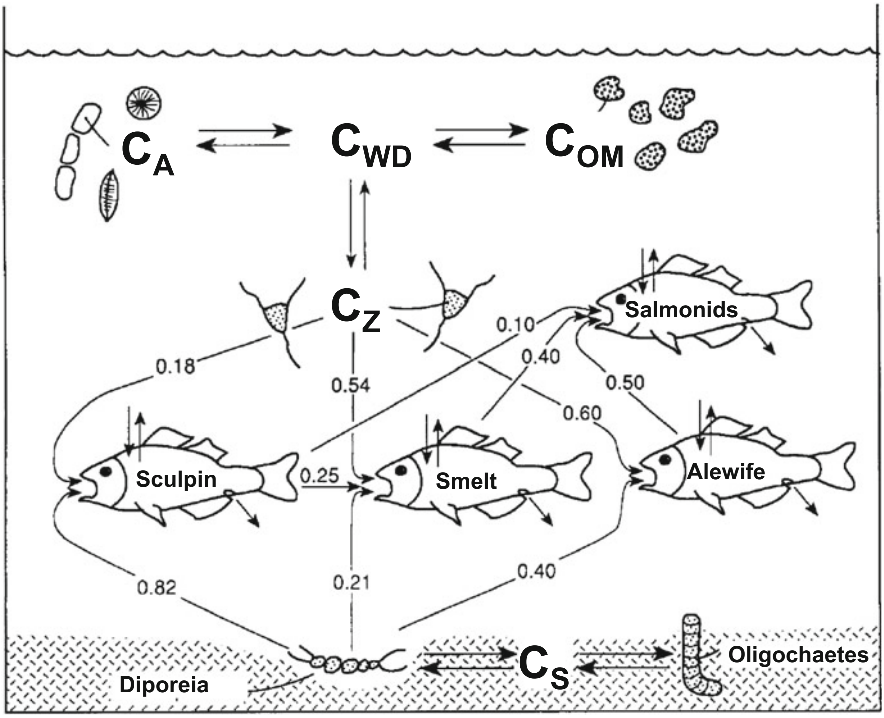

Fig. 5 Schematic illustrating the chemical transfer in the Lake Ontario food-web (Gobas 1993) with salmonids, including lake charr *Salvelinus namaycush* as top predators. C_A = chemical concentration in the organism, C_{WD} = bioavailable (dissolved) concentration in the water, C_{OM} = concentration on organic carbon, C_S = concentration in sediment, and C_Z = concentration in zooplankton

2.2.1 Bioaccumulation of Mercury

A mass balance model was used to predict age-specific Hg concentration in lake charr in Lake Memphremagog (Trudel and Rasmussen 2001). Compared to a bioenergetics approach for modeling food consumption and uptake of organic contaminants by lake charr (Thomann 1989; Madenjian et al. 1993; Luk and Brockway 1997), using a ^{137}Cs method to model food consumption and bioenergetics activity rates (Rowan and Rasmussen 1996) required accurate estimates of feeding rates to predict Hg concentrations in fish (Trudel and Rasmussen 2001). The key to accurately predicting Hg accumulation in fish is to adequately describe activity costs as a mechanism regulating bioenergetics processes in wild fish under natural conditions (Trudel and Rasmussen 2006).

Key pharmacokinetic parameters for modelling inorganic Hg and methyl Hg bioaccumulation in lake charr have not been measured directly, like other studies of organic contaminants. Based on a compilation of studies, the elimination rate of Hg is a function of fish size and water temperature (Trudel and Rasmussen 1997).

Elimination rate of inorganic Hg from fish is 2.8 times greater than that of methyl Hg, which combines with a higher assimilation efficiency of methyl Hg from food to cause a predominance of methyl Hg in fish (Trudel and Rasmussen 1997). However, lack of methyl Hg elimination rate data for lake charr as of the mid-1990s has forced modelers to use estimates for uptake from water and food and elimination rates based on data for other species. For example, modelling efforts assumed an assimilation efficiency (net trophic transfer efficiency) for methyl Hg of 80% (Norstrom et al. 1976; Trudel and Rasmussen 2001, 2006) and 84% (Borgmann and Whittle 1992).

In a large laboratory experiment to determine net trophic transfer efficiency (γ) and elimination rates of methyl Hg and inorganic Hg in adult (1 kg) lake charr fed naturally contaminated bloater from Lake Michigan, γ was 76.6% for methyl Hg and 63.5% for inorganic mercury, and did not differ between active and inactive lake charr (activity level was compared by adjusting water flow and volume for a subset of fish; Madenjian et al. 2012a). The lower transfer of inorganic Hg was likely due to its greater elimination rate, while the elimination rate of methyl Hg (0.000244 day^{-1}, Madenjian et al. 2012a) was 5.5 times lower than predicted by the chronic exposure equation for elimination of methyl Hg (Trudel and Rasmussen 1997). Lake whitefish *Coregonus clupeaformis* eliminated Hg at a rate nearly three times higher than lake charr, even though the two species were roughly equal in size and kept at similar temperatures (Madenjian et al. 2012a). Studies of methyl Hg depuration by northern pike *Esox lucius*, a large top predator following exposure to isotope-enriched methyl Hg in a whole-lake Hg experiment at ELA, showed that elimination rates were 1.2- to 2.7-fold lower than predicted by the Trudel–Rasmussen model (Van Walleghem et al. 2013), which was developed from estimates of methyl Hg elimination rates for fish from the literature published up to the mid-1990s, including rainbow trout, but not lake charr. These more recent experimental data showed that Hg elimination rate varied substantially among species and for adult lake charr was likely much lower than predicted. Further refinement of Hg mass-balance models for fish should account for species-specific elimination rates (Madenjian et al. 2016).

Male lake charr were 8% higher in Hg concentration and 22% higher in PCB concentration than females from Lake Ontario (Madenjian et al. 2010, 2011), because male lake charr ingest Hg at a higher rate than females, but also eliminate Hg at a higher rate than females (Madenjian et al. 2016). Sexual differences in gross growth efficiency (GGE; amount of growth divided by the amount of food eaten) do not explain sexual difference in Hg concentrations because Wisconsin bioenergetics modeling (Stewart et al. 1983) revealed that GGEs did not appreciably differ between sexes of lake charr (Madenjian et al. 2010). The bioenergetics model did not contain sex-specific parameters for standard metabolic rate (SMR) or swimming activity, but higher PCB concentration in male lake charr was likely due to a higher rate of energy expenditure stemming from a higher SMR and swimming activity, which led to a higher rate of food consumption and a higher rate of PCB accumulation (Madenjian et al. 2010). A higher male-to-female ratio of PCB concentration in lake charr in Lake Ontario (1.22) than Hg concentration (1.08) was likely because males eliminated Hg at a greater rate than females, whereas long-term elimination of

PCBs is negligible for both sexes. This higher level of accumulation in males has now been documented in eight species of fish (Madenjian et al. 2016).

2.2.2 Trophic Magnification Studies of Contaminants in Lake Charr Food Webs

In the western Lake Superior food web, PCBs, and DDT biomagnified through zooplankton, *Mysis diluviana* (formerly *M. relicta*), forage fishes (e.g., sculpins *Myoxocephalus thompsonii* and *Cottus cognatus;* rainbow smelt *Osmerus mordax*), and lake charr, although trophic magnification factors (TMFs) were not estimated (Veith et al. 1977). An early attempt to model biomagnification of contaminants in a food web with lake charr as the top predator was based on allometric relationships between body size and trophic level (Borgmann and Whittle 1983). Discovery of the fractionation of heavy isotopes of nitrogen (^{15}N) and carbon (^{13}C) relative to their light isotopes, and the stepwise increase of $\delta^{15}N$ from one trophic level to the next (Peterson and Fry 1987), led to their use in describing contaminant bioaccumulation in lake charr food webs. For example, concentrations of $\delta^{15}N$ and Hg were significantly correlated in lake charr from Canadian Shield lakes (Cabana and Rasmussen 1994) and concentrations of DDT, toxaphene, and hexachlorocyclohexanes (HCH) were significantly correlated with $\delta^{15}N$ in biota from Lake Laberge, Yukon (Kidd et al. 1995). Similarly, $\delta^{15}N$ was strongly correlated with wet-weight concentrations of p,p′-DDE, mirex, and PCBs, and slopes of relationships for individual compounds provided ecological measures of biomagnification in the Lake Ontario food web (Kiriluk et al. 1995). Lack of correlation between $\delta^{15}N$, fish age, or size and the organochlorine concentrations in lake charr indicated that N isotope fractionation was independent of metabolic factors and could be a valid indicator of trophic relationships (Kiriluk et al. 1995). The method used in the above-cited work was later refined by calculating integer-based trophic level (TL) or trophic position (TP) from $\delta^{15}N$ using trophic enrichment factors (fractionation of ^{15}N from prey to predator, called $\Delta^{15}N$; Fisk et al. (2001)) where primary producers and primary consumers included in the calculations occupied discrete trophic levels of 1 and 2, respectively:

$$\mathrm{TL}_{\text{consumer}} = \left(\delta^{15}\mathrm{N}_{\text{consumer}} - \frac{\delta^{15}\mathrm{N}_{\text{primary producer}}}{\Delta^{15}\mathrm{N}}\right) + 1$$

The slope of the relationship between Log[Contaminant] and TL represented the average change in contaminant concentration per trophic level (rather than per $\delta^{15}N$) and is analogous to the average biomagnification of a contaminant through the food web (Borgå et al. 2012; Jardine et al. 2006), where TMF = antilog [slope contaminants vs TL]. In a review of literature up to 2013 on TMFs for organic contaminants, 13 of 69 studies were of lake charr food webs, with a wide range of TMFs for eight classes of brominated and chlorinated organics reported (Fig. 6; Walters et al. 2016).

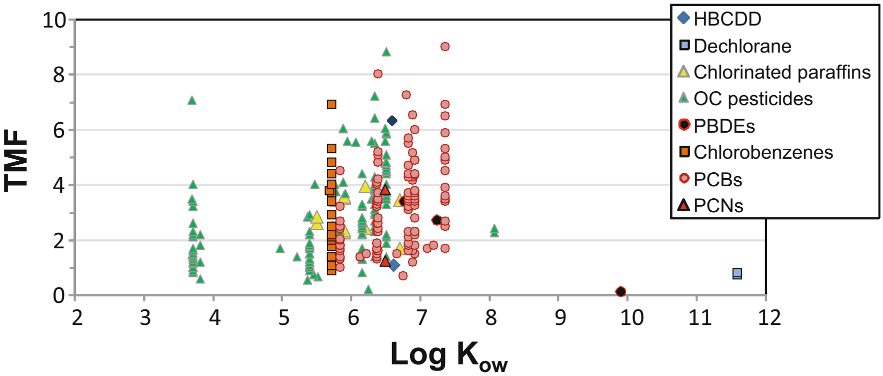

Fig. 6 Trophic magnification factors (TMF) versus log octanol–water partition coefficient (K_{ow}) of brominated and chlorinated organic contaminants in lake charr *Salvelinus namaycush* food webs. Data are from the review by Walters et al. (2016)

For example, HCH isomers (log K_{ow} 3.7) had TMFs from 0.75 to 7 while hexachlorobiphenyls (log K_{ow} 6.8–6.9) had TMFs from 1 to 7 (Fig. 6; Walters et al. 2016). In one of the largest studies of TMFs in lake charr food webs (17 lakes in Canada and the northeastern United States sampled between 1998 and 2001), average TMFs for 14 individual PCBs or organochlorine pesticides (OCPs) were significantly correlated with log K_{ow} (Houde et al. 2008). TMFs of PCBs, hexachlorobenzene, α-HCH, and lindane were weakly correlated with lake area, latitude, and longitude, which suggested that TMFs for PCBs and OC pesticides were only weakly influenced by lake location. Total phosphorus (unfiltered) was correlated to TMFs of PCBs, HCB, and α-HCH, and phytoplankton composition was correlated to HCB, and all parameters were also correlated with latitude and longitude, which confounded the influence of water chemistry (Houde et al. 2008). In summary, a combination of food-web characteristics, such as number of higher and lower trophic level taxa sampled, lake to lake variation in trophic enrichment factors for $\delta^{15}N$, combined with differences in primary productivity and water chemistry may play a role in the wide range of TMFs of chlorinated organics in lake charr food webs (Walters et al. 2016).

Food-chain length affects contaminant concentrations in lake charr. For example, lake charr from Ontario lakes with the shortest food chains (Class 1, $n = 23$, lake charr with small zooplankton, but lacking Mysis and pelagic forage fishes) had the lowest PCB levels and those from lakes with the longest food chains (Class 3; $n = 32$, lake charr with both Mysis and forage fishes, such as smelt and coregonines) had the highest PCB levels (Class 2 lakes lacked only Mysis; Rasmussen et al. 1990). Multiple linear regression showed that PCB levels in lake charr were best predicted by a model including lake class and % lipid as independent variables (Rasmussen et al. 1990). Similarly, PCB and DDT concentrations were each proportional to lipid content in all three lake classes for inland lakes and the Great Lakes, and slopes of relationships of concentrations versus lipid were the same

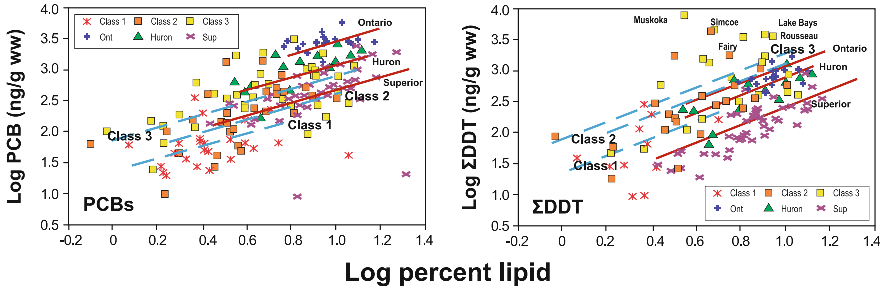

Fig. 7 Relationship between PCBs and total (Σ) DDTs versus percent lipid (all log10 transformed) for PCBs in lake charr *Salvelinus namaycush* from 87 lakes in Ontario (redrawn from (Bentzen et al. 1996). Results for analysis of covariance fit of % lipid, PCB, and ΣDDT are overlaid on lake averages. For the ΣDDT results, lakes that are identified were excluded from the ANCOVA because of possible previous DDT use in their watersheds. Red lines are results for the Great Lakes and blue-dash lines are for the Class 1, 2, or 3 inland lakes

across all lake classes, while intercepts generally differed (Fig. 7; Bentzen et al. 1996).

On the basis of five studies from 24 Canadian lake charr lakes, the slope of log Hg concentration versus $\delta^{15}N$ (trophic magnification) TMS exceeded 0, thereby indicating Hg biomagnification in lake charr food webs (Lavoie et al. 2013). The largest dataset was from a study (Kidd et al. 2012) in which Hg TMS in 14 lake charr lakes in Ontario, northern Saskatchewan, and Alberta were best predicted by log lake surface area (positive) and log total phosphorus concentration (positive), which indicated greater Hg biomagnification occurs in larger, more productive systems (Lavoie et al. 2013). However, Hg concentrations in lake charr (size adjusted) that were not correlated with TMS indicated that Hg in lake charr was not directly predicted by the rate of biomagnification through the food web.

In a study of Hg concentrations in lake charr muscle from 96 Ontario lakes, average Hg concentration increased with pelagic food chain length, and ranged 0.03–0.64 µg/g wet wt (ww) among Class-1 lakes, 0.04–1.53 µg/g among Class-2 lakes, and 0.23–3.94 µg/g among Class 3 lakes (Cabana et al. 1994). Lake class and fish weight (wt) both predicted Hg concentration (log Hg (µg/g ww) $= -2.72 + 0.21 \pm 0.04$ (class 1, 2, or 3) $+ 0.61 \pm 0.09$ log wt; $r^2 = 0.56$; Cabana et al. 1994). Mean PCBs and Hg in lake charr from the same lake were significantly correlated (Cabana et al. 1994), which illustrates that presence/absence of pelagic forage fishes and Mysis explained elevated concentrations of substances with biomagnification potential in lake charr.

3 Geospatial Trends of Contaminants in Lake Charr

3.1 Mercury

Trends of contaminants in the same species of fish across large numbers of lakes have proven valuable for understanding sources (e.g., atmospheric deposition versus local emissions), biogeochemistry (e.g., mercury methylation), and food-web biomagnification of Hg. For example, the Canadian Fish Mercury Database (Depew et al. 2013; Canadian Mercury Science Assessment, ECCC 2016; http://www.smu.ca/research/fish-mercury-datalayer.html) assessed Hg in fish across Canada based on data during 1967–2010. Lake charr represented 5.6% ($n = 21{,}865$) of individual results in the database and had the highest average concentrations of Hg of all fish species. Highest concentrations were generally found in eastern and northern ecozones (http://ecozones.ca/english/introduction.html), while lowest concentrations were found in Great Lakes lake charr (McGoldrick and Murphy 2016; Fig. 8; Table 11). For example, Hg concentrations averaged 0.80 μg/g ww ($n = 2025$) in the eastern Taiga Shield (northern Quebec) and 0.81 μg/g ww ($n = 473$) in the eastern Boreal Shield (central Quebec). By contrast, total Hg averaged 0.124 μg/g ww ($n = 358$) in Lake Ontario during 2008–2012 (McGoldrick and Murphy 2016). Concentrations depicted in Fig. 8 were not corrected for fish size or food chain length, but mean lengths did not vary widely (range = 44–64 cm; ECCC 2016).

A large study involving composite samples of fish muscle (predators) and whole fish (benthic foragers) from 500 lakes (not including the Great Lakes) selected randomly across the lower 48 states during 2000–2003 included Hg and

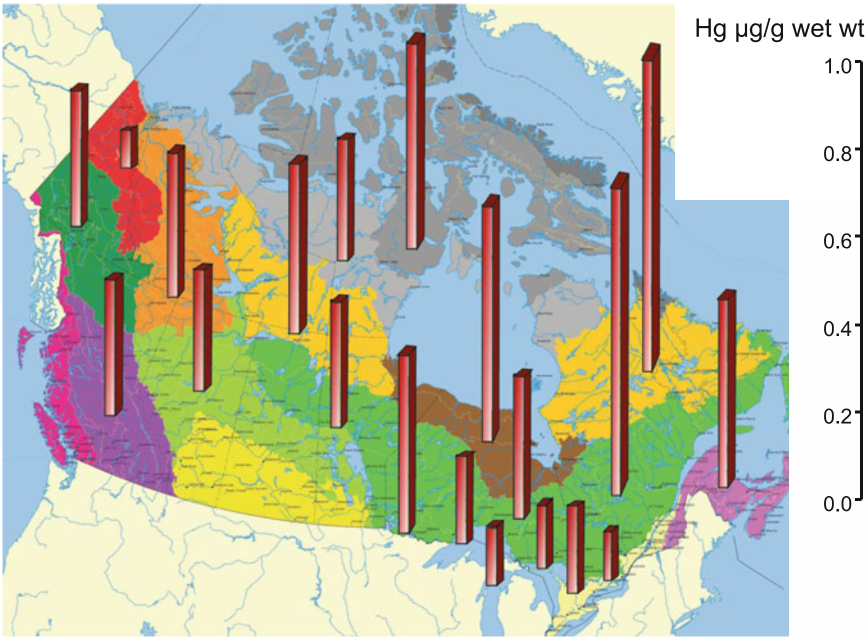

Fig. 8 Total Hg in lake charr *Salvelinus namaycush* muscle grouped by terrestrial ecozone. Bars represent arithmetic means for sample numbers ranging from 5 fish (Taiga Cordillera, northern Yukon) to 6996 (Southern Boreal Shield, central Ontario). Results are from the Mercury Science Assessment Table 10.11 in Chapter 10 (ECCC 2016)

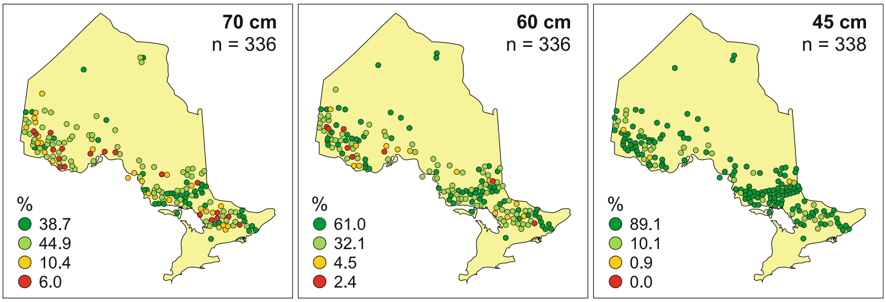

Fig. 9 Mercury concentrations (μg/g wet weight) in skin-off fillets of small, medium, and large-sized lake charr *Salvelinus namaycush* from Ontario lakes collected between 2000 and 2012. Reproduced from Gandhi et al. (2014b) with permission

268 individual chemicals including 209 polychlorinated biphenyl (PCB) congeners (yielding 159 measurements based on co-eluting congeners), five arsenic species, PCDD/Fs, 46 OCPs, and organophosphate (OP) pesticides, and 40 semivolatile organic compounds (mainly polycyclic aromatic compounds) (Stahl et al. 2009; U.S. EPA 2009; https://www.epa.gov/fish-tech/national-lake-fish-tissue-study). Mean Hg concentrations in composite muscle samples of lake charr from 10 lakes in the northern United States ranged 0.012–0.59 μg/g ww, at the low end of the range for lake charr in Canadian lakes, and was highest in Torch Lake, northern Michigan (Stahl et al. 2009).

Lake charr, mainly from Alaska and Canada, were among the fish species with highest Hg concentrations, ranking 7th out of 208 species in a recent survey with a size-adjusted average of 0.27 (0.010–12.3) μg/g ww Hg (285 sites, $n = 4383$) (Eagles-Smith et al. 2016). Fish Hg concentrations (but not specifically lake charr) were weakly correlated with sediment methyl Hg concentrations, which led to the suggestion that factors influencing methyl Hg production may be more important than inorganic Hg loading for determining fish Hg levels. As discussed previously, Hg in lake charr was not directly predicted by the rate of biomagnification (Kidd et al. 2012), while lake class (a measure of food chain length) and fish weight predicted Hg concentrations in lake charr (Cabana et al. 1994). Spatial trends of Hg of three standard fish lengths (45, 60, and 70 cm) for lake charr from 338 lakes in Ontario during 2000–2012 did not differ significantly between northern ($n = 243$) and southern Ontario ($n = 92$-94) locations (Fig. 9; Gandhi et al. 2014b).

Although all studies of spatial trends of Hg in fish reviewed herein were of large geographic scope (western North America, Canadian shield, northern and southern Ontario) and showed substantial variation among lakes, no latitudinal or longitudinal trends were evident for Hg in lake charr. The relatively similar gaseous elemental Hg and total Hg in precipitation over much of Canada (Cole et al. 2014; ECCC 2016) implies similar atmospheric inputs to most lake charr lakes in north-temperate North America. Exceptions would be the lower Great Lakes and some lakes near sources such as smelters located in regions where higher localized atmospheric deposition and/or urban sources have been predicted or observed (ECCC 2016). In a study to assess Hg sources in Great Lakes sediments using Hg isotope ratios included lake charr from Lakes Ontario and Superior, bioaccumulated Hg was isotopically more like atmospherically derived Hg than to the isotope signature in lake sediment, based on mass-independent fractionation (MIF) of ^{200}Hg relative to the major isotope ^{202}Hg (Lepak et al. 2015). Earlier work that showed a lack of MIF for Hg during dietary exposure of lake charr suggested that Hg isotope measurements can provide direct linkages between Hg sources and Hg in fish tissues (Kwon et al. 2012).

Lack of latitudinal trends in lake charr Hg is likely due to the strong influence of food-chain length and complexity (Cabana et al. 1994). For example, invasive species such as non-native smallmouth bass, rainbow smelt, and spiny water flea *Bythotrephes longimanus* have influenced fish diversity and prey abundance for lake charr (Van der Zanden et al. 2004). This food-chain factor may be more influential in lakes nearer population centers that have greater fishing and recreational uses. These factors are further discussed below in relation to temporal trends of Hg in lake charr.

3.2 Legacy POPs

Unlike Hg, lake charr mean PCB concentration declined with latitude (i.e., from south to north) due to higher PCBs in the Laurentian Great Lakes, Michigan, Huron, and Ontario (Rasmussen et al. 1990; Bentzen et al. 1996; $n = 83$ and 87 lakes, respectively). While the main focus of these studies was to understand the effect of food-chain length and percent lipid on PCB concentration in fish, these studies also provided insight into levels of PCBs in remote lakes in northern Ontario and near urban regions (Fig. 10; Bentzen et al. 1996). The model for predicting PCBs in lake charr and other pelagic fishes included lake class, latitude, and % lipid (Rasmussen et al. 1990):

$$\mathrm{Log_{10}PCB\ (ng/g\ wet)} = 1.63 + 0.40(\pm 0.05) \times \mathrm{Lake\ class} - 0.14(\pm 0.02) \times \mathrm{Latitude}\ (^{\circ}\mathrm{N\ of\ 42}) + 0.73(\pm 0.14) \times \mathrm{log\%lipid}\ (r^2 = 0.74; n = 97)$$

The model illustrates a significant negative relationship of declining concentrations of PCBs with increasing latitude in Ontario.

Additional evidence for effects of lipid and lake characteristics on PCBs and OCPs in lake charr comes from a comparison of PCBs and OCPs in lake charr from 14 lakes in British Columbia, Alberta, and Saskatchewan (Donald et al. 1993), with selected data from 14 lakes (Rasmussen et al. 1990). They evaluated food-web length of each lake by identifying key species in lake charr diets and found PCB concentration was positively related to lake area, but not to percent lipid content or lake trophic structure (Fig. 11). Larger catchments received greater loading of PCB and thereby greater concentrations in lake charr. Omitting the Great Lakes (Superior, Huron, and Ontario) results from the model did not change the findings.

Spatial trends of PCBs in lake charr from 23 lakes in Canada and the northeastern United States sampled during 1998–2001were inferred from stable carbon isotope ratios (δ^{13}C), an indicator of littoral feeding because lipid-corrected δ^{13}C was

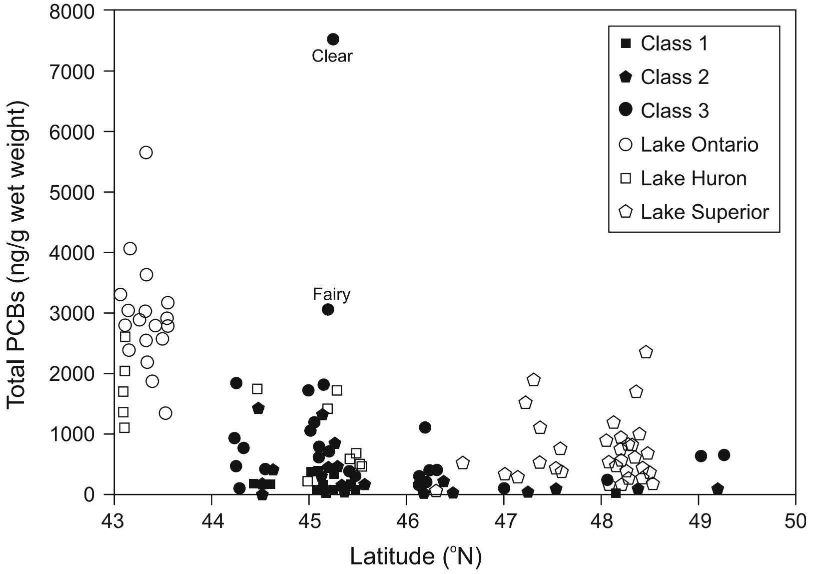

Fig. 10 Lake-averaged PCB concentrations in lake charr *Salvelinus namaycush* muscle versus latitude for the three classes of inland lakes ($N = 87$) and three Great Lakes from Ontario Ministry of Environment data for the late 1980s (Crawford and Brunato 1978). Clear Lake is identified as an outlier due to known PCB contamination reported by Macdonald et al. (1992). Reproduced from Bentzen et al. (1996)

negatively correlated to total (Σ) PCB concentrations (sum of 57 congeners), which supports the hypothesis that increasing access to littoral habitat results in lower concentrations of POPs in lake charr (Guildford et al. 2008). They also found a negative relationship of ΣPCBs with latitude and a positive relationship to lake area:

$$\log_{10} \sum \text{PCB} = 6.222 + 0.158 \log_{10} \text{Area} - 0.073 \times \text{latitude} \; (r^2 = 0.733)$$

Lake area may serve as a surrogate for littoral habitat because the proportion of deep water increases and the proportion of shallow water decreases with lake size (Guildford et al. 2008).

Geospatial trends of organic contaminants in lake charr are shown in Fig. 12, which combines lipid normalized results for Σ_{10}PCBs and ΣDDT from samples collected in 2010 from Lakes Kusawa and Laberge, Yukon (Ryan et al. 2013) and in Great Slave Lake, Northwest Territories (Evans et al. 2012; Muir et al. 2013), and from the Great Lakes (Chang et al. 2012). Σ_{10}PCBs (sum of congeners 28, 31, 52, 99, 105, 118, 138, 153,156, 180) were used to enable comparison with the more limited suite of congeners measured in lake charr from Alaskan lakes and the lower 48 states. In Alaska National Parks during 2004–2011 (Ackerman et al. 2008; Flanagan Pritz et al. 2014), concentrations of Σ_7PCBs (sum of 7 congeners), and

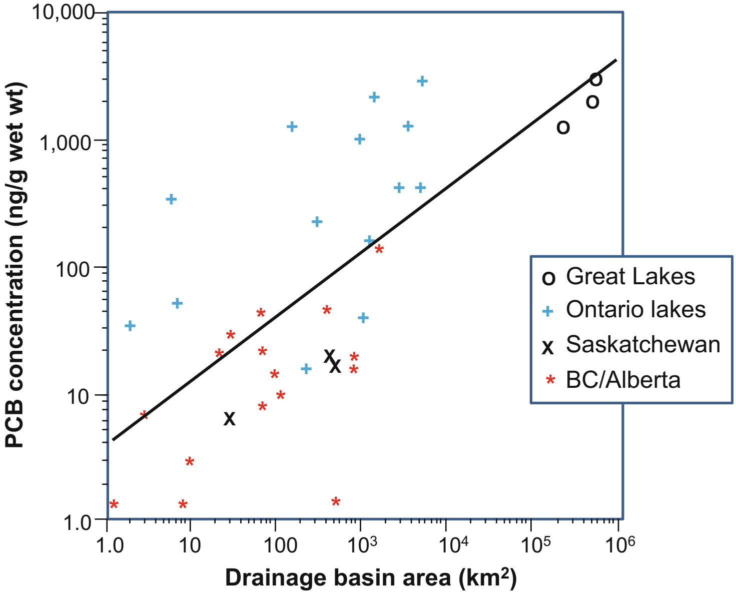

Fig. 11 Relationship between PCB (ng/g wet wt) in lake charr *Salvelinus namaycush* fillets and lake drainage basin area (km^2) for lakes in British Columbia, Alberta, Saskatchewan, and Ontario (Donald et al. 1993)

ΣDDT were highest in Kijik Lake, a small, remote lake in Lake Clarke National Park, Alaska (Fig. 12). Concentrations in Kijik lake charr were higher than in most other remote lake locations, but similar to Lake Laberge, where elevated concentrations of many organochlorine contaminants, especially PCBs and toxaphene, have been attributed mainly to food chain length (Kidd et al. 1998; Ryan et al. 2013). Three- to fourfold higher concentrations of Σ_{10}PCBs and ΣDDT in lake charr from the east arm than from the west basin of Great Slave Lake (Fig. 12) illustrate the effect of food chain and water chemistry on PCB concentration in fishes. Low productivity in the east arm may provide less opportunity for contaminant dilution through fish growth while high suspended particle loadings in the west basin may limit bioavailability (Evans and Muir 2016). Legacy sources from historical use of DDT, which was widely used for biting fly control in the 1950s and 1960s, may explain higher ΣDDT/PCB ratios in Laberge, Brooks, Kekekabic, Upper Two Medicine, and Lewis Lakes than in Kusawa and Great Slave Lakes, although this is not well documented (Fig. 12). Σ_{10}PCBs and ΣDDT concentrations in lake charr (muscle) from six US lakes west of the Great Lakes region were generally similar to those in Alaskan lakes while PCBs were higher in three of the four eastern lakes (Fig. 12). Highest PCBs in lake charr were in Torch Lake (near Rapid City, Michigan), which was designated as an Area of Concern under the 1987 Great Lakes Water Quality Agreement and has three small communities in its catchment

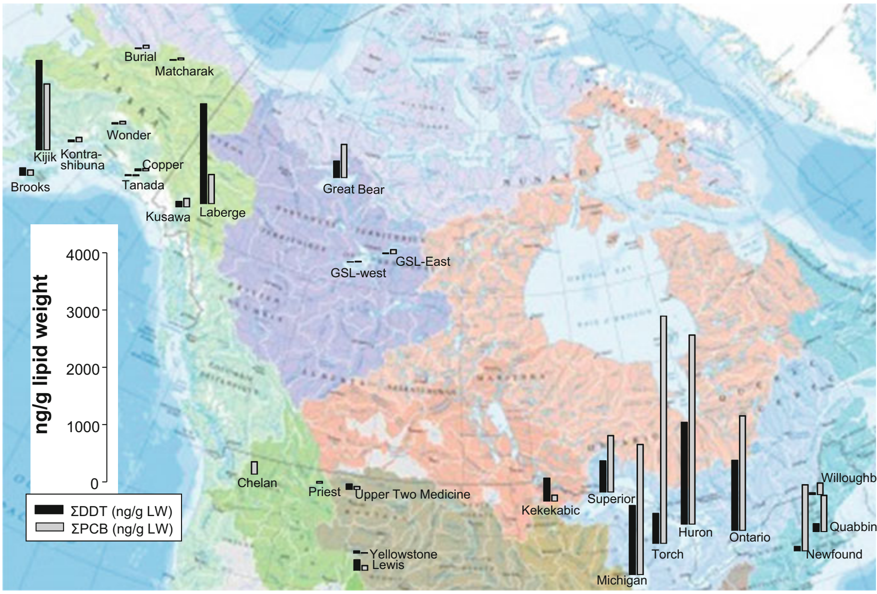

Fig. 12 PCBs (sum of 7–10 congeners) and ΣDDT (6 isomers) in lake charr *Salvelinus namaycush* muscle (or whole fish Great Lakes only). Results (ng/g lipid weight) are from samples collected between 2004 and 2011 in Alaska, 2007 in Great Bear Lake, 2010 in Great Slave Lake, Kusawa Lake and Lake Laberge, and 2009 in four Great Lakes and by the U.S. EPA National Fish Contaminants Study (2000–2003) (U.S. EPA 2009)

and legacy sources of pollution related to mining and industrial operations (U.S. EPA 2018).

Concentrations of legacy contaminants, such as PCBs and OCPs, and more recently measured organic contaminants, in Great Lakes lake charr, ranked by relative concentration in Lake Ontario, were relatively consistent among lakes during 2008–2012 (Fig. 13; McGoldrick and Murphy 2016). First, concentrations of major organic contaminants and Hg in whole fish homogenates indicate that PCBs remain the predominant contaminant in all five lakes despite bans and phaseouts in the late 1970s and 1980s in the USA and Canada (CEC 1996). Next, the combined sum of tetra-, penta-, hexa-, and heptachlorobiphenyls greatly exceed levels of other contaminants (Fig. 13). Next, legacy OCPs, banned in the 1970s and 1980s (ΣDDT, toxaphene, dieldrin, and chlordane-related compounds) are also prominent contaminants, particularly in Lakes Michigan and Superior (Fig. 13). Last, mirex remains a major OCP in lake charr from Lake Ontario, but not in other lakes (Fig. 13).

3.3 *New Organic Contaminants*

Several chemical substances have only been measured since the mid-1990s, including PBDEs, short-chain chlorinated paraffins (SCCPs), nonylphenol-related

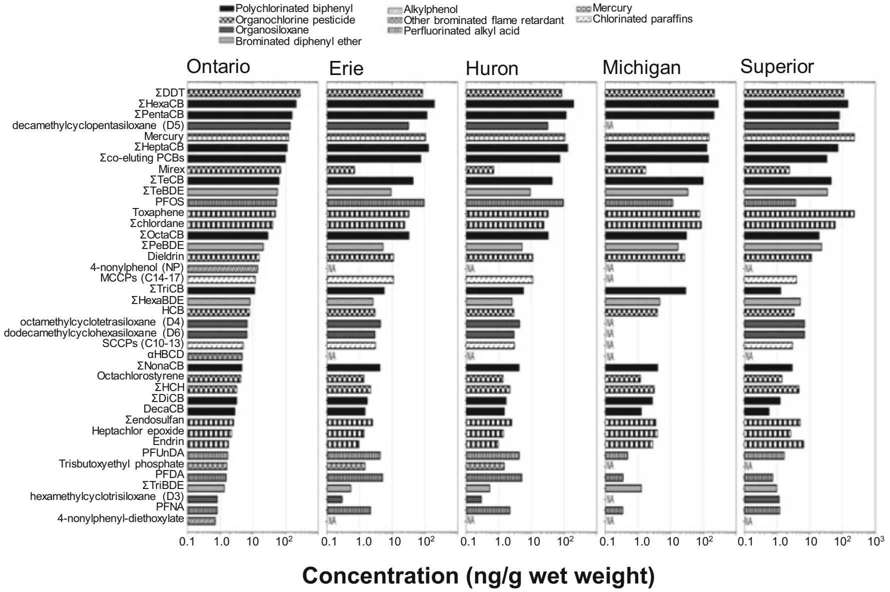

Fig. 13 Mean concentrations of the top 40 compounds (by mass) measured in whole-body homogenates of lake charr *Salvelinus namaycush* from five Great Lakes. Redrawn from McGoldrick and Murphy (2016)

compounds, cyclic methyl siloxanes (D4, D5, D6), medium-chain chlorinated paraffins (MCCPs), perfluorooctanesulfonate (PFOS) perfluorocarboxylates (PFCAs; PFNA, PFDA, PFUnA), and tris(2-butoxyethyl) phosphate (TBOEP; McGoldrick and Murphy 2016). These substances are high production-volume industrial chemicals or persistent transformation products in the case of PFOS and PFCAs that have been in commercial use for the past 30 years or more based on their listing in the chemical inventories of the U.S. EPA and Environment Canada (Howard and Muir 2010). Thus, none are new to commerce but their analysis in lake charr reflects advances in analytical methodology, including availability of appropriate analytical standards, particularly for PFOS and PFCAs and the cyclic siloxanes.

The combined concentrations of cyclic siloxanes D4, D5, D6 places them among the most prominent organic contaminants in lake charr in the Great Lakes (Fig. 13). In lake charr from Lakes Superior, Erie, Huron, Ontario, Athabasca (northern Alberta), and Kusawa (Yukon), cyclic siloxanes were detectable in all lakes, but lowest in Athabasca and Kusawa, the two most northerly lakes (McGoldrick et al. 2014). D5 was the most prominent siloxane with the highest concentration in lake charr collected near the Niagara River outflow into Lake Ontario (45–719 ng/g ww). Higher concentrations of cyclic siloxanes in lake charr from Lakes Ontario, Erie, and Huron were consistent with wastewater effluents and atmospheric emissions from urban areas being the main sources for these compounds (Xu et al. 2014).

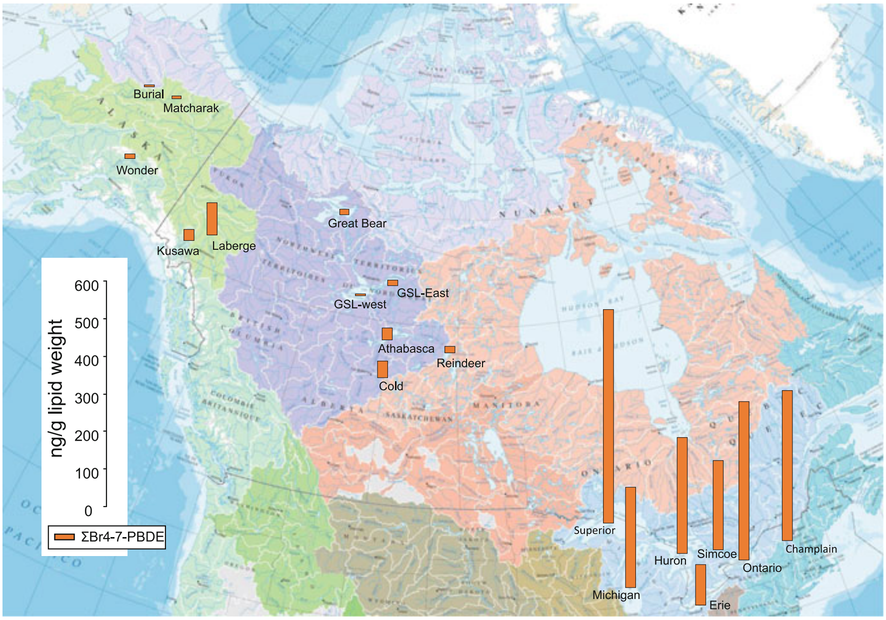

Fig. 14 PBDEs (sum of tetra to heptabromo congeners) in lake charr *Salvelinus namaycush* muscle (Alaska, Yukon, and Northwest Territories) or whole fish (all other sites). Results (ng/g lipid weight) are from samples collected between 2004 and 2011 in Alaska (Ackerman et al. 2008), 2007 Great Bear Lake (Evans and Muir, unpublished data), 2010–2011 in Great Slave Lake, Kusawa Lake, and Lake Laberge (Evans et al. 2012; Muir et al. 2013), and 2009 in four Great Lakes. Data sources are Gewurtz et al. (2011d)

PBDEs are another prominent group of organohalogen compounds in lake charr in the Great Lakes. The combined total for tetra-, penta-, and hexabromo BDEs brings ΣPBDEs to similar levels as siloxanes and PFASs (Fig. 13). Relatively elevated ΣPBDE concentrations in Lake Simcoe and Lake Champlain likely reflect emissions from urban centers on these lakes (Fig. 14). Much lower concentrations of ΣPBDEs in lake charr from Alaskan and northwestern Canadian lakes reflect mainly atmospheric deposition pathways to these lakes (Fig. 14). As with DDT, Lake Laberge stands out as having somewhat higher ΣPBDE than other lakes in the region, possibly reflecting food chain length, although wastewater sources from the city of Whitehorse could also be important.

Concentrations of PFASs in lake charr have a similar geospatial pattern as PBDEs, with highest concentrations in the Great Lakes and nearby lakes with smaller urban centers releasing municipal wastewaters (Peninsula, Champlain) (Fig. 15). In a cross-Canada survey, geometric mean PFOS and ΣPFCAs concentrations were highest in lake charr from Lakes Erie (90 ng/g ww) and Ontario (62 ng/g ww; Gewurtz et al. (2013). In a more detailed analysis of PFAS in Lake Ontario lake charr, PFASs were not related to possible fish covariates, % lipid, length, weight, age, growth rate, δ^{15}N, and δ^{13}C, when using all data from 1997 to 2008 (Gewurtz et al. 2012). In contrast to results for lipophilic compounds such as PCBs,

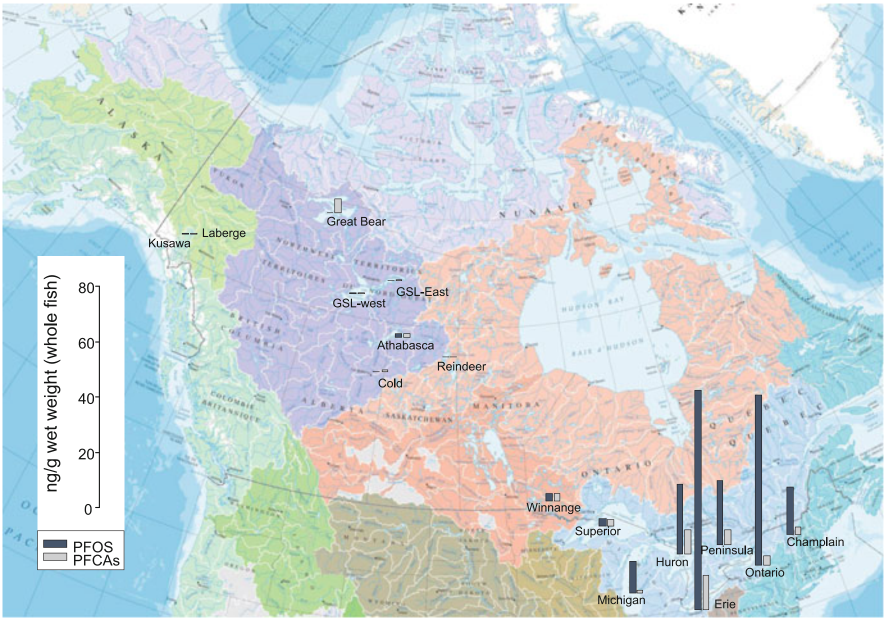

Fig. 15 Concentrations of PFOS and ΣPFCAs (C9–C12) in whole lake charr *Salvelinus namaycush* from the Great Lakes (McGoldrick and Murphy 2016) and lakes across Canada (Gewurtz et al. 2013)

lack of fish covariates may reflect the association of PFASs with proteinaceous tissue and also that uptake from water could be more important for these water-soluble contaminants found at relatively high levels in Lake Ontario (Gewurtz et al. 2013).

Concentrations of SCCPs and MCCPs in lake charr from large lakes in Canada (Kusawa, Athabasca, Superior, Huron, Erie, Ontario), as expected, were higher for MCCPs in the Great Lakes, with highest levels in Lake Huron, but unexpectedly higher for SCCPs from Lake Athabasca and Kusawa Lake, a remote lake in the Yukon (Saborido Basconcillo et al. 2015). Taken together, these results support the hypothesis that atmospheric sources are important for SCCPs in northern large lakes and the upper Great Lakes, while wastewater emissions are the predominant source of MCCPs in the lower Great Lakes.

Among organophosphate ester flame retardant/plasticizers (OPEs) surveyed from the Great Lakes and several large lakes across northwestern Canada, TBOEP and tris (chloroethyl) phosphate (TCEP) were highest in concentration in lake charr (McGoldrick et al. 2014). However, TCEP was only detected in several northwestern lakes (Athabasca, Cold, Kusawa, Great Bear) but not in lake charr from the Great Lakes (McGoldrick et al. 2014). TBOEP was detected in lake charr in all lakes and was the most prominent OPE in Great Lakes waters (Venier et al. 2014). Concentrations of TCEP (geomeans of 6.5–12.8 ng/g lw) were low in Great Lakes lake charr and TCEP and triphenyl phosphate (TPHP) were the most prominent OPEs in Great Lakes lake charr, although TBOEP was not determined (Guo et al. 2017).

4 Temporal Trends

Lake charr were used beginning in the 1970s for monitoring contaminants in fish, particularly in the Great Lakes (Gewurtz et al. 2011a) and since then robust temporal trend studies have built on this early work in programs operated by the U.S. EPA (Great Lakes National Program Office), Environment and Climate Change Canada's Water Quality Monitoring and Surveillance Division (and previously Canada's Department of Fisheries and Ocean (DFO), Great Lakes Laboratory for Fisheries and Aquatic Sciences), and by the Ontario Ministry of the Environment, Conservation and Parks (ECCC and U.S. EPA 2017). Similarly, studies of contaminants in lake charr from the Great Slave Lake, Kusawa Lake, and Lake Laberge began in the 1990s under the Northern Contaminants Program (NCP) of Indigenous and Northern Affairs Canada (NCP 2018), and built on earlier measurements of Hg by DFO's Fish Inspection Division (Lockhart et al. 2005). The time series with greatest statistical power to detect a trend in sample measurements when a trend is occurring, despite "noise" in the data, are from annual sampling (Table 4). Using data for PCBs in lake charr from Lake Ontario, for example, 10–15 years of sampling with 10–15 samples per year are needed to detect a 5% decrease in total PCB concentrations with a 5% significance level (Gewurtz et al. 2011a). This level of sampling had only been achieved for PCBs, OCPs, and Hg in lake charr from Lakes Michigan, Superior, Huron, Erie, and Ontario by the three major monitoring programs. Power analysis on lake charr contaminant data from Great Slave Lake, Kusawa, and Laberge (Macdonald 2014) indicates that these shorter time series had not achieved the NCP objective of 80% power based on 11 to 14 sampling years from the 1990s to 2012, although continued annual sampling would likely achieve it soon.

Lake charr contaminant programs in the Great Lakes have received continued support from environmental agencies because they produced valuable results in support of chemical management and assessment commitments under Canada's Chemicals Management Plan (CMP) and the Great Lakes Water Quality Agreement (GLWQA) related to reducing or eliminating releases of anthropogenic chemicals into waters of the Great Lakes (GLWQA [Great Lakes Water Quality Agreement] 1978). Trends of major contaminants reported in State of the Great Lakes reports (ECCC and U.S. EPA 2017) complement other long-term trend data, such as herring gull egg monitoring and atmospheric measurements (ECCC and U.S. EPA 2017). Contaminant trend data also provide an indicator of aquatic ecosystem health and data for estimating human and fish-eating wildlife exposure to contaminants. These commitments were reaffirmed under Annex 3 (Chemicals of Mutual Concern) of the 2012 protocol amending the GLWQA (GLWQA [Great Lakes Water Quality Agreement] 2012). In 2009, the U.S. EPA eliminated analysis of POPs in sport fish and expanded effort to identify emerging contaminants in whole fish. The program name was changed from the Great Lakes Fish Monitoring Program to the Great Lakes Fish Monitoring and Surveillance Program (ECCC and U.S. EPA 2017).

Table 4 Long-term temporal trend programs for contaminants in lake charr *Salvelinus namaycush*

Program	Water bodies	Frequency	Sample type	Contaminants
Ontario Ministry of the Environment, Conservation and Parks	Lakes Superior, Huron, Ontario, and Erie	Generally on an annual or biennial basis from 1970	Skinless dorsal muscle. Individual fish 60 and 70 cm	Total Hg, 12 metals, PCBs, OCPs, selected new organics
Environment Canada, WQMSD—Great Lakes	Lakes Superior, Huron, Ontario, and Erie	Annual collections since 1977; 2–4 offshore sites per lake	Whole fish (Aged 4–6); individual fish homogenates.	Total Hg, PCBs, OCPs, PBDEs, PFAS, other selected priority organics, and metals
Environment Canada, WQMSD—Chemicals Management Plan	Lakes Kusawa, Great Bear, Athabasca, Reindeer, Cold	Annual collections since 2009	Whole fish; individual fish homogenates	Total Hg, PBDEs, PFAS, non-BDE flame retardants, other selected priority organics, and metals
U.S. EPA GLNPO (Great Lakes Fish Monitoring Program)	Lakes Superior, Michigan, Huron, Erie, and Ontario	Annual collections in US waters from early 1970s; 2 sites per lake on alternate years	Whole fish, (600–700 mm length). 10 composite samples of 5 fish	Total Hg, metals, PCBs, OCPs, PBDEs, PFAS, other chemicals of emerging concern
Northern Contaminants (INAC) and Yukon Contaminants Committee	Kusawa and Laberge	Annual sampling since 2000	Skinless dorsal muscle and liver for PFASs, individual fish	Total Hg, Se, PCBs, OCPs, PBDEs, PFAS
Northern Contaminants (INAC) and Environment Canada	Great Slave Lake	Annual sampling since 1998	Skin on muscle, individual fish	Total Hg, 32 multielement suite, PCBs, OCPs, PBDEs, PFAS

Contaminant time-trend studies in northern lakes also contributed to chemical assessment and management, mainly at an international level. Results for PCBs and OCPs were part of data assembled for the Stockholm Convention on POPs (http://www.pops.int/) and also for the Minamata Convention on Mercury (http://www.mercuryconvention.org/). In addition, results for POPs in lake charr from the Lake Laberge were a key factor in the decision to close the fishery in the lake in 1991–1992 to reduce human exposure. Continued monitoring under the NCP has been in support of that early decision (Ryan et al. 2013).

4.1 Mercury Trends in Lake Charr

4.1.1 Overview

Several recent studies have synthesized spatial and temporal trends of Hg in the Canadian environment, with a focus on long-range atmospheric transport sources (Chételat et al. 2015; Depew et al. 2013; Eagles-Smith et al. 2016; ECCC 2016). Temporal trends in Hg concentrations in lake charr are influenced by several variables. Localized anthropogenic perturbations, such as gold mines, can increase Hg concentrations in lake charr and other fish species, which may decline with a reduction in mining (Armstrong and Scott 1979; Moore and Sutherland 1980; Weech et al. 2004). Reservoir creation that floods the landscape and results in substantial methyl Hg production can result in high Hg concentrations in lake charr that gradually subside as organic matter decomposes (Anderson et al. 1995; Jackson 1991). In the Great Lakes region, while industries such as chlor-alkali plants contributed to localized Hg contamination of the environment and fish, most Hg was atmospheric in source (Bhavsar et al. 2010; Hatch et al. 1987). A recent study using stable Hg isotopes linked Hg signatures of lake charr from all five Great Lakes with precipitation sources, and suggested that methylation of mercury deposited into the upper water column was an important source of mercury to lake charr (Lepak et al. 2018). Mercury emissions in North America and Europe declined in recent decades with improvements in coal-fired power-plant technologies and waste management improvements, while emission rates increased from Asia with expansion in various economic sectors, particularly coal-fired power plants (Durnford et al. 2010; Jaffe and Strode 2008). Global warming, with a longer growing season in many regions of Canada, is resulting in increased primary productivity with a concomitant increase in particulate flux, including Hg, to lake sediments, while methyl-Hg production rates may increase with enhanced productivity (Lehnherr et al. 2018; Outridge et al. 2007; Stern et al. 2012). Increasing productivity may enhance fish growth rates to biodilute Hg in lake charr. Alternatively, an increase in forage fish abundance may result in a richer fish diet and an increase in Hg concentrations. Changes in food-web structure as a result of exotic species and increased fish harvesting pressure changes fish age structure and growth rates that also may result in changes in Hg concentrations in fishes (Lavigne et al. 2010; Rasmussen et al. 1990).

4.1.2 Great Lakes

Annual monitoring of mercury in lake charr from Lakes Superior, Huron, Erie, Ontario, and Michigan by provincial, tribal, state, and federal agencies has shown a substantial decline from the 1970s to 2000, with a further decline, albeit less drastic, during 2000–2015 in most lakes (Bhavsar et al. 2010; Dellinger et al. 2014; Visha et al. 2015; Zhou et al. 2017). Concentration of Hg in lake charr declined significantly in Lakes Superior, Huron, Erie, and Ontario during 1973–2007

(Bhavsar et al. 2010). An apparent increase in Hg concentration in Lake Superior lake charr since 2006 was caused by fish being older at a given length than from 1980 through the 1990s, so fish had more time to accumulate Hg. Declines in Hg were related to decreased Hg emissions from incinerators and smelters while Hg from coal-fired power generation remained relatively constant. Continued Hg inputs from the watershed were inferred as the cause of delayed responses to reduced Hg emissions (Bhavsar et al. 2010). Hg in lake charr from Lakes Superior, Huron, and Michigan did not decline during 1992–2011 (6–7 sampling years) (Dellinger et al. 2014). Concentration of Hg in lake charr from Lake Ontario from the late 1970s to 2011 generally declined, but with short-term increases and decreases in the rate of decline when fish length was considered (Visha et al. (2015). Hg inputs to Lakes Superior and Huron were dominated by atmospheric sources and concentrations in lake charr declining at rates of 5.2–7.8% per year during 2004–2015 (Zhou et al. 2017). Mercury concentrations decreased in Lake Michigan (3.9% per year), increased in Lake Erie (1.2% per year), and exhibited no temporal trend in Lake Ontario over the same period (Zhou et al. 2017). While rates of decline were attributed to decreasing regional Hg emissions, other factors, such as eutrophication, warming, increased local Hg emissions, and food-web changes may have altered trends. In lake charr from Canadian waters of the Great lakes (1977–2015 with gaps from the mid-1990s to mid-2000s), mercury declined at annual rates of 3–5% from the mid-80s until mid-1990s (Blukacz-Richards et al. 2017). From the mid-2000s to 2015, Hg increased slightly in Lakes Superior (2–3%), Huron (2%), Erie (1%), and western Lake Ontario (1%). Studies of temporal Hg trends by Blukacz-Richards et al. (2017) and Zhou et al. (2017) included similar periods (mid-2000s to 2015) and results mostly agreed for Lakes Erie and Ontario, but differed for Lakes Superior and Huron. Blukacz-Richards et al. (2017) used a dynamic linear model incorporating length and lipid whereas Zhou et al. (2017) used age normalization, so different approaches may account for different results for temporal trends of Hg in lake charr from Lakes Superior and Huron.

4.1.3 Ontario Inland Lakes

Since the early 1970s, Hg concentrations in lake charr (also walleye and northern pike) have been measured in more than 100 lakes under programs designed to provide fish consumption advice for the Ontario recreational fishery (Gandhi et al. 2014b, 2015; Tang et al. 2013). Overall, Hg concentrations declined in lake charr at more than half of the locations studied during 1970–2012 (Fig. 16). Rates of decline were particularly large during 1970–1990 in southern Ontario for medium (60 cm length) and large (70 cm) lake charr. However, rates of decline were much lower than those reported from the Great Lakes. Moreover, Hg concentrations increased in some lakes, particularly for medium and large lake charr in southern Ontario during 1970–1990 and 1995–2012, with a weak decline during 1985–2006. Overall findings were consistent with generally observed patterns of decreasing Hg concentrations since the 1970s, with increases in recent years. Recent increases in Asian Hg

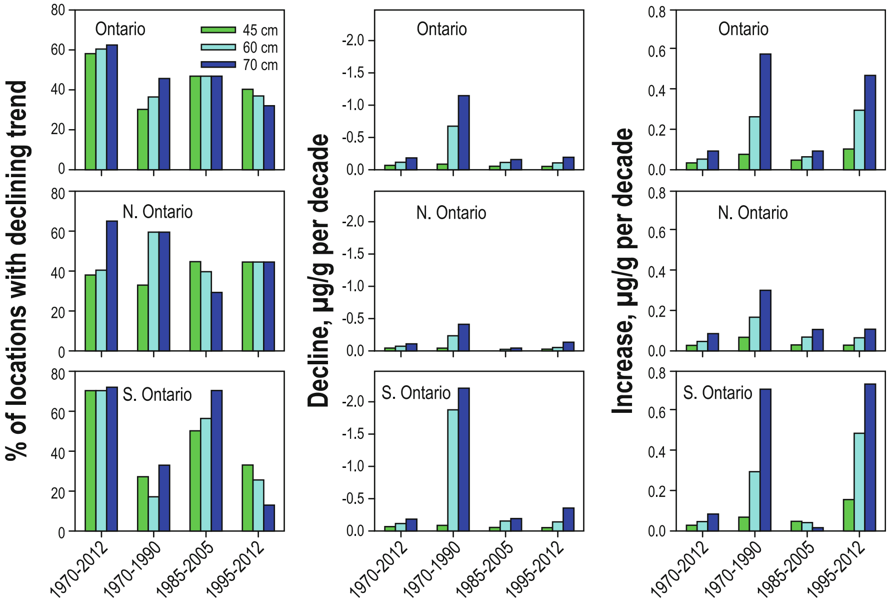

Fig. 16 Spatial and temporal trends in Hg concentrations in lake charr *Salvelinus namaycush* from Ontario lakes. Panels A, B, and C represent % of locations with a declining trend for all of Ontario, northern, and southern Ontario, respectively. To the right of each panel is the decline or increase expressed as µg/g per decade. From Table 1 in Gandhi et al. (2014b)

emissions may have played a role in recent increases in Hg concentrations in Ontario lakes, but warming temperatures may also be important. Few studies reported Hg trends in specific inland lakes, but Hg concentration in lake charr declined significantly in Lake Simcoe, Ontario, between 1970 and 2009 (Gewurtz et al. 2011c).

4.1.4 Other Southern Canada Inland Lakes

Mercury trends have not been monitored in Québec lakes due to the small number of lakes sampled more than three times and the general paucity of lake charr in those lakes, which tend to be walleye and northern pike dominated (Lucotte et al. 2016). Mercury trend studies have not been conducted in Canada's Maritime province lakes (apart from Anderson et al. 1995). Hg concentrations in lake charr measured as part of fish inspection studies showed no temporal trend in Cold Lake, Alberta, and Reindeer Lake, Saskatchewan during 1977–2014 (ECCC 2016). Similarly, Hg concentration showed no detectable trends in lake charr from western Lake Athasbaca during 1978–2009 (Evans and Talbot 2012).

4.1.5 Northern Canada

Mercury concentrations in lake charr have been monitored annually in Great Slave Lake since 1998. More limited data going back to 1977 are available from the west basin commercial fishery and some data from the east arm during the early 1990s (Evans et al. 2013). Mercury increased significantly through time in west basin lake charr and in large (>590 mm) lake charr from the east arm from the early 1990s to 2012, but decreased in small (<590 mm) lake charr from the east arm (Evans et al. 2013) (Fig. 17). Higher Hg concentrations in west basin lake charr were also associated with cooler years and a more positive Pacific North American oscillation index. Cooler years potentially were associated with less productive conditions, slower growth, and a lower condition factor than warmer years. Lake charr Hg concentrations in Lake Laberge and Kusawa Lake were slightly higher in the early 1990s than 2000–2001, particularly in Kusawa lake, although no trends were detected (Chételat et al. 2015).

4.2 *Temporal Trends of POPs*

4.2.1 Overview

Lake charr is one of the main target organisms for basin-wide assessments of POPs in the Great Lakes due to their availability, large home range, and position as a top

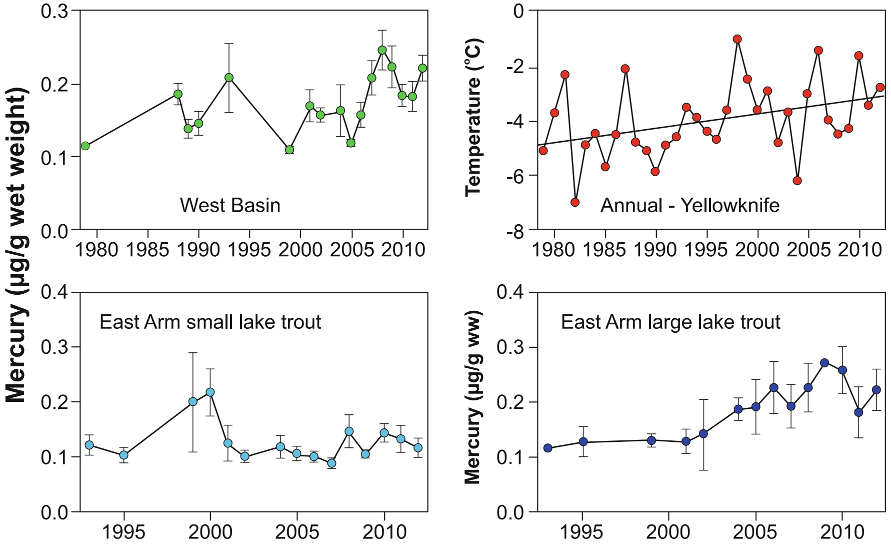

Fig. 17 Trends time in Hg concentrations in lake charr *Salvelinus namaycush* from the west basin and east arm of Great Slave Lake. Also shown is the year-to-year variation in mean annual air temperatures at the city of Yellowknife. Modified from Evans et al. (2013)

predator in the food web (Murphy et al. 2013). Canada and the USA have operated biomonitoring programs to monitor the status and trends of POPs in lake charr tissues from the Great Lakes since the 1970s (Gewurtz et al. 2011a; Murphy et al. 2013). The Province of Ontario and eight Great Lakes states also have long-term monitoring programs related to trends of contaminant concentrations in edible portions of fish (see Section “Human Dietary Exposure and Advisories”). The number of time series of POPs in lake charr is more limited than for Hg due to the high cost of analysis that limits the numbers of samples analyzed and sampling locations.

Since POP monitoring programs began, they have directly supported commitments made in the Great Lakes Water Quality Agreement between Canada and the USA to track progress toward reducing or eliminating releases of organic pollutants in the waters of the Great Lakes (GLWQA [Great Lakes Water Quality Agreement] 1978), and domestic chemical management initiatives. Long-term trend studies of POPs in lake charr began in the Arctic during the early 1990s with studies in Lake Laberge, Yukon, and Great Slave Lake, Northwest Territories (Muir et al. 2013). These studies were initiated because of concerns about human exposure from traditional diets by indigenous peoples.

Long-term monitoring of POPs in lake charr initially focused on PCBs and OCPs in the Great Lakes and Arctic lakes. However, in the early 2000s, attention began to shift toward other classes of POPs that were being reported in environmental media, such as PBDEs and PFASs, as discussed above under “New organic pollutants”. The availability of archived tissue samples from Environmental Specimen Banks enabled temporal trends of these new contaminants to be examined retrospectively. The importance of specimen banking was recognized early on during the development of protocols in the Great Lakes (Gewurtz et al. 2011a; McGoldrick et al. 2010) and was part of long-term monitoring of lake charr from lakes in the Yukon and Northwest Territories.

4.2.2 Northern Lakes

Concentrations of POPs were found to be elevated in lake charr from Lake Laberge in the Yukon in the early 1990s (Kidd et al. 1995, 1998), a finding that led to investigative studies in other Yukon lakes intended to ascribe cause. Lake Laberge and nearby Kusawa Lake were later established as long-term POPs (and later for Hg) trend monitoring sites for lake charr under the Northern Contaminant Program. Great Slave Lake, Northwest Territories, was established as a second long-term monitoring site because of its importance to local communities and concern that development in the south, primarily in Alberta, was contributing to significant contaminant loading to the lake (Evans et al. 2005b). An overview of these trends is discussed below.

In 1993, PCBs, DDT, and toxaphene concentrations were substantially higher in Lake Laberge lake charr fillets (averaging 328 ± 121 ng/g, 392 ± 133 ng/g, and 311 ± 62 ng/g, respectively) than in Kusawa Lake lake charr fillets (86 ± 26 ng/g, 44 ± 22 ng DDT/g, and 121 ± 25 ng/g, respectively). While high by northern

Canada standards, these lake's concentrations were lower than those measured in Lake Michigan (at Saugatuck in 1992), where PCBs averaged 3490 ± 450 ng/g, DDT averaged 1160 ± 180 ng/g, and toxaphene averaged 1730 ± 220 ng/g (De Vault et al. 1996). Higher lake charr POPs concentrations in Lake Laberge than Kusawa Lake were attributed to local sources and food chain length, as discussed previously.

Trends in POPs of Yukon lake charr up to 2011 indicate that ΣPCB, ΣDDT, ΣChlordane, ΣHCH, ΣCBz, and toxaphene concentrations declined sharply in Lake Laberge and Kusawa Lake from the 1990s through the early 2000s and then subsequently leveled off (Table 5; Fig. 18; Muir et al. 2013; Ryan et al. 2013). Trends were significant except for ΣDDTs in Lake Laberge and ΣCBz in Kusawa. ΣHCH declined the most (17% per year for Laberge and 14% per year for Kusawa) followed by ΣChlordane (12% per year and 13% per year, respectively) and ΣPCB (7.5% per year and 14% per year). In Lake Laberge, some of the decline in POPs was due to growth dilution, lower lipid content, increased forage fish abundance, and possible shifts in zooplankton community structure (Ryan et al. 2013). However, in the absence of other biological monitoring in Lake Laberge (and Kusawa Lake), a cause of changes in POP concentrations is difficult to confidently ascribe. Other studies in the Great Lakes noted reductions in the rate of POPs decline since the 1990s, with trend reduction related to continued recycling of POPs from sedimentary sinks, inputs from the watershed, and changes in food-web structure (Bhavsar et al. 2007). In Yukon lakes, which have mountain glaciers within their catchments, continued inputs of POPs from glacial melt may also delay reduction (Donald et al. 1999).

In contrast to Yukon lakes, ΣPCBs in lake charr from Great Slave Lake declined slower at a nonsignificant rate (Fig. 18). Initial measurements in 1993 showed that ΣPCBs concentrations averaged 14 ± 7 ng/g in west basin lake charr and 25 ± 19 ng/g in east arm lake charr, like other POPs (Evans and Muir 2016). A closer examination of the data showed that concentrations of other POPs appeared to be declining from the 1990s to 2002, then increased sharply in 2004, and declined thereafter, particularly in recent years. ΣDDT declined significantly in the west basin (8.3% per year) and east arm (6.0% per year). p,p′-DDE became the predominant DDT degradation product in recent years. ΣChlordane declined in the west basin but not east arm lake charr, in contrast to Yukon lakes where concentrations consistently declined, and concentrations are higher in Great Slave Lake than Yukon lakes. ΣHCH declined in both the east arm (10%/year) and west basin 15%/year) at a rate similar to Yukon lakes, although concentrations tend to be higher in Great Slave Lake. Toxaphene declined in lake charr (14%/year) from west basin, Great Slave Lake, although the decline was not significant in east arm lake charr. The lack of a significant decline of ΣPCBs and total (tetra-hexa) chlorobenzenes (ΣCBz) may be related to past sources in urban and industrial areas of the lake and its large watershed. Riverine inputs and atmospheric deposition are important sources of contaminants to Great Slave Lake. The major inflow is the Slave River formed by the confluence of the Peace and Athabasca Rivers. Development, particularly pulp and paper mills but also agriculture, oil sands activities, and urban development

Table 5 Percent annual decline or increase per year[a] for legacy POPs in lake charr fillets from Lake Laberge and Kusawa Lake in the Yukon and the west basin and east arm of Great Slave Lake (GSL). From Chapter 4 of the Canadian Arctic Contaminants Assessment Report (Muir et al. 2013)

Lake	Period	Years	ΣPCBs[b]	ΣDDT	ΣChlordane	ΣHCH	ΣCBz	Toxaphene
Laberge	1993–2011	13	−7.5	3.7 ns	−12	−17	−7.1	−9.6
Kusawa	1993–2011	13	−14	−23	−13	−14	−4.5 ns	−8.5
GSL west	1993–2011	12	−3.9 ns	−8.3	−5.8	−15	+2.0	−14
GSL east	1993–2011	13	−0.1 ns	−6.0	−0.6 ns	−10	+0.9 ns	−9.0 ns

[a] Percent annual change per year was determined from the half-lives ($t_{½}$), estimated from the log mean concentrations versus time (year) using the equation (LN (2)×100/$t_{½}$

[b] NS = not statistically significant ($P > 0.05$)

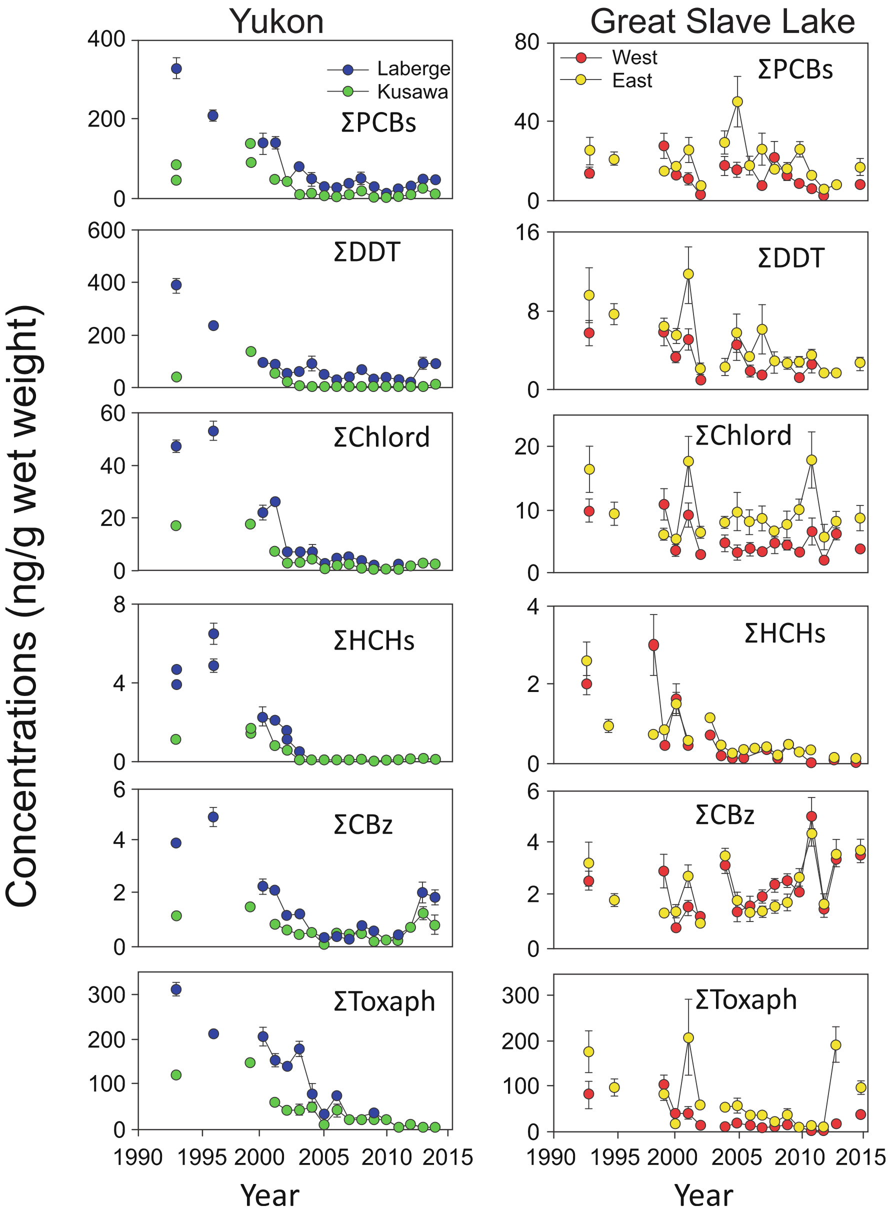

Fig. 18 Temporal trends in persistent organic pollutants (mean and standard error) in lake charr *Salvelinus namaycush* muscle from Lake Laberge and Kusawa Lake in the Yukon and the west basin and east arm of Great Slave Lake. Data from Muir et al. (2013) and Ryan et al. (2013)

fueled concerns that the lake is being adversely impacted by contaminant input via the Slave River and long-range atmospheric inputs (Evans and Muir 2016; Mudroch et al. 1992). The west basin is profoundly affected by the Slave River inflow, while the east arm has clearer and less productive waters that are more strongly influenced by long-range atmospheric inputs.

4.2.3 Great Lakes Region

A large number of studies have examined temporal trends of POPs and Hg in lake charr in the five Great Lakes. Detailed interpretation of annual collections started to be published in the 1980s with studies initially describing the first 10–12 years of data collection (Baumann and Whittle 1988; Borgmann and Whittle 1991; DeVault et al. 1986), and subsequently, temporal trends of POPs from the 1970s to the late 1990s and early 2000s (Hickey et al. 2006); Carlson et al. 2010). As monitoring studies continued, data were incorporated into peer-reviewed publications, government reports, and public documents such as the triennial State of the Great Lakes Reports (SOGLR) (ECCC and U.S. EPA 2017). The Toxic Chemicals in Whole fish sub-indicator of the SOGLR included summaries of the current status and trends for several different contaminants. Here, we describe trends of selected contaminants from the 1970s to 2017, review the most recent temporal trends of lake charr, and examine factors influencing trends. Given the large number of studies, we focus on three legacy contaminants (PCBs, DDT, and PCDD/F) and three new contaminants (PBDEs, PFOS, and HBCDD).

PCBs have been monitored in lake charr from the Great Lakes since the onset of monitoring in 1977. High levels of PCBs were present in Great Lakes fishes and in other environmental media, which led to bans on production and most uses of PCBs in both Canada and the USA by 1979 and globally under the Stockholm Convention in 2004 (although not ratified by the USA). Since the bans, concentrations in lake charr from all Great Lakes declined 2–9% per year (ECCC and U.S. EPA 2017) (Fig. 19). From 1999 to 2014, concentrations of PCBs in lake charr from Lakes Huron, Michigan, Ontario, and Superior, after age normalization, declined 6.0–17.2% per year (Zhou et al. 2018). Declines were smallest in nonindustrial sampling sites on Lake Michigan and most rapid in remote sites on Lake Superior. Despite continued long-term declines, PCBs are still the most predominant class of contaminants measured in lake charr from the Great Lakes (Fig. 13). PCB concentrations remain above the target of 100 ng/g ww in the 1987 amendment to the GLWQA, and are the primary cause of fish consumption advisories in the Great Lakes (Bhavsar et al. 2011; Guo et al. 2017; McGoldrick and Murphy 2016).

DDT and its environmental metabolites DDE and DDD (ΣDDT) are the most abundant organochlorine pesticide in whole-body homogenates of lake charr monitored by ECCC and the U.S. EPA (McGoldrick and Murphy 2016). Like PCBs, DDT was one of the original contaminants added to Annex A of the Stockholm Convention and has been measured since the onset of monitoring in the Great Lakes. Registration and uses of DDT were banned in the USA and Canada in the 1970s and

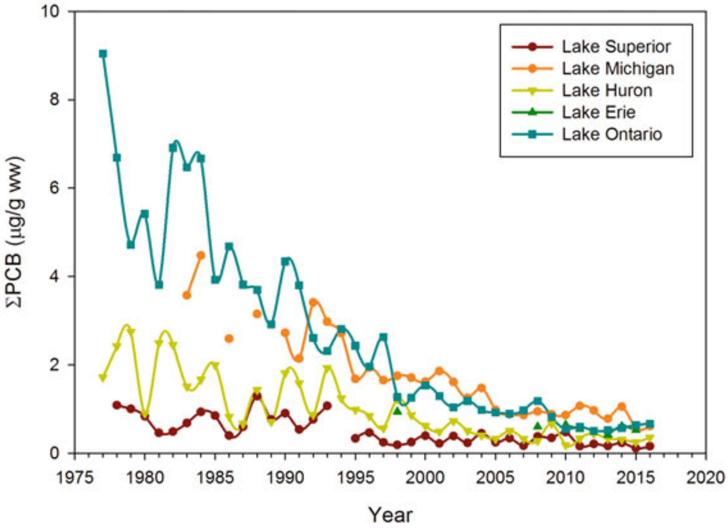

Fig. 19 Annual mean concentrations of ΣPCBs measured by ECCC and U.S. EPA in whole-body homogenates of lake charr *Salvelinus namaycush* from each of the Great Lakes (1977–2016)

all existing stocks of DDT in Canada were to be disposed by 1990. Concentration of ΣDDTs in lake charr declined substantially after the onset of monitoring, with current levels 88–95% lower than the maximum observed concentration in each Great Lake, well below the target of 1.0 μg/g specified in the 1987 GLWQA (Fig. 20). Age-adjusted ΣDDT concentrations in lake charr during 2004–2014 also declined 8.5–18.4%, with the slowest decline in Lake Ontario and the fastest decline in Lake Michigan (Zhou et al. 2018).

Lake Simcoe is a moderately large lake north of Lake Ontario and south of Georgian Bay. Situated relatively close to the urban area of southern Ontario and to intensively farmed areas south of the lake, it presents an interesting case study for temporal contaminant trends. An early study documented elevated ΣDDT concentrations in lake charr averaged 9460 ng/g in 1970 fall-caught lake charr and a rapid decline to 4430 ng/g for fish caught in fall 1975 and 1976 (Frank et al. 1978). Similarly, ΣPCBs concentrations averaged 5050 ng/g in 1970 and 1570 ng/g in fall 1975–1976 and PCBs and ΣDDT continued to decline in lake charr with lipid-based concentrations fitting a first-order exponential decay model over the 36-year period (1970–2006) (Gewurtz et al. 2011c). Mercury concentrations in Lake Simcoe lake charr also declined exponentially from 1970 to 2006, and length was not a significant covariate due to use of a limited size range (55–65 cm lengths) of lake charr (Gewurtz et al. 2011c). Declines of all three of these contaminants (DDT, PCB, and Hg) reflect reductions in local municipal wastewater and agricultural emissions to the lake similar to observations in the Great Lakes.

The final legacy contaminant group to be discussed, PCDD/Fs, are produced as by-products in industrial processes or through combustion of chlorinated

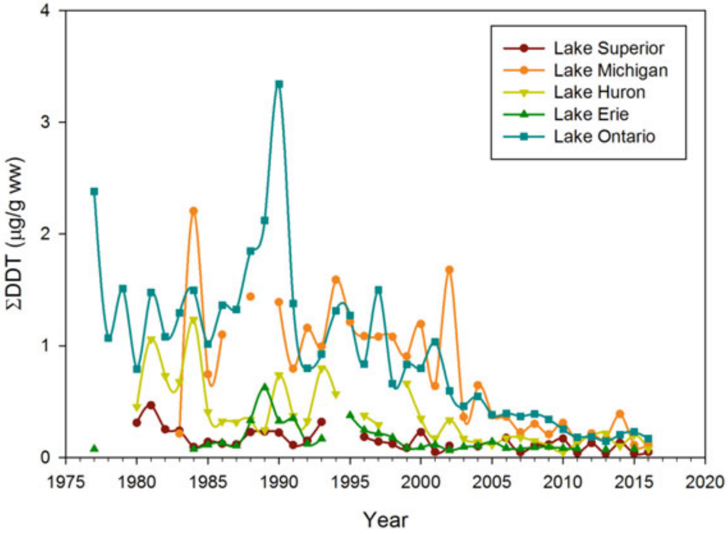

Fig. 20 Annual mean concentrations of ΣDDT measured by ECCC and U.S. EPA in whole-body homogenates of lake charr *Salvelinus namaycush* from each of the Great Lakes (1977–2016)

compounds. These highly toxic contaminants have also been measured and monitored in various media since being detected in Great Lakes biota, including lake charr (Bhavsar et al. 2008; Hallett 1985; Huestis et al. 1997). During 2004–2014, concentrations of 2378-TCDD and 2378-TCDF declined 41–73% across the Great Lakes (Pagano et al. 2018). Despite these declines, toxic equivalents (TEQ) based on PCDD/F exceeded Canadian Tissue Residue Guidelines (TRG) for protection of mammalian consumers of aquatic biota (0.71 pg/g diet). Based on trend models, TEQ based on TCDD/F and non-ortho PCBs in lake charr will remain above the TRG beyond 2050 (Pagano et al. 2018).

In the early 2000s, attention began to shift toward other classes of POPs that were being detected in Great Lakes biota. Unlike many legacy contaminants used in industrial applications or applied for pest control, several POPs were being used as additives to consumer products as flame retardants or as water or stain repellants. The first reports of PBDEs in lake charr from the Great Lakes were published in the early 2000s (Luross et al. 2002; Stapleton and Baker 2003). Subsequent retrospective investigation of trends using archived tissue samples from the U.S. EPA specimen bank demonstrated that concentrations of PBDEs increased exponentially in lake charr from all Great Lakes between 1980 and 2000 (Zhu and Hites 2004). PBDEs were added as routine analytes by ECCC and the U.S. EPA in Great Lakes monitoring programs starting in 2005 and through the additional use of retrospective analysis of archived samples filled in gaps to create a long-term picture of PBDEs in lake charr from the Great Lakes (Zhu and Hites 2004). Levels of all PBDEs appear to have peaked in or prior to 2000, and have since declined with estimated halving times of 3–5 years in Lakes Michigan, Huron, and Ontario, 13 years in Lake

Superior, and although declining, without significant trend in Lake Erie (Crimmins et al. 2012). These declines preceded official industry production phase outs and government regulatory actions, so were likely a result of replacement of PBDEs with other products in anticipation of restriction on use (Alcock et al. 2003; Hardy 1999). The most abundant PBDE congeners measured in lake charr were tetra-brominated BDE-47, penta-brominated BDE-99 and -100, and hexa-brominated BDE-153 and -154 (Gewurtz et al. 2011d). Of these congeners, penta-brominated BDEs are of most concern despite their declines due to the frequency and magnitude of exceedances of Canadian Federal Environmental Quality Guidelines for fish tissues (1.0 ng/g ww) (Fig. 21).

Perfluorooctane sulfonate (PFOS) is a chemical within a large group of per- and polyfluoroalkyl substances (PFAS) that was used as a water, oil, and grease repellant on paper products and fabrics and in firefighting foams. Similar to PBDEs, the primary manufacturer of PFOS voluntarily phased out its manufacture and use in products in 2002 due to concerns surrounding its persistence and potential for causing environmental harm and impending government restrictions and regulations. PFOS levels in lake charr from Lake Ontario increased from 43 ng/g in 1980 to 180 ng/g by 2001 (Martin et al. 2004). Follow-up investigations of trends of several PFAS compounds in lake charr from Lake Ontario that combined current monitoring with analyses of archived tissues from ECCCs specimen bank and previous published studies found the best-fit model for the trend in PFOS was an exponential rise at estimated rates of ~6% per year until levelling off in the 1990s and remaining stable to 2009 (Furdui et al. 2008; Gewurtz et al. 2012). Continued monitoring by ECCC and U.S. EPA in the Great Lakes have since shown high interannual

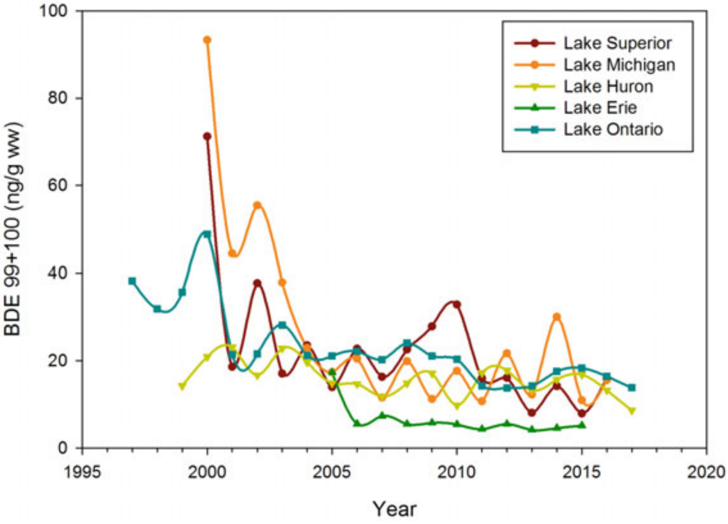

Fig. 21 Annual mean concentrations of BDE99+100 measured by ECCC and U.S. EPA in whole-body homogenates of lake charr *Salvelinus namaycush* from each of the Great Lakes (1997–2017)

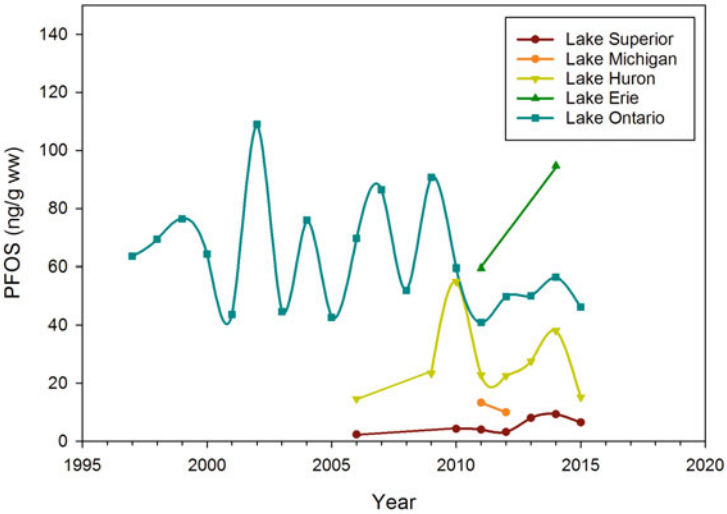

Fig. 22 Annual mean concentrations of PFOS measured by ECCC and U.S. EPA in whole-body homogenates of lake charr *Salvelinus namaycush* from each of the Great Lakes (1977–2016)

variability in the concentration of PFOS in lake charr (Fig. 22). In Lakes Superior, Michigan, Huron, or Erie, PFOS concentration in lake charr exhibited no temporal trends since the phase out of manufacture in 2002, whereas in Lake Ontario PFOS concentrations have started to decline (U.S. EPA and FDA 2017).

Concentrations of hexabromocyclododecane (HBCDD), a chemical widely used as replacement for PBDEs (Koch et al. 2015), especially α-HBCDD, the most abundant HBCDD isomer in lake charr, were fairly constant from 1980 to 2000 and then rose post-2000 through to 2010, after which the increase in concentration ceased and may be decreasing (Su et al. 2018). The rise and plateau of HBCDD in lake charr closely mimicked when PBDEs were phased out of production by government regulation of HBCDD through international and domestic actions. Levels of γ-HBCDD, the primary component of the technical mixture, declined significantly from 1975 to 2015, possibly because new releases of HCBDD to the environment are declining in response to regulatory restrictions (Su et al. 2018).

Long-term monitoring of contaminants in lake charr in the Great Lakes, in conjunction with retrospective analyses of fish tissue from specimen banking programs, identified chemicals that were causing or may cause harm to the environment. The data not only helped support actions to restrict use of these chemicals but also served to track progress of actions to reduce levels in the environment (McGoldrick and Murphy 2016). Concentrations of legacy contaminants in lake charr from the Great Lakes all declined significantly from high levels when first identified in the 1970s. Availability of preserved specimens in ECCC and U.S. EPA specimen banks also allowed for quick determination of trends for new chemicals as they emerged and contributed to decisions by governments and industry that halted increases

(PFOS and HBCDD) and initiated declines (PBDEs). Continuous technological improvements in analytical capabilities, such as recent advancements in nontarget analysis, will allow monitoring programs to adopt new and improved methods to identify contaminants of concern in lake charr from the Great Lakes (Fernando et al. 2018).

4.3 Effects of Changing Climate and Food Webs on Contaminant Temporal Trends

Climate warming may have unexpected effects on contaminant cycling due to the balancing effects of uptake rates and growth dilution in fishes, and because of temperature sensitivities of individual species (Ng and Gray 2011). Increasing trends of mercury in lake charr from lakes in southern and northern Ontario from the early 2000s through 2012 were attributed to remobilization of Hg, accelerated conversion to MeHg, and changes in food-web structure caused by invasive species (Gandhi et al. 2014b). Similar qualitative observations have been made in the Great Lakes. In Lake Ontario, Hg and PCBs in lake charr muscle declined overall but year-to-year variation was related to food-web changes and variation in Hg and PCB fluxes from atmosphere or sediments (Visha et al. 2015). Concentration of Hg in lake charr in Lake Ontario decreased 6.7–7.5% per year from 2004 to 2009 and then increased 3.3–4.6% per year from 2010 to 2015 (Zhou et al. 2017). The increasing Hg trend in Lake Ontario lake charr contrasted with lakes Superior and Michigan, where Hg declined from 2004 to 2015, likely because atmospheric emissions of Hg increased and Hg reservoirs in sediments that could be resuspended by increasing storms and less ice cover were greater in Lake Ontario than the other lakes (Zhou et al. 2017).

Changes in Great Lakes food webs have affected health of Great Lakes' fishes over the past 20 years, including changes in bioaccumulation potential of contaminants in top predators, such as lake charr (Murphy et al. 2018). Food-web structure has been stressed by nutrient availability, invasive species, anthropogenic change, declines in prey availability, increases in predator density, shifts in predator–prey ratios, and density-dependent growth declines resulting in higher chemical concentrations of POPs and mercury (He et al. 2015, 2016; Lake Michigan Lake Trout Working Group 2016; Tsehaye et al. 2014). Consequently, long-term chemical monitoring and surveillance programs in the Great Lakes are incorporating fish age into their assessments of concentrations and trends as a result.

Minor oscillations (within an order of magnitude) in temporal trends of POPs in lake charr from Lakes Ontario, Huron, Michigan and Superior from 1999 to 2009 were attributed to trophodynamic, meteorological, or climatological changes (Chang et al. 2012). Surface water temperature was not correlated to fish POP concentrations in any lakes, thereby suggesting that temperature alone was not directly responsible for the oscillations (Chang et al. 2012). Modelling of the effect of a warming climate on PCB 77 (2,4,2′4′-tetrachlorobiphenyl) uptake by lake charr predicted indirect effects due to changing growth and consumption rates of major prey species that might lead to higher chemical uptake (Ng and Gray 2011).

5 Human and Wildlife Contaminant Exposure

5.1 Human Dietary Exposure and Advisories

In general, fish consumption is an important pathway for human exposure to contaminants. For example, PCB concentration in anglers was positively related to years of Great Lakes sport fish consumption and the number of fish meals consumed (Cole et al. 2002). Similarly, blood Hg levels were higher among anglers consuming fish caught in Great Lakes areas of concern than within the general population (Cole et al. 2004). First-Nations communities in northern Ontario and Manitoba with exposure to PCBs and DDE via fish consumption had higher incidence of type-2 diabetes (Marushka et al. 2018). Lake charr form a significant portion of the fish diet of First Nations communities in Ontario (Marushka et al. 2017) and are a popular sport fish (Gandhi et al. 2014b). Monitoring of lake charr for assessment of human health-related exposure has been conducted primarily by the US Great Lakes states and Provincial and Territorial governments in Canada. These programs have focused on analyzing fillets for Hg and in some cases for other priority chemicals such as PCBs.

Consumption advisories are generally based on risk assessments that consider tolerable daily intakes and exposure rates to contaminants. Tolerable daily intake (TDIs) for human consumers of fish have been developed by health agencies around the world. Many consumption advisories are related to contaminants in lake charr, especially Hg. Provincial, Territorial, and State agencies post advisories on web sites and in fishing regulation guides (http://ec.gc.ca/mercure-mercury/default.asp?lang=En&n=DCBE5083-97AD-4C62-8862). Advisory program managers from U.S. government health, water quality, and fisheries agencies bordering the Great Lakes have developed protocols for issuing fish consumption advice (MDH 2018).

Mercury fish consumption advisories are not evenly distributed across the lake charr range, but are most numerous in areas with strong sport fish monitoring programs, with Hg often measured as part of stock and other assessments. Regions where Hg in fish has not been identified as a wide-spread problem have no or limited Hg monitoring programs, such as Nunavut and British Columbia. For example, lake charr are uncommon in British Columbia and advisories have been issued for only three locations: Williston Reservoir and two lakes near two historical gold mining sites. In the Yukon, advisories are precautionary, nonspecific to any lake and river, and only for women of childbearing years and children less than 12 years old. The advisory states that lake charr under 40 cm can be consumed without limit while fish >60 cm should be consumed only 1–2 times per week. Several Hg advisories have been issued for lake charr (and other predatory fishes) in the Northwest Territories (NWT HSS 2018). Advisories are most strongly associated with small to medium size lakes (<500 km^2), Hg methylation rates are greater, and with older fish populations (Evans et al. 2005a; Lockhart et al. 2005; Stephens 1995). In contrast, hundreds of Hg consumption advisories have been issued for Great Lakes lake charr. Large sport fisheries, relatively easy access for study, and significant local Hg emissions all contribute to the prevalence of Hg advisories in the Great Lakes basin. Consumption advisories typically are based on length categories of lake charr with large fish having more stringent consumption limitations due to bioaccumulation and biomagnification (Bhavsar et al. 2011; Gandhi et al. 2015; Gewurtz et al. 2011b).

The number of Hg advisories for fish consumption is projected to increase in regions such as the Great Lakes where climate is warming. For example, the percentage of lakes in northern Ontario with “do not consume” advisories for lake charr is expected to increase from 0–6% to 0–52% for the general population and from 21–72% to 24–88% for sensitive populations by 2050, based on an apparent slow increase in Hg concentrations (Gandhi et al. 2015). Similarly, the number of health advisories is also predicted to increase in southern Ontario from 0–7% to 0–24% for the general population and 13–66% to 25–95% for sensitive populations (Gandhi et al. 2015).

Consumption advisories based on POPs are fewer in number than for Hg, with more advisories in the five Great Lakes than inland lakes in the region (Dellinger 2004). PCBs are the major driver of consumption advisories, with PCDD/PCDFs of secondary importance, toxaphene, and mirex only occasionally high enough to result in advisories (Gandhi et al. 2014a, 2017). While DDT has been implicated in many measures adversely affecting bird health, the advisory benchmark for human consumption of fish is high (Table 6) relative to environmental concentrations. Average concentrations of PCBs, OCPs, PBDE congeners, and PFOS in lake charr from lakes Superior, Michigan, Huron, and Ontario did not exceed Province of Ontario benchmarks (Dellinger et al. 2014; Table 6), whereas total TEQs for PCDD/Fs and dioxin-like PCB congeners exceeded guidelines (Pagano et al. 2018). In Lake Simcoe, PCBs in large lake charr (>65 cm) exceeded the consumption guideline (211 ng/g) for sensitive populations, while PBDEs (BDE-47, BDE-99, BDE-153-, BDE-209) were below consumption guidelines (Gewurtz et al. 2011c). In the early 1990s, Health Canada issued a consumption advisory for lake charr and burbot *Lota lota* liver from Lake Laberge in the Yukon based on high toxaphene concentrations, but this advisory was discontinued due to declining contaminant levels (Ryan et al. 2013). Lake charr from four northern Québec lakes had PCB and PCDD/PCDF concentrations below Health Canada guidelines (Laliberté and Tremblay 2002).

Consumption advice related to Hg in lake charr and other fishes varies, particularly with respect to subsistence consumers who are more likely to consume fish regularly and in larger quantities than occasional recreational anglers (Table 7). For example, the U.S. Food and Drug Administration (U.S. FDA) set an action level of 1000 ng/g for Hg, while the U.S. EPA set a screening value of 400 ng/g ww for recreational anglers and 49 ng/g for subsistence fishers for total Hg. The U.S. FDA action level used for commercial fish is an indicator of chemical residue levels in fish and shellfish that should not be exceeded for the general population (U.S. EPA

Table 6 "Do not eat" fish consumption advisory benchmarks used by the Province of Ontario and potential health effects for major contaminants found in Great Lakes fishes, including the lake charr *Salvelinus namaycush*. Sensitive population refers to women of childbearing age and children. Modified from Gandhi et al. (2017). Data sources for concentration are provided in the footnote

Contaminant	Units (wet wt)	General population	Sensitive Population	Range of mean concentration[a]	Potential health effects
Mercury	ng/g	>1800	>500	99–159	Neurotoxicant, can also damage immune, digestive, and nervous systems
PCBs	ng/g	>844	>211	53–207	Neurotoxicant, affects reproductive and immune systems, developmental effects, potential carcinogen
Dioxin/furan/dioxin-like PCBs (TEQs)	pg/g	>21.6	>5.4	22–51	Neurotoxicant, affects reproductive, immune, and endocrine systems
Mirex	ng/g	>657	>164	1–7	Can affect stomach, intestines, liver, kidneys, eyes, thyroid, nervous system, reproductive health
Toxaphene	ng/g	>1877	>469	49–173	Potential carcinogen, convulsions, liver and kidney damage
Chlordane	ng/g	>469	>117	–	Affects nervous and digestive systems and liver
DDT	ng/g	>5000	>5000	21–83	Affects nervous system, potential carcinogen, developmental, reproductive effects
HCB	ng/g	>2534	>634	2–6	Affects nervous system, liver, thyroid, possible carcinogen, endocrine disruptor
PFOS	ng/g	>640	>160	0.85–46	Potential carcinogen, endocrine disruptions, oxidative stress
Aldrin + dieldrin	ng/g	>939	>235	–	Potential carcinogen, convulsions, nervous system effects, kidney damage
BDE-47		>939	>235	55–135	Can affect thyroid and liver, behavioral changes, may affect immune system, possible carcinogen, BDE 47 and 99 more toxic than BDE 209
BDE-99		>939	>235	15–29	
BDE-153		>1877	>469	3.8–4.4	
BDE-206		>65,701	>16,425	–	

[a] Range of average concentrations of PCBs and OCPs (except toxaphene) in lake charr *Salvelinus namaycush* reported during 1999–2011 for Lakes Superior, Michigan, and Huron from Dellinger et al. (2014). Range of average concentrations for Lakes Superior, Michigan, Huron, and Ontario for BDE 47, 99, and 153 during 2004–2009 from Crimmins et al. (2012) for PFOS during 2008–2009 from Guo et al. (2012), for toxaphene during 2009 from Xia et al. (2012), and for dioxin/PCB TEQs from Pagano et al. (2018)

2000). As of 2017, the U.S. EPA and U.S. FDA issued joint advice for mercury in fish and shellfish (U.S. EPA and FDA 2017). The National Lake Fish Tissue Study (Stahl et al. 2009; U.S. EPA 2009) used a fish tissue criterion of 300 ng/g based on a criterion for methyl Hg (U.S. EPA 2001). The Great Lakes Fish Consortium, Fish Advisory Workgroup from Great Lake states issued protocols for fish consumption advisories for PCBs and mercury and discussion papers related to chlordane and toxaphene (MDH 2018). Their guidelines for mercury are similar to those issued by the U.S. FDA and U.S. EPA. However, the tissue concentration for unrestricted consumption for PCBs (50 ng/g) is 20-fold higher than the U.S. EPA screening value (Table 7). In northern Canada, an Hg guideline of 200 ng/g was initially considered for subsistence fishers (Lockhart et al. 2005; Wheatley 1979), in addition to the Health Canada guideline of 500 ng/g for commercial sale of fish, but has not been used for advisories. Rather, guidelines generally are issued only for lakes where average Hg concentration in the species exceeds 500 ng/g, with consumption of small fish in greater quantities than larger fish (Health Canada 2007). Concentrations of 370 ng/g (average for walleye or yellow perch) resulted in average consumption of 70% of TDI values for women (60 kg) and 110% for children 1–4 years old (Health Canada Hg risk assessment 2007), and are likely similar for lake charr consumption.

The U.S. FDA action level for PCBs is 2000 ng/g (ww) while U.S. EPA screening values (SV) are 20 ng/g for recreational and 2.45 ng/g for subsistence fishers (Table 7). SVs are defined as the concentration of a chemical in fish tissue that is of potential public health concern and used as a threshold value against which tissue residue levels of the contaminant in fish are compared. Screening values are based on both noncarcinogenic and carcinogenic effects of the chemical contaminant (U.S. EPA 2000). Screening values for dieldrin and heptachlor epoxide are also quite low relative to other OCPs. As a consequence of these stringent guidelines for subsistence fishers, lake charr in several lakes in Alaska exceeded consumption thresholds for dieldrin, chlordane, and p,p′-DDE (Ackerman et al. 2008; Flanagan Pritz et al. 2014). Σ_7PCBs (sum of seven major congeners) in lake charr from Alaskan lakes (Fig. 12) generally did not exceed subsistence consumption values, but likely would have if based on a larger suite of congeners. Lake charr from inland lakes in the Great Lakes region and from Kusawa Lake, Lake Laberge, and Great Slave Lake in northern Canada exceed subsistence limits for PCBs (Fig. 18).

A more recent approach to consumption advice for contaminants is based on risk-benefit assessment and a recognition that fish contain high levels of healthy omega-3 fatty acids (Dellinger 2004; Dellinger and Ripley 2016; Knuth et al. 2003; Reyes et al. 2017; Turyk et al. 2012; Williams et al. 2017). Furthermore, a shift in diet from wild-caught fish to alternate foods that are higher in unhealthy fats, sugars, and salts poses a different health risk. Subsistence fish consumers may also not have the means to purchase or have access to alternate foods. Therefore, an increasingly large number of studies are investigating fatty acids in fish in addition to contaminant levels when developing more tailored consumption advice, such as research to optimize the balance between contaminant and fish fatty acid consumption. Advice will be lake- and fish-size-specific. For example, lake charr in Lake Ontario are high

Table 7 Comparison of FDA Action Levels and Tolerances with U.S. EPA screening values (SV), Health Canada guidelines, and Great Lakes Consortium advisory guidance. Modified from Tables 1 and 2 in the U.S. EPA guidance document for fish advisories (U.S. EPA 2000)

Chemical	Units	FDA action level	EPA SV: recreational fishers	EPA SV subsistence fishers	Health Canada	Great lakes consortium DNE[a]	Great lakes consortium unrestricted consumption
Mercury	ng/g	1000	400	49	500	950	50
Chlordane	ng/g	300	114	14			
Dieldrin	ng/g	300	2.5	0.307			
Heptachlor epoxide	ng/g	300	4.39	0.540			
Mirex	ng/g	100	800	98			
Total DDT	ng/g	5000	117	14			
PCBs	ng/g	2000	20	2.45		1890	50

[a] "Do not eat" values

in eicosapentaenoic (EPA) and docosahexaenoic acid (DHA) fatty acids that can be good food choices (Strandberg et al. 2017), although, Hg and POP concentrations also need to be considered when weighing the merit of consuming lake charr versus other species such as lake whitefish or yellow perch. The lake charr is somewhat lower in fatty acid concentration, but substantially higher in POPs and Hg than other species.

5.2 Comparison to Guidelines for Piscivorous Fish and Fish-Eating Wildlife

Sandheinrich et al. (2011) proposed a toxicity reference value (TRV) for Hg of 300 ng/g wet weight (whole body) for piscivorous fishes (not lake charr) and concluded that fish inhabiting inland lakes were at more risk than species inhabiting the Great Lakes, based on lowest observable effect levels for sublethal effects of mercury on freshwater fish, including changes in reproductive health (Dillon et al. 2010; Sandheinrich and Wiener 2011). Based on an assessment of the large OMECC database, 70% of lake charr populations in northern Ontario and 57% in southern Ontario exceeded a TRV for Hg of 470 ng/g in fillet (or 330 ng/g ww whole body) for mature lake charr, with exceedances projected to increase to 76–92% for northern and 79–89% in southern lakes by 2050 due to slowly increasing contaminant concentrations (Gandhi et al. 2015). Similarly, Hg in lake charr in northern Quebec and in many lakes in Northwest Territories also exceeded the 470 ng/g TRV (Laliberté and Tremblay 2002).

Tissue residue guidelines (TRG) for protection of fish eating wildlife are available for selected POPs and Hg (CCME 1999; U.S. EPA 1995), but do not specifically consider lake charr as prey. Because adult lake charr inhabit cold deep waters (Marsden et al. 2021), they are unlikely prey for most fish-eating mammals and birds except during spring when they forage in shallow nearshore waters or at the surface over deep waters (Vinson et al. 2021). Nevertheless, a comparison of guidelines is useful to illustrate the relevance of contaminant measurements. For example, total TEQ (PCDD/F +dioxin-like PCBs) in Great Lakes lake charr (Table 6) that exceeded Canadian TRGs (CCME, 2001) for fish-eating mammals and birds indicate the potential for adverse effects if consumed (Pagano et al. 2018). Based on an assessment of U.S. EPA wildlife contaminant health thresholds, chlordane concentrations in lake charr from three of eight Alaskan lakes exceeded the health threshold for kingfisher (4.5 ng/g), but not for mink (830 ng/g) or river otter (1140 ng/g), and dieldrin and pp-DDE thresholds were not exceeded for any wildlife species (Table 8; Flanagan Pritz et al. 2014; Ackerman et al. 2008).

Table 8 Wildlife contaminant thresholds and tissue residue guidelines (ng/g wet weight). Data sources provided in the footnotes

Chemical	Kingfisher[a]	Mink[a]	River Otter[a]	Fish	CCME TRG for fish consuming wildlife[b]
Chlordane	4.5	830	1140		–
Dieldrin	360	20	30		–
Total DDT	490	360	490		14
PCBs	440	130	180		0.00079–0.0024 (TEQs)
PCDD/Fs	–	–	–		0.00071–0.00475 (TEQs)
Toxaphene	–	–	–		6.3
Methyl Hg	–	–	–	300[c]	33

[a] Ackerman et al. (2008)

[b] CCME (http://st-ts.ccme.ca/en/index.html); (CCME 1999)

[c] Sandheinrich et al. (2011)

6 Conclusions

The contaminants literature for lake charr is substantial, and encompasses trend measurements, bioaccumulation, and adverse biological effects. Nonetheless, many data gaps are evident. For adverse effects, lake charr have not been extensively studied as test organisms (with much more work on rainbow trout), which increases the uncertainty of risk assessments of contaminant exposure. Notably, lake charr were the most sensitive of 11 species to TCDD in tests of free embryo mortality (Walker et al. 1996). Most of the 1980s and 1990s and new or emerging contaminants (outlined by McGoldrick and Murphy 2016) have not been tested for their toxicity to lake charr. The combined effects of exposures to chemical mixtures are also unknown and remain a major knowledge gap. Another major knowledge gap is the extent to which lake charr populations are vulnerable to the combined effects of contaminants with other stressors, such as increased primary production, prey abundance, and invasive species all of which are changing in respect to a changing climate.

Long-term monitoring of POP and Hg concentrations in lake charr has been invaluable in assessing the effectiveness of domestic regulatory programs for chemical management, like Canada’s CMP and the binational Great Lakes Water Quality Agreement, and for judging progress on global bans on POPs through the Stockholm Convention. Continuing these trend monitoring studies is important because they become more statistically powerful with each new sampling year. Long-term trend data are increasingly being interpreted with consideration of climate change impacts on food webs and contaminants (e.g., greater methylation of Hg). Climate warming is already emerging as a serious concern for Hg in lake charr, with concentrations increasing in Ontario (Gandhi et al. 2014b, 2015) and in Great Slave Lake (Evans et al. 2013). However, compensating factors, such as increased growth rates and increased fishing pressure as lakes become more accessible, may counteract this. Bioenergetics modelling of effects of climate warming on PCBs in lake charr have illustrated the complexity of this issue (Ng and Gray 2011). Understanding future contaminant trends and possible adverse effects will require strong ancillary data, such as data on prey fish populations, stomach contents, stable isotope ratios, other indicators of diet and food-web relationships, measures of primary productivity, and climate parameters such as lake thermal regimes and ice out times.

The suite of contaminants measured in Great Lakes lake charr is extensive, but more limited for other lakes across Canada and the northern USA, except Hg. Concentrations of POPs and new contaminants such as chlorinated paraffins and volatile methyl siloxanes are likely lower in lake charr across Canada than in the Great Lakes (Gewurtz et al. 2011d, 2013; Saborido Basconcillo et al. 2015), but perhaps not for all organic pollutants, especially where local sources are available (Ackerman et al. 2008) or where long food chains lead to lake charr (Kidd et al. 1998; Rasmussen et al. 1990; Ryan et al. 2013). Thus, carefully revising and possibly expanding the number of contaminants is important to keep monitoring programs relevant. This has begun under the U.S. EPA Great Lakes, Environment and Climate Change Canada monitoring programs, and Northern Contaminants Program. The number of contaminants measured should also be expanded under provincial, state, tribal, and territorial programs to more fully assess human exposure, especially from subsistence fish consumption. Maintenance and availability of archived samples in formal specimen banking programs, such as by ECCC and the U.S. EPA, for assessing new contaminants is also important and requires ongoing commitment from funding agencies for long-term storage costs.

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Appendix 1

Acronyms and chemical terminology

AhR	Aryl hydrocarbon receptor
Aroclor	Commercial name for PCB mixtures, e.g., Aroclor 1254 (54% Chlorine)
BAF	Bioaccumulation Factor (concentration in field collected biota (usually lipid adjusted)/dissolved concentration in water)
BCF	Bioconcentration Factor (concentration in lab exposed biota (usually lipid adjusted)/dissolved concentration in water)
BSAF	Biota-Sediment Accumulation Factor (concentration in field collected biota (usually lipid adjusted)/concentration in sediment (usually organic carbon adjusted)
DHA	Docosahexaenoic acid - a long-chain polyunsaturated fatty acid: 22:6n-3

(continued)

AhR	Aryl hydrocarbon receptor
Dieldrin	Insecticide with a hexachloro-1,3-cyclopentadiene ring. Also, a degradation product of Aldrin
DDT	Insecticide. Chemical name dichlorodiphenyltrichloroethane. Has p,p′ and o,p′ isomers. Also with degradation products DDD and DDE
D4, D5, D6	Cyclic methyl siloxanes. Widely used silicon-based chemicals
EPA	Eicosapentaenoic acid—a long-chain polyunsaturated fatty acid: 20:5n-3
EROD	Ethoxyresorufin o-deethylase. A measure of Hepatic mixed-function oxidase activity, specifically induction of cytochrome p4501A1
GC	Gas chromatography
HBCDD	Hexabromocyclododecane. A flame retardant and replacement for PBDEs
HCH	Hexachlorocyclohexane (isomers α-HCH, lindane or γ-HCH)
log K_{ow}	Logarithm of the octanol–water partition coefficient
MCCPs	Medium-chain chlorinated paraffins (C14–C17 chlorinated n-alkanes)
MeHg	Methyl mercury. The toxic and bioaccumulative form of mercury (Hg)
mirex	Insecticide based on a chlorinated cyclopentadiene caged ring structure
net trophic transfer efficiency (γ)	$\gamma = \Delta$PCB body burden (ng) $\div$ amount of PCB ingested (ng)
Non-ortho PCBs	PCB congeners lacking chlorine substitution in the ortho or 2,6 positions on the phenyl ring. Also referred to as “dioxin-like PCBs”
OCPs	Organochlorine pesticides. DDT, chlordane, HCH, dieldrin, mirex, aldrin, toxaphene, etc.
OPEs	Organophosphate ester flame retardant/plasticizers
PBDEs	Polybrominated diphenyl ethers. Tetra-brominated BDE-47, penta-brominated BDE-99 and -100, and hexa-brominated BDE-153 and -154
PCB congener	One of 209 possible structural isomers having 1–10 chlorines on the biphenyl rings
PCBs	Polychlorinated biphenyls
PCDDs	Polychlorinated dibenzo-p-dioxins
PCDFs	Polychlorinated dibenzofurans
PFASs	Poly/perfluoro alkyl substances
PFCAs	Perfluorocarboxylates. Typically consist of perfluorinated 4 carbon to 16 carbon chains
PFOS	Perfluorooctane sulfonate. Contains a perfluorinated 8 carbon chain
POPs	Persistent organic pollutants. Includes PCBs, OCPs. Refers to the chemicals listed by the Stockholm Convention on POPs
PPCPs	Pharmaceuticals and personal care products
SCCPs	Short-chain chlorinated paraffins (C10–C13 chlorinated n-alkanes)
TBARS	Thiobarbituric acid reactive substances. An oxidative stress indicator
TBOEP	Tris(2-butoxyethyl) phosphate, a phosphorus-based flame retardant
TCDD	2,3,7,8-tetrachlorodibenzo-p-dioxin. The most toxic dioxin congener
TCEP	Tris (chloroethyl) phosphate
TEFs and TEQs	TCDD toxic equivalents or factors. Toxicity relative to 2,3,7,8-TCDD = 1.

(continued)

AhR	Aryl hydrocarbon receptor
TL	Trophic level = $TL_{consumer} = ((\delta^{15}N_{consumer} - \delta^{15}N_{primary\ producer})/\Delta^{15}N) + 1$
TMF	Trophic Magnification Factor. TMF = antilog [slope contaminants vs Trophic Level of individual food-web organisms]
TMS	Trophic magnification slope. TMS = antilog [slope contaminants vs $\delta^{15}N$ of individual food-web organisms]
Toxaphene	Insecticide also called polychlorocamphene. Complex mixture of chlorinated bornanes
TP	Trophic position = $TP_{consumer} = \delta^{15}N_{primary\ producer} + (\delta^{15}N_{consumer} - \delta^{15}N_{primary\ producer})/\Delta^{15}N)$
TPHP	Triphenyl phosphate
TRG	Tissue Residue Guidelines
TRV	Toxicity reference value. A toxicological index is used to qualify or quantify a risk of adverse effects to human or wildlife health.
T3	Tri-iodothyronine. Thyroid hormone
VTG	Vitellogenin. A precursor protein of egg yolk used as a biomarker in vertebrates of exposure to estrogenic substances
$\Delta^{15}N$	Trophic enrichment factors (fractionation of ^{15}N from prey to predator)
$\delta^{13}C$	Carbon stable isotope ratio ($^{13}C/^{12}C$). Expressed as parts per thousand (‰) relative to a standard
$\delta^{15}N$	Nitrogen stable isotope ratio ($^{15}N/^{14}N$). Expressed as parts per thousand (‰) relative to a standard

Appendix 2

Aquatic toxicity of 39 pesticides and selected industrial chemicals to lake charr (i.e., Lake trout) *Salvelinus namaycush*. Data extracted from the acute toxicity database (https://www.cerc.usgs.gov/data/acute/acute.html.)

Chemical	Units (/L)	Use	CAS RN	Temp (°C)	Hardness	Type	Duration (hrs)	N	Average 96 hr LC50	Range
2,4-D	mg	Herbicide	94-75-7	5	44	Static	96	6	58.1	44.5–105
2,4-D Butyl ester	µg	Herbicide	94-08-4	10	44	Static	96	14	1040	500–2800
2,4-D Propylene Glycol butyl ether ester	µg	Herbicide	1928-45-6	5	44	Static	96	14	1151	390–2930
Antimycin A	ng	Pesticide	1397-94-0	12	44	Static	24	1	53	45–63
Captan	µg	Fungicide	133-06-2	12	44	Static	96	3	54.4	49–63.2
Carbaryl	µg	Insecticide	63-25-2	12	40	Static	96	5	783	690–2300
Carbofuran	µg	Insecticide	1563-66-2	12	314	Flow-through	96	1	164	119–226
Chlorpyrifos	µg	Insecticide	29921-88-2	12	44	Static	96	6	148	73–227
Coumaphos	µg	Insecticide	56-72-4	12	162	Static	96	1	593	416–846
Diazinon	µg	Insecticide	333-41-5	12	162	Static	96	1	602	400–906
Dichlorvos	µg	Insecticide	62-73-7	12	162	Static	96	2	185	183–187
Dicofol	µg	Acaricide	115-32-2	12	162	Static	96	1	87.0	53–142
Dinitramine	µg	Herbicide	29091-05-2	12	44	Static	96	1	920	776–1090
Dinoseb	µg	Herbicide	88-85-7	10	162	Flowthrough	96	12	202	2.2–1440
Diuron	mg	Herbicide	330-54-1	15	44	Static	96	13	3.0	1.1–11.5
D-Trans Allethrin	µg	Insecticide		12	40	Static	96	2	16.7	16–17.3
EPTC	mg	Herbicide	759-94-4	10	44	Static	96	8	13.7	11.5–1450
Fenthion	µg	Insecticide	55-38-9	12	44	Static	96	3	1573	1370–1900
Flit Mlo	mg	Mosquito Larvicide		12	162	Static	96	1	>700	–
Folpet	µg	Fungicide	133-07-3	12	44	Static	96	2	55.3	24–86.5

(continued)

Chemical	Units (/L)	Use	CAS RN	Temp (°C)	Hardness	Type	Duration (hrs)	N	Average 96 hr LC50	Range
Lethane 384	mg	Insecticide	112-56-1	12	162	Static	96	2	4.0	3.9–4.1
Lindane	µg	Insecticide	58-89-9	12	44	Static	96	2	28.0	24–32
Malathion	µg	Insecticide	121-75-5	12	162	Static	96	2	109	76–142
Methoxychlor	µg	Insecticide	72-43-5	12	162	Static	96	2	16.5	16–17
Methyl parathion	µg	Insecticide	298-00-0	12	162	Static	96	2	3570	3360–3780
Mexacarbate	mg	Insecticide	315-18-4	12	162	Static	96	1	8.2	3.69–18
Naled	µg	Insecticide	300-76-5	12	162	Static	96	1	87.0	53–142
Parathion	µg	Insecticide	56-38-2	12	162	Static	96	2	1705	1490–1920
PCB Aroclor 1016	µg	Industrial	12674-11-2	10	170	Static	96	2	685	480–890
Picloram	mg	Herbicide	19180-02-1	10	44	Static	96	13	3.9	1.6–16.8
Pydraul 50e	mg	Hydraulic Fluid		10	170	Static	96	3	2.4	1.5–2.9
Pyrethrum	µg	Insecticide	8003-34-7	12	44	Static	96	2	28.4	19.7–37
Resmethrin	µg	Insecticide	10453-86-8	12	44	Static	96	2	1.2	0.74–1.68
Ronnel	µg	Insecticide	299-84-3	12	162	Static	96	2	378	265–490
Ru-11679 (bioethan-omethrin)	µg	Insecticide	51202-40-5	12	44	Static	96	1	0.20	0.14–0.20
Ru-11679 (bioethan omethrin)	µg	Insecticide	51202-40-5	12	314	Flowthru	24	1	0.27	0.25–0.30
Temephos	mg	Insecticide	3383-96-8	10	40	Static	96	4	2.7	1.05–4.8
Thanite	µg	Insecticide	115-31-1	12	162	Static	96	2	116	109–123
Trichlorfon	µg	Insecticide	52-68-6	12	162	Static	96	2	790	550–1030

Appendix 3

Half-lives and absorption efficiencies for PBDE congeners in lake charr (i.e., lake trout) *Salvelinus namaycush* and other fish species based on data from the Arnot and Quinn (2015) database for dietary bioaccumulation studies

PBDE Congener	Species	Temp. (°C)	Feeding rate[a] (g/g BW/d)	Exposure Duration (d)	Depuration (d)	Growth rate constant (/d)	Food concentration (ng/g)[b]	Tissue analyzed[c]	Half-life ± SE (d)	Assimilation efficiency	References[d]
BDE 47	sole	19	0.008	84	149	0.008	82.2 ww	M + L	59 ± 21	0.15	1
BDE 47	Common carp	22	0.033	60	100	0.009	174 ww	WB − GIT	30 ± 12	0.93	2
BDE 47	Lake charr	12	0.015	56	112	0.013	2.1 dw	WB −(L & GIT)	39 ± 8	0.22	3
BDE 47	Lake charr	12	0.015	56	112	0.015	11.4 dw	WB −(L & GIT)	346 ± 173	0.43	3
BDE 99	sole	19	0.008	84	149	0.008	85.7 ww	M + L	37 ± 7	0.13	1
BDE 99	Common carp	22	0.033	60	100	0.009	490 ww	WB − GIT	N/A	0.00	2
BDE 99	Lake charr	12	0.015	56	112	0.013	1.1 dw	WB −(L & GIT)	87 ± 11	0.31	3
BDE 99	Lake charr	12	0.015	56	112	0.015	10.8 dw	WB −(L & GIT)	346 ± 173	0.42	3
BDE 100	sole	19	0.008	84	149	0.008	93.1 ww	M + L	62 ± 24	0.14	3
BDE 100	Lake charr	12	0.015	56	112	0.013	1.1 dw	WB −(L & GIT)	63 ± 17	0.42	3
BDE 100	Lake charr	12	0.015	56	112	0.015	6 dw	WB −(L & GIT)	173 ± 173	0.53	3
BDE 183	Zebrafish	26	0.020	42	14	NR	86700 ww	WB	10	0.09	4
BDE 183	Zebrafish	26	0.020	42	14	NR	635.8 ww	WB	15	0.09	4

(continued)

PBDE Congener	Species	Temp. (°C)	Feeding rate[a] (g/g BW/d)	Exposure Duration (d)	Depuration (d)	Growth rate constant (/d)	Food concentration (ng/g)[b]	Tissue analyzed[c]	Half-life ± SE (d)	Assimilation efficiency	References[d]
BDE 183	Lake charr	12	0.015	56	112	0.013	2.1 dw	WB −(L & GIT)	69 ± 14	0.23	3
BDE 183	Lake charr	12	0.015	56	112	0.015	15.8 dw	WB −(L & GIT)	346 ± 173	0.33	3
BDE 209	Lake charr	12	0.015	56	112	0.015	27.5 dw	WB −(L & GIT)	26 ± 5	0.05	3
BDE 209	Rainbow trout	12	0.010	150	0	0.003	940 ww	WB	N/A	0.04	5
BDE 209	sole	19	0.008	84	149	0.008	184 ww	M + L	43 ± 8	0.01	1
BDE 209	Zebrafish	26	0.020	42	14	NR	69055 ww	WB	6.5	0.01	4
BDE 28	Common carp	22	0.033	60	100	0.009	96 ww	WB − GIT	36.5 ± 17	0.20	2
BDE 28	Lake charr	12	0.015	56	112	0.015	12.6 dw	WB −(L & GIT)	58 ± 10	0.53	3
BDE 28	Lake charr	12	0.015	56	112	0.013	1.3 dw	WB −(L & GIT)	NR	0.48	3
BDE 28	sole	19	0.008	84	149	0.008	84.4 ww	M + L	86 ± 27	0.16	1
BDE 28	Zebrafish	26	0.020	42	14	NR	313 ww	WB	23	0.97	4
BDE 28	Zebrafish	26	0.020	42	14	NR	28076 ww	WB	25	1.20	4

[a] Feeding rate = g-ww-food/g-ww-body weight (BW) fish/day

[b] dry wt (dw) or wet wt (ww)

[c] Tissue analyzed: *M* muscle, *L* liver, *GIT* gastrointestinal tract, *WB* = whole body

[d] References: 1—Munschy et al. (2011); 2—Stapleton et al. (2004); 3—Tomy et al. (2004); 4—Nyholm et al. (2009); 5—Stapleton et al. (2006)

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A General, Life History-Based Model for Sustainable Exploitation of Lake Charr Across Their Range

Nigel P. Lester, Brian J. Shuter, Michael L. Jones, and Steve Sandstrom

Abstract Guidance for sustainable exploitation of lake charr *Salvelinus namaycush* needs to account for an enormous diversity within an ecological context. In this chapter, we expand earlier work to develop a framework for managing lake charr fisheries across the zoogeographic range of the species. We describe how environmental attributes influence two key determinants of sustainable harvest: natural mortality rate and biomass at maximum sustained yield (MSY). Evidence is presented that mean air temperature, lake size, and lake morphometry determine lake productivity and habitat suitability for lake charr, which combine with adult body size to influence biomass density. Variation in adult body size is associated with natural mortality rates, along a climatic gradient. Our model predicts that, on average, MSY decreases with lake surface area and mean annual air temperature. MSY is also influenced by lake depth because of the need for a hypolimnetic cold-water refuge is greater in warmer climates. The model provides a basis for developing regional-scale management and assessment strategies. We demonstrate its application using three MSY-based reference points (i.e., biomass density, total mortality rate, angling effort), which can be calculated from readily available habitat data.

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Keywords Angling effort (E) · Angling effort at MSY (E_{msy}) · Biomass at carrying capacity (B_{max}) · Biomass at MSY (B_{msy}) · Body size · Catchability (q) · Exploitable biomass (B) · Exploitation status · Fishing mortality rate (F) · Fishing mortality at MSY (F_{msy}) · Habitat suitability · Maximum sustainable yield (MSY) · Natural mortality rate (M) · Population abundance · Population dynamics · Productivity · Reference points · Sustainable fishing · Temperature · Total mortality rate (Z) · Total mortality at MSY (Z_{msy})

1 Introduction

As noted elsewhere in this volume (Hansen et al. 2021), the lake charr *Salvelinus namaycush* (more commonly known as lake trout) is relatively long-lived and late maturing, particularly when compared to other economically important freshwater fishes in North America. When fish with this type of life history become the object of a fishery, especially one that can target immature fish, they are particularly vulnerable to overexploitation. As detailed below, lake charr are targeted by subsistence, recreational, and commercial fisheries across North America and overfishing has occurred, especially from the Laurentian Great Lakes, that (Lawrie and Rahrer 1972; Ryder and Johnson 1972). Because lake charr fisheries are found in hundreds of lakes throughout the species' range, spanning a wide range of lake sizes, fish assemblages, and environmental conditions, guidance for sustainable exploitation needs to account for the enormous diversity within the ecological context that these fisheries experience. In this chapter, we extend our earlier work (Shuter et al. 1998) by incorporating new theory and a broader empirical description of how lake charr demographics vary across the zoogeographic range of the species. The result is an extended modeling framework that provides management reference points for lake charr fisheries across most of the species range in North America.

As the largest charr and an "esteemed food fish" (Scott and Crossman 1973), lake charr are a popular target for many fisheries. Its native range (see Distribution map, Muir et al. 2021) includes all the mainland provinces of Canada and the northern fringe of the USA (including Alaska, Indiana, Illinois, Maine, Michigan, Minnesota, Montana, New Hampshire, New York, Pennsylvania, Vermont, and Wisconsin). Historically, the lake charr was recognized as the second most important freshwater food fish in Canada, next to the lake whitefish *Coregonus clupeaformis* (Martin and Olver 1980).

Lake charr has been a primary target of commercial fisheries in the Laurentian Great Lakes for more than 150 years, and coastal populations were likely an important component of subsistence fisheries for centuries before European colonization of the region (Bogue 2000). Intensifying commercial fishing and invasion of the upper Great Lakes by sea lamprey *Petromyzon marinus* in the 1930s decimated lake charr stocks, leading to extirpation in Lake Michigan, near extirpation in Lake Huron, and sharp reductions in abundance in Lake Superior (Hansen 1999). With the advent of sea lamprey control in the 1960s and restoration efforts in the USA and

Canada, wild lake charr populations recovered in Lake Superior by the late 1990s (Hansen 1999). More recently, substantial recruitment of wild lake charr has been observed in Lakes Huron and Michigan (Riley et al. 2007; Hanson et al. 2013). Commercial and subsistence fishing for lake charr also occurs on large lakes in Ontario, Saskatchewan, and the Northwest Territories. Long-term records of lake charr harvests, and other species, have been used historically to infer the environmental determinants of fish production (e.g., Ryder 1965; Matuszek 1978; Schlesinger and Regier 1983; Christie and Regier 1988) and provide a conceptual foundation for our work.

Recreational fishing for lake charr increased dramatically during the latter half of the twentieth century (Post et al. 2002; Gunn and Sein 2004; Olver et al. 2004). Increased pressure on lake charr, especially in Ontario and Quebec, has led to concerns that some stocks were suffering from overexploitation (Evans et al. 1991; Shuter et al. 1998). Whereas commercial fishing is restricted mainly to large lakes, recreational fishing occurs on lakes of all sizes, across the entire range of the species.

Our analysis of lake charr demographics, focused on the lean morphotypes (see Chavarie et al. 2021 for morph description), is framed around a simple conceptual model (Fig. 1) of how environmental attributes influence two key determinants of sustainable harvest rates: natural mortality rates and biomass at maximum sustained yield (MSY; see Table 1 for list of acronyms). Mean air temperature, lake size, and lake morphometry appear to determine lake productivity and habitat suitability for lake charr, which combine with adult body size to inform biomass density. Similarly, we show that variation in adult body size is associated with natural mortality rates along a gradient of climate described by the mean air temperature. This evidence is then integrated into a model that describes how sustainable harvest varies across a gradient of lake types spanning the full range of environmental conditions experienced by lake charr. This work extends our earlier analysis (Shuter et al. 1998) by (1) incorporating new developments in life history theory (Lester et al. 2004a; Shuter et al. 2005; Giacomini et al. 2013) and ecological theory (Gillooly et al. 2001; Andersen and Beyer 2006); and (2) using a larger dataset (>300 populations) that spans the entire climatic range of this species.

2 A Conceptual Model of Fishing

We begin with a well-known equilibrium model of fishing (Fig. 2). When a population is not fished, the total mortality rate (Z) equals the natural mortality rate (M) and exploitable biomass (B) equals carrying capacity ($B_{\max}$). Fishing creates an additional source of mortality (F) that increases total mortality ($Z = M + F$) and reduces equilibrium biomass. The rate of decline depends on compensatory mechanisms (e.g., increased growth or survival of young fish), which ultimately dictate how much fishing can be sustained. Fishing mortality rate that results in $B = 0$ (F_{ext}) sets a limit to sustainable harvest rates: F must be less than F_{ext} to be sustainable. Equilibrium yield is calculated as Yield $= F \times B$. Because B decreases with

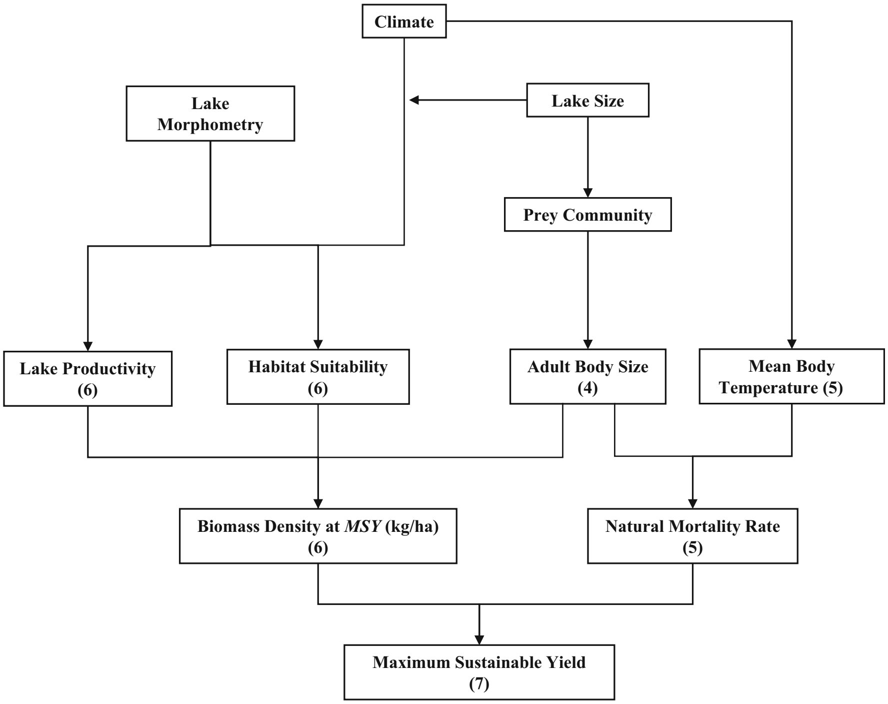

Fig. 1 An influence diagram relating lake characteristics to lake charr *Salvelinus namaycush* yield potential. Climate, lake size, and lake morphometry influence lake productivity and habitat suitability for lake charr, which combine with adult body size to influence the biomass density associated with maximum sustainable yield (MSY). Biomass density combined with the natural mortality rate determines the yield potential for a lake. The natural mortality rate depends on adult body size and mean body temperature, which is influenced by lake morphometry and climate. Adult body size depends on the prey community, which is influenced by lake size. The numbers in parentheses refer to the relevant section of this chapter

increasing F, maximum sustainable yield (MSY) occurs at an intermediate value of F, referred to as F_{msy}. For the example shown in Fig. 2, biomass decreases linearly with F and MSY occurs when $F = F_{\text{ext}}/2$. In this example, we also assume that MSY occurs when fishing mortality equals natural mortality (i.e., $F_{\text{msy}} = M$).

The hypothesis that $F_{\text{msy}} = M$ was originally proposed by Gulland (1971). It has been challenged and supported by theoretical arguments (see summary by Zhou et al. 2012), but rarely investigated using empirical data. However, a recent meta-analysis of 245 fish species worldwide found strong support for this rule (Zhou et al. 2012) and the best model for teleost species implied $F_{\text{msy}} = 0.87\ M$, which we generalize to $F_{\text{msy}} = {\sim}M$ for simplicity in developing our model.

The model depicted in Fig. 2 indicates that MSY occurs when biomass has been reduced to one-half of carrying capacity, and thus MSY $= 0.5\ B_{\max} \times M$. The constant “0.5” results because this model is based on the logistic Graham-Schaefer model (Graham 1935). Its value shifts slightly if we assume other forms of

Table 1 Abbreviations and symbols used in this chapter

Abbreviation	Description	Units
A	Lake surface area	ha
B	Biomass density of a population	kg/ha
$B_{\max}$	Biomass density when a population is unexploited	kg/ha
B_{msy}	Biomass density when a population is exploited at MSY	kg/ha
B'	Biomass of a population in relative units of weight	wt
B'/V	Volumetric biomass density in relative units of weight	wt/ha-m
B'/A	Areal biomass density in relative units of weight	wt/ha
D	Depth	m
$D_{\max}$	Maximum depth of the lake	m
D_{mn}	Mean depth of the lake	m
D_{th}	Thermocline depth	m
DR	Depth ratio (ratio of maximum to mean depth)	
E	Angling effort intensity	hr/ha-year
E_{msy}	Angling effort intensity that produces F_{msy}	hr/ha-year
F	Fishing mortality rate	/year
F_{ext}	Fishing mortality rate which results in $\mathrm{B} = 0$ (extinction)	/year
F_{msy}	Fishing mortality rate when the population is exploited at MSY	/year
g	Index of reproductive effort	/year
h	Juvenile growth rate	mm/year
K	Von Bertalanffy parameter—relative rate of growth toward L_{∞}	/year
L_{m}	Fork length at maturity	mm
L_{∞}	Asymptotic fork length (terminal body length)	mm
M	Natural mortality rate of a population	/year
MSY	Maximum sustained yield	kg/ha-year
$pA_{\mathrm{lake}}(D)$	Proportion of the lake area where depth $> = D$	
pV_{eb}	Proportion of the lake volume in the epibenthic zone	
pV_{hy}	Proportion of the lake volume in the hypolimnetic zone	
$pV_{\mathrm{lake}}(D)$	Proportion of the lake volume where depth $> = D$	
S	Habitat suitability index for lake trout	
T	Mean annual air temperature	°C
T_{body}	Mean annual body temperature	°C
V	Lake volume ($= D_{\mathrm{mn}} \times A$)	ha × m
W_{∞}	Asymptotic weight: $W_{\infty} = (L_{\infty}/451)^{3.2}$	kg
ω	Von Bertanffy parameter—initial rate of growth (i.e., slope at origin $= K \times L_{\infty}$)	mm/year
Z	Total mortality rate ($Z = F + M$); annual mortality (%) $= 100 \times (1\text{-}e^{-Z})$	/year

Fig. 2 A conceptual model of sustainable fishing, based on an equilibrium model of surplus production model (Graham 1935). The graph demonstrates how exploitable biomass (B, solid line) decreases as the fishing mortality rate (F) increases. Yield (dashed line) increases and then decreases with F, reaching its maximum value when $F = M$ (natural mortality). See the text for more details

density-dependence. Given the constraint that $F_{\mathrm{msy}} = M$, the equilibrium yield model developed by Shuter et al. (1998) implies $B_{\mathrm{msy}}/B_{\mathrm{max}}$ ranges from 0.31 to 0.44 depending on the form of density-dependence. Thus, the logistic surplus production model yields slightly higher estimates of B_{msy} (i.e., $0.5 \times B_{\mathrm{max}}$) relative to predictions from our 1998 model. A more general model proposes that $\mathrm{MSY} = f \times B_{\mathrm{max}} \times M$, where the value of f is expected to lie between 0.31 and 0.50, depending on the form of density-dependence.

If estimates of biomass are available, this model can be used to estimate the annual harvest expected when fishing at F_{msy}. This information is especially important because it helps to set realistic expectations when planning a fishery. It sets a ceiling for how much harvest should be allowed, providing a basis for allocating harvest among fishers, and adjusting this allocation as the number of users changes. In commercial fisheries, harvest quotas are often used to manage the total harvest. In recreational fisheries, management of total harvest is typically achieved through regulations that limit the number of fish harvested per angler per day.

One important detail not explicit in our model is that size of fish harvested may vary. If harvesting begins when fish are small relative to their size at maturity, then

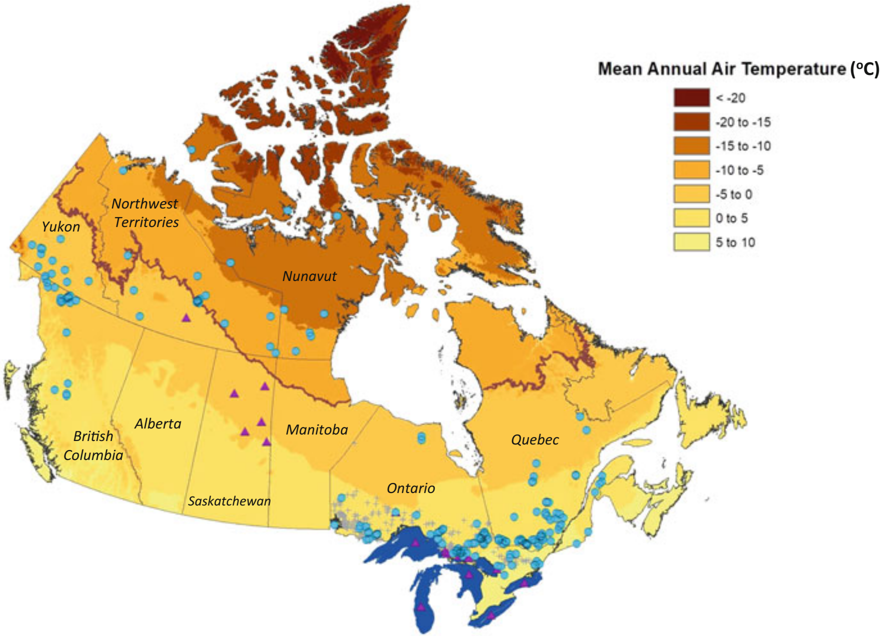

Fig. 3 Map of mean annual air temperature in Canada (1981–2010 norms), showing locations of the lake charr *Salvelinus namaycush* lakes referred to in this chapter. Lake symbols identify the three primary data sources: Canada-wide life history (blue circles), Ontario Broad-scale Monitoring (plus sign), and long-term sustained yield lakes (triangles). A thick line highlights the −5 °C isocline

the sustainable level of fishing will be lower. Conversely, if the size at harvest is larger than the size at maturity, then F_{msy} could be very large. Size at harvest (relative to size at maturity) may account for some variation in estimates of F_{msy}/M, but these data were not available in Zhou et al. (2012). In general, one expects harvesting will begin shortly before fish become mature because the biomass of the stock increases rapidly as fish approach size at maturity and then declines. For lake charr fisheries, we showed (Shuter et al. 1998; Fig. 3) that length at harvest (i.e., mean length where vulnerability to fishing is 50% of maximum) is approximately 82% of length at maturity. We will use this criterion to define the exploitable biomass of lake charr and assume that $F_{\mathrm{msy}} = M$.

Our model shows how information about biomass and mortality rate can be used to predict a sustainable harvest for an exploited population. However, this information is rarely available for the many lake charr fisheries on small lakes, with economic values too low to justify an expensive stock assessment approach to estimating M and B_{msy}. Here we propose an alternative approach that predicts M and B_{msy} from environmental variables. Predicted values serve as a means of estimating sustainable harvest, and, more importantly, as joint reference points on a landscape scale to identify regions where populations are showing signs of overexploitation.

3 Sources of Data

Three main sources of data were used to develop our lake charr fishing model: (1) Canada-wide life history data, (2) Ontario fish biomass data, and (3) harvest monitoring from commercial and recreational fisheries. These datasets include 456 Canadian lakes where lake charr have been sampled. Lake locations are included on a map showing variation in mean annual air temperature (Fig. 3). Each dataset is briefly described below.

The Canada-wide life history dataset is based on data provided by government agencies in Nunavut, Northwest Territories, Yukon, British Columbia, Ontario, and Quebec, which span the climatic range of lake charr in Canada. The mean annual air temperature of the lakes ($n = 153$) ranged from -16 to 8 °C, based on IPCC climate norms during 1961–1990, the period most relevant to sampling dates in the life history dataset. Most populations were surveyed using multi-mesh gill-netting methods designed to capture a wide size range of fish. An initial analysis of these data included estimates of immature growth rate, length and age at maturity, and maximum length (McDermid et al. 2010). We expanded the analysis to include estimates of von Bertalanffy growth parameters and total mortality rate.

Lake charr biomass estimates (relative units) were obtained from the Ontario Broad-scale Monitoring Program for Inland Lakes (BsM), conducted by the Ontario Ministry of Natural Resources and Forestry. This program monitors fish communities, water chemistry, and angling pressure on a stratified random sample of Ontario lakes (Sandstrom et al. 2013). We used data from 650 lakes sampled between 2008 and 2012 to develop a model for predicting a relative measure of lake charr biomass density. Four hundred and seventy two (73%) of these lakes were thermally stratified and lake charr were present in 277 (60%) of the stratified lakes (Table 2). The surface area of stratified lakes ranged from 50 to 34,518 ha and mean annual air temperature ranged from -1.9 to 7.5 °C, based on climate norms during 1981–2010 (see Cross et al. 2012). Maximum depth, lake volume, and mean depth were obtained from bathymetric maps of each lake. The dataset gave a comprehensive view of lake charr lakes in Ontario smaller than 35,000 ha, but did not include the Great Lakes and several other large inland lakes (e.g., Lake Nipigon, Lake Simcoe, Lake of the Woods, Big Trout Lake).

In the BsM program, fish communities were assessed during the period of thermal stratification using depth-stratified overnight sets of small and large mesh gillnets (details in Sandstrom et al. 2013). The large mesh method (referred to as NA gillnetting) is a standard protocol proposed by the American Fisheries Society for sampling lakes in North America (Bonar et al. 2009). The gear is effective for capturing fish larger than 250 mm, although retention selectivity increases with body size (Walker et al. 2013; Schoup and Ryswyk 2016; Smith et al. 2017). We

Table 2 Summary of environmental and biomass data for the BsM lakes in Ontario. Relative biomass density refers to fish larger than 250 mm fork length

Subset	Variable	Mean	Median	Minimum	Maximum
Stratified lakes ($N = 472$)	Lake area (ha)	1646	679	50	34,518
	Maximum depth (m)	37	31	11	186
	Mean depth (m)	10.9	8.7	1.9	40.1
	DR (depth ratio)	3.6	3.4	1.5	14.6
	Total phosphorus (ug/L)	8.4	7.2	1.7	51.6
	Mean annual air temperature (°C)	3.4	3.0	−1.9	7.5
	Thermocline depth (m)	10.0	9.7	5.3	19.5
	Relative epibenthic volume	0.32	0.29	0.03	0.85
	Relative hypolimnetic volume	0.29	0.27	0.02	0.70
	Relative biomass density—All species (wt/ha)	23.0	19.4	0.6	102.7
	Relative biomass density—Lake charr (wt/ha)	1.8	0.5	0.0	24.6
Lake charr lakes ($N = 277$)	Lake area (ha)	2001	879	50	34,518
	Maximum depth (m)	47	41	13	186
	Mean depth (m)	13.9	12.1	3.1	40.1
	DR (depth ratio)	3.5	3.3	1.5	8.1
	Total phosphorus (ug/L)	6.4	6.1	1.7	16.3
	Mean annual air temperature (°C)	3.3	3.0	−1.3	7.5
	Thermocline depth (m)	10.8	10.8	6.1	19.5
	Relative epibenthic volume	0.23	0.19	0.03	0.65
	Relative hypolimnetic volume	0.37	0.37	0.07	0.70
	Relative biomass density—All species (wt/ha)	20.4	18.0	0.6	74.6
	Relative biomass density—Lake charr (wt/ha)	3.1	12.3	0.1	24.6

used the CPUE data from large mesh nets (stretch mesh size = 38 to 127 mm, net length = 24.8 m) to estimate the relative biomass density of lake charr and the entire fish community. Because sampling was depth-stratified, we calculated a whole lake index of CPUE as the area-weighted mean of CPUE in each depth stratum. We assumed that area-weighted CPUE (# fish/net) would be an index of fish density (# fish/ha): CPUE $= q \times$ Density, where q is the catchability coefficient. Based on mark-recapture studies in 13 lakes, the average q for lake charr was 0.30 but variation among lakes indicated it increased proportionally to the mean weight of fish. These results implied CPUE $= 0.18 \times \overline{w} \times$ Density, where $\overline{w}$ is mean weight (kg) of fish and biomass density (i.e., $\overline{w} \times$ Density) was estimated as CPUE/0.18. We used this formula to estimate relative biomass density of lake charr and other species. Given the uncertainty in this estimate of catchability, we report our results (B'/A) in relative biomass units (wt/ha). From relative biomass density (B'/A), we calculated total biomass (wt) as $B' = B'/A \times A$, where A is lake area. Volumetric density (wt/ha-m) was calculated as B'/V, where lake volume (V) was measured as lake area times mean depth (units = ha-m). Fish biomass was analyzed using volumetric density measures, but final results are expressed in units of relative biomass density (i.e., wt/ha).

The third data source included estimates of lake charr harvest from commercial and recreational fisheries. These data included estimates of MSY for 17 fisheries, based on long-term monitoring of harvests (see Marshall 1996), and point-in-time estimates of recreational yield from 36 non-stocked Ontario lakes (Evans et al. 1991). Lakes in the MSY dataset range from 54 to 8,241,400 ha in surface area and from −5.2 to +9.4 °C in mean air temperature. This dataset was used to test MSY predictions based on environmentally based estimates of M and B_{msy}. Lakes in the point-in-time yield dataset ranged from 105 to 6622 ha in surface area and 1.8–4.8 °C in mean air temperature. These results were used to test whether predicted MSY accounted for variation in observed yield of lake charr.

4 Adult Body Size

The potential yield of a fish population is heavily influenced by adult body size because it affects both exploitable biomass and natural mortality rate, two determinants of MSY (Fig. 1). Knowledge of potential yield is especially important for managing lake charr fisheries because size at maturity, which correlates with maximum size, is highly variable in this species. Size-spectrum theory provides an empirically well-founded account of the size structure of aquatic communities and life histories of top predators that live in these communities (Andersen and Beyer 2006; Andersen et al. 2009; Chu et al. 2016; Giacomini et al. 2016; Shuter et al. 2016; Mehner et al. 2016). Bioenergetic constraints on the overall size structure of the community force a systematic decline in abundance of member populations, as trophic level increases, with the force of the constraint increasing with adult body size. Consequently, adult biomass density is expected to vary inversely with maximum size (Andersen and Beyer 2006). Given that length of the smallest harvested fish is a fixed proportion of length at maturity (i.e., 0.82), exploitable biomass decreases with maximum size, thereby reducing potential yield. Body size also negatively affects potential yield via natural mortality rate M that is expected to decrease with body size (Andersen et al. 2009), a prediction for which there is strong empirical support (Peterson and Wroblewski 1984; McGurk 1986; Lorenzen 1996).

Adult body size of lake charr is highly variable and tends to increase with lake size (Shuter et al. 1998). This trend is probably due to changes in species richness and community complexity associated with lake size. The smallest reported size at maturity of lake charr is for a tiny (8 ha) sub-alpine lake (Sassenach Lake, Alberta) where females matured at ~220 mm and reached a maximum size of 333 mm (Donald and Alger 1986). Here, lake charr fed on zooplankton and benthos

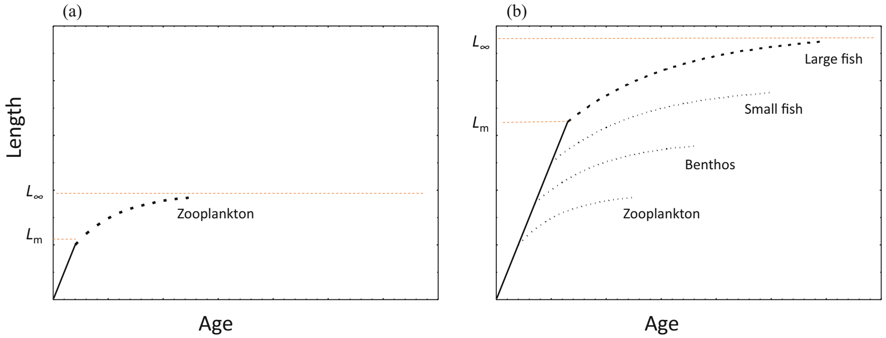

Fig. 4 Conceptual model of lake charr *Salvelinus namaycush* growth illustrating how adult body size is limited by prey size based on the biphasic growth model (Lester et al. 2004a; Quince et al. 2008). The solid line shows juvenile growth; the thick dashed line is adult growth. Length at maturity (L_m) and asymptotic length (L_∞) are indicated by thin dashed lines. (**a**) Only small prey (i.e., zooplankton) are available; the initial growth rate cannot be sustained as fish get larger, so the optimum size at maturity is small. (**b**) All prey sizes are available; ontogenetic shifting of prey size maintains growth efficiency so that the initial growth rate can be sustained at larger sizes, thus, optimum size at maturity is larger and lake charr attain a larger adult body size than when only small prey are available. Thin dotted lines show expected growth for cases where the maximum prey size is small (Zooplankton, Benthos, Small fish). The maximum age increases with body size because the natural mortality rate is inversely related to body size

throughout their lifetime, because larger items such as amphipods, mysids, and other fish species were not available. The maximum body mass attained in this lake (0.45 kg) is about 100 times smaller than the world record for lake charr (46.3 kg). This population was labeled as "stunted," but may represent one end of a wide and continuous range of adult lake charr body size generated by local adaptation to lake-specific differences in diversity of available prey.

The body size of lake charr depends on the breadth of the prey size spectrum (Fig. 4). Species-poor and species-rich environments offer very different opportunities for growth of lake charr because ontogenetic shifting of prey size is needed to sustain a fast growth rate (Martin 1952; Martin 1966; Kerr 1971a, b; Kerr and Ryder 1977; Sherwood et al. 2002; Pazzia et al. 2002; Cruz-Font et al. 2019). Typically, the diet of lake charr progresses through zooplankton, benthos, small fish, and large fish as lake charr grow. Growth is limited if this progression to larger prey sizes is blocked, so fish mature at a smaller size and attain a smaller maximum size (Fig. 4). This prey size effect is observed when comparing mean length at age among lakes with different prey communities, but can also be seen within lakes when individual differences in diet are compared (e.g., Houde and Scrosati 2003). In some lakes, the lake charr population may contain some cannibalistic fish, which attain a much larger size than the other individuals in the population (Martin 1970).

Variation in the lifetime growth pattern of lake charr is well-described using the biphasic growth model (Lester et al. 2004a; Shuter et al. 2005; Quince et al. 2008). This model predicts that prior to maturation, growth in length is approximately linear, and after maturation growth becomes asymptotic. Asymptotic length (L_∞)

is directly proportional to the juvenile growth rate (h) and inversely proportional to reproductive investment (g): $L_\infty = 3\ h/g$. The model also predicts that as mortality rate increases, optimal length at maturity (L_m) decreases, and optimal reproductive investment increases (Lester et al. 2014). For long-lived species like lake charr, $g \approx M$ and $L_m \approx 2\ h/M$. Jointly, these relationships imply $L_m/L_\infty \approx 2/3$, a property that is widely observed in lake charr populations.

In a recent summary of lake charr life history traits (Hansen et al. 2021), average size at maturity (L_m) was 420 mm and ranged from 212 to 660 mm across 202 lakes, and average maximum length (i.e., largest fish in the lake) was 851 mm and ranged from 422 to 1200 mm across 271 lakes. The same study reported that asymptotic length (L_∞) averaged 717 mm and was correlated with length at maturity. On average, L_m/L_∞ equaled 0.603, close to the value of 0.67 predicted above by life history theory (see also Jensen 1996).

Analysis of life history data in our Canada-wide dataset also supports this finding. The analysis by Hansen et al. (2021) was based on estimates of L_∞ obtained from fitting Von Bertalanffy growth curves. One problem with this curve-fitting method is that, because fishing mortality typically removes the larger (and older) fish, L_∞ can exceed the largest fish in the sample and severely overestimate the expected average size at terminal age (Goodyear 2019). This issue arises especially when the sample size is small, as it was for many of the populations in our dataset. Instead, we estimated maximum body size for each population in our data set as the mean fork length of the largest 10% in our sample, after removing fish smaller than 300 mm. These indirect estimates of L_∞ agreed very well with estimates based on growth curve fits for those populations where curve-fitting gave sensible results (e.g., $L_\infty <$ the maximum observed length). Analyses based on this indirect method showed that the relationship with length at maturity agreed precisely with the prediction that $L_m/L_\infty = 2/3$ (Fig. 5a).

Our estimates of L_∞ also indicate the positive effect of lake size, initially described by Shuter et al. (1998) for Ontario lakes, is evident across a much broader landscape. The Canada-wide dataset showed that adult body size was independent of climate and increased asymptotically with lake surface area (A) (Fig. 5b):

$$L_\infty = 957 \times \left(1 - e^{-0.14\times(1+\log_e A)}\right). \tag{1}$$

This relationship, based on 129 lakes, accounted for 58% of the variation in L_∞. These length measurements of adult body size can be converted into body mass using the following weight-length (kg-mm) relationship:

$$W = (L/451)^{3.2} \tag{2}$$

Our analysis of weight-length data across the Canadian landscape revealed that this pooled relationship was independent of climate. The formula is almost identical to the mean weight-length parameters reported by Hansen et al. (2021).

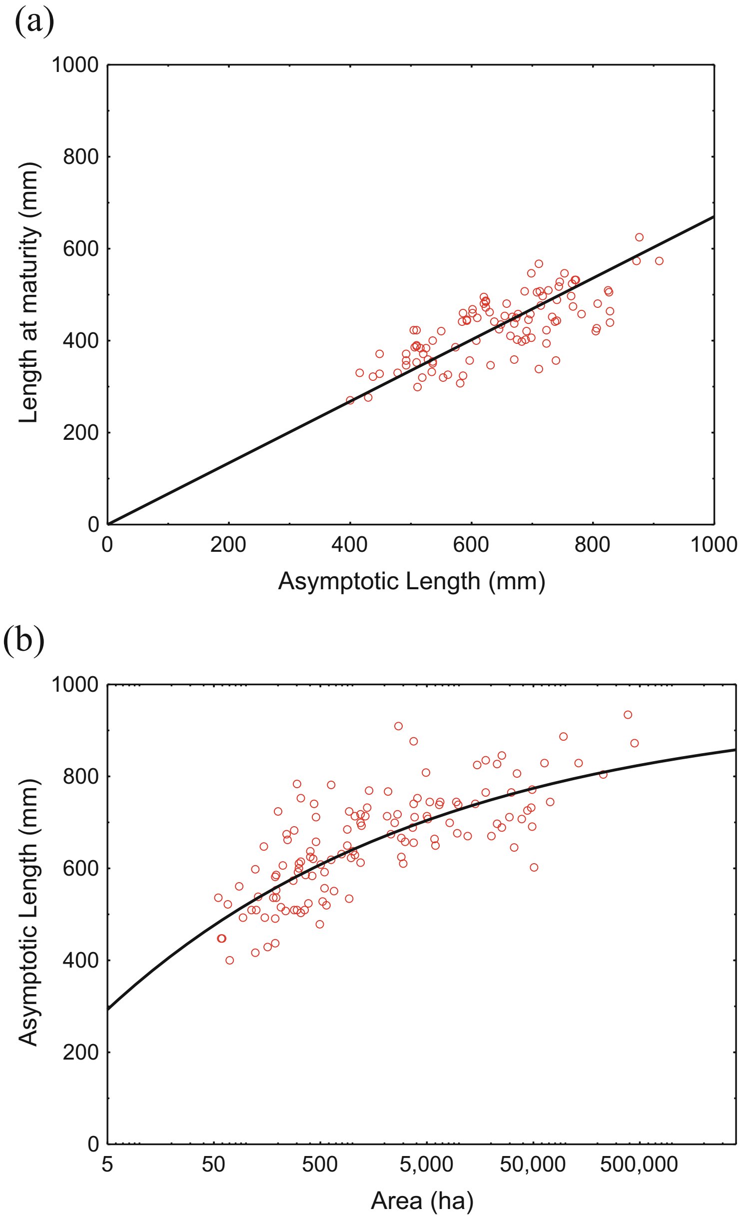

Fig. 5 Adult body size of lake charr *Salvelinus namaycush* populations across Canada. (**a**) Length at maturity (L_m) is approximately 2/3 of asymptotic length (L_∞). (**b**) Asymptotic length increases with lake area: $L_\infty = 957 \times \left(1 - e^{-0.14\times(1+\log_e A)}\right)$. $n = 129$ lakes, $r^2 = 0.58$, SE of the asymptote $(957) = 52.3$

5 Natural Mortality Rate

Many empirical methods have been proposed for estimating M from life history traits (see review by Kenchington 2013). Most methods rely on information about the lifetime growth of a fish and use parameters such as growth rate, size at maturity, maximum body size, and maximum age. Shuter et al. (1998) found that natural mortality of lake charr in Ontario lakes could be predicted using the Pauly (1980) method, which is based on the von Bertalanffy growth parameters (K, L_∞) and mean annual body temperature (T_{body}). Within Ontario, predicted values of M ranged from 0.13 to 0.36 and were associated mainly with variation in body size.

Reliance on growth parameters is problematic when working with exploited populations because parameters change due to density-dependent processes (Post et al. 1999; Lorenzen and Enberg 2002; Lorenzen 2008; Lester et al. 2014). An alternative approach based on metabolic theory avoids this issue (McCoy and Gillooly 2008) by predicting M based solely on body size and body temperature. We adapted this method to estimate M for lake charr populations and found it to be a useful alternative to the Pauly (1980) method (see Appendix 1).

The metabolic approach assumes that the mortality rate depends on body size and temperature like the individual metabolic rate (Gillooly et al. 2001; McCoy and Gillooly 2008). The theory implies

$$M = \frac{a f\left(T_{\mathrm{body}}\right)}{W_\infty^b} \tag{3}$$

where a, b are parameters, $f(T_{\mathrm{body}})$ is a function of mean annual body temperature, and W_∞ serves as an index of adult body size. Parameter b is the complement of the production exponent (i.e., $b = 1 - \beta$) in the relationship between somatic growth and body weight (i.e., $\frac{dW}{dt} \propto W^\beta$). Because Quince et al. (2008) have shown that growth in lake charr supports a value of $\beta = 0.70$, we set $b = 0.30$. We re-analyzed fish mortality data reported in McCoy and Gillooly (2008) to solve for other model parameters (see Appendix 1). Equation 3 was then applied to estimate M for 122 lakes where estimates of W_∞ were available. A temperature model (Shuter et al. 1983) predicted water temperature (and hence body temperature) from mean air temperature (T). In calculating the body temperature of lake charr, we assumed a desired body temperature of 10 °C and that lake charr would thermoregulate by moving to the hypolimnion when the surface temperature exceeded this criterion (details in Appendix 1).

Our results implied the following equation for estimating M:

$$M = \frac{0.26\, e^{0.021 \times T + 0.0004 \times T^2}}{W_\infty^{0.30}} \tag{4}$$

where T is mean annual air temperature. This equation becomes:

$$M = \frac{91.8\ e^{0.021 \times T + 0.0004 \times T^2}}{L_\infty^{0.96}} \tag{5}$$

when body weight is converted to length using (Eq. 2).

We estimated M across a broad latitudinal gradient, where mean annual air temperature ranged from −16 to +7 °C (Fig. 6). Our water temperature model implied that surface temperatures during summer rose above 10 °C when mean annual air temperature exceeded −10 °C (Fig. 6a). This threshold indicates that water temperature in many Nunavut lakes may never exceed the preferred temperature of lake charr, but that further south, thermal stratification would be needed to allow fish to thermoregulate to 10 °C. Annual mean body temperature ranged from approximately 2 to 7 °C when we used 10 °C as the desired temperature (Fig. 6a). Our results show M ranged from 0.11 to 0.31 (Fig. 6b). For a given body size, M increased 1.5 times from north to south. For a given climate, M varied 2.2 times due to body size, which ranged from 400 to 900 mm (0.7 to 10 kg).

Estimates of M based on the metabolic method are similar to estimates obtained using the Pauly method (see Appendix 1). Across 122 populations of lake charr, estimates were strongly correlated ($r = 0.72$) and mean values from each method were almost identical (M-metabolic = 0.19, M-Pauly = 0.18). One difference was that the Pauly method produced lower estimates for northern populations. We assessed the validity of each method by comparing the maximum age ($T_{\max}$) in each population to estimated M, given the expectation that $T_{\max} = \frac{5.67}{M^{1.09}}$ (Then et al. 2015). Our results showed that metabolic estimates followed this expectation very well and much better than estimates based on the Pauly method (details in Appendix 1).

6 Biomass at MSY

We hypothesized that lake charr abundance, in the absence of fishing, is primarily determined by the suitability of water temperature, and availability of food and oxygen. In the far north, where surface temperatures never exceed the optimal temperature for lake charr, all lakes provide suitable summer habitat. However, in the south, the surface temperature often exceeds the lethal temperature for lake charr (>24 °C—Hasnain et al. 2013) and lake charr are found only in lakes where summer thermal stratification creates a cold-water, oxygenated refuge in the hypolimnion. In some small shallow lakes, groundwater provides cold-water habitat refugia (Snucins and Gunn 1995).

Thermal constraints have two important implications affecting biomass of lake charr in southern lakes. First, lake charr have restricted access to shallow, warm parts of lakes where food is more plentiful. In spring and fall, lake charr exploit nearshore areas for feeding (e.g., King et al. 1999), but the primary residence of lake charr in summer is the hypolimnion (Cruz-Font et al. 2019). Although lake charr are known

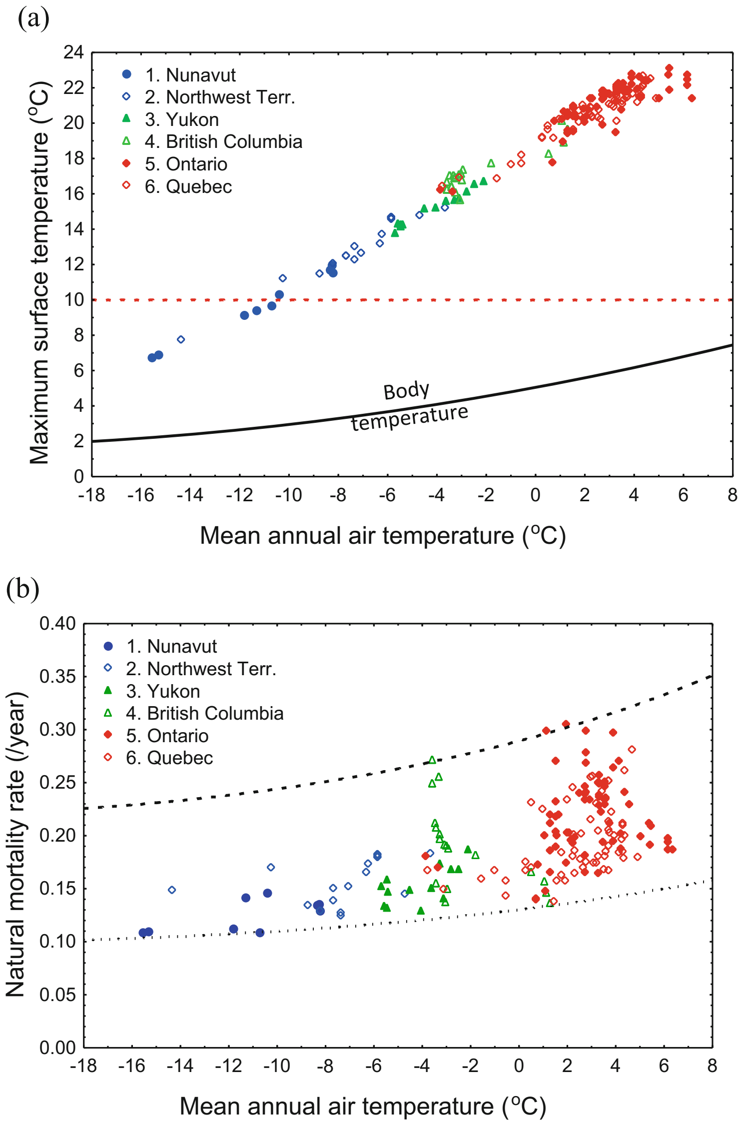

Fig. 6 Estimating natural mortality (M) of lake charr *Salvelinus namaycush*. (**a**) Estimates of maximum surface temperature and mean body temperature of lake charr in lakes from different regions of Canada (assuming lake charr use the hypolimnion to thermoregulate at 10 °C when the surface temperature exceeds this value). (**b**) Estimated M for populations shown in (**a**), based on the metabolic method. Curved lines show expected M for a large-bodied population (lower line: $W_\infty = 10$ kg, $L_\infty = 926$ mm) and small-bodied population (upper line: $W_\infty = 0.7$ kg, $L_\infty = 403$), where W_∞ is the asymptotic weight

to make feeding excursions into warm water (Martin 1970; Sellers et al. 1998; Morbey et al. 2006; Cruz-Font et al. 2019), the duration of such visits must be relatively short to avoid higher metabolic costs of living in warm water. In lakes where cold-water forage fish are lacking, nearshore benthic resources account for 83% of lake charr diets (Vander Zanden and Rasmussen 1996). While lake charr may make extensive use of nearshore resources, the increased metabolic cost of traveling to, and living in, warm water should reduce foraging efficiency, thereby making them less competitive with species adapted to warmer water and limiting their abundance (Cruz-Font et al. 2019).

The second implication of this thermal constraint is that dissolved oxygen in the hypolimnion may limit lake charr abundance (MacLean et al. 1990; Dillon et al. 2003; Evans 2007). Oxygen concentration in the hypolimnion depends on the initial supply at spring overturn, the rate of oxygen depletion during summer, and time between mixing events (Charlton 1980; Cornett and Rigler 1980; Ryan and Marshall 1994). Demand by lake charr depends on the amount of time spent in the hypolimnion (i.e., residence time) that is imposed by unfavorable temperatures in the epilimnion. As air temperature increases farther south, the period of stratification increases, hypolimnetic residence time increases, and, consequently, the required hypolimnetic volume increases.

Various habitat models based on thermal and oxygen requirements have been developed for lake charr, but none offer a means of predicting lake charr biomass across its entire geographic range. Some models focused on thermal requirements as a means of explaining variation in productivity related to climate and morphometry (e.g., Christie and Regier 1988). Others focused on oxygen requirements, typically raising concerns about loss of suitable habitat due to increased phosphorus loading and climate change (Ryan and Marshall 1994; Dillon et al. 2003; Jacobson et al. 2008, 2010). Here, we develop a model that bridges this gap and acknowledges the potential effect of trophic levels (Andersen and Beyer 2006).

Our model proposes that lake charr biomass depends on the lake productivity, habitat suitability for lake charr, and adult lake charr body size. We test each component of the model using biomass estimates for Ontario lakes. Lake productivity is expected to increase with the relative volume of epibenthic habitat. This habitat zone is the nearshore portion of the epilimnion where water depth is shallower than the thermocline. Being shallow and warm, it is a primary source of food. We begin by using the biomass density of all fish species to characterize how lake productivity is affected by the amount of epibenthic habitat. Next, we use the presence/absence of lake charr in Ontario lakes to develop a habitat suitability index based on mean air temperature, a correlate of epibenthic temperature, and hypolimnetic volume. These two model components (productivity and suitability) are described in the following sub-section. We then address the question of how biomass predicted by these components is affected by the body size of lake charr. In doing this, we test the prediction that lake charr biomass density varies inversely with adult body size (Andersen and Beyer 2006).

6.1 Lake Productivity and Habitat Suitability

We calculated hypolimnetic and epibenthic volumes (see Appendix 2) for 472 thermally stratified lakes in Ontario where fish biomass had been estimated from index fishing surveys. Relative habitat volumes (habitat volume/lake volume) were then compared across lakes. As expected, these indices have a predictable relationship with mean depth (Fig. 7), wherein an increase in mean depth is accompanied by an increase in relative hypolimnetic volume and a decrease in relative epibenthic volume. Among-lake variability is due partly to variation in lake shape (maximum depth divided by mean depth), but also to variation in mean air temperature, which is inversely related to thermocline depth (Shuter et al. 1983). One relationship not affected by climate is the inverse relationship between relative hypolimnetic and epibenthic volume (see Appendix 2):

$$pV_{\mathrm{hy}} = -0.216 \times \log_e(pV_{\mathrm{eb}}) \tag{6a}$$

or, inversely,

$$pV_{\mathrm{eb}} = e^{-4.63\, pV_{\mathrm{hy}}} \tag{6b}$$

This relationship is very useful because both habitat measures are used to predict lake charr biomass and this formula allows model results to be shown using either measure. Below, we use relative epibenthic volume (Fig. 8).

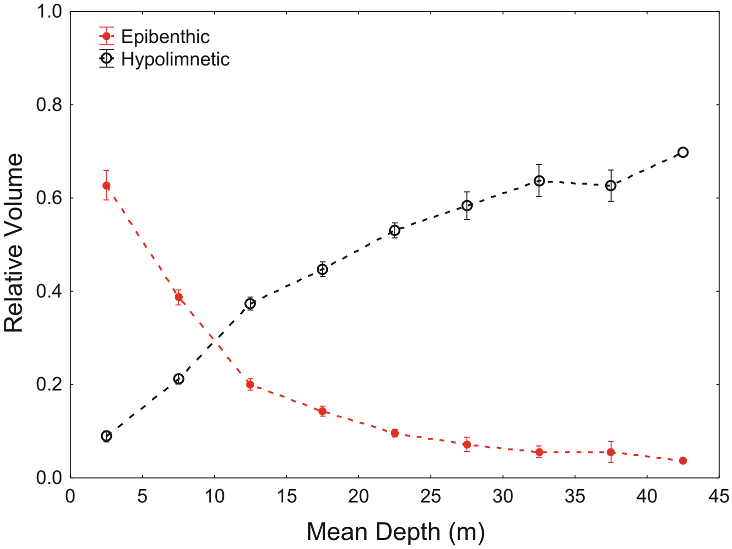

Fig. 7 Relative habitat volumes (hypolimnetic and epibenthic) in Ontario lakes. Means (and 95% confidence limits) are shown for 5 m interval of mean depth, based on 472 thermally stratified lakes

Biomass estimates of the fish community support the hypothesis that lake productivity increases with relative epibenthic volume. In thermally stratified lakes, large fish community biomass (i.e., all species, fork length $>$ 250 mm) increased in proportion to epibenthic volume (Fig. 8a). Variation in pV_{eb} accounted for 63% of the observed variation in log-transformed volumetric relative biomass density (B'/V), with a regression coefficient of 1.0 that implies B'/V is proportional to pV_{eb} (Fig. 8a). Mean air temperature, total phosphorus, species richness, mean body size, and lake area accounted for an additional 9% of the variability. Given the relatively small effect of other factors, our biomass model uses pV_{eb} as an index of lake productivity (Fig. 8b).

The presence of lake charr in these lakes supports our assumption that habitat suitability depends on epibenthic temperature and availability of hypolimnetic water. The probability of lake charr being present was highest in very deep lakes (where hypolimnetic volume is large and epibenthic volume is small (Fig. 8c)), but the relationship was affected by temperature. Logistic regression indicated that lake charr presence increased with relative hypolimnetic volume and decreased with mean annual air temperature, thereby implying the following relationship to describe habitat suitability:

$$S = \frac{1}{1 + e^{2.47+0.386\ T-16.8\ pV_{\mathrm{hy}}}} \tag{7}$$

Given (Eq. 6a), this formula can be restated in terms of epibenthic volume as:

$$S = \frac{1}{1 + e^{2.47+0.386\ T+3.62\ \log_e (pV_{\mathrm{eb}})}} \tag{8}$$

Habitat suitability scores, based on this equation, for each lake are related to relative epibenthic volume (Fig. 8d).

The combined effect of lake productivity and habitat suitability implies that biomass of lake charr, B'/V, initially rises with relative epibenthic volume, but then declines progressively towards zero (Fig. 8e). This pattern is consistent with a model (Fig. 8f) that assumes biomass is the product of lake productivity (defined by the relative epibenthic volume, Fig. 8b) and habitat suitability (Fig. 8d). The scatter of points in Fig. 8f illustrates the variation in optimum epibenthic volume associated with differences in temperature in Ontario. Within Ontario, the peak ranges from $pV_{\mathrm{eb}} \approx 0.2$ to 0.4. However, in a colder region (e.g., −5 °C), the predicted optimum pV_{eb} is much larger. Figure 8f also illustrates that the maximum lake charr biomass (i.e., when pV_{eb} is optimal) also increases as mean annual air temperature decreases.

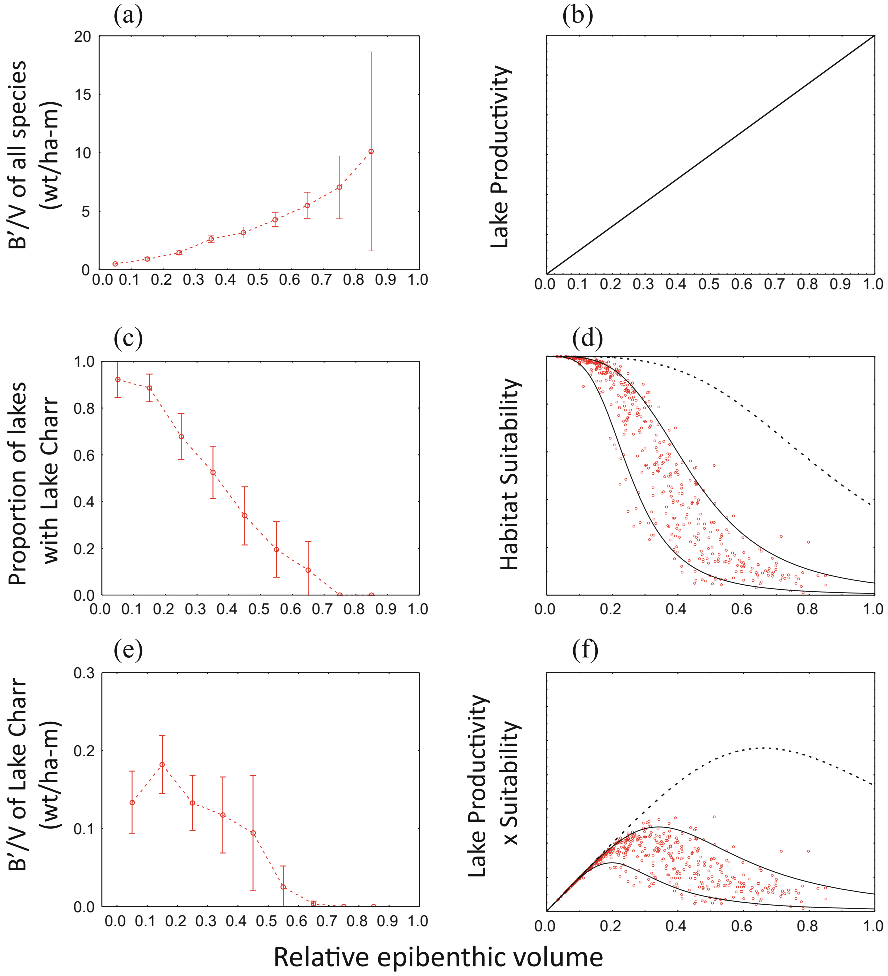

Fig. 8 Predicting lake charr *Salvelinus namaycush* biomass from lake productivity and habitat suitability. Results shown in panels **a**, **c**, and **e** are based on 473 thermally stratified lakes. (**a**) Mean (and 95% confidence limits) of community biomass density (B'/V) for 0.1 classes of pV_{eb}. The linear relationship implies pV_{eb} serves as an index of lake productivity, as shown in panel **b**. (**c**) The probability of lake charr being present in a lake decreases with pV_{eb}, but this relationship depends on mean air temperature. (**d**) Points are habitat suitability scores for lakes, based on (Eq. 8); solid lines are predicted scores for mean annual air temperature = 1.2 (upper line) and 6.4 °C (lower line), bounding 90% of the Ontario lakes; dashed line is the expected habitat suitability in a much colder region ($T = -5$ °C). (**e**) Mean (and 95% confidence limits) of lake charr biomass density (B'/V) increases and then decreases with pV_{eb}. (**f**) Product of lake productivity × habitat suitability increases and then decreases with pV_{eb}; points are individual lakes; the lines show results for fixed temperatures as in panel **d** (dashed line −5 °C, upper solid line = 1.2 °C, lower solid line = 6.4 °C. See the text for more details

6.2 The Effect of Body Size

Theory predicts that lake charr biomass varies inversely with maximum body size (Andersen and Beyer 2006). We tested this hypothesis by measuring the effect of body size (W_∞), after correcting for lake productivity (P) and habitat suitability (S).

For well-sampled lakes (i.e., number of sampled lake charr >50), we estimated asymptotic length (L_∞) and then converted this measure to asymptotic weight (W_∞) using the weight-length relationship (Eq. 2). We then calculated the initial size at harvest (L_c) for each lake and used the CPUE of fish larger than L_c to estimate the exploitable biomass of lake charr. Given $L_c = 0.82 \times L_m$ (from Shuter et al. 1998) and $L_m = 0.67 \times L_\infty$ (Fig. 5a), $L_\mathrm{c} = 0.55 \times L_\infty$. For 80 lakes assessed in this manner, exploitable biomass volume density (B'/V) ranged 0.06–1.5 wt/ha-m and W_∞ ranged 0.9–6.2 kg.

The model proposes that lake charr biomass scales with body mass (W_∞):

$$B'/V = c \times P \times S \times W_\infty{}^{d} \tag{9}$$

where P is a volumetric index of lake productivity ($= pV_\mathrm{eb}$), S is habitat suitability (Eq. 8), and c and d are estimated parameters. Logarithmic transformation yields the following linear model:

$$\log_e\,(B'/[V \times P \times S]) = \log_e(c) + d \times \log_e(W_\infty) \tag{10}$$

We estimated parameters of this model using data from lakes in the more remote northwest region of Ontario, where mean angling pressure was low (2.9 h/ha-year) relative to the northeast (8.4 h/ha-year) and southern (12.4 h/ha-year) regions. Regression analysis of 45 lakes in the northwest implied:

$$\log_e(B'/[V \times P \times S]) = 2.262 - 1.33 \times \log_e(W_\infty) \tag{11}$$

$$\left[n = 45, \text{adjusted } r^2 = 0.58, \text{SD of regression} = 0.49, \text{SE of slope } (d) = 0.17\right]$$

As expected, body size had a strong negative effect ($d = -1.33$). Back-transformation (with correction based on the standard deviation of the regression) gives:

$$B'/V = 10.83 \times P \times S \times W_\infty{}^{-1.33} \tag{12}$$

Given that $V = A \times D_\mathrm{mn}$ and $P = pV_\mathrm{eb}$, biomass density (i.e., wt/ha) is expressed as:

$$B'/A = 10.83 \times D_\mathrm{mn} \times pV_\mathrm{eb} \times S \times W_\infty{}^{-1.33} \tag{13}$$

Observed relative biomass density in northwest lakes were typically within a factor of 2 of values predicted by (Eq. 13) (Fig. 9a). This variation is expected given that some of these lakes are unexploited while others have considerable angling pressure. Observed biomass in other regions, where angling pressure is higher, demonstrate the effect of angling. As angling pressure increases across regions, observed biomass declined relative to predicted biomass. In the south (Fig. 9c), where mean angling pressure is four times higher than in the northwest, lakes are heavily depressed (i.e., less than ½ predicted biomass). Lakes in the northeast, where angling pressure is intermediate, biomass was intermediate.

Because the northwest region is lightly exploited, the model developed from this region (Eq. 13) is expected to provide estimates of biomass density when lake charr are close to carrying capacity, and biomass density at MSY (B_{msy}) would therefore be some proportion (e.g., 50%) of (Eq. 13). Because the biomass model is expressed in relative units, we cannot use these results to predict B_{msy} in units of kg/ha. However, given (Eq. 13), we can predict that

$$B_{\text{msy}} = C \times D_{\text{mn}} \times pV_{\text{eb}} \times S \times {W_\infty}^{-1.33} \tag{14}$$

where B_{msy} is measured in units of kg/ha and C is a parameter to be determined, which reflects both the ratio of $\mathrm{B_{msy}/B_{max}}$ and the conversion from relative to absolute units of biomass. As demonstrated in the next section, we can test whether MSY predictions based on the structure of this model account for variation in sustained yield of lake charr, and, in this process, obtain an expression that predicts B_{msy} in units of kg/ha.

7 Maximum Sustainable Yield

The final step in predicting the potential yield of lake charr is to combine sub-models developed for natural mortality rate and biomass density. We predict that MSY is the product of M (Eq. 4) and B_{msy} (Eq. 14). Combining these equations gives

$$\text{MSY} = \frac{C \times 0.26 \times e^{0.021\,T + 0.0004\,T^2} \times D_{\text{mn}} \times pV_{\text{eb}} \times S}{{W_\infty}^{1.63}} \tag{15}$$

where C is a parameter to estimate. We tested this model by predicting MSY for a different set of lakes where regular harvest monitoring provided reliable estimates of long-term sustained yield, which we used as empirical estimates of MSY. This dataset (Table 3) includes sustained yield data from 14 commercial and five recreational lake charr fisheries. Sustained yield for lakes with recreational fisheries (surface area = 59 to 5894 ha) was estimated as the average yield during a 12- to 17-year period when angling pressure was moderate to high and the lake charr population was relatively stable (details in Payne et al. 1990). Sustained yield for

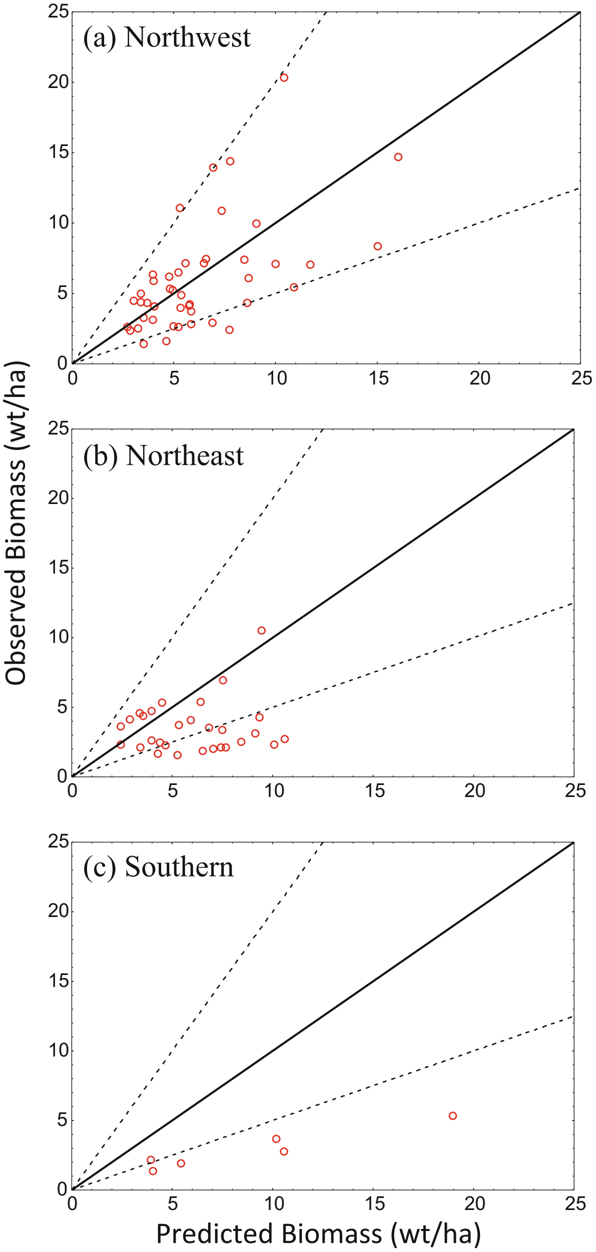

Fig. 9 Predicted and observed relative biomass density of lake charr *Salvelinus namaycush* (wt/ha) within three regions of Ontario: (**a**) Northwest, (**b**) Northeast, and (**c**) Southern. Angling pressure (hr/ha-year) on lake charr increases across these regions (2.9, 8.4, and 12.4, respectively). Diagonal lines indicate (1) the line of equality (thick), (2) Observed = 2 × Predicted (top line), and (3) Observed = 0.5 × Predicted (bottom)

lakes with commercial fisheries (surface area = 115,200 to 8,241,400 ha) was estimated as the maximum 15-year running average (details in Christie and Regier 1988). Across all lakes, the mean annual air temperature ranged from −5.2 to +9.4 °C, and mean depth ranged from 7 to 148 m. Previous reports have noted that sustained yield, which ranged from 0.08 to 2.12 kg/ha-year was inversely related to lake area (Payne et al. 1991; Marshall 1996).

To test the model, we first examined whether MSY scaled with body size as predicted. From (Eq. 15), the expected relationship was

$$\log_e(\mathrm{MSY}/f1) = \log_e(C) - 1.63\ \log_e(W_\infty) \tag{16}$$

where $f1 = 0.26 \times e^{0.021\ T + 0.0004\ T^2} \times D_{\mathrm{mn}} \times pV_{\mathrm{eb}} \times S$. This equation uses $f1$ to isolate the effects of temperature, lake morphometry, and habitat suitability, to focus on the effect of body size. We assigned W_∞ based on the lake area (using Eq. 1) because this variable was not available in the original dataset. Regression of sustained yield (SY) implied

$$\log_e(\mathrm{SY}/f1) = 2.28 - 1.76\ \log_e(W_\infty) \tag{17}$$

$$\left[n = 19, \text{adjusted } r^2 = 0.86, \text{SD of regression} = 0.376, \text{SE of the slope} = 0.17\right]$$

The estimated slope (−1.76) is close to the predicted value (−1.63) and within statistical limits given its standard error, which supports the structure of our biomass and mortality models. Constraining the slope to the predicted value (−1.63) led to the following model to predict MSY:

$$\mathrm{MSY} = 8.47 \times f1 \times W_\infty^{-1.63} \tag{18}$$

which accounts for 75% of the observed variation in sustained yield (Fig. 10a). Residuals were not correlated with lake area or mean air temperature, indicating that the model successfully accounted for the effects of these variables. Substituting for $f1$ in (Eq. 18) gives:

$$\mathrm{MSY} = \frac{2.2\ e^{0.021\ T + 0.0004\ T^2} \times D_{\mathrm{mn}} \times pV_{\mathrm{eb}} \times S}{W_\infty{}^{1.63}} \tag{19}$$

Since this equation is the product of M and B_{msy}, it implies:

$$B_{\mathrm{msy}} = 8.47 \times D_{\mathrm{mn}} \times pV_{\mathrm{eb}} \times S \times W_\infty{}^{-1.33} \tag{20}$$

The complete the set of equations needed to estimate MSY is shown in Fig. 11.

Additional support for the model comes from a larger dataset (Evans et al. 1991), which included estimates of recreational yield from creel surveys on 36 non-stocked Ontario lakes (Fig. 10b). Yield estimates for these lakes were not classified as

Table 3 The sustained yield dataset, compiled by Marshall (1996), including predicted MSY based on our model

Lake Name	*Area* (ha)	T (°C)	$D_{\max}$ (m)	D_{mn} (m)	pV_{eb}	pV_{hy}	S	Predicted W_{∞} (kg)	Predicted MSY (kg/ha-year)	Sustained *Yield* (kg/ha-year)
Christman	59	2.5	18	7.0	0.27	0.27	0.75	1.28	2.22	1.59
Bone	121	2.2	33	7.7	0.28	0.30	0.85	1.70	1.79	2.12
Flack	951	2.5	70	19.9	0.11	0.51	0.99	3.04	0.84	1.35
Chiblow	2675	2.4	66	23.9	0.10	0.51	0.99	3.75	0.64	0.59
Opeongo	5894	3.9	49	14.6	0.23	0.34	0.85	4.28	0.63	0.68
Amisk	32,100	−0.4	40	13.1	0.42	0.17	0.63	5.37	0.49	0.42
Cree	115,200	−2.3	60	14.9	0.47	0.16	0.75	6.12	0.58	0.87
La Ronge	130,700	−0.8	42	13.5	0.52	0.12	0.45	6.19	0.35	0.49
Wollaston	206,200	−3.3	97	20.6	0.37	0.23	0.94	6.44	0.70	0.77
Nipigon	448,100	0.0	127	54.9	0.09	0.52	1.00	6.84	0.47	0.29
Huron—North Channel	455,000	5.4	77	22.0	0.27	0.30	0.60	6.85	0.39	0.56
Reindeer	556,900	−5.2	215	17.0	0.52	0.16	0.90	6.95	0.68	0.50
Erie—Central Basin	623,700	9.4	64	24.3	0.39	0.20	0.06	7.00	0.07	0.08
Huron—Georgian bay	1,375,200	6.2	165	51.0	0.10	0.52	0.98	7.37	0.50	0.48
Ontario	1,947,700	8.1	236	84.0	0.05	0.66	1.00	7.53	0.38	0.16
Great slave	2,538,200	−4.4	614	62.0	0.16	0.48	1.00	7.64	0.71	0.40
Huron—Main Basin	4,165,900	6.6	218	67.0	0.08	0.56	0.99	7.85	0.49	0.36
Michigan	5,801,600	7.2	282	84.6	0.06	0.62	0.99	7.98	0.46	0.56
Superior	8,241,400	3.9	358	148.0	0.03	0.70	1.00	8.11	0.35	0.23

Sustained yield values are means from stable periods when the lake was fished at a moderate to high level (see text for details). Values for pV_{eb}, pV_{hy}, habitat suitability (S), predicted W_{∞}, and predicted MSY are calculated from a combination of lake surface area (*Area*), mean annual air temperature (T), maximum depth ($D_{\max}$), and mean depth (D_{mn}). See Fig. 11 for empirical equations

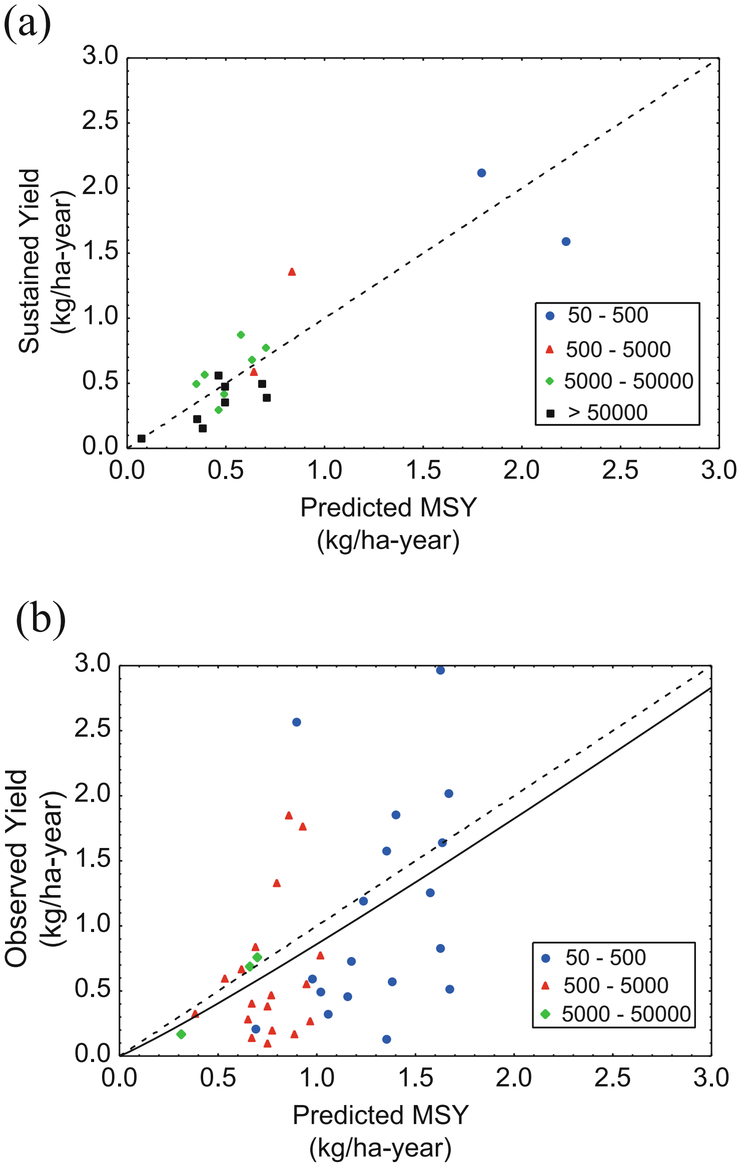

Fig. 10 Predicted maximum sustainable yield (MSY) and observed yield of lake charr *Salvelinus namaycush*. (**a**) Sustained long-term yield for 19 lakes (see Table 3). (**b**) Point-in-time estimates of yield for 36 non-stocked Ontario lakes (from Evans et al. 1991). The solid line is the predicted relationship based on log-log regression. Dashed lines are 1:1 lines

"sustained" because estimates were simply point-in-time observations of yield (mostly based on a single year of assessment) and lakes were not selected for having a moderate level of fishing pressure. Angling pressure was highly variable, and

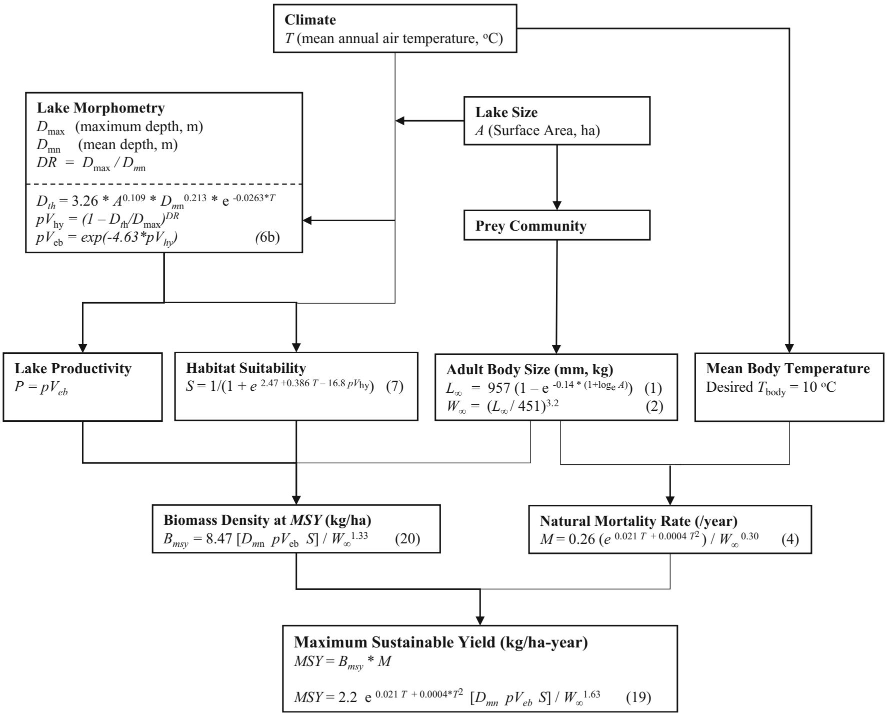

Fig. 11 Expansion of the influence diagram in Fig. 1 showing empirical equations used to predict maximum sustainable yield (MSY) of lake charr *Salvelinus namaycush*. Numbers in parentheses refer to equations in the text

consequently, yield estimates were much more variable than estimates of sustained yield. Nevertheless, the predicted relationship (solid line in Fig. 10b) indicated that the observed yield followed the pattern predicted by our model of MSY.

Given the support shown in Fig. 10, we are confident that our empirical models (Fig. 11) can be used to generate reasonable MSY estimates for lake charr populations. Predictions based on this model are not very precise (as indicated in Fig. 10a), but are still useful for fishery management. The potential yield of lake charr populations is highly variable, but our model indicates that much of this variation can be explained by a few easily measured lake variables. Thus, the model offers a reasonable estimate of a target level of harvesting for a typical lake population in a given region, before a fishery develops, or in the absence of lake-specific stock assessment data. Obviously, a more detailed assessment, based on fishery-dependent data and fishery-independent surveys, would provide more precise estimates of potential yield.

Detailed assessment may be feasible on large lakes, where individual harvests are economically significant, and management on a lake by lake basis can be justified. However, the vast majority of lake charr lakes are too small (e.g., 50–5000 ha) and it is impractical to manage these lakes individually. Our model provides an alternative basis for the management of lake charr fisheries using a landscape approach that aims to diagnose resource status in a geographic area based on a statistical sample of lakes (e.g., Lester et al. 2003; Lester and Dunlop 2004). This approach relies on the establishment of biological reference points for lake charr populations. In the following section, we provide examples of reference points based on the MSY model and demonstrate their application in diagnosing the status of lake charr populations at the landscape level.

8 MSY Reference Points: Landscape Variation

Increasingly, the management of exploited fish populations is guided by the specification of reference points to which population or fishery status is compared. Target reference points represent a desired state for the fishery, while limit reference points commonly represent fishery status that would trigger corrective action (i.e., reductions in future harvest). Our model shows that lake charr population dynamics are influenced by climate, the lake area, and lake morphometry that imply differences in both MSY and fishery target reference points among different types of lakes. To illustrate this effect, we generated both population (biomass) and fishery (F) reference points for lakes in three climatic zones over the range of lake size and mean depth in central Ontario. Reference points for the first climatic zone (labeled $T = +3$ °C) were generated using 267 Ontario lakes where the mean annual air temperature was 2–4 °C, the surface area was 50–20,000 ha, and mean depth was 3–40 m. Results for the other climate zones were generated using the same lakes (surface area and depth ranges) but assuming mean air temperature was 8 degrees colder ($T = -5$ °C) or 6 degrees warmer ($T = +9$ °C). These climatic zones span the temperature range for which the model was calibrated from sustained yield data (Table 3). This temperature range (see isotherms in Fig. 3) includes southern parts of Yukon and the Northwest Territories but excludes more northern areas, including all of Nunavut. For each climatic zone, we calculated MSY and reference points using the set of equations listed in Fig. 11.

Application of the model to lakes in the far north is a question for future investigation. The model measures habitat suitability for lake charr based on summer conditions (availability of cold water) and does not address winter limitations. When winters are very cold, ice thickness during winter likely limits habitat more than epilimnion thickness during summer. In that case, a model based on summer habitat suitability is likely to overestimate lake charr biomass. Given this uncertainty, we show reference points for a limited climatic range where we believe summer habitat is the important bottleneck for lake charr.

Predicted MSY values for lakes in these climatic zones are shown in Fig. 12. The model predicts a negative relationship with the lake area, which is consistent with empirical studies (Goddard et al. 1987; Payne et al. 1990; Marshall 1996; Hansen et al. 2021). It also predicts that MSY decreases as mean air temperature

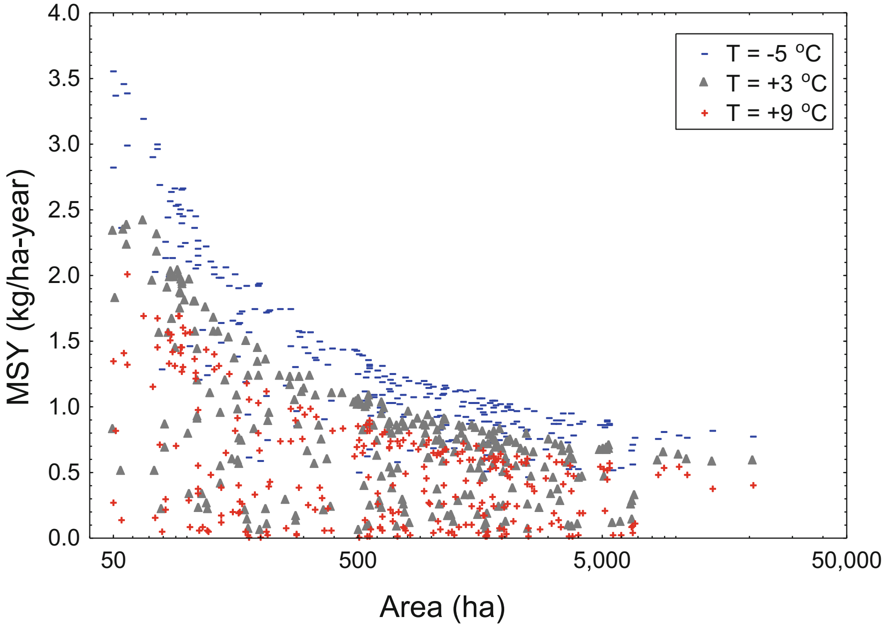

Fig. 12 Predicted maximum sustainable yield (MSY) for lakes in three climatic zones plotted against the surface area. The solid triangles show predicted biomass density (kg/ha) for 267 Ontario lakes where mean annual air temperature (T) was between +2 and + 4 °C (labeled as T = +3 °C). The surface area ranged from 50 to 20,000 ha and the mean depth ranged from 3 to 40 m. Blue minus signs show the predicted MSY in these lakes if the air temperature was 8 °C colder (T = −5 °C). Red plus signs show the predicted MSY in these lakes if the air temperature was 6 °C warmer (T = +9 °C)

increases. This prediction is counter to observations of Hansen et al. (2021, in Fig. 5) who reported a weak negative correlation ($r = -0.17$) between yield and latitude, although their analysis did not control for multiple factors affecting MSY. For example, the lake area has a strong negative effect on MSY, so an increase in lake area with latitude would offset positive effects related to a lower temperature at higher latitudes. Our model predicts that yield increases with latitude because lake charr biomass density is higher in northern lakes. Although F_{msy} is lower in northern lakes, thereby contributing to lower MSY, the effect is outweighed by a stronger positive effect on biomass.

8.1 Biomass Density at MSY

Our model predicts that biomass density at MSY is higher in northern lakes, where the mean air temperature is lower (Fig. 13a, b). In our simulations, the maximum B_{msy} is ~15 kg/ha in the north ($T = -5$ °C) and ~ 5 kg/ha in the south ($T = +9$ °C), which indicates that a 14 °C decrease in mean air temperature results in a threefold increase in biomass. This result is due to the effect of temperature on habitat suitability for lake charr (see Fig. 8d).

In each climatic zone, B_{msy} is expected to rise and then fall as mean depth increases (Fig. 13a). Optimum mean depth increases with mean air temperature because southern lakes are warmer and more hypolimnetic water is needed as a cold-water refuge. The optimum mean depth is around 12 m in the south and slightly less in the north, but Fig. 13a does not demonstrate the interaction with the lake area. More detailed simulations demonstrate that optimum mean depth is higher in larger lakes.

B_{msy} is inversely related to the lake area (Fig. 13b). For a given lake area, B_{msy} varies widely depending on climate and morphometric traits, but the maximum B_{msy} for a given climate declines progressively with lake area. This result is due to the effect of lake area on body size (as summarized in Fig. 11). Large lakes typically have more diverse prey communities that are capable of supporting higher trophic levels and larger predator body sizes.

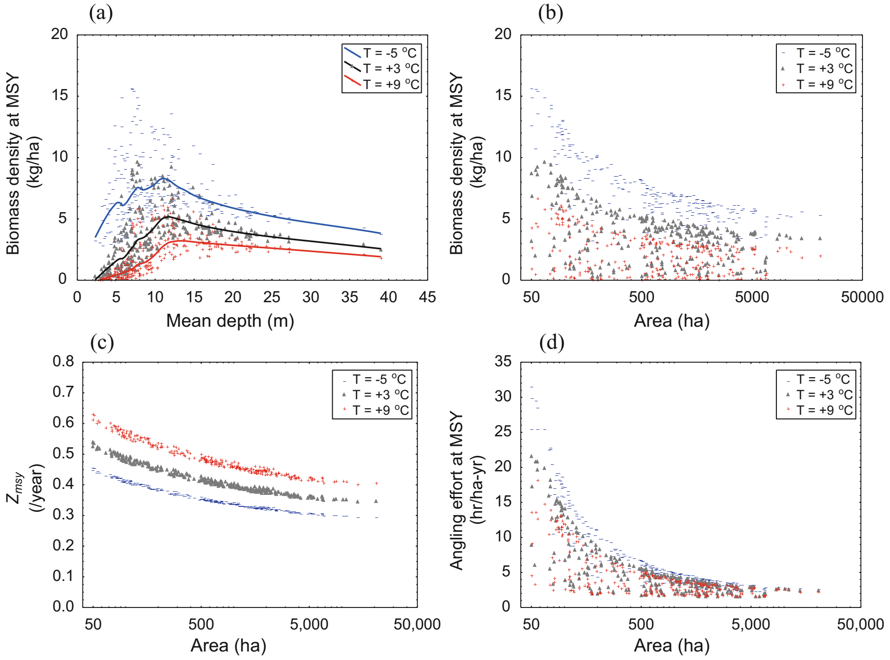

Fig. 13 Maximum sustainable yield (MSY) reference points for lakes in three climatic zones. Predicted values of biomass density at MSY B_{msy} (**a**, **b**), total mortality at MSY Z_{msy} (**c**), and Angling effort intensity E_{msy} (**d**) are shown for the lakes depicted in Fig. 12. The black lines in panel (**a**) are LOESS fits, illustrating that B_{msy} peaks at an intermediate value of mean depth (which varies depending on climate and lake area)

8.2 *Fishing Mortality, Total Mortality, and Angling Effort at MSY*

Natural mortality rate is expected to decrease with the lake area and increase with temperature. The same rule applies for F_{msy} because we assumed $F_{\mathrm{msy}} = M$. Given that total mortality (Z) is the sum of natural and fishing mortality, $Z_{\mathrm{msy}} = 2 \times M$. Our estimates of Z_{msy} range from 0.60 to 0.40 in the warmest zone and from 0.45 to 0.30 in the coldest zone (Fig. 13c).

To estimate the angling effort expected to generate this level of mortality (E_{msy}, Fig. 13d), we used an estimate of lake charr angling catchability (q) reported by Shuter et al. (1998), which applied to the angling regime operative in Ontario during the 1980s. A similar estimate has been reported for lake charr fisheries in the Yukon (Wilson et al. 2019). Angling catchability (q) describes the relationship between angling effort (hr/ha-year) and fishing mortality rate (/year):

$$F_{\mathrm{msy}} = q\, E_{\mathrm{msy}} \tag{21}$$

Catchability q was inversely density-dependent, increasing as fish density (D) decreased (Shuter et al. 1998):

$$q = 0.14/(1 + 0.35 \times D) \tag{22}$$

Consequently, the value of q when $F = F_{\mathrm{msy}}$ depends on fish density at MSY (D_{msy}).

Given that

1. $D_{\mathrm{msy}} = B_{\mathrm{msy}}/w$ (where w is the mean weight of harvested lake charr), and
2. creel survey data for Ontario fisheries indicate w averages $0.25 \times \mathrm{W}_{\infty}$.

Catchability at MSY can be calculated as:

$$q_{\mathrm{msy}} = 0.14/\left(1 + 1.4 \times B_{\mathrm{msy}}/W_{\infty}\right) \tag{23}$$

implying

$$E_{\mathrm{msy}} = 7.14 \times F_{\mathrm{msy}} \times \left(1 + 1.4 \times B_{\mathrm{msy}}/W_{\infty}\right). \tag{24}$$

Our model predicts that sustainable fishing effort (measured as angler hours per hectare per year) decreases with lake area and mean air temperature (Fig. 13d), like mortality (Fig. 13c), except the effect of mean air temperature is less pronounced, especially in large lakes.

9 Exploitation Status of Lake Charr Across Canada

To demonstrate the application of reference points at the landscape level, we assessed the exploitation status of lake charr in different regions of Canada using estimates of total mortality rate. For each lake in the Canada-wide dataset, we estimated the total mortality of fish in the exploited segment of the population ($L_c > 0.82\ L_m$), using the Robson-Chapman method (details in Appendix 3). We then compared Z estimates to predicted values of M. We calculated Z/M for each lake and then pooled values within regions (i.e., province or territory) to describe the exploitation status of each region (Fig. 14). Because $Z_{\text{msy}} = 2 \times M$, $Z_{\text{msy}}/M = 2$ supplies a reference point for identifying overexploitation. Our results demonstrate that the intensity of exploitation increased from north to south, an expected result given that fishing pressure is much higher in the more densely populated south.

A more complete diagnosis would include a similar analysis of biomass density. As Z/M increases, equilibrium B/B_{msy} decreases and equals 1.0 when $F = F_{\text{msy}}$ (i.e., $Z/M = 2$). Plotting the two ratios against each other produces a standardized method of summarizing the exploitation status for a group of lakes (Fig. 15). This plot classifies lakes into four stages of fishery development (Lester et al. 2003):

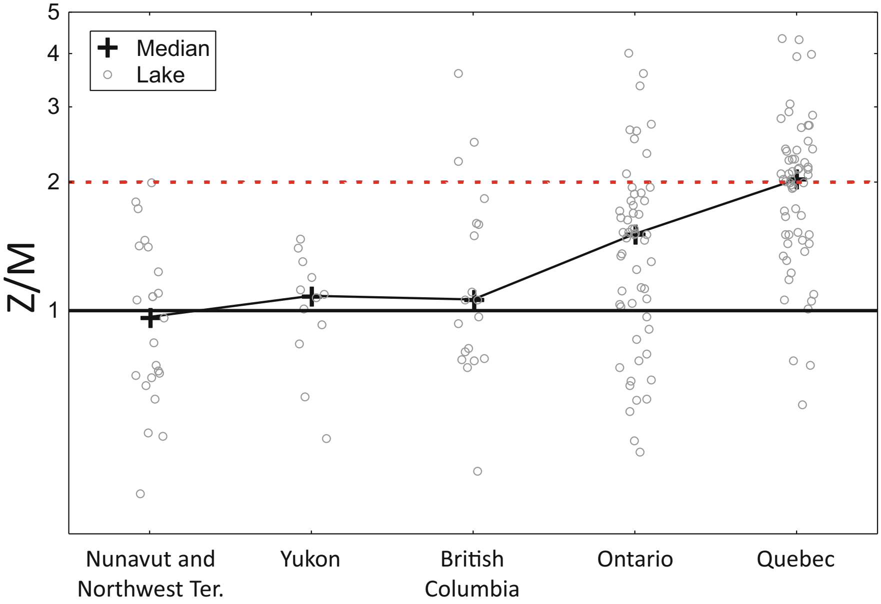

Fig. 14 Exploitation status of lake charr *Salvelinus namaycush* across Canada. Estimates of Z/M (total mortality/natural mortality; small circles) are shown for lakes in different regions. The median value (plus sign) in each region illustrates that exploitation is higher in southern regions (Ontario and Quebec) than in the north. The dashed line ($Z/M = 2$) is an overexploitation threshold (i.e., $F > M$), where F is fishing mortality. Z was estimated assuming that size selectivity is proportional to body weight (see Appendix 3)

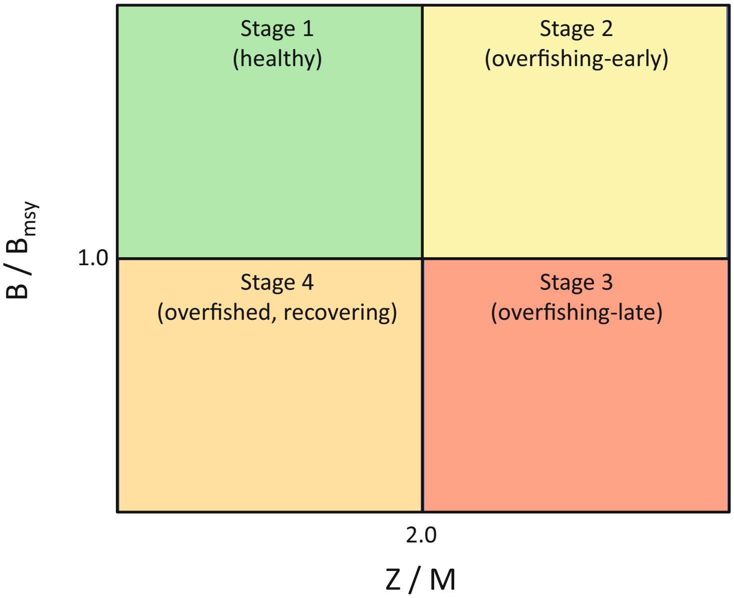

Fig. 15 Use of mortality and biomass reference points for classifying lakes into various stages of fishery development. The identification of each stage is based on the conceptual equilibrium model of fishing shown in Fig. 1

- Stage 1 (healthy)—low fishing mortality and high biomass. This state is expected during the early stages of fishery development.
- Stage 2 (overfishing, early)—high fishing mortality and high biomass. This state is expected only during the early stages of overexploitation because stable combinations of fishing mortality rates and biomass do not exist in this quadrant.
- Stage 3 (overfishing, late)—high fishing mortality and low biomass. This state indicates that the population is being overexploited and fish biomass has declined as expected.
- Stage 4 (overfished, recovering)—low fishing mortality and low biomass. This state indicates that the stock was probably overexploited in the past, as expected in the natural course of fishery development because anglers are likely to shift effort to other lakes once catch rates on one lake suffer due to a decline in biomass. Stable (i.e., equilibrium) combinations of abundance and mortality are not expected in this quadrant. If the fishing mortality rate remains low, a gradual transition to stage 1 should occur. This recovery process may be inhibited, however, by changes in the fish community resulting from heavy exploitation of one species (e.g., Walters and Kitchell 2001).

If estimates of lake charr biomass were available for the lakes shown in Fig. 14, this classification method could be used to describe the status of lake charr in different regions of Canada. Status estimates were not possible for the data that we analyzed because the various index fishing methods used in different regions have not been calibrated.

10 Discussion

Critical ingredients for long-term success of fisheries include: (1) realistic expectations of potential harvest, (2) a regulatory framework for controlling harvest and adapting to new information, and (3) monitoring populations to assess the abundance and the level of exploitation. In this chapter, we focused on the first ingredient and developed a model that predicts potential harvest for lake charr fisheries across the species' range. Intensive lake-by-lake management and assessment are not practical for fisheries that are spread across numerous, relatively small lakes and populations, so we offer our model as a basis for developing regional-scale management and assessment strategies that recognize how landscape variation affects lake charr population dynamics.

The model presented herein differs from a previous lake charr exploitation model (see Appendix 4) in two useful ways. First, we explicitly incorporate a climatic (i.e., latitudinal) gradient to make the model applicable across the geographic range of lake charr. Second, the model was constructed by combining separate sub-models for natural mortality and population biomass, both of which can serve as informative reference points for monitoring population status across the landscape. This model offers a promising basis for regional management of lake charr fisheries, but like all models should be treated as a hypothesis whose validity can be further tested through targeted monitoring of populations in contrasting habitats. Further validation of the biomass sub-model for cold northern regions is critical, because much of the data to inform this model came from lakes in the southern portion of the species' range.

We constructed our model by integrating a set of principles, derived from both studies of lake charr populations and from the wider ecological literature, into a simple and coherent structure to estimate sustainable harvest for a lake charr population given a set of relatively easily obtained measures of critical habitat for that population. The key to our approach is that these principles have a theoretical foundation but were informed by empirical evidence from lake charr lakes. We emphasize three fundamental principles:

1. Critical habitat variables, particularly temperature, nutrients, and oxygen, are significant determinants of the standing biomass of freshwater fish communities and the presence/absence of particular species.
2. Body size is a significant determinant of both physiological rates and life history traits.
3. Community diversity plays a significant role in determining the life history of top predators.

Appreciation of the role of habitat in determining fisheries yield and, implicitly, fish community biomass began with Ryder's (1965, 1982) morphoedaphic index

(MEI). The MEI focused on two simple variables that captured basic morphometric (mean depth) and nutrient (total dissolved solids) characteristics of limnetic habitat supporting a fish community. The effects of climate on fish community harvest were first evaluated quantitatively by Schlesinger and Regier (1982, 1983). Christie and Regier (1988) went on to evaluate the role of climate in shaping sustainable harvests for populations of particular species. This approach was elaborated for other species (e.g., Lester et al. 2004b; Lester et al. 2014) and was extended to examine the role of climate in shaping the zoogeographic boundaries of a variety of North American freshwater fish (e.g., Shuter and Post 1990; Alofs et al. 2014). Our model of standing biomass incorporates (directly or indirectly) the full set of habitat measures listed above. Climate and lake morphology are included explicitly and are linked empirically to lake charr occurrence and biomass (Eqs. 7 and 20) that interact to shape population characteristics through basic limnetic productivity and specific thermal and oxygen requirements of lake charr.

The link between body size and natural mortality has long been recognized in fisheries literature (e.g., Beverton and Holt 1959; Peterson and Wroblewski 1984; Beverton 1987). More recent work (e.g., Lorenzen 1996; Gislason et al. 2010) confirmed the generality of this relationship in fish. Broader ecological work on metabolic theory (Brown et al. 2004) demonstrated the ubiquity of this relationship for ectotherms, as well as the role of temperature in modifying it. We found that metabolic theory could account for the observed variation in estimated lake charr natural morality rates, and consequently chose to use this method for predicting natural mortality, rather than the empirical method proposed by Pauly (1980) that we used in an earlier model (Shuter et al. 1998).

The natural mortality formula developed for lake charr (Eq. 4) assumed that behavioral thermoregulation would maintain body temperature at 10 °C when surface waters exceeded this criterion. In reality, this “desired” temperature probably varies depending on the availability of cold-water food resources. For this reason, we explored the sensitivity of M estimates to variation in this parameter. For values that ranged from 8 to 12 °C, we showed that variation in M was very small (i.e., $<6\%$ deviation from estimates based on 10 °C), which confirmed that the 10 °C rule produced reasonable estimates. Further assessment of this method could examine its performance for other species with different temperature preferences.

Empirical relationships linking population biomass, adult body size, and lake size are consistent with expectations from size-spectrum theory (Andersen and Beyer 2006; Andersen et al. 2009). These relationships also improved our ability to account for among-lake variation in sustainable harvest indices. The fact that they were consistent with theory added to our confidence in their reliability and supported their inclusion in our model.

We used our model to propose three reference points for the sustainable harvest that can be easily derived from readily available habitat data for most North American lakes (i.e., the lake area, mean annual air temperature): (1) $Z < 2 \times M$; (2) $E < E_{\mathrm{msy}}$; (3) $B > B_{\mathrm{msy}}$. We suggest considering these indices as landscape, regional-level limit reference points: if lakes in a region, after accounting for among-lake habitat variation, show evidence of exceeding these limits, this should be regarded as a warning sign of possible overexploitation in the region. We discuss this view in detail below.

10.1 $\mathbf{Z < 2 \times M}$

Healey (1978) suggested that total annual mortality for lake charr should not exceed 50% (i.e., $Z = 0.69$). Our model suggests that this value is too high for most lake charr populations (Fig. 13c). Shuter et al. (1998) suggested that a "safe" level of F would decrease with M. This conclusion was presented prior to Zhou et al.'s (2012) convincing demonstration that F_{msy} varies directly with M for a wide range of wild fish populations. We have incorporated Zhou et al.'s finding directly in our model and when we applied it to assess the status of lake charr fisheries across Canada, it produced a credible diagnosis—fisheries in more densely populated areas (i.e., south) were more heavily exploited (Fig. 14). Note that the $F_{\mathrm{msy}} = M$ rule depends on the size of fish being harvested relative to size at maturity (see Lester et al. 2014). As size at capture decreases relative to size at maturity, F_{msy} (and hence Z_{msy}) should also decrease.

10.2 $\mathbf{E < E}_{\boldsymbol{msy}}$

Another reference point we explored is recreational fishing effort: how many hours per hectare per year can be sustained when a population is fished at the MSY level? The relationship between angling effort and sustainable fishing mortality rates depends on both angler practice and regulations that re-shape angler practice. Our previous work, based on the practice and regulations in place in Ontario in the 1980s, suggested that safe angling effort averaged about 4 h/ha-year and ranged 2–6 h/ha-year depending on lake size (Shuter et al. 1998). Our newer model predicts a similar range of values for medium and large lakes, but somewhat higher levels for small lakes (due to the smaller size and higher biomass of lake charr in these lakes). In contrast to our earlier work (Shuter et al. 1998), which suggested that small lakes are more vulnerable to overexploitation, the newer model suggests that small lakes can sustain higher fishing mortality and higher angler effort. Note that the translation of fishing mortality to angler effort depends on an estimate of angler catchability. We do not present any new evidence on landscape variation in catchability in this chapter, so understanding factors affecting catchability for recreational fisheries remains a high priority for management.

10.3 $\mathbf{B} > \mathbf{B}_{msy}$

We found that the expected biomass density of lake charr varies depending on lake-specific factors related to air temperature, lake size, and lake morphometry. Given the complexity of these interactions, biomass predictions are not precise (Fig. 9), which limits their utility at the individual lake level. At a landscape level, however, biomass reference points can be very useful (see Lester and Dunlop 2004 and Fig. 15). If a landscape region experiences high fishing intensity one expects biomass to be depleted in many of the lakes in that region. The average condition will indicate this status, even though low precision might prohibit a firm diagnosis for individual lakes. Lake charr biomass can be efficiently assessed using calibrated index netting methods. Calibration implies that the relationship between biomass density and CPUE has been determined. In this chapter, we used a North American index netting standard (Bonar et al. 2009) and relied on a tentative model of lake charr catchability for this gear to estimate relative differences in biomass. Further studies are needed to refine a calibration model so that the biomass of lake charr and other species can be estimated from index netting data across the entire geographic range of lake charr. Another potential tool for estimating lake charr biomass is SPIN (Summer Profundal Index Netting), which was developed and calibrated in Ontario (Sandstrom and Lester 2009) and has been widely used in other areas.

11 Final Thoughts

We are encouraged by the consistent pattern of variation in lake charr population dynamics across a very broad range of lake types and climatic zones. Our goal was to propose a practical, broadly applicable tool, and thus our focus was on readily observable lake characteristics, likely at the expense of precision that would result from using a more detailed characterization of lake charr habitat. For this reason, reference points we propose should not be viewed as precise indicators to be used to specify management targets for individual lakes—targets that, if adopted, will ensure sustainable fisheries in these lakes. Instead, they represent targets that should result in sustainability, on average, across the group of lakes used to inform our analysis. They can also be considered as thresholds that, when passed, flag potential risks of overexploitation.

Our analysis focused on describing among-lake variation in lake charr habitat and population attributes, and on deriving broad generalizations about how, on average, these attributes vary across the landscape. A useful next step will be to focus on the unexplained variability among lakes to inform a risk assessment for management strategies (effort level or fishing mortality targets). This residual variability (ideally the component of this variability that is not a result of measurement error) provides an indication of uncertainty about the general relationships we have proposed and therefore can help define a range of possible outcomes for a management strategy applied across a group of lakes for which little if any assessment information is available on lake charr populations. The risk assessment results could then be used to prescribe management actions that are formally precautionary, as determined by risk tolerances of fishery managers.

Although the model developed in this chapter is focused on lake charr, it has potential applications to other species. The potential yield of other temperate-zone species, such as walleye *Sander vitreus* or smallmouth bass *Micropterus dolomieu*, could be predicted in a similar manner by updating a few species-specific components: habitat suitability, mean body temperature, and adult body size (see Fig. 11). Mean body temperature for cool-water and warm-water species is easily predicted based on mean surface temperature, because these species do not rely on hypolimnetic waters to thermoregulate during summer. Thus, the natural mortality rate of these species could be predicted based on mean water surface temperature and adult body size. Habitat suitability indices for these species could be generated using methods applied to lake charr: species presence in lakes across a broad geographical gradient could be very informative in defining habitat suitability indices for different species. Given these modifications, and an assigned value for adult body size, MSY could be predicted for other species by following the schema described in Fig. 11.

We expect our approach will work best when applied to species in thermally stratified lakes because the index of lake productivity, a common factor for all species, applies to this type of lake. In thermally stratified lakes, the epibenthic volume serves as an index of lake productivity because these lakes have relatively clear water and the entire epibenthic zone is productive. Habitat suitability and trophic level of each species dictate how this productivity is shared among species. In shallow non-stratified lakes, this measure of lake productivity may not apply. For shallow lakes, the entire lake is epibenthic, but reduced water clarity may limit light penetration and hence production. Consequently, a more complex measure of lake productivity, such as Secchi depth, would be needed. Regardless, we expect that the principles of our model would still apply. Given a suitable measure of lake productivity, the potential yield of various species could be predicted based on body size, mean body temperature, and habitat suitability.

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Appendix 1: Comparison of the Metabolic and Pauly Methods for Estimating *M*

This appendix describes and compares the metabolic and Pauly (1980) methods for estimating the natural mortality rate (M). For the metabolic method, we derive an operational formula for lake charr based on (1) re-analysis of data supplied by McCoy and Gillooly (2008) and (2) the use of a water temperature model (Shuter et al. 1983) to predict body temperature. For the Pauly method, we describe the empirical formula originally developed by Pauly (1980). We apply both methods to estimate M for 122 lake charr populations which span the climatic range of this species. We then contrast the estimates and assess their validity by comparing M to the maximum observed age in each population.

The Metabolic Method

A long history of work exists relating body size and temperature to biological rate processes (e.g., Peters 1983). The metabolic approach to estimating natural mortality assumes that this rate shows the same body size and temperature dependence as the individual metabolic rate (Gillooly et al. 2001; McCoy and Gillooly 2008). Specifically, McCoy and Gillooly (2008) proposed that

$$M = \frac{a \times e^{-c \times f\left(T_{\text{body}}\right)}}{w^b} \text{ where } f\left(T_{\text{body}}\right) = \frac{1}{k}\left(\frac{1}{T_{\text{body}} + 273} - \frac{1}{293}\right), \tag{25}$$

a, b, c are parameters, w is dry weight in grams, T_{body} is mean body temperature in degrees Centigrade, and k is the Boltzman constant (8.62×10^{-5}). They analyzed data from 234 fish populations (168 species) and reported temperature-corrected estimates of weight-dependence. Their results implied $b = 0.27$, with 95% confidence limits of 0.35 to 0.19. This parameter is the complement of the production exponent (i.e., $b = 1 - \beta$) in the relationship between somatic growth and body weight (i.e., $\frac{dW}{dt} \propto W^{\beta}$). Quince et al. (2008) showed that growth in lake charr supported a value of $\beta = 0.70$, implying $b = 0.30$. We therefore re-analyzed the McCoy and Gillooly data assuming $b = 0.30$. Our results imply

$$\log_e\left(M \times w^{0.30}\right) = 1.198 - 0.529 \times f\left(T_{\text{body}}\right)$$
$$\left(n = 234, \text{adjusted } r^2 = 0.47, \text{SD of the regression} = 0.667\right).$$

Back-transformation of this equation implies

$$M = \frac{4.14\ e^{-0.529 \times f\left(T_{\text{body}}\right)}}{w^{0.30}} \tag{26}$$

The coefficient (4.14) in this equation included a correction based on the SD of the log-log regression (see Ricker 1975, p. 274): 4.14 = exp(1.198 + $0.667^2/2$). We converted the units of w (dry mass in grams) to wet weight in kilograms ($W = 4000\ w$). Using W_∞ as the measure of body size,

$$M = \frac{49.8\ e^{-0.529 \times f\left(T_{\text{body}}\right)}}{W_\infty^{0.30}} \tag{27}$$

To apply this formula to lake charr, we estimated the mean annual body temperature for lakes in our Canada-wide dataset. We assumed that, during ice-cover body, the temperature is 1 °C and that during the ice-free period lake charr strives to maintain body temperature at 10 °C. After ice-out, body temperature initially matches the surface water temperature, but once the water exceeds 10 °C lake charr will use the hypolimnion to thermoregulate. Calculations were made using empirical formulae for ice-free times and surface warming rates based on mean annual air temperature, lake surface area, and mean depth (Shuter et al. 1983).

The choice of 1 °C for winter body temperature was based on field studies. Bergstedt et al. (2003) used surgically implanted archival tags to monitor the body temperature of lake charr in Lake Huron and found that mean body temperature during ice-cover was approximately 1 °C. This finding is consistent with results from telemetry studies on much smaller lakes. Blanchfield et al. (2009) showed that the winter depth distribution of lake charr varied with light intensity. Reduced light under the ice, due to the accumulation of snow, resulted in an upward migration so that lake charr reside just below the ice, where the water temperature is expected to be around 1 °C.

The choice of 10 °C as the ‘desired’ temperature in the wild is supported by both laboratory preference studies and field data. Hasnain et al. (2013, 2018) summarized all available laboratory-based estimates of lake charr preferred temperature and reported an overall average result of 11.8 °C. Cruz-Font et al. (2019) reported temporally fine scale (10 min) summer exposure temperatures for four lakes that differed greatly in primary prey types (i.e., *Mysis*, littoral minnows, perch, cisco) and showed that typical exposure temperatures ranged from 8 to 14 °C, with 12 °C a common value for most individuals in all four lakes. Because the formula reflects core temperature not exposure temperature, with core temperature being the average of long-term exposure temperatures, a value in the neighborhood of 12 °C is reasonable and matches laboratory-based expectations. Sellers et al. (1998) reported that in small lakes lake charr may spend long periods of time living in warm water. On the other hand, a single study in a very large and deep lake (Lake Huron) has shown that mean body temperature during mid-summer was approximately 8 °C (Bergstedt et al. 2003). This discrepancy suggests that the summer body temperature of lake charr probably varies depending on the availability of cold-water food resources. In large lakes, a species-rich cold-water community is more likely to exist and the optimal foraging strategy for lake charr may be to reside exclusively in the hypolimnion. In small lakes, the lack of cold-water food resources would favor more foraging in warmer waters. Given these considerations, we chose an average value of 10 °C as the 'desired' temperature, but we explored how variation in this parameter (from 8 to 12 °C) affects estimates of natural mortality.

Our water temperature model implied that surface temperatures during the summer rose above 10 °C when mean annual air temperature surpassed −10 °C (Fig. 6a). This threshold indicates that water temperature in many Nunavut lakes may never exceed the preferred temperature of lake charr, but further south thermal stratification would be needed to thermoregulate at 10 °C. Across an air temperature gradient of −16 to +7 °C, mean body temperature ranged from approximately 2 to 7 °C when we used 10 °C as the desired temperature (Fig. 6a). Using alternative values (8 and 12 °C), shifted the high value in this range to 6 and 8 °C, respectively. The resulting estimates of M ranged from 0.11 to 0.31 for a desired temperature of 10 °C (Fig. 6b). The alternative values (8 and 12 °C) had no effect on the minimum value of M, but they produced a 6% shift in the high value (i.e., 6% lower for 8 °C and 6% higher for 12 °C). The relatively small effect of changing the desired temperature indicates that assuming 10 °C in all lakes is sufficient.

Calculation of M is tedious when mean body temperature is estimated in the manner described above, but this process can be simplified using a formula based only on mean air temperature (T):

$$M = \frac{0.26\, e^{0.021\, T + 0.0004\, T^2}}{W_\infty^{0.30}}. \tag{28}$$

This equation is an almost exact fit ($r^2 = 0.99$) to results obtained from the more complex equation based on $f(T_{\text{body}})$ above. It offers a simple means of applying the metabolic model, requiring only two measures, mean annual air temperature (°C) and maximum body size (kg). Given that $W_\infty = (L_\infty/451)^{3.2}$, the formula can be also expressed in terms of fork length (mm):

$$M = \frac{91.8\, e^{0.021\, T + 0.0004\, T^2}}{L_\infty^{0.96}}. \tag{29}$$

The Pauly Method

Pauly's (1980) method of predicting M is based on an analysis of 175 fish stocks distributed across 84 species, both freshwater and marine, and across a broad temperature gradient. Regression analysis indicated that:

$$\begin{aligned}\log_{10} M = &-0.0066 - 0.279\ \log_{10} L_\infty + 0.6543\ \log_{10} K \\ &+ 0.4643\ \log_{10} T_{\text{body}}\end{aligned} \tag{30}$$

$$\left(n = 175, r^2 = 0.847, \text{SD of the regression} = 0.245\right)$$

where L_∞ (cm) is asymptotic total length, K (1/year) is the von Bertalanffy growth coefficient (1/year), and T_{body} is the mean annual water temperature in which the stock lives. For Polar fishes, Pauly (1980) used an empirical adjustment to convert environmental temperature to "effective physiological temperature." We did not apply this correction when applying the Pauly model to lake charr.

Back-transformation of (Eq. 30), with correction for the SD = 0.245, implies

$$M = \frac{1.06\ K^{0.6543} T_{\text{body}}^{0.4643}}{L_\infty^{0.279}} \tag{31}$$

The von Bertalanffy equation, usually defined in terms of L_∞ and K, can also be expressed in terms of L_∞ and ω where ω (= $K\ L_\infty$) is the initial slope of the growth curve. Substituting for K in (Eq. 32), and converting units from cm to mm, implies the alternative formula:

$$M = \frac{2.01\ K^{0.6543} T_{body}^{0.4643}}{L_\infty^{0.933}} \tag{32}$$

In this form, the denominator in the Pauly method is almost the same as in the metabolic method. The equations differ mainly in the numerator. In the metabolic method, the numerator is determined strictly by body temperature. In the Pauly method, the numerator is a combination of body temperature and an index of the juvenile growth rate (ω). For this reason, the Pauly method is vulnerable to bias resulting from density-dependent growth. If a decline in density resulting from fishing caused an increase in growth rate, *M* would be overestimated by this method.

Comparison of M *Estimates*

We used both methods to estimate *M* for lake charr populations in our Canada-wide dataset (Fig. 16). The estimates from 122 populations were highly correlated ($r = 0.72$) and mean values from each method are almost identical (*M*-metabolic = 0.19, *M*-Pauly = 0.18). One difference was that the Pauly method produced lower estimates for northern populations.

We assessed the validity of each method by comparing the maximum age ($T_{\max}$) in each population to estimated *M* (Fig. 17). Analyses by Then et al. (2015) imply that $T_{\max} = \frac{5.67}{M^{1.09}}$. Our results demonstrate that the metabolic estimates of *M* follow this pattern very well (Fig. 17a). With few exceptions, the maximum age falls on or

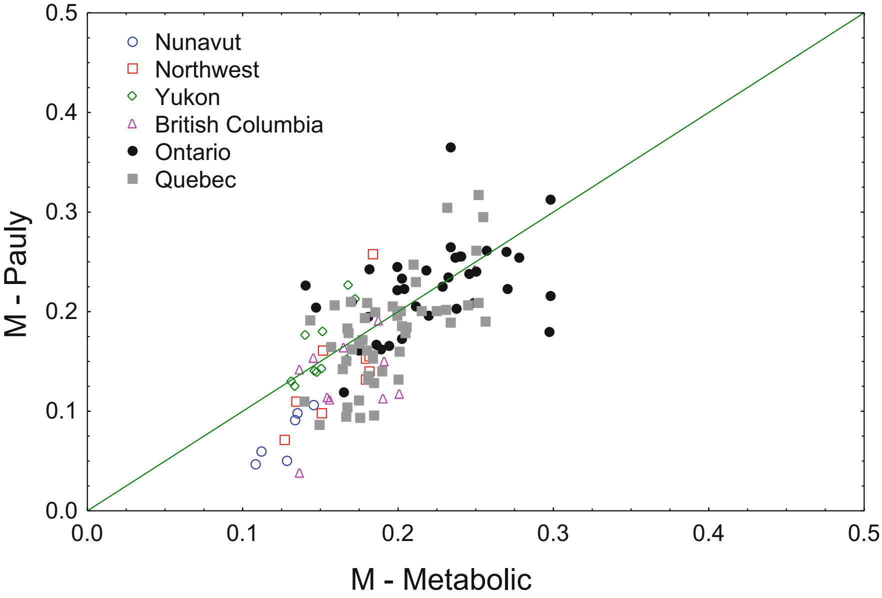

Fig. 16 Comparison of natural mortality (*M*) estimates based on the metabolic and Pauly (1980) methods. Each point is one lake. Estimates are compared only for lakes where at least 50 fish were aged. The diagonal line is the line of equality

below this line. This direction of deviation is expected given that many of the populations are exploited. It is also expected when the sample size is small. The results for Pauly estimates of *M* are less consistent with predictions (Fig. 17b). In general, maximum age deviates further from the predicted line, especially for northern populations (e.g., Nunavut, Northwest Territories, and Yukon). In these cases, the Pauly estimate of *M* is much lower than the metabolic estimate, but the maximum age assessment favors the metabolic method. The metabolic method also performs better in southern populations (e.g., Ontario and Quebec), although the differences are less severe. The ability of the metabolic estimator to “better” capture the effects of temperature is not surprising given that: (1) it was derived from a larger sample size covering a broader range of temperatures; (2) its structure is founded on well-validated theory (the Arrhenius equation) rather than a simple empirical fit.

Estimates of total mortality (*Z*) derived from the life history database provide additional confirmation of the validity of the metabolic method for estimating *M*: see Appendix 3 for details.

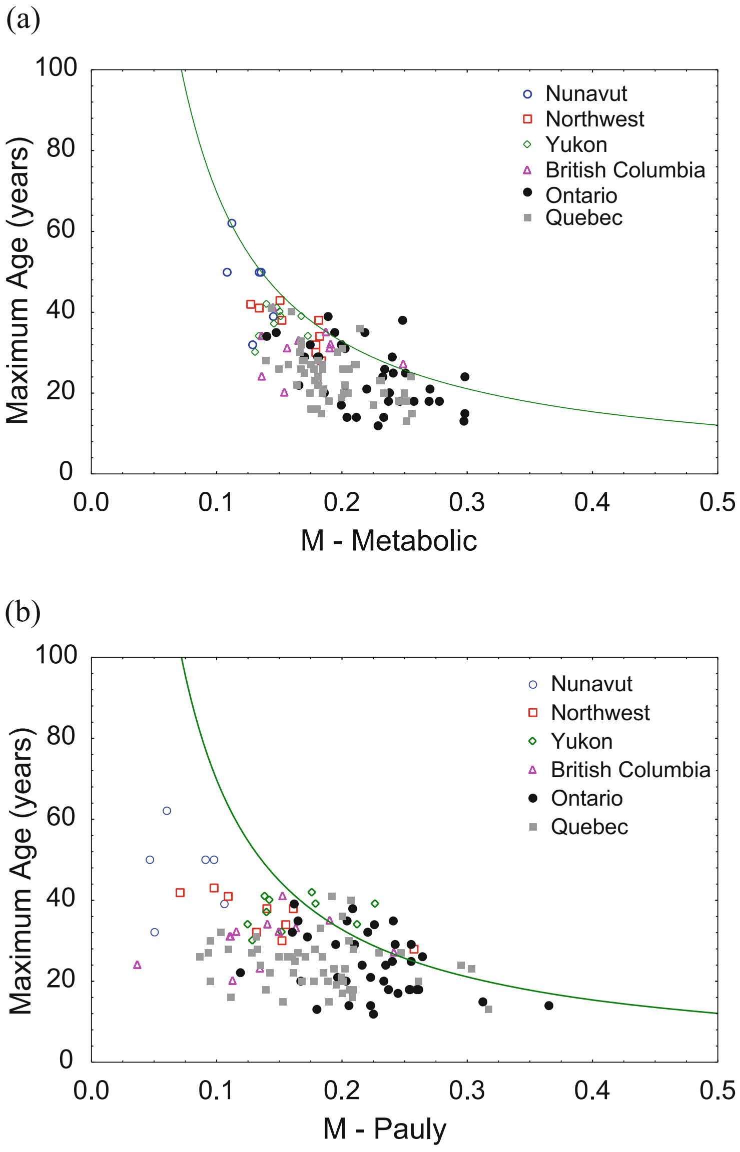

Fig. 17 Use of maximum age ($T_{\max}$) to assess the validity of natural mortality (M) estimates. (**a**) Maximum observed age versus M-metabolic. (**b**) Maximum observed age versus M-Pauly. For large sample sizes, the expected relationship is $T_{\max} = 5.67/M^{1.09}$ (Then et al. 2015) as shown on the graphs. Deviation below the line is expected if the sample size is small or fishing mortality is high. The metabolic estimates of M follow the expected line better than the Pauly estimates

Appendix 2: Habitat Volumes in Thermally Stratified Lakes

Bathymetric data and empirical models of thermocline depth were used to estimate hypolimnetic and epibenthic volumes in Ontario lakes. Thermocline depth (D_{th}) was predicted using an empirical formula from Shuter et al. (1983) with lake area (A) being used to estimate lake fetch (see Lester et al. 2004b):

$$D_{\mathrm{th}} = 3.26 \times A^{0.109} \times D_{\mathrm{mn}}^{0.213} \times e^{-0.0263\ T} \tag{33}$$

where D_{mn} is mean depth (m). Inspection of the hypsographic curves for these lakes showed that depth profiles for most lakes could be re-constructed from the values for mean and maximum depths, using the following relationship (Livingstone and Imboden 1996):

$$pA_{\mathrm{lake}}(D) = \left(1 - \frac{D}{D_{\max}}\right)^{DR-1} \tag{34}$$

where $pA_{\mathrm{lake}}(D)$ is the proportion of lake area deeper than D, $D_{\max}$ is maximum depth, and DR is the ratio of maximum depth to mean depth (referred to here as the depth ratio). Integration of this equation supplies a formula for estimating the volumetric proportion by depth ($pV_{\mathrm{lake}}(D)$):

$$pV_{\mathrm{lake}}(D) = \left(1 - \frac{D}{D_{\max}}\right)^{DR} \tag{35}$$

We estimated relative hypolimnetic volume (pV_{hy}) using this equation, with $D =$ thermocline depth. We also estimated the relative volume of the epibenthic zone (pV_{eb}) (i.e., depth shallower that the thermocline):

$$pV_{\mathrm{eb}} = 1 - pV_{\mathrm{hy}} - pA_{\mathrm{hy}} \times \left(DR \times \frac{D_{\mathrm{th}}}{D_{\max}}\right) \tag{36}$$

where pA_{hy} is the proportion of lake area deeper than the thermocline. This equation results from calculating epibenthic volume as lake volume minus the sum of the hypolimnetic volume and the epilimnetic volume which is directly above the thermocline. Relationships between these habitat volumes and mean depth are shown in Fig. 18.

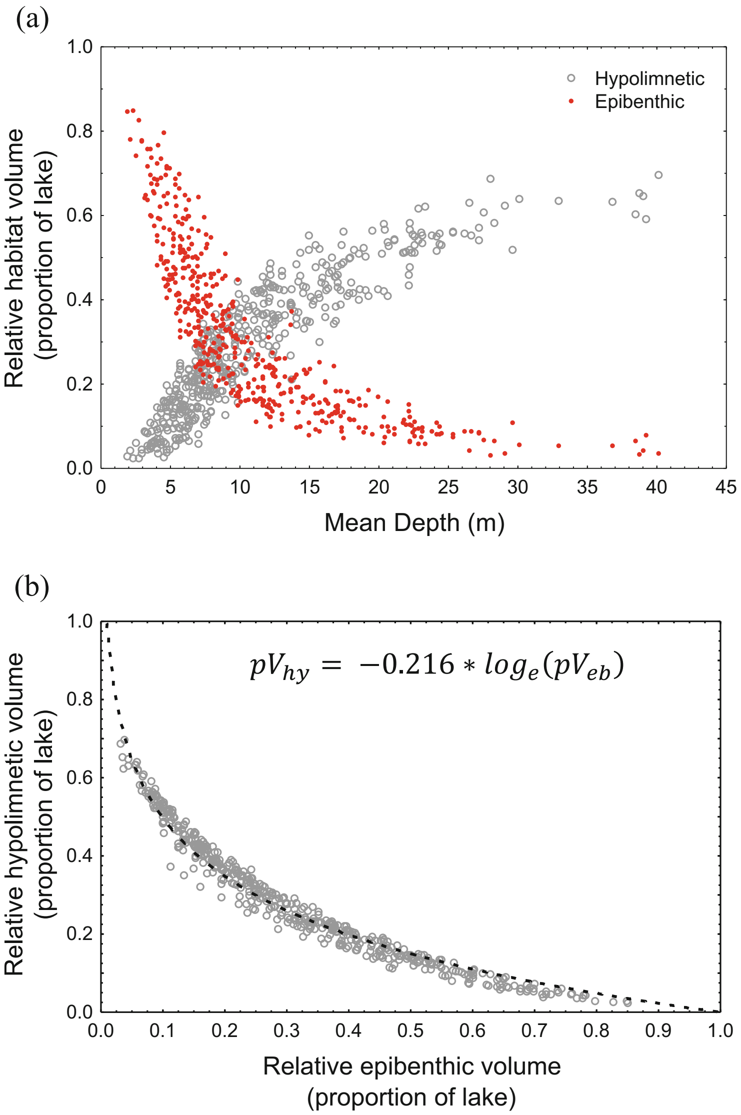

Fig. 18 Habitat volumes in 472 thermally stratified lakes within Ontario. (**a**) Relative epibenthic and hypolimnetic habitat volumes (i.e., proportions of lake volume) are plotted against mean depth. (**b**) Relative hypolimnetic volume plotted against epibenthic volume. The inverse relationship between these volumes is well described by the formula shown on the graph

Appendix 3: Method of Estimating Total Mortality Rate (Z)

The total mortality rate of the exploitable fish population was estimated using the Robson-Chapman method (Robson and Chapman 1961; Smith et al. 2012). This method uses the mean age (Age_{mn}) of fish in a designated segment of the population to estimate the probability of annual survival (*Survival*), from which the instantaneous mortality rate (Z) can be calculated. The population segment is defined by a minimum age (Age_{min}), which was assigned based on the estimated initial size at harvest (= 0.82 times size at maturity). Given that n is the number of aged fish, the relevant formulae for calculating Z (and its variance) are:

$$\text{Survival} = \frac{\text{Age}_{\text{mn}} - \text{Age}_{\text{min}}}{1 + \text{Age}_{\text{mn}} - \text{Age}_{\text{min}} - {}^{1}\!/_{n}} \tag{37}$$

$$\text{Z} = -\log_e(\text{Survival}) \tag{38}$$

$$\text{var}(Z) = \frac{\text{Survival}^2}{n\,(1 - \text{Survival})} \tag{39}$$

We used a size-stratified approach to estimate the mean age because age was not determined for every sampled fish. Populations were divided into 100 mm fork length bins, estimated the mean age within each bin, and then calculated a weighted mean age based on the frequency of fish in each length bin.

Our estimates of the total mortality rate were used to investigate the potential impact of size selectivity due to the sampling method. We assumed a range in size selectivity by assigning selectivity coefficients equal to L^x, where x ranged from 0 to 3. $x = 0$ implies that all sizes of fish are equally vulnerable to being captured. $x = 3$ implies selectivity is roughly proportional to fish weight (because the weight-length relationship is approximately cubic). To apply selectivity, the mean age was calculated as a weighted mean, where the weight assigned to each fish was inversely proportional to the selectivity coefficient (i.e., L^x).

We estimated Z for 170 lake charr populations in the Canada-wide dataset. Our results showed that estimated Z increased roughly in proportion to the magnitude of the size selectivity parameter (x). When selectivity increases proportional to fish weight (i.e., proportional to L^3), the total mortality rate averages about 1.5 times the value produced under the assumption of no selectivity ($x = 0$). We assumed this level of selectivity to produce the results shown in Fig. 14, the same value that was used when estimating biomass density in Ontario lakes. We compared these estimates of Z to estimates of *M,* which were based on the metabolic method. As expected, we found that M set a reasonably well-defined lower bound for our estimates of Z (Fig. 19).

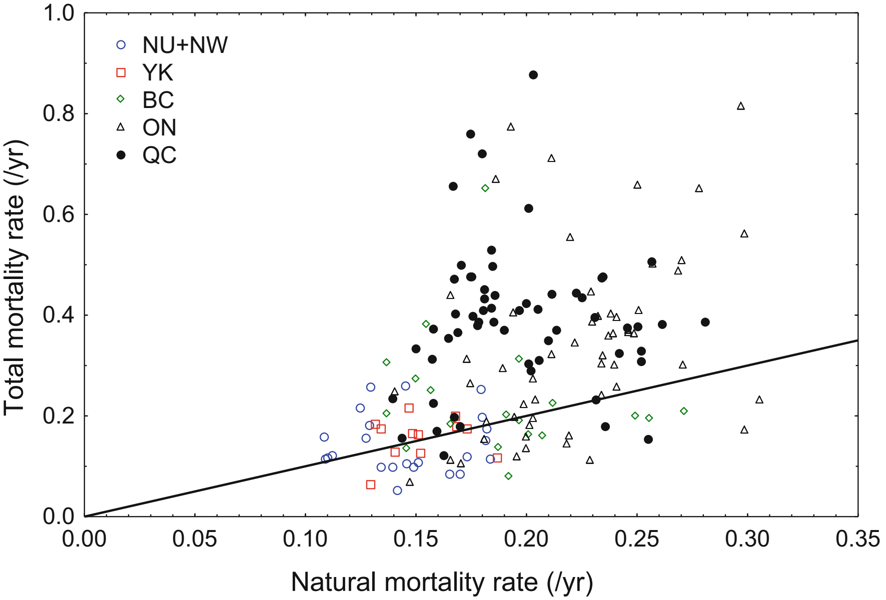

Fig. 19 Comparison of total mortality (Z) to natural mortality (M) estimated by the metabolic method. The diagonal line is the line of equality

Appendix 4: Comparison to the 1998 Lake Charr Exploitation Model

The model developed in this chapter (Fig. 11) is an extension of the model developed by Shuter et al. 1998. The new model contains:

- A more explicit description of how habitat is influenced by lake morphometry (i.e., area, mean depth, and maximum depth) and climate and the effect this has on B_{msy}; and
- A broader characterization of how climate influences natural mortality and thus affects $F_{\mathrm{msy.}}$

The old model characterized lake charr habitat using lake area alone and predicted natural mortality for lakes in an Ontario climate. Each model includes empirical descriptions of life history relationships (e.g., asymptotic length versus lake area, length at maturity versus asymptotic length). Whereas the old model developed relationships using data only from Ontario lakes, the new model's relationships are based on data from the entire geographic range of lake charr. Despite these differences, relationships predicted by each model are similar, indicating that the data from Ontario alone foretells body size relationships across the entire geographic range (Fig. 20). Also, natural mortality predictions are almost identical when the new mortality model is applied to the climate of Ontario (see Fig. 20e).

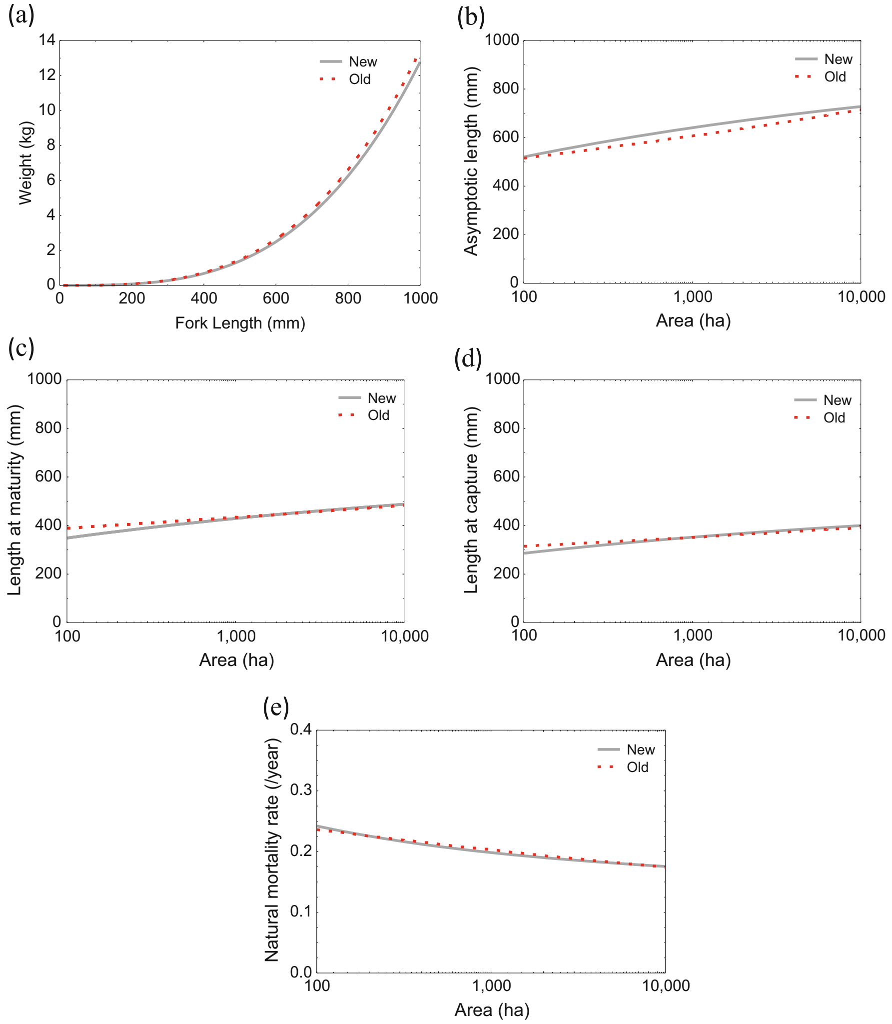

Fig. 20 Comparison of the empirical relationships developed in the new (solid line) and old (dashed line) models. (**a**) Weight-length relationship. (**b**) Asymptotic length versus lake area. (**c**) Length at maturity versus lake area. (**d**) Length at capture versus lake area. (e) Natural mortality rate (M) versus lake area. The old model relationships in **c**, **d**, and **e** are shown for $\omega = 100$ m/year, the average rate of growth in Ontario lakes, where ω is the initial growth rate from the Von Bertalanffy model. The new model for natural mortality (**e**) is shown for mean annual air = +3 °C, the average for Ontario lakes

MSY reference points from each model are compared (Fig. 21) using a subset of Ontario lakes where mean annual air temperature ranges from +2 to +4 °C (as in Figs. 12 and 13). The old model predicts a single MSY value for each lake area; the new model predicts a range of values depending on lake morphometry (Fig. 21a).

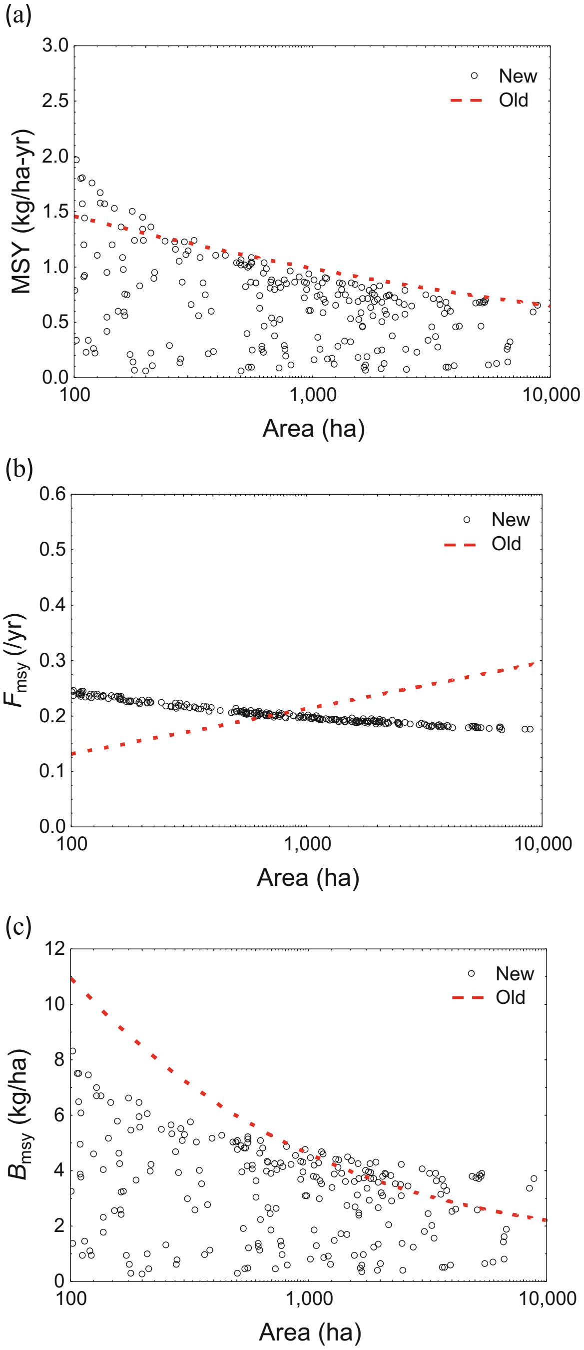

Fig. 21 Comparison of maximum sustainable yield (MSY) predictions for the new model (points) and old model (dashed red line). New model results are generated for BsM lakes where mean annual air temperature ranges from +2 to +4 °C (as in Figs. 12 and 13). Old model results are generated for the same lakes; only one prediction for each value of lake area occurs because the old model does not incorporate lake morphometry and climate. (**a**) MSY versus lake area. (**b**) F_{msy} versus lake area. (**c**) B_{msy} versus lake area, where F_{msy} is fishing mortality at MSY and B_{msy} is biomass density at MSY

The old model predicts the approximate maximum value (i.e., ceiling) of the new model's MSY. This result is expected because Shuter et al. (1998) used sustained yield data from deep lakes to calibrate their model; that model did not show how variation in lake morphometry (and hence the availability of suitable habitat) affects MSY. The range of values generated by the new model (see Fig. 21a, c) illustrates the degree to which observed differences in the morphometry of Ontario lakes can affect both MSY and $B_{\text{msy.}}$

One striking difference between the predictions of the two models is in the level of fishing mortality (F_{msy}) that results in MSY. The new model predicts that F_{msy} decreases with increases in the lake area, while the old model predicts that F_{msy} increases with lake area. Since B_{msy} equals MSY/F_{msy}, this difference in F_{msy} predictions leads to differences in B_{msy} predictions as well, with the old model overestimating B_{msy} for small lakes (e.g., <1000 ha—Fig. 21c). In addition, the old model predicts that small lakes are more susceptible to overexploitation than larger lakes; this prediction disappears in the new model.

These differences stem from the fact that the two models make different assumptions about the density-dependence of biomass production. For the old model, density dependence is embodied in a stock-recruit relationship built on the following assumptions: (1) a Shepherd recruitment function (Shepherd 1982), structured largely on qualitative arguments current in the literature of the time; (2) a common maximum recruitment rate (i.e., number of recruits per biomass of spawners) for all populations. For the new model, we have not described a stock-recruitment function in this chapter, but, as we show below, the assumption that $F_{\text{msy}} = M$ implies maximum recruitment rate cannot be the same for all populations; it must vary with M and body size. This constraint applies to any stock recruit relationship which is consistent with the new model (e.g., Logistic, Ricker, Beverton-Holt, Shepherd). It is most easily demonstrated by assuming logistic density dependence, which produces a linear relationship between fish biomass and fishing mortality rate (as illustrated in Fig. 2). For simplicity, we also assume that harvesting begins when fish reach maturity (i.e., $L_c = L_m$) so that the exploitable biomass equals spawning biomass.

Building on the structure of the stock-recruit equation in the old model (Eq. A4 in Shuter et al. 1998), net production of exploitable biomass is given by:

$$
\begin{aligned}
dB/dt &= \{\text{ biomass gain from recruitment }\} - \{\text{biomass loss due to mortality}\} \\
dB/dt &= \left\{\alpha_{\max} \times \text{fec}_{\max} \times g(B) \times B \times e^{-M \times (t_m - 1)} \times W_m \right\} - \{Z \times B\} \qquad (40)
\end{aligned}
$$

where:

- $\alpha_{\max}$ is the maximum survival egg to age 1,
- $\text{fec}_{\max}$ is the maximum relative fecundity (eggs per unit weight of mature females),

- $g(B)$ is the density-dependent part of the stock recruit relationship, here assumed to have a logistic form such that $g(B) = 1 - B/B_{\max}$ where $B_{\max}$ is the adult biomass density required for the total suppression of recruitment,
- $e^{-M\times(t_m-1)}$is survival from age 1 to age at maturity (t_m), given natural mortality rate of M
- W_m is weight at age of maturity.
- Z is the total mortality rate, the sum of both fishing and natural mortality.

Solving (Eq. 40) for equilibrium conditions (i.e., $dB/dt = 0$) implies

$$\left\{\alpha_{\max} \times \mathrm{fec}_{\max} \times g(B) \times e^{-M\times(t_m-1)} \times W_m\right\} = Z \tag{41}$$

An equation for Z_{ext} (the level of total mortality required to drive spawning biomass to zero) is then obtained by letting $B = 0$ (implying $g(B) = 1$):

$$\left\{\alpha_{\max} \times \mathrm{fec}_{\max} \times e^{-M\times(t_m-1)} \times W_m\right\} = Z_{\mathrm{ext}} \tag{42}$$

Given the constraint that $F_{\mathrm{msy}} = M$, the logistic model implies $F_{\mathrm{ext}} = 2 \times M$ and thus $Z_{\mathrm{ext}} = 3 \times M$. Substituting for Z_{ext} in (Eq. 42) implies

$$\left\{\alpha_{\max} \times \mathrm{fec}_{\max} \times e^{-M\times(t_m-1)} \times W_m\right\} = 3 \times M \tag{43}$$

The term $e^{-M\times(t_m-1)}$ is approximately constant (~Q) because M and t_m are inversely related (Lester et al. 2014). Therefore, the maximum recruitment rate per spawner ($\alpha_{\max} \times \mathrm{fec}_{\max} \times Q \times W_m$) is conditioned by adult natural mortality—the higher the natural mortality rate, the higher the maximum recruitment rate.

Empirical support exists for this prediction. Given that M is inversely related to maximum adult size, $\alpha_{\max} \times \mathrm{fec}_{\max} \times Q \times W_m \propto M$ implies that maximum recruitment rate per spawner should be inversely related to maximum adult size; Denney et al. (2002) showed this to be the case in their analysis of recruitment data from over 50 marine populations. The consistency of these results with Zhou et al.'s (2012) empirical finding that $F_{\mathrm{msy}} \sim M$ for many harvested stocks provides strong support for the contention that the model of lake charr exploitation presented in this chapter provides better estimates of F_{msy} than those provided by the old model.

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Terminology Issues in Lake Charr Early Development

J. Ellen Marsden, Andrew M. Muir, David L. G. Noakes, and Charles C. Krueger

> *. . . biases have been caused by 'fishery biologists' who, in the necessary attempt at cooperation, adjust their 'terminology' to the jargon of their non-biologist counterparts in management, trade and politics. The result is a ridiculous life history sequence: egg–larva–fry–fingerling–subadult–spawner. . .*
>
> *Balon (1999)*

Abstract Accurate and precise terminology is critical for clarity and information transfer. Lake charr *Salvelinus namaycush* developmental terminology is often incorrectly and inconsistently applied and consists of terms borrowed from other salmonids. Terms currently used may not identify developmental stages, are not synonymous with formal terminology, and are not ecologically relevant. We propose a standard lake charr-specific terminology consisting of: (1) *egg*: a haploid, unfertilized gamete; (2) *pre-hatch embryo*: a developing embryo within a chorion; (3) *free embryo*: post-hatch embryo, used until absorption of the external yolk sac; (4) *post-embryo*: lake charr with internal or fully

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absorbed yolk sac, usually with parr marks and inflated gas bladder, and still resident on a spawning area; (5) *age-0*: lake charr during the period between leaving spawning grounds and December 31 of the first year of life; (6) *juvenile*: interval between the end of age-0 (January 1) and the onset of maturity; (7) *adult*: life stage after reproductive maturity; and (8) *senescent*: stage after growth and reproductive capacity cease. The recommended terminology is specific to lake charr and strikes a balance between accurate life-stage specific terms that reflect development, and the practicality of life-stage terms that can be assigned by field biologists and fishery managers.

Keywords Alevin · Cumulative degree days · Developmental biology · Larvae · Eleutheroembryo · Emergent fry · Fingerling · Life history · Life stages · Adult · Age-0 · Egg · Fertilized egg · Free embryo · Juvenile · Post-embryo · Pre-hatch embryo · Senescent · Young-of-year · Ontogeny · Parr · Swim-up fry · Yolk sac

1 Introduction

Development and use of accurate and precise terminology are critical for clarity and information transfer in the scientific endeavor; however, terminology also constrains how we think about science. Discussion of lake charr *Salvelinus namaycush* early developmental stages is confounded by the use of terms that are incorrectly borrowed from adfluvial and anadromous species, used inconsistently, do not identify actual developmental stages, are not synonymous with formal terminology, are not ecologically relevant, and do not reflect differences in behavior between riverine versus lacustrine salmonids. Our purpose here is to review early life-stage terminology and illustrate how the erroneous transfer of terminology across salmonid taxa has led to misassumptions about lake charr life history. Like other authors before us (Hubbs 1943; Balon 1999), we suggest the adoption of a more accurate and informative species-specific terminology for field practitioners and use in publications, with specific reference to the lake charr. Our recommendations are not intended to replace developmental or physiological terms, instead, we suggest a set of terms for stages that can be identified by a field biologist with the naked eye. The term "stage" is widely used, but also widely misused; we use the term "stage" herein to refer to an *interval* of development, not a brief period of time during ontogeny.

2 Developmental Stages, Terminology, and Misuse

To clarify early life-stage terminology, we distinguish between terms that are used by ichthyologists and developmental biologists, and terms that have an ecological significance and are useful in practice by fishery managers and researchers in fishery science and ecology, particularly terms for stages that can be identified by superficial examination of very small fish in the field. We also need to distinguish between

Table 1 General developmental types in fishes, and developmental stages and processes (i.e., metamorphosis) that occur in each type

Direct	Intermediate	Indirect
Embryo	Embryo	Embryo
Juvenile	Free embryo	Larva
Adult	Juvenile	Metamorphosis
Senescent	Adult	Juvenile
	Senescent	Adult
		Senescent

terms that apply to stream-spawning salmonids but not to lake charr, which are primarily lacustrine spawners, and identify terms that incorporate behavior and ontogeny in addition to morphology. Although few adfluvial (stream-spawning; lake-dwelling) or anadromous (stream-spawning; ocean-dwelling) populations of lake charr have been documented, they occur, but are not sufficiently well studied to know whether their behavior and development are similar to anadromous salmons, including a smolt stage. Thus, specific terminology may be needed in the future to describe their development.

Developmental biologists have struggled to find a set of terms that can be applied universally to fishes, and have been challenged by the range of fish developmental patterns from placental incubation in elasmobranches to the complex pre-adult stages in catadromous eels (for a review of challenges and attempts at standardization see Blaxter 1988), and the impossibility of finding terms that apply to all fish taxa. We will circumvent these debates by first reviewing terms for general teleost development, and then restricting our discussion to the development and specific terms applicable to salmonid species, particularly to the lake charr. We note here that the timing and duration of stages are not fixed, but highly temperature-dependent (and in later stages, food-dependent), so any stated intervals in development are approximations that must be applied by subsequent writers with appropriate context and definition.

The basic stages of fish development are, in sequence: *embryo*, which terminates with the transition to exogenous nutrition; *larva*, which terminates with complete development of the axial skeleton; *juvenile*, which terminates at reproductive maturity; and *adult*, an individual capable of reproduction (Balon 1975). Not all stages are present in all species. Fishes with *direct development* do not have a larval stage and fishes with *indirect development* have a larval stage with true metamorphosis into the juvenile stage (Table 1; Balon 1986). *Hatching* is a relatively unimportant event that allows more scope for the continued growth of the embryo and does not define any development stage. Hatching releases an embryo from the chorion (egg envelope) and is affected by extrinsic factors including dissolved oxygen and temperature (Balon 1980). In some fishes, we may recognize *metamorphosis*, a substantial and relatively abrupt transformation from larvae to juvenile that occurs in only a few taxa, such as eels (Anguilliformes) and lampreys (Petromyzontiformes). In lake charr, most of the developmental processes into a juvenile occur during the embryo stage and metamorphosis does not occur. Many fishes, including coregonines, hatch with a vestige of the yolk sac, which comprises less than 10% of the total body mass and is soon absorbed. These species complete their development during an extended larval period after the yolk sac is fully absorbed and exogenous feeding has become the predominant nutritional source. Although exogenous feeding often begins while the yolk sac is still present, the interval of combined endogenous and exogenous feeding is very brief. In contrast, salmonines (*Oncorhynchus*, *Salmo*, and *Salvelinus*) hatch with a substantial yolk sac that comprises up to 75% of the total body mass at hatching (Alanärä 1993) and is absorbed over an extended period, usually several weeks, while axial skeletal development is completed at, or before, yolk-sac absorption. Thus, salmonine fishes develop from an embryo into a fully competent juvenile with a brief or non-existent larval stage (see Goetz et al. 2021). Parenthetically, we note that referring to "salmonid" fishes in reference to development is inappropriate, as salmonine and coregonine fishes within Salmonidae have substantially different developmental types. Unlike salmonines, coregonine species (whitefishes and ciscoes) have a true larval state. Replacement of the commonly used but the incorrect term "coregonid" with "coregonine" is encouraged, because "Coregonidae" is not a family.

A diversity of loosely defined and overlapping terms appears in the salmonid literature, including egg, green egg, ripe egg, embryo, fry, sac fry, emergent fry, post-emergent fry, swim-up fry, larva, fingerling, and age-0. For example, *fry*, a broadly used but loosely defined term for a young or small fish, has been variously modified to indicate the presence of the yolk sac ("sac fry"), or stages before, during, or after emergence from the substrate. The term "larva," generally used to mean any small, immature fish, is also found in the salmonine literature despite the absence of a true larval stage in salmonines (e.g., "larval lake trout," Fitzsimons et al. 2009, 2010; Schmitt 2011). The distinction between larva and embryo is important, because both are stages when feeding can occur, but free embryos have prolonged access to endogenous resources that buffer them against periods of low food availability. Post-embryonic stages, when yolk sac absorption is complete, must seek, catch, ingest, and digest prey, and consequently are exposed to predation. In the salmon literature *alevin*, *parr*, and *smolt* are added to the plethora of confusing terminology. Similar to the previously described stages, these terms are also confusingly misused. For example, alevin has been used to mean stages from hatching ("newly hatched alevins," "alevins at hatching stage;" Jaroszewska et al. 2009; Mirza et al. 2001; Sternecker and Geist 2010), post-yolk sac adsorption and first feeding (Balon 1975), or a stage synonymous with larva (Hubbs 1943; Simpson et al. 2016). Even Blaxter (1988), in his extensive review of patterns of fish development, makes a confusing synonymy of three independent stages: "In the salmonids. . .although the yolk sac is still large, the larva (alevin) is better developed. . . ." *Parr*, a free-swimming stream stage, and *smolt*, the stage when anadromous salmons undergo physiological preparation for a saltwater environment, are terms specific to anadromous species and have no relevance for lacustrine lake charr.

3 Misappropriation of Terms from Adfluvial Salmonids and Hatchery Culture

Terminology for lake charr early life stages is confounded with terms used for adfluvial (river-spawning with freshwater lake residence) salmonids and influenced by hatchery culture practices. Appropriation of these terms results in highly misleading assumptions. The most loosely borrowed terms are those that link developmental periods with specific behavioral events in salmonine early life, including *emergence* and *swim-up* (Table 2). For example, "emergent fry traps" are used to collect post-hatch lake charr prior to leaving a spawning site (Collins 1975; Stauffer 1981). The name is a holdover from the original use as traps for stream-spawning salmonids (e.g., Phillips and Koski 1969). The use of "emergent" implies that lake charr "emerge." In salmon and trout, "emergence" describes an abrupt, distinct, post-hatch stage where all or most of the yolk sac has been absorbed and the fish leave the gravel redd (i.e., nest), fill their gas bladder, and begin a free-swimming stage (e.g., Gustafson-Marjanen and Dowse 1983). The nature of the redd, constructed in stream gravel, combined with stream current, largely precludes young fish from returning to the redd after departing. Thus, the term "emergence" is synonymous with a one-way exit from the substrate, and the onset of exogenous feeding. Exogenous feeding is believed to be rare prior to emergence. In contrast, lake charr embryos incubate in large rocky substrate with large interstitial spaces. Hatched embryos move laterally and vertically within the substrate (to at least 1 m deep depending on the size of the substrate). By 3 weeks after hatching, free embryos make regular nocturnal forays into the water column above the substrate (Baird and Krueger 2000). This behavior allows free embryos to begin mixed feeding (i.e., feeding endogenously from the yolk sac while also becoming competent at exogenous foraging on small plankton) early in development, while they have access to the substrate, which provides refuge from predators before the free embryos are fully capable swimmers (Ladago et al. 2016). Consequently, "emergent" fry traps collect lake charr throughout the first 4–6 weeks of life, from newly hatched free embryos through past yolk sac adsorption.

The term "emergent" in lake charr is not a description of emergence from spawning substrate, but more correctly refers to the distinct event when lake charr embryos swim to the surface to fill their gas bladder (Tait 1960), a stage synonymous with "swim-up." However, "swim-up" also appears to be somewhat arbitrarily borrowed from adfluvial salmonine species. Deep-water spawning lake charr, such as those hatching on the Lake Michigan Mid-Lake Reef Complex (Janssen et al. 2007), likely do not risk predation by swimming upward through depths of 50 m or more simply to fill their gas bladder. Lake charr may either delay filling the gas bladder until buoyancy compensation becomes important as a consequence of their increasing size, or they may fill the gas bladder without access to surface air (Tait 1960; Marsden unpublished data; Goetz et al. 2021). In short, "emergence" and "swim-up" are misleading in reference to lake charr because they are essentially synonymous, but are derived from taxa in which distinct life stages associated with

Table 2 Developmental periods of salmonines, adapted from Balon (1975, 1980), with commonly used terms for each period in lake charr, and behavioral events that occur during each period

	Period		Events		Terms
Period	Developmental Stage	Lake charr common terms	Anadromous and adfluvial species	Lake charr (lacustrine)	Proposed terminology for lake charr
Egg	Unfertilized gamete	Egg	Within female or pre-fertilization	Within female or pre-fertilization	Egg
Embryo	Chorion-bound embryo	Egg	In redd (lotic)	Entrained in lentic rocky interstices	Pre-hatch embryo, fertilized egg
	Free embryo (eleutheroembryo)	Sac fry	In redd (lotic)	Diel movements from substrate; begin exogenous feeding; period of mixed feeding	Free embryo
Alevin	Alevin	Emergent fry	Gas bladder inflation; emerge from redd; begin exogenous feeding	Leave spawning site	Post-embryo
Juvenile	Parr	Post-emergent fry; fingerling; age-0	Stage not present or synonymous with smolt	Lake-resident	Age-0, young-of-year
	Smolt	Stage not present	Downstream migration; adaptation to salt water	Stage not present	
	Juvenile	Juvenile, age-1 +	Lake- or ocean-resident	Deep-water resident, but considerable uncertainty exists whether this is common across the range	Juvenile
Adult	Adult	Adult	Reproductively mature	Reproductively mature	Adult
Senescent	Senescent	Senescent	Post-reproductive	Post-reproductive	Senescent

specific behaviors occur, whereas these stages and behaviors do not occur in lake charr. Similarly, the use of "fry" or "larval lake charr" is too non-specific to be informative. Are the lake charr feeding? Has the yolk sac been adsorbed? Has the individual left the spawning reef?

The use of the terms "alevin" and "juvenile" are also problematic. For stream-spawning salmonines, "alevin" is most correctly used to indicate a stage between the embryo and juvenile, after the fish leave their redd, inflate their gas bladder, and begin exogenous feeding (e.g., Balon 1975; Rimmer and Power 1978). As regards the lake charr, this term is confounded by the early onset of exogenous feeding prior to complete yolk sac absorption, and the difficulty of sampling the stage between leaving the spawning site and becoming true juveniles. However, lake charr with completely internalized or adsorbed yolk sacs are frequently sampled in traps on spawning reefs. Though somewhat unwieldy, the term "post yolk-sac age-0" is descriptive and accurate. "Juvenile" is also a problematic general term in most salmonines that refers to a period of five or more years for lake charr, between completion of age-0 development and beginning of maturation. This term also leaves a significant gap in terminology for the first year of life, between approximately June and end of the first winter when the first annulus (i.e., annual growth demarcation on bony structures) is formed, a period critical for survival and often for the establishment of year-class strength (Hjort 1914). The term "age-0," while encompassing the entire period after hatching but before age-1, is useful for describing post-hatch juveniles during the first year of life and distinguishing the first critical year from the next five-plus years of juvenile growth.

Artificial propagation or hatchery culture has also caused misleading assumptions about lake charr developmental stages and behavior. When propagated, young salmonines are provided artificial feed rather than live plankton. While they are feeding on their yolk sac, these fish do not respond to non-moving food, so culturists do not introduce food until the yolk sac is fully adsorbed and the post yolk sac age-0 fish are seeking alternative sources of nutrition. In fact, Balon (1975) who conducted his observations on hatchery-reared fish, defined "emergence" as the stage at which feeding begins. In the wild, however, when free embryos are exposed to moving zooplankton prey, feeding commences considerably earlier (Ladago et al. 2016). The free embryo period is therefore an interval of mixed feeding, which supplements maternally provisioned nutritional resources and can protract yolk sac adsorption.

4 Proposed Terminology for Lake Charr Early Life Stages

To conform to ichthyological terms that specify important developmental transitions, while maintaining useful and identifiable categories for field biologists, we suggest the adoption of the following terminology, simplified from Balon (1975), and illustrated in Table 2. We have not adopted Balon's use of "phase," in preference to "period" and "stage" for developmental intervals.

Egg: a haploid, unfertilized gamete.

Pre-Hatch Embryo: A developing embryo within a chorion. Also, the term "*fertilized egg*" is acceptable for this stage. The alternative term, "embryo," defined by Balon (1975), does not readily convey the concept of a chorion-bound stage. Balon stated that hatching "is a fairly artificial character as a boundary between phases." While this is correct from a developmental standpoint, embryos are trapped while contained in a chorion and cannot avoid predation or move if incubation water quality degrades (Blaxter 1988). In addition, sampling methods (and seasons) for fertilized eggs and mobile (hatched) free embryos, defined below, are very different.

Free Embryo: Post-hatch embryo until absorption of the external (visible) yolk sac that is generally resident on or within spawning substrate. Here, we again depart from Balon's use of "eleutheroembryo," which is unfamiliar to most non-developmental biologists. "*Sac fry*" is a commonly used alternative to free embryo, though not ideal because of the aforementioned vagueness of the word "fry," and is a term in very common use that is descriptive of the stage when an external yolk sac is visible.

Post-Embryo: Lake charr with internal or fully absorbed yolk sacs, usually with parr marks and inflated gas bladder, and still resident on a spawning area. This stage is recognizable by the absence of the external yolk sac. Balon (1975) uses the term alevin (an undefined term, as described above) to describe this stage as ending with complete scalation or ossification of the vertebrae, characters that are not readily evaluated in the field. From a practical standpoint, this stage ends once fish are no longer on spawning grounds, have moved offshore, or are larger than approximately 35 mm total length.

Age-0, Young-of-Year: The period between leaving spawning grounds and December 31 during the first year of life, which by convention ends with the first "birthday" of fishes on January 1 (Blaxter 1988). This term was not used by Balon, but is useful for, and familiar to, fishery biologists. Age-0 lake charr from fall-spawning populations are highly identifiable by size (<100 mm by the end of the year, and substantially smaller at any time of year than age-1 or older) and relatively easy to sample (compared to developing pre-hatch embryos or free embryos) as an indicator of pre-recruitment. While technically including the period from hatching to December 31 in North America, the term age-0 is useful in practice to distinguish lake charr that are post-embryos until December 31, a stage not associated with spawning areas. Use of terminology that terminates this stage on December 31 is confounded by spring-spawning lake charr that presumably hatch in summer, such that their first "year" may be less than 6 months. Nevertheless, for consistency, we suggest using the same terminology for these fish. Consistent with the American Fisheries Society Style Guide, "young-of-the-year" may be used in lieu of "age-0," but it may not be abbreviated to "YOY."

Juvenile: The interval between the end of age-0 (January 1) and the onset of maturity. For most populations, this stage extends beyond age 5. Juveniles progress through ecological and morphological changes that may include diet shifts and changes in depth distribution. However, the size and age at which these shifts occur vary among lakes and morphotypes and are not readily identifiable in the field. No unambiguous terms are available to define different juvenile stages, so authors who may need to make such distinctions to define groups when reporting results, such as "ages 1 through 3," or "pre-piscivory juveniles."

Adult: Stage after reproductive maturity. In practice, this stage is identified by the presence of gametes or the presence of lake charr on spawning sites.

Senescent: Stage after growth and reproductive capacity cease. This stage is difficult to identify in practice and the term may not have much practical value, because this stage is likely limited or non-existent in fish.

The recommended terminology above is intended to standardize communication and minimize confusion. The terminology is specific to lake charr to strike a balance between accurate life-stage specific terms that reflect development, and the practicality of meaningful language for field biologists and fishery managers. The field of fish development and ontogeny has progressed beyond simple descriptive terminology and classification systems (e.g., Balon 1980; Allen et al. 2005). We now have a better understanding of lake charr genetics (Wellband et al. 2021) and life history (Hansen et al. 2021), and approaches have been extended to merge ecology, evolutionary biology, and developmental ontogeny into eco-evo-devo approaches to understanding diversity (Campbell et al. 2017; Skulason et al. 2019).

As a final note concerning the classification of developmental stages within the embryo stage, cumulative degree days (CDD) or temperature units (TU) are frequently used to identify embryonic life stages, particularly by culturists or in controlled laboratory studies. However, the number of degree days to reach a particular point in development varies with incubation temperature (Allen et al. 2005) and potentially with photoperiod. Under natural conditions, the temperature experienced by pre-hatch embryos fluctuates overwinter. Thus, the standard hatchery metric of "50 days at 50 ° F to 50% hatch" does not apply if pre-hatch embryos are incubated at other temperatures, and CDD cannot be used to denote a developmental stage. Similarly, free embryos are classified by total length (e.g., Swedberg and Peck 1984) or by the proportion of yolk sac length to body length (Ladago et al. 2016). However, the growth rate in length is semi-independent of yolk sac absorption and depends on the amount of exogenous food ingested (Simard et al. 2019). The growth rate in early development can be affected by egg size (yolk volume) and the nutritional quality of yolk lipids, which vary among females and within embryos from a given female. Thus, measures of absolute size only provide an estimate of the developmental stage. Ideally, authors should report both total length and an approximate measure (yolk sac length as a proportion of total length, or % of yolk sac remaining) to characterize developmental stages in lake charr embryos.

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