

Perspectives on the ecomorphology of bony fishes

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Synopsis

The field of ecomorphology has a long history with early roots in Europe. In this half of the century the application of ecomorphology to the biology of fishes has developed in the former Soviet Union, Poland and Czechoslovakia, The Netherlands, and in North America. While the specific approaches vary among countries, many North American studies begin by comparing morphological variation with variation in ecological characteristics at the intra or interspecific levels. These initial correlative studies form the ground work for hypotheses that explore the mechanistic underpinnings of the observed ecomorphological associations. Supporting these mechanistic hypotheses are insights from functional studies which demonstrate the limits to potential resource use resulting from a particular morphology; however, the actual resource use is likely to be more limited due to additional constraints provided by internal (e.g., behavior, physiology) and external (e.g., resource abundance, predator distribution) factors. The results from performance studies in the laboratory or field can be used to test specific ecomorphological hypotheses developed from the initial correlational and functional studies. Such studies may, but rarely do, incorporate an ontogenetic analysis of the ecomorphological association to determine their effect on performance. Finally, input from phylogenetic analyses allow an investigator to examine the evolution of specific features and to assess the rates and directionality of character evolution. The structural and ecological diversity of fishes provides a fertile ground to investigate these interactions. The contributions in this volume highlight some of the specific directions for ecomorphological research covering a variety of biological processes in fishes. These include foraging, locomotion, reproduction, respiration, and sensory systems. Running through these papers are new insights into universal ecomorphological issues, i.e., the relationships between form and ecological role and the factors that modify these relationships.

Introduction

Ecological morphology or ecomorphology, as presented in this volume, is a comparative discipline; its central focus is the study of the interaction of morphological and ecological diversity among organisms both in the present and over evolutionary

time (Motta & Kotrschal 1992). These interactions can be studied at multiple levels: among individuals within a species, among species and higher taxa, and among guilds and communities. The mechanistic underpinning of ecomorphology is that some aspects of interindividual morphological variation will lead to functional and performance differences

that result in differences in how these individuals use the available resources. In turn, ecological factors may influence further morphological changes (1) over evolutionary time as selection on these characters leads to changes in gene frequencies in a population or through extinction/speciation of taxa (e.g., Wiens 1977, Crowder 1986, Schluter 1988, Swain 1992, Hori 1993), or (2) over the life span of the organism through use-induced changes in morphological structures (e.g., Ehlinger & Wilson 1988, Ehlinger 1990, Meyer 1990, Wimberger 1991, Mittelbach et al. 1992). A key feature of this particular ecomorphological paradigm is that morphological variation among individuals or among species can be causally linked to variation in performance and ultimately to variation in resource use and fitness (Wainwright 1994). Ecomorphology therefore becomes a framework for addressing adaptation.

Individual perceptions of ecomorphology are in part affected by one's background and approach to the field. Functional morphologists are generally interested in understanding the function of a specific morphological feature. Their understanding can then form the foundation for exploring the performance consequences of anatomical differences among species (or individuals within species) that may result in ecological differences among these organisms (Wainwright & Reilly 1994).

In general ecologists are interested in understanding resource use by organisms and the interactions among species. From an ecological perspective ecomorphological studies have three aims: (1) measurements of the correlation between general morphological variation and ecological variation; (2) making ecological inferences from morphological pattern; and (3) determination of the underlying morphological mechanism that influences resource use by an organism and the degree to which ecomorphological relationships are influenced by other factors (paraphrased from Ricklefs & Miles 1994). Expanding beyond any specific community, ecologists might attempt to identify universal forces structuring ecological communities, especially through the determination of morphological commonalities and convergences in community organization among different assemblages.

Viewing ecomorphological relationships from the perspective of only current utility ignores the important role of evolution in producing these relationships. One of the most exciting conceptual advances in recent studies has been the incorporation of explicit phylogenetic hypotheses into ecomorphological studies. Historical interpretations of ecomorphological relationships provide important information on rates of evolution and the extent of morphological and ecological coevolution (e.g., symecomorphosis, Liem 1993). On a practical level, the addition of a phylogenetic component to an ecomorphological study resolves the statistical dilemma of the nonindependence of characters for those taxa which share a trait due to common ancestry (see Felsenstein 1985, Losos & Miles 1994, and Westneat 1995 for further discussion).

Historical overview

Attempts to draw connections between the form of an organism and its ecological role have a long history. Probably the first comments that can be interpreted as ecomorphological can be found in the Hindu text 'Sursuta-samhita', describing a link between body form and habitat in freshwater fishes, and in the writings of Aristotle (Lindsey 1978). While a clear understanding of both the field of morphology and the field of ecology is necessary for a well-designed ecomorphological investigation, progress in these fields has not proceeded at an equal pace historically. Ecology is a relatively young science, developing primarily in this century, but the roots of morphology in the western world can be traced to Plato and Aristotle. The 18th and 19th centuries saw tremendous progress in understanding the influences of phylogenetic history, development, and function on morphology. In this century, morphological diversity has been increasingly interpreted as being the consequence of adaptation to specific environmental conditions. More recently, the increased application of experimental approaches to morphological analysis has provided great insights into the functional significance of intra- and interspecific morphological diversity (see Liem 1991).

While the recognition of ecology as a distinct field of biology dates from about 1900, its antecedents reach back into the natural history studies of 18th and 19th centuries (Odum 1971). Applying this holistic approach to biology, natural historians such as van Leeuwenhoek, Darwin, and Haeckel, proposed the term 'oecology' in 1869 to refer to the study of the organism-environment interactions (Kingsland 1991). Important ecological concepts such as the niche, succession, food webs, and the competitive exclusion principle were developed early in this century as a result of attempts to describe ecological communities qualitatively.

The interest in the fit of the organism to the environment predates Darwin, however the theoretical underpinnings of ecomorphology can be dated to Darwin's publication of 'On The Origin of Species' in 1859 (Bock 1990). Within this evolutionary framework the study of adaptation could be applied to the relationship between form and function. In the early 1900's there were sporadic studies dealing with ecological morphology (see Bock 1990 for a review), but an explicit blending of ecology and morphology began to emerge in the 1940's in Europe. Remane (1943), a morphologist, and Kuhnelt (1943), an ecologist, published separately their concepts of 'Lebensform', in which similarities in morphological constructions are attributed to constraints imposed by a similar environment, even in different taxonomic groups (Goldschmid & Kotrschal 1989). Van der Klaauw (1948, 1951), influenced by the earlier work of Hans Boker, clearly stated that ecological morphology is the relationship between the structure of the organism and its environment (Bock 1990). With the increased interest in functional anatomy in the 1950's there was a resurgence of interest in vertebrate morphology. However there were few works on ecological morphology until Bock & von Wahlert (1965) clearly set out guidelines for the study of adaptation and differentiated between function and biological role (Bock 1990). This work helped to clarify the distinction between functional morphology and ecological morphology. At about the same time functional morphologists again became interested in ecological morphology, ecologists saw morphology as a tool for addressing questions about the niche, competi-

tion, community structure and resource partitioning. In 1975 Karr & James (1975) introduced the term 'ecomorphology' in their study of avian communities [for a review of the history of ecomorphology see Goldschmid & Kotrschal (1989) and Bock (1990)]. Since then there has been a steady growth in interest in ecomorphology both by ecologists and morphologists.

Modern ecomorphological research has benefited greatly from the quantitative and experimental approaches that have developed independently in the fields of morphology and ecology. In addition, recent ecomorphological studies have borrowed insights and methodologies from other fields, including evolutionary biology, behavior, physiology, and biomechanics (Liem 1991). One of the major goals of this volume is to identify the current state of knowledge of ecomorphological research, specifically for fishes, and to chart out promising areas for future research.

Application of ecomorphology to fishes

Fishes exhibit tremendous morphological and ecological diversity. They occupy a wide variety of ecological niches, forage on almost anything of energetic value, demonstrate a full range of reproductive styles, and utilize more sensory modalities than any other group of organisms. To access these ecological niches, fishes have evolved complex suites of foraging, locomotory, respiratory, reproductive, and sensory structures. As a result of their long evolutionary history, their high biodiversity, and their often multi-stage life histories, fishes have provided fertile grounds for examination of the relationship between form and ecological role.

The application of the ecomorphological approach to ichthyology has played an important role in our understanding of biological diversity in fishes. Research groups utilizing this approach have developed independently in the former Soviet Union, Czechoslovakia and Poland; the Netherlands, and in North America. Many of these early works include some of the first ecomorphological studies of ontogenies, life histories and reproductive styles in

fish communities (e.g. Kryzhanovsky 1949, Kryzhanovsky et al. 1953).

In the west, seminal works by Fryer & Iles (1972) laid the groundwork for interpreting the tremendous morphological diversity of the speciose lacustrine cichlids of Africa in an ecological content. The importance of the ecomorphological approach to fish biology was recognized by research groups in the Netherlands (Barel 1983, 1984, Barel et al. 1989, Hoogerhoud et al. 1983, Hoogerhoud 1987, Witte et al. 1990, Nagelkerke et al. 1994). This resulted in the formation of the Ecological-Morphology Research Group at the Rijksuniversiteit Leiden with research focused on the African Rift Lake communities.

The approach by many in this research group is termed ultramechanistic by Zweers (1988). This approach is deductive in nature, where optimality modeling plays a central role in the generation of hypotheses. In these models the optimal gain in energy is realized if the underlying anatomical and functional systems perform at the highest possible efficiencies (Barel et al. 1989 in Liem 1993, Barel 1993). The predictions of these models would then be tested against laboratory or field data. In determining the optimum energetic efficiency, these models assume (1) energy is a limiting resource for which there is competition; (2) historical factors are not important (Liem 1993). While the former may ultimately be true, under many circumstances there may be no competition for energy (see Wiens & Rotenberry 1980). Regarding the second assumption, under many circumstances a clear understanding of the evolutionary history and ontogeny of the organisms that are being modeled is necessary to understand constraints imposed on their biological interactions (see Brooks & McLennan 1991, Harvey & Pagel 1991).

In North America, studies by Keast & Webb (1966), Ciardelli (1967), Werner & Hall (1976, 1979), Werner et al. (1977), Chao & Musick (1977), and Gatz (1979a, b) set the stage for a burst of interest in the interrelationship of morphology and ecology related to resource partitioning and feeding in fishes. Currently, the ecomorphological approach is being applied on a broad front to investigate nearly every area of potential interaction between morphology and ecology of fishes at both the intra- and

interspecific level (e.g., Wikramanayake 1990, Vergina 1991, Ekau 1991, Norton 1991, Winemiller 1991, Douglas & Matthews 1992, Motta & Kotrschal 1992, Sturmbauer et al. 1992, Swain 1992, Purcell & Bellwood 1993, Norton & Brainerd 1993, Robinson et al. 1993, Turingan 1994).

The initial studies in North America were conducted by ecologists, and they used an inductive/comparative approach. Many of them employed what Motta & Kotrschal (1992) and Liem (1993) have termed the scattershot strategy, in which numerous morphological and ecological characters were analyzed with the hope of discovering relevant patterns of correlation. Choice of the characters in these studies was often based on the intuition of the investigator (Dullemeijer 1980) or simply included traditional taxonomic characters. Under these conditions, providing a plausible mechanism for many of the correlations that were produced was problematic. In many of the recent studies, choice of morphological characters has been restricted to those for which there is experimental evidence for their potential adaptive significance (e.g., Ricklefs & Miles 1994, Norton 1995). While the early studies on the ecomorphology of fishes focused on ontogeny and life history, these areas are generally under-represented in current studies with few exceptions (e.g. Balon 1975, 1986, Galis 1993, Crawford & Balon 1994).

An approach to ecomorphology

Despite the active interest in ecomorphology there is little consensus on definitions and hypotheses of ecomorphology, and considerable confusion concerning the distinctions between ecomorphology and similar morphological analyses (i.e., functional morphology) (for discussions see Leisler & Winkler 1985, Barel et al. 1989, Goldschmid & Kotrschal 1989, Bock 1990, Motta & Kotrschal 1992, Wainwright 1994). The terms ecology and morphology are often used rather imprecisely, explicitly or implicitly including behavior, physiology, biochemical traits and the like (see Motta & Kotrschal 1992, Garland & Losos 1994). In our view ecomorphologists attempt to determine the strength of the rela-

tionship between variation in form and variation in actual resource use among individuals, populations, species and higher taxa, or communities.

In contrast to ecomorphology, one goal of functional morphology is to determine the potential function or biological role of structures, particularly in an adaptive context (Liem 1991). The difficulty with many functional studies is that the artificial laboratory conditions or simplified ecological challenges may be poor mimics of the diverse ecological challenges and conditions under which these structures must operate in the wild. In spite of these limitations, the results of functional morphological studies play an important role: (1) *a priori* in identifying which morphological variables are likely to influence a particular ecological variable, and (2) *a posteriori* by providing a plausible mechanism for an observed ecomorphological correlation (e.g., Barel 1983, Norton & Brainerd 1993).

Insights from a functional analysis of structural variation among a group of organisms may provide part of the information necessary to predict the fundamental niches that these organisms may inhabit. The realized niches (as measured as part of an ecomorphological analysis) may be different due to the complex interplay of internal and external constraints (see discussion in Bock & von Wahlert 1965, Bock 1980, Motta & Kotschal 1992, Reilly & Wainwright 1994). Moreover, the support provided by a functional morphological analysis of an anatomical structure is still insufficient to demonstrate that this structure determines the observed ecological patterns. To move beyond correlation (even when supported by functional inference) requires a demonstration that the differences in morphological features identified in the ecomorphological component lead to differences in performance that would result in the ecological patterns observed under natural conditions (e.g., Wainwright 1987, 1988, Norton 1991).

It is unreasonable to expect a perfect match between morphological variation and ecological variation. In fact, the authors of several ecomorphological studies have concluded that limited or no correlation existed between ecological and morphological variables (e.g., Wiens & Rotenberry 1980, Grossman 1986, Motta 1988, Block et al. 1991, Dou-

glas & Matthews 1992). The lack of ecomorphological correlations in these studies may be artifactual or real. Of course, these results fall into the difficult conceptual problem that the absence of evidence of an ecomorphological pattern provides only weak inference that no such pattern could exist. For example, choosing other morphological and ecological variables or analyzing them differently may produce a correlation where none was found earlier (see Norton 1995). Alternatively, the results of these studies may reflect reality, i.e., no correlation between morphological and ecological variation. A complex interplay of factors (e.g., behavioral, ecological, physiological, historical, and morphological constraints) may influence the morphological and ecological characters that are being studied (e.g., Baker et al. 1995, Cech & Massingill 1995). This interplay might prohibit a perfect fit between morphological and ecological parameters, result in a sub-optimal fit or leave no connection at all (see Gould & Lewontin 1979, Motta & Kotschal 1992, Losos & Miles 1994, Ricklefs & Miles 1994).

While the statement, 'the ecology of a fish is determined wholly by its morphology', is clearly not correct, it is also clear that the alternative hypothesis, 'the morphology of a fish plays no role in its ecology' is also not correct. Repeatedly, studies have demonstrated close ecomorphological relationships; among these are the relationship between interspecific differences in visual pigments, retinal morphology, and the electromagnetic spectrum characteristic of the habitats of fishes (e.g., Munz & McFarland 1977, Levine & MacNichol 1979, Hobson et al. 1981, Pankhurst 1987, Hueter 1990, Mas-Riera 1991, McFarland 1991), between gut length and diet in fishes (e.g., De Groot 1969, Montgomery 1977, Horn 1989, Zihler 1982, Stoner & Livingston 1984, Motta 1988, Vergina 1991, Eggold & Motta 1992, Sturmbauer et al. 1992), and between the body shape, and position and shape of fins and the primary habitats of fishes (e.g., Keast & Webb 1966, Watson & Balon 1984, Webb 1984, 1988, Wikramanayake 1990, Douglas & Matthews 1992). Clearly, reality lies somewhere between the first statement and its alternative.

In our view, the initial goal of an ecomorphological research program is to identify which features

of an organism's form are correlated with particular features of its ecology. The choice of features should be based on an understanding of the putative functional links between the morphological variables and the ecological variables in the study. A functional analysis then provides the causal mechanism for the correlation. This analysis can be used to generate predictions on the role of morphological variation in determining the potential niche. Performance tests then provide a powerful mechanism to evaluate the ecomorphological hypotheses generated by the analyses. Ideally, these performance tests should be either direct or indirect indicators of fitness, e.g., growth, survival, fecundity (Jayne & Bennett 1990, Liem 1993, Ricklefs & Miles 1994, Garland & Losos 1994). Such analyses could be applied to an ontogenetic series to ascertain ontogenetic ecomorphological associations and their effect on performance. Comparisons between the potential and realized niche are particularly important to ecologists who are interested in community structure and interspecific interactions. Finally, incorporation of a phylogenetic component could be used to provide evidence of convergence, divergence and parallelism, to assess the rates of morphological and ecological evolution, and to describe adaptive character complexes (Lauder 1981, 1982, Brooks & McLennan 1991, Losos & Miles 1994, Wainwright & Reilly 1994).

An overview of the contributions in this volume

This is an exciting time to be pursuing ecomorphological research. A continuous stream of new books (e.g., Wainwright & Reilly 1994) and articles (e.g., Schluter 1994) demonstrate the continued vitality of this interdisciplinary approach to biology. As the hybrid title implies, ecomorphology is a synergistic endeavor; progress in ecomorphology has come not only from increased understanding of ecology and morphology, but also through progress made in other disciplines, especially functional morphology, biomechanics, embryology, ethology, physiology, and evolutionary biology.

The goal of the symposium that we organized for the 1992 annual meeting of the American Society of

Ichthyologists and Herpetologists and the papers included in this volume was to explore the implications of new strides along this broad front to ecomorphological research and to identify promising areas for future research. For some contributors, investigations of the ecomorphology of fishes is the major focus of their research programs. Others would consider their primary focus to be on some other aspect of adaptive biology (e.g., ecophysiology, biomechanics), but their research clearly contributes to our understanding of the relationship between ecology and morphology. Continued interdisciplinary interactions can greatly increase the pace of progress.

We organized the symposium and the contributions in this volume around major processes that are important in the biology of fishes, including foraging, locomotion, sensory perception, respiration, and reproduction. Specific studies in this volume examine: (1) adaptations for the acquisition and utilization of sensory information from the environment (Kotrschal, Mensinger, van der Meer et al.); (2) general and specific adaptations for locomotion in aquatic environments (Long, Motta et al., Winemiller et al.); (3) the ability to capture food (Luczkovich et al., Motta et al., Norton, Wainwright & Richard, Westneat); (4) the need to acquire sufficient oxygen to support metabolic activities (Cech & Massingill, Chapman & Liem, Martin), and (5) constraints on reproductive styles (Baker et al., Foster & Baker). Several studies look at potential interactions between these processes (e.g., Baker et al., Cech & Massingill). The contributions include analyses of ecomorphological variation within a species (e.g., Chapman & Liem, Foster & Baker, Luczkovich et al.), among closely-related species (Norton, Westneat, van der Meer), within a community (Motta et al., Wainwright & Richard) and among several communities (Martin, Winemiller et al.).

Running through these papers are general ecomorphological questions that are broadly applicable to more than just fishes and their specific systems. These include: (1) How good is the basic fit between an organism's structure and its use of ecological resources when traditional taxonomic variables are used? (2) Can we improve our conceptual

or statistical fit between ecology and morphology by choosing non-traditional parameters that reflect a clearer understanding of the functional potentials of individual structures and the ecological complexities facing fishes? (3) When a structure plays a role in several ecological contexts, does its form represent a compromise among optimal solutions to these contexts or are some ecological roles more important than others in the evolution of form? (4) How responsive are ecomorphological patterns to changes in scale, either temporal (e.g., during the ontogeny of any individual or over the evolutionary history of a clade) or spatial (e.g., between different communities of fishes or different habitats)? (5) In a broader context, how does an organism's morphology interact with other intrinsic characteristics (e.g., behavioral repertoire, physiology) to define the fundamental niche, and with the environment to produce the realized niche?

We asked each of the contributors to address the following issues: to review past works in fish ecomorphology, to present new approaches, data, and ideas in their area of interest, and finally to suggest future directions for research in ecomorphology. As we learned and as you can see from this volume, some areas sustain active ecomorphological research programs (e.g., foraging, respiration, vision), while others are ripe for future research (e.g. non-visual sensory systems). In other fields, approaches other than ecomorphology (e.g., ecophysiology, behavioral ecology) may dominate an area (e.g., the central role of physiology in respiration), but there are important insights that would accrue from an ecomorphological analysis. Our desire is that this volume will highlight the unique perspectives and approaches that these investigators bring to ecomorphological research. We are sure that this synthesis of ideas will stimulate continued progress in ecomorphological research.

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