

The role of ecomorphological studies in the comparative biology of fishes

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Synopsis

The goal of an ecomorphological study is to understand the interactions between the morphology of organisms and their ecology. Both the morphology and the ecology presented by an organism are directly or indirectly under the influence of the environmental conditions that the organism experiences and its heritable composition. The development and interpretation of the central element of ecomorphological studies, the comparison between patterns of variation of morphological and ecological characters, depends heavily on the mechanistic framework provided by functional morphological and biomechanical studies. The cause-and-effect hypotheses derived from this comparison can be tested with performance trials. Ecomorphology forms an integral part of comparative biology, along with ecophysiology, behavioral ecology, and evolutionary ecology. Current issues in ecomorphological research that are addressed in this volume include application of a more functional approach to the choice of characters, integration of morphological, behavioral, and physiological information to address adaptation, and the expansion of spatial and temporal (ontogenetic and evolutionary) scales of ecomorphological questions. Future directions for ecomorphology include broadening the knowledge base, further integration of information from other disciplines, examination of the role of environmental and genetic factors in producing and maintaining ecological and morphological diversity, and application of ecomorphological insights to questions of community structure.

Introduction

Ecomorphology is a comparative, often strictly observational, approach to biology. While its antecedents have a long history, its modern integrated form is relatively young (Motta et al. 1995b). Ecomorphological comparisons are pitched at two levels: (1) among taxonomic units or life history intervals and (2) between their phenotypic characteristics (e.g. their morphology) and their use of ecological resources (i.e. their realized niche) in a particular environment. The core element of an

ecomorphological study consists of a comparison between patterns of variation in ecological characteristics and patterns of variation in morphological characteristics measured among the taxonomic units (e.g. genera, life history intervals, allopatric populations). These comparisons may be strictly qualitative (e.g. 'Species with morphology A tend to be found in habitat 1 . . .') or highly quantitative (e.g. 'The results of a canonical correlation analysis showed a correlation between morphological features X, Y, and Z and ecological features 2 and 4'). After developing these comparisons, ecomorpho-

logical studies may involve experimental tests of the inferred causal relationships or tracking changes in morphological and ecological characters through evolutionary history.

There have been a variety of attempts to conceptualize the interactions between morphology and ecology (e.g. Bock & von Wahlert 1965, Bock 1980, 1990, Barel 1983, Balon 1985, Liem 1991, 1993, Motta & Kotrschal 1992, Reilly & Wainwright 1994; see also Motta et al. 1995b, Smirnov et al. 1995). In our view, the phenotype of an organism and its realized niche are both products of complex interactions between the environment and factors intrinsic to an organism (Fig. 1). These intrinsic factors, which include its unique genotype, epigenetic interactions, and maternal effects, would lead to a defined set of phenotypic characteristics if independent of ecological influences. For many characters, the influence of the environment may modify the phenotypic expression of the intrinsic factors directly (i.e. triggering genetically-based phenotypic plasticity – Conover & Kynard 1981) or indirectly (through use-induced changes in phenotype under specific environmental conditions – Meyer 1987, Wainwright et al. 1991, Wimberger 1991). The realized niche of a species depends on the interactions of the phenotypic characteristics of an individual (defining its potential niche) and the physical and biological conditions present in the environment. The realized niche can influence environmental conditions through biogenic changes in the environment (e.g. changes in the prey community, alterations of local hydrological conditions). The realized niche can influence phenotype through use-induced changes. The realized niche can also influence intrinsic factors through its differential effects on fitness (growth and survival) among genetically-varying individuals over many generations (e.g. changes in gill raker numbers due to a competitor – Crowder 1986, see also Robinson & Wilson 1994).

In ecomorphological studies as in other multivariate studies, the choices of ecological characteristics (i.e. aspects of the realized niche) and morphological characteristics (i.e. aspects of the phenotype) are critical and should reflect those characters that the researcher regards as most important to the functional relationship being examined. Traditional

taxonomic or ecological characteristics may not be the best choices. The decision concerning characters in the analysis should be based on the results of functional morphological and biomechanical studies, which may also provide a causal framework for interpreting the ecomorphological correlations (e.g. Norton & Brainerd 1993). Development of an explicit cause-and-effect hypothesis between the morphological and ecological characters is critically important in order to separate spurious correlations or autocorrelations from those with a potentially causal basis.

Performance tests, conducted either in the laboratory or in the field, can be used to test this cause-and-effect hypothesis. Usually, one presents individuals of different morphotypes with the same ecological challenges and then monitors their performance under these conditions (e.g. Moody et al. 1983, Wainwright 1988, Norton 1991, 1995, Hernandez & Motta personal communication). An alternative strategy is to manipulate morphotypes experimentally and then to present them with the ecological challenge, but this has been used rarely because of the technical difficulties (but see Sinervo & Licht 1991, Sinervo et al. 1992). One of the assumptions of performance tests is that the ecological challenges being presented mimic conditions that would produce differences in fitness among the morphotypes under natural conditions (Arnold 1983, Lauder et al. 1993). Ideally, performance experiments should be designed to manipulate direct measures of fitness: fecundity and survivorship (e.g. Basolo 1990, Bronmark & Miner 1992, Moller 1992). Where this is not possible Arnold (1983) has proposed a two-step process in which the correlation between morphological variation and performance is determined first and then the relationship between variation in performance and fitness is measured. The appropriate performance standards will depend on the functional relationship under review and have included growth rate (e.g. Schluter 1994, 1995), locomotory rates (e.g. Webb 1986, Jayne & Bennett 1989, Losos 1990a,b, Nicoletto 1991, Garland & Losos 1994), and capture efficiency (e.g. Moody et al. 1983, Wainwright 1988, Norton 1991, 1995) among others.

Implicit in the invocation of fitness in perform-

ance studies is the concept of adaptation, that the correlation between morphological and ecological characteristics is the product of the natural selection among the taxa under examination. This ecomorphological correlation may result either from direct selection on the phenotypic characteristics of taxa to fit the unique physical and biotic characteristics of a particular site or from selective invasion from a broader species pool of those members whose phenotypic characteristics (evolved elsewhere) are appropriate to the new site. In either case, several authors (e.g. Gould & Lewontin 1979, Brooks & McLennan 1991, Lauder 1992, Lauder et al. 1993) have argued that to describe a specific morphological feature as having evolved to access an ecological resource requires demonstration that these historical transitions in morphology are coincident with ecological transitions. Discrepancies may be examples of exaptations (Gould & Vrba 1982), but this is a topic of debate (Reeve & Sherman 1993). Techniques to address the patterns of historical transitions in ecology and morphology are proliferating quickly (e.g. Pagel & Harvey 1988, Brooks & McLennan 1991, Losos & Miles 1994, Westneat 1995).

Ecomorphology of fishes and comparative biology

Ecomorphology forms part of the broader developing field of comparative biology. The goal of this growing field is to explore the interactions between the intrinsic characteristics of individuals or taxonomic units and their environment. Other interdisciplinary fields that embrace this goal include ecophysiology and behavioral ecology. Of these three fields, ecomorphology has tended to be more correlative and observational (see Wainwright & Reilly 1994), behavioral ecology has been driven more by optimality models (e.g. Krebs & Davis 1978) and ecophysiology by laboratory experimentation (e.g. Feder et al. 1987). Regardless of these differences in emphasis, each field examines the implications of individual variation in a phenotypic character on the ecological differences between species or other taxonomic units or the implications of ecological differences on phenotypic characters. Emerging

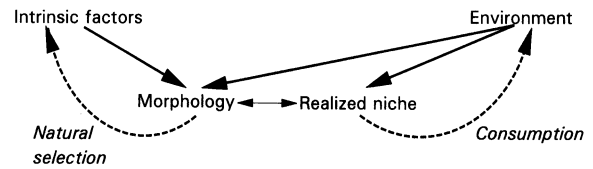


Fig. 1. Aspects of an organism's morphology (i.e. its phenotype) may be the result of the interaction between the environment, its use of resources, and intrinsic factors (e.g. genotype). Its morphology and the environment interact to produce its realized niche. The consumption of resources by an individual may alter its environment. Its relative success at turning resources into components of fitness (survival and reproduction) will affect the genotypes of subsequent generations via natural selection.

from these three interdisciplinary fields, which focus on the present, is evolutionary ecology which attempts to trace the historical patterns in the evolution of these phenotypic characteristics and to link them to environmental conditions where possible (e.g. Brooks & McLennan 1991, Nitecki 1990).

Clearly a complete understanding of the links between form (or any other phenotypic characteristic), function, and realized niche requires a synergistic attack incorporating ecology, behavior, physiology, morphology, genetics, and evolution. Very few systems have been studied in such a holistic way, but several of the most complete examples can be found in fishes. Block and her coworkers have examined the biological implications of regional endothermy among scombroid fishes. They have identified the morphological and physiological specializations that make regional endothermy possible; they have demonstrated the behavioral and ecological consequences of regional endothermy in the field and have traced its historical development among scombroid fishes (e.g. Block 1991, Block et al. 1993). Endler, Reznick, and their coworkers have manipulated the environmental conditions in streams to understand the reproductive biology and life-history styles of guppies (e.g. Endler 1983, Houde & Endler 1990, Reznick et al. 1990, Rodd & Reznick 1991). This work has been especially insightful in documenting the dynamic tension that exists between sexual selection and natural selection in field populations. Freshwater sticklebacks have been the focus of a variety of interdisciplinary studies (see Bell & Foster 1994). A large portion of these studies highlight stickleback foraging biology

(e.g. Lavin & McPhail 1985, 1986, Schluter & McPhail 1992, Schluter 1994, 1995) and their morphological defenses to predators (e.g. Reist 1980a, b, Bell et al. 1985, Reimchen et al. 1985, Baumgartner 1992, Reimchen 1992, Baker et al. 1995). The foraging biology of the North American centrarchids has also received extensive attention (e.g. Werner & Hall 1979, Mittelbach et al. 1992, Wainwright & Lauder 1992, Norton & Brainerd 1993, Wainwright & Richard 1995).

Contributions from the ecomorphology of fishes volume

It is our view that further progress in ecomorphological research will come from the broader context of comparative biology. This perspective was a major consideration as we organized a symposium for the 1992 Annual Meeting of the American Society of Ichthyologists and Herpetologists and is reflected in the contributions to this volume. The diversity of opinions and approaches included here clearly indicates the vigor of comparative biology, especially that subset that focuses primarily on the relationships between an organism's morphology, its realized niche, and the environment. The contributors include individuals whose primary research focus is the relationship between ecology and morphology and others whose primary focus may be described as more physiological, biomechanical, or evolutionary. While the individual papers contribute a wealth of new information and new ideas concerning specific ecomorphological relationships, particular taxa and communities, and biological systems, we have synthesized their more general contributions and conclusions on the ecomorphology of fishes. We center our discussion around five critical issues in current ecomorphological research. Ten years ago these questions would have been quite different, emphasizing the search for broad correlations between large numbers of ecological and morphological variables or for patterns of morphology and ecology consistent with the idea of a Hutchinsonian niche. Quite likely in another ten years the most pressing questions will be different from the five

that we have emphasized. Clearly ecomorphology, especially of fishes, is a dynamic field.

(1) How good is the basic fit between an organism's structure and its use of ecological resources when traditional taxonomic and ecological variables are used?

The use of traditional morphological and ecological variables may obscure ecomorphological relationships because of the confounding influence of evolutionary history or because these variables are not relevant to important functional relationships. In many ecomorphological studies the initial correlational analysis is based on morphological characters derived from systematic studies and ecological characters derived from phylogeny (e.g. prey types by taxa) or from broad habitat categories (e.g. benthic versus midwater). Often clear functional connections between the ecological and morphological characters are lacking. Such a 'shotgun' approach (e.g. Gatz 1979a, b) may produce correlations between morphology and ecology, but separating meaningful correlations from spurious correlations or autocorrelations is difficult. Potential ecomorphological relationships may be swamped by phylogenetic influences (Norton 1995). Even after narrowing the choice of morphological characters to those found important by other studies, Motta et al. (1995a) detected little overall ecomorphological correlation in a seagrass fish assemblage that spans a large part of the phylogenetic breadth of bony fishes. Some morphological associations did emerge when subsets of the ecological and morphological characters were analyzed for a part of the assemblage (Felley 1985). Motta et al. (1995a) also highlighted the morphological characters that most often appear to be influencing ecomorphological associations in their study and others. In contrast to the findings of Motta et al. in a taxonomically diverse system, Winemiller et al. (1995) have been successful in using a broad character set to document clear ecomorphological patterns for a single family of fishes, the Cichlidae, living in 3 riverine drainages: in central Africa, in Central America, and in South America. They also document pat-

terns of diversification and convergence in morphological structure and ecological niche among these cichlid faunas. Thus, the 'shotgun approach' appears to be more useful in ecomorphological studies when the suite of characters is narrowed to those that demonstrate some functional relevance and when they are applied with a narrow taxonomic focus (see also Douglas & Matthews 1992).

(2) Can we improve our conceptual or statistical fit between ecology and morphology by choosing non-traditional characters that reflect a clearer understanding of the functional potentials of specific structures and the ecological complexities facing fishes?

The characters chosen in an ecomorphological study should be restricted to those for which we have some knowledge of the potential functional relationship. The choice of appropriate morphological characters requires a clear understanding of the basic function of a particular structure, of the functional significance of morphological variation, and of the relationship between function and biological role (Bock & van Wahlert 1965, Bock 1980, Long 1995, Westneat 1995). Beginning in the 1970's, biomechanical and experimental functional morphological studies have increased greatly our understanding of the potential ecological role of particular morphological structures (e.g. Levine & MacNichol 1979, Sibbing 1982, 1988, Weihs & Webb 1983, Webb 1984, Sanderson et al. 1991, Liem 1993, and see Motta et al. 1995b). Kotschal's (1995) review of the current knowledge of the functional properties of solitary chemosensory cells in gadids and other fishes highlights the importance of functional morphology at the cellular level in interpreting ecomorphological diversity. The types of stimuli to which these diverse cells respond in the laboratory provide critical insights into their potential biological role in the field and into the design of appropriate performance tests. Similarly, van der Meer et al. (1995) show that in haplochromine cichlids interspecific differences at the cellular level can be related to differences in visual sensitivity and resolution, although not to ecological differences. Long (1995) approaches ecomorphology from a primarily

biomechanical perspective; specifically he examined the role of variation in the notochord and its biomechanical properties on the swimming performance of white sturgeon. One result of his study was a lack of correlation between swimming performance and those aspects of notochord morphology that he measured (e.g. curvature, angular stiffness, and diameter), yet the biomechanical properties of the notochord regions were correlated with performance. His conclusion was that this apparent contradiction may be resolved by modeling the notochord of the sturgeon as a pressurized cylinder, rather than a simple beam, thus requiring the measurement of different morphological characteristics. Alternatively, the performance of the swimming apparatus was due to the emergent properties of the locomotor morphology taken as a whole, rather than as separate elements. His research highlights the critical need to identify relevant morphological features as part of both performance tests and broader ecomorphological studies.

One important difference in recent ecomorphological studies is a trend to rely less on purely correlational approaches and to move towards the generation of predictions that can be tested in performance studies. Both Wainwright & Richard (1995) and Norton (1995) use insights derived from functional morphological studies of fish feeding to highlight a restricted set of characteristics of the oral jaws of the predators that appears to influence the prey composition in fish diets. Both of these studies make explicit, testable predictions of the relationship between morphological variation and ecological variation. The biomechanical model of Wainwright & Richard (1995) assesses the importance of variation in jaw morphology for the kinematics of mouth opening versus mouth closing; this model has clear ecological implications that are consistent with field diet data from a broad spectrum of fishes. In Norton (1995), predictions regarding the relationship between mouth size and feeding ecology in cottid fishes were supported by the results of performance studies in which elusive and non-elusive prey were presented to various species of cottids and their capture success was recorded. In another experimental study, Mensinger (1995) addresses the burglar alarm hypothesis for the evolution of biolu-

minescence in marine algae. In these innovative laboratory experiments he demonstrated the value of the concordance between the luminescence produced by dinoflagellates and the visual system of the midshipman to the foraging ecology of this fish. These fishes are capable of using the light flashes that are produced by dinoflagellates in response to disturbance by swimming mysids to increase feeding efficiency on these mysids. These studies represent a shift in ecomorphological studies away from a purely correlative, post hoc approach to a more predictive, a priori approach.

Just as a clear understanding of the functional roles of morphological features is critical to a proper ecomorphological analysis, a clear understanding of the demands placed on an organism by a particular environment is also critical. A poor ecomorphological correlation may be due to improper categorization or superficial understanding of the environmental conditions. In addressing the difficulties in ecological categorization, Luczkovich et al. (1995), Norton (1995) and Wainwright & Richard (1995) have all argued that prey types in the diet of a predator should be assorted by the functional challenges that the prey pose to the predator, not by their taxonomic affinities (see also Motta 1988). As an example of underlying ecological complexities, Martin (1995) demonstrates that the voluntary emergence of fishes from the water may be better considered as several distinct ecological styles in response to very different environmental conditions. The activities of amphibious marine fishes range from very active lifestyles by species that may forage or court when emerged to those of other species that show only minimal activity when emerged. These different styles have very divergent implications for the kinds of morphological structures that would be required to support these activities (e.g. locomotion, respiration). Thus, an alternative to the 'shotgun' approach is to focus on only a few morphological and ecological characters which are relevant to important functional challenges in the environment.

(3) When a structure plays a role in several biological 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?

It is unlikely that observed ecomorphological relationships will be perfectly matched to some theoretical optimum. Structures operate not in isolation, but in coordination with other structures and often in multiple contexts (Barel 1983). Deviation from some hypothetical ecomorphological optimum may reflect the constraints that other features impose on our targeted structure-function-ecology relationship. Alternatively, deviation from the hypothetical optimum may be due to interactions among the multiple functions that a single structure must perform; here the observed morphology represents a compromise among several functions and not the optimum solution to any single function.

The morphological variation present in allopatric populations of sticklebacks has proven to be a fertile area to examine these relationships. Baker et al. (1995) investigated the potential constraining role of a defensive structure (the pelvic girdle complex) on the reproductive ecology of three-spined sticklebacks. They had proposed that reductions in the development of the pelvic girdle could lead to increased clutch volumes of female sticklebacks. However, individuals with a fully developed pelvic girdle actually had larger clutch volumes than individuals lacking this defensive structure. They argue for a more holistic examination of the factors driving variation in clutch volume. Foster et al. (1995) had predicted that populations of the three-spined stickleback with larger mouth sizes (a potential adaptation for foraging on benthic prey) would be more predisposed toward courtship cannibalism of eggs, a life-history style, than would populations characterized by smaller mouth sizes. While comparisons among populations that differ in mouth size demonstrated no correlation between gape and courtship cannibalism, body size differences within populations did appear to be linked with courtship cannibalism. They present several alternative hypotheses for this pattern.

Similarly, Cech & Massingill (1995) explore the

potentially conflicting constraints operating on the pharyngeal apparatus of Sacramento blackfish in which the gill bars function not only in support of respiration, but also as the primary prey-capture surface for these suspension-feeding fishes. Blackfish altered a number of gill ventilation behaviors in response to both hypoxia and feeding. Regional separation of respiratory surfaces and prey capture surfaces within the gill apparatus allow this species to forage efficiently under both normoxic and hypoxic conditions. Understanding the potential constraints provided by other structures or other ecological roles should be one of the major focuses of ecomorphological research.

(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)?

Ecomorphological relationships do change as we expand either temporal or spatial scales. As a result of their often complex life-histories and pattern of indeterminate growth, fishes provide abundant opportunities to investigate ontogenetic changes in ecomorphological relationships. Individuals of many freshwater and marine fishes begin their lives as planktonic embryos and larvae, settle out of the water column into specific juvenile or nursery habitats and then gradually move into their adult habitats. These different habitats present dramatically different abiotic and biotic challenges, including changes in the hydrodynamic regime and habitat structure and a vastly different array of potential prey, competitors, and predators (e.g. Balon 1986, Crawford & Balon 1994, Wainwright & Richard 1995). Separate from these ecological transitions during growth, individual structures or groups of structures may demonstrate non-isometric growth, modifying their mechanical relationships to other structures and altering the functional abilities of fishes. Taken together, the often-abrupt ecological changes and smoother phenotypic changes may alter dramatically the ecomorphological patterns observed in fishes.

For many fish species ontogenetic transitions in their feeding ecology follow similar general trajectories that appear to be correlated with changes in body size and correlated structures (Norton 1991, Wainwright & Richard 1995). Not all fishes follow this general pattern however; Luczkovich et al. (1995) document contrasting ontogenetic changes in the trophic ecology and morphology of two important marine fishes. For snook, changes in body size lead to little change in the functional groups included in their diet, but growth by pinfish leads to dramatic shifts in functional groups in the diet: from prey types that can be captured by ram-feeding or suction to prey that can only be captured by biting. The importance of a clear understanding the implications of relative versus absolute size relationships between predators and their prey have also been discussed by Wainwright (1988), Galis (1990), and Wainwright & Richard (1995).

Intraspecific ecomorphological differences are not confined to ontogenetic changes alone; many studies have documented morphological and ecological differences among the individuals of a single nominal species (e.g. Turner & Grosse 1980, Crowder 1986, Lavin & McPhail 1986, Ehlinger 1990, Mittelbach et al. 1992). The focus may be on allopatric populations of a putative species complex (e.g. Foster & Baker 1995, Baker et al. 1995), on allotopic populations of a species (e.g. Baumgartner 1992, Chapman & Liem 1995), or on sympatric morphs of a single species (e.g. Kornfield et al. 1982, Sundland et al. 1992, Hori 1993). For example, the study by Chapman & Liem (1995) clearly documents differences in gill morphology between populations of a small cyprinid that inhabit a hypoxic swamp and populations that inhabit a well-oxygenated river. These intraspecific studies put the spotlight on the degree of morphological and ecological plasticity present in a species and may shed insights on the interaction between genetic, developmental, and environmental contributions to the morphological phenotype and niche breadth of a species.

Through much of its development, one of the central focuses in morphological research has been the desire to understand the patterns of historical change in morphological features and the evolutionary forces driving these changes (Liem 1991).

For the most part, ecology has been far less concerned with evolutionary history, and yet ecological interactions among species are subject to evolutionary pressures and are the product of their unique evolutionary histories. One potential outcome of ecomorphological studies is an understanding of the degree of co-evolution of morphology and ecology. However, morphological and ecological characteristics may have completely independent evolutionary histories. This creates both conceptual and practical problems for ecomorphological analyses. On a conceptual level, separating co-evolution of morphological and ecological characteristics from chance historical co-occurrence of these characteristics is a difficult task (Gould & Vrba 1982, Huey & Bennett 1986, Douglas & Matthews 1992). On a practical level, the statistical tests used to establish the initial ecomorphological correlation assume that each data point (e.g. species) in the morphology-ecology correlation matrix represents an independent historical event, an unlikely occurrence when analyzing closely-related species (see Felsenstein 1985, Losos 1990a). The incorporation of explicit phylogenetic information is becoming the new standard in the diverse fields that comprise comparative biology, including ecomorphology (e.g. Wainwright & Reilly 1994). Methods of addressing these problems are developing rapidly (e.g. Brooks & McLennan 1991). Westneat (1995) presents several alternative solutions to these evolutionary problems in ecomorphological studies. He illustrates their application by examining the evolution of the feeding ecology and feeding morphology among chelone wrasses. In his analysis Westneat traces the multiple evolution of suites of jaw characteristics and dietary patterns in this lineage. The value of this evolutionary approach is also clearly demonstrated by Winemiller et al. (1995). In this study information from morphology and feeding ecology was incorporated into the existing phylogeny to identify ecomorphological convergence and to compare the rate of evolutionary change among three independent cichlid faunas. The scope of ecomorphological research should be expanded to encompass broader spatial scales, longer temporal scales, and all stages of development.

(5) In a broader context, how does an organism's morphology interact with other phenotypic characteristics (e.g. behavioral repertoire, physiology) to define the fundamental niche and with environmental conditions to produce the realized niche?

With rare exception, morphological structures require appropriate behaviors and physiological support to function properly and therefore to meet the challenges presented by the environment. We have argued earlier that morphology, behavior, and physiology must be considered together to fully understand the abilities of an individual to survive in a specified environment. Any one of these aspects may limit its ability to respond to changes in environmental conditions. In many cases there are tight correlations among morphology, behavior, and physiology to meet a specific extrinsic challenge (e.g. Block 1991, Martin 1995). For example, the structure of the midshipman eye, the physiology of its photoreceptors and photosystems, and its behavioral repertoire are coordinated to use bioluminescence to improve prey capture success (Mensing 1995). Sacramento blackfish may alter several respiratory behaviors (e.g. ventilation rate) that are integrated with structural features (e.g. gape) to enable them to survive and even to feed under hypoxic conditions (Cech & Massingill 1995). These types of interdisciplinary studies highlight the importance and the advantages of integrating ecophysiology, behavioral ecology, and ecomorphology.

The future of ecomorphological research in fishes

Ecomorphology is a relatively young discipline (Motta et al. 1995b) and we foresee tremendous gains in a number of different areas. First, we need to add to the knowledge base. We need to apply ecomorphology analyses to additional functional systems, to broaden the taxonomic coverage, to include a wider range of habitats, and to incorporate all life history intervals. This comprehensive approach will allow us to estimate which ecomorphological interactions are general and which apply only narrowly to particular taxa, environments, life intervals, or systems. Second, we need to integrate

the results of ecomorphological studies with those from the other comparative fields: ecophysiology, behavioral ecology and evolutionary ecology. Clearly an understanding of phylogenetic relationships of the taxa under investigation is fast becoming a new sine qua non in ecomorphological research. Third, we need to apply the insights gained from ecomorphology to address the formation and maintenance of morphological and ecological diversity and the development of new species. Finally, ecomorphological studies can be critical to an understanding of community organization. In particular, ecomorphological studies can contribute to assessing the relative contributions to community structure by stochastic processes (e.g. chance invasion of species from another community) versus deterministic processes (e.g. interspecific differences in ability to invade or persist in a local habitat). This information can also be used to predict changes in community structure after disturbance.

Additions to the knowledge base

Progress in our understanding of ecomorphological diversity among the various functional systems of fishes has been uneven. The relationships between patterns of morphological diversity and patterns of ecological diversity are well known in some systems (e.g. vision, digestion, and foraging), incompletely known for some systems (e.g. locomotion and electroreception) and poorly known in others (e.g., sound detection, chemosensory abilities, and life-history characters). For example, the role of mouth size in determining diet has been explored by many studies (e.g. Schmitt & Holbrook 1984, Motta 1988, Schluter & McPhail 1992, Luczkovich et al. 1995, Norton 1995, Wainwright & Richard 1995). Interspecific differences in dentition have clear associations with interspecific differences in diet (e.g. Lauder 1983, Kotrschal & Goldschmid 1983, Stoner & Livingston 1984, Norton 1988, Motta 1989). Other studies have documented similar results for intraspecific differences in dentition and diet (e.g. Sage & Selander 1975, Turner & Grosse 1980, Kornfield et al. 1982, Turner et al. 1983, Liem & Kaufman 1984, Galis 1990, Wainwright et al. 1991, Mittelbach et al.

1992, Luczkovich et al. 1995). Often linked with specific dental features, digestive adaptations, including the structure and length of the intestinal tract, have clear correlations with the digestive demands that particular prey present to the predator (e.g. De Silva et al. 1980, Zihler 1982, Verigina 1991, Sturmbauer et al. 1992). Among visual systems, intra and interspecific differences in ocular structures, retinal pigments, and retinal organization are strongly correlated with the spectral environment and habitat characteristics (e.g. Levine & MacNicol 1979, Hobson et al. 1981, Herring 1982, Partridge 1989, Hueter 1990, Mas-Riera 1991, McFarland 1991).

The incompletely known or poorly known systems await the development of a better understanding of the functional role of morphological diversity and its ecological implications. Often basic descriptions of the environmental conditions (e.g. odor plumes, hydrodynamic regime) have proven to be difficult. Compared to our understanding of the visual system, the ecomorphological relationships for other sensory systems, such as mechanoreception and olfaction, are poorly known. For example, there is tremendous diversity among fishes in the placements and numbers of lateral line and cephalic canals, in degree to which these canals are open or closed, and in the distribution of canal versus superficial neuromasts (e.g. Blaxter 1987, Janssen et al. 1987, Coombs et al. 1988, Kalmijn 1989, Webb 1989). The functional significance and ecological correlates of this structural diversity is an area of research only now undergoing explosive growth (e.g. Jones & Janssen 1992, Denton & Gray 1993). The importance of chemoreception of environmental cues by olfactory organs or through solitary chemosensory cells is another fast-developing areas of sensory biology (e.g. Kotrschal et al. 1993, Whitear & Moate 1994, Kotrschal 1995). Progress in understanding the interactions of morphological diversity and ecological role in these systems will follow the development of a firm understanding of the biomechanics and functional morphology of these systems.

A majority of ecomorphological studies have been conducted in temperate freshwater lakes and streams from Europe and North America and in the tropical African Rift lakes (especially the cichlid

fauna). Surprisingly, there have been general ecomorphological surveys of only a few tropical reef systems (e.g. Davis & Birdsong 1973, Emery 1973, Motta 1988, 1989, Bellwood & Choat 1990, Purcell & Bellwood 1993, Wainwright & Richard 1995, Westneat 1995). This effort pales in comparison to the challenge of understanding the interrelationships among the diverse, complex faunas present in modern reef systems. Many other habitats have received only cursory treatments, including pelagic habitats (Ebeling & Cailliet 1974), meso- and bathypelagic environments (Casinos 1978, McLellan 1977), the non-cichlid faunas of tropical lakes (Nagelkerke et al. 1994), and the tremendously seasonal river systems of South America (Winemiller 1991, Winemiller et al. 1995), Asia (Wikramanayake 1980, Moyle & Senanayake 1984, Watson & Balon 1984), and Australia.

Most ecomorphological studies have focused on adult fishes. More studies are needed that examine communities composed of earlier life-history intervals. Largely unexplored are the ecomorphological relationships that may exist among the planktonic larvae of many fishes. There is clearly tremendous morphological diversity among fish embryos, larvae and juveniles (Lasker 1981, Balon 1985), but the ecological correlates have not been well-established. Functional studies and performance tests involving fish embryos and larvae are just beginning (Drost 1987, Drost et al. 1988, Osse 1990, Coughlin 1991).

Only a few ecomorphological studies have been conducted that have examined changes during the entire ontogeny of a species; a quick overview of the results of these studies reveals a diversity of responses in the interactions between morphological and ecological characteristic during ontogeny, not a consensus. Some features (e.g. visual pigments) demonstrate quick discrete morphological changes, apparently in response to the changing environment during habitat shifts (Boehlert 1978, 1979). As Luczkovich et al. (1995) and Wainwright & Richard (1995) have demonstrated some species may show gradual changes in their ecomorphological relationships during ontogeny, while other species do not. Further, the interaction of morphological changes during ontogeny and environmental condi-

tions may lead to unexpected threshold effects (Gallis 1990, Luczkovich et al. 1995). Tremendous potential exists for additional studies. The transition from planktonic larva to benthic juvenile is likely to be a fruitful area for in-depth investigation as the pace of morphological change is often increased during this abrupt habitat transition.

The majority of ecomorphological studies have been conducted on actinopterygian fishes, especially those groups either in or related to the Perciformes (e.g. Centrarchidae – Keast & Webb 1966, Werner 1977, Werner & Hall 1979, Wainwright et al. 1991, Mittelbach et al. 1992; Cichlidae – Hoogehoud et al. 1983, Witte et al. 1990, Winemiller 1991, Hori 1993, Winemiller et al. 1995; and the Labridae – Wainwright 1988, Sanderson 1990, Westneat 1990, 1995). Non-percomorph taxa that have been examined include the salmonids (e.g. Malmquist et al. 1992) and the cyprinids faunas of North America (e.g. Felley 1984, Douglas & Matthews 1992) and Europe (Kryzhanovsky 1949, Lammens & Hoogenboezem 1991), but large open horizons remain. For example, the morphologically and ecologically diverse catfishes and characins of Central and South America should be a very fertile area for ecomorphological research. Similarly, the diverse clinid and gobiid fishes of temperate and tropical marine waters are ripe candidates for this approach. While the feeding mechanics of bony fishes is well understood, experimental functional morphological studies of the feeding of elasmobranchs (Wu 1995, Motta et al. personal communication) is now in progress and will add to our understanding of ecomorphological relationships among these fishes.

Integration with other comparative fields

As we have already pointed out, there are tremendous advantages to viewing ecomorphological research within the synergistic framework of comparative biology. Morphological structures rarely operate in isolation; the appropriate behavioral and physiological supports are necessary for their proper function. For example, interspecific morphological specializations among centrarchids have been accompanied by modifications of motor patterns

used during the strike (Wainwright & Lauder 1986) that lead to differences in patterns of subambient pressure generation (Norton & Brainerd 1993) and produce interspecific differences in diet (Werner 1977, Werner & Hall 1979, Wainwright & Richard 1995). Among some embiotocids, the development of winnowing, a specialized prey handling activity, is the result of coordination of behavioral and morphological specializations that produce a unique diet in these species (Laur & Ebeling 1983, Drucker & Jensen 1991). Ontogenetic changes in the diets of pinfish are accompanied by morphological, behavioral, and physiological changes (Stoner & Livingston 1984, Luczkovich & Stellwag 1993, Luczkovich et al. 1995).

These ecological, morphological, behavioral, and physiological changes need not appear simultaneously. Tracing the co-evolution of these changes requires an understanding of the historical relationships among taxa. This information is critical to identifying morphological and ecological convergence and divergence within a taxon (e.g. Wainwright & Lauder 1992, Winemiller et al. 1995, Westneat 1995). In the future, ecomorphological studies will need to address the phylogenetic history of its taxa as an integral part of the analysis.

The generation of ecological and morphological diversity

It is clear from examining the contributions of this volume and of other investigations that there is a split in ecomorphological studies between those that focus on intraspecific ecomorphological patterns and those that compare ecomorphological relationships between species, either because they are closely related or because they are members of a local assemblage. The intrinsic advantage of intraspecific studies is a closer adherence to the *ceteris paribus* assumption central to ecomorphological investigations and freedom from some of the statistical difficulties in interspecific comparisons (see Westneat 1995).

Intraspecific variation in ecomorphological patterns can be studied at three scales, ontogenetically, allopatrically, and sympatrically. In the first, the de-

gree of concordance between morphological and ecological characteristics can be examined during the ontogeny of a species either throughout its range or locally (see above). In the second, ecomorphological comparisons can be made among allopatric populations of a species especially if these allopatric sites appear to show great differences in their abiotic or biotic environments (Endler 1983, Lavin & McPhail 1985, Wainwright et al. 1991, Mittelbach et al. 1992, Swain 1992a, b, Baker et al. 1995, Chapman & Liem 1995). Finally, the presence in sympatry of multiple morphs of a single fish species has garnered considerable scientific attention (reviewed by Robinson & Wilson 1994). Intraspecific trophic polymorphisms have been identified in a variety of taxa including salmonids (Malmquist et al. 1992, Sandlund et al. 1992), sticklebacks (Lavin & McPhail 1985, 1986, Schluter & McPhail 1992, Schluter 1994), cichlids (Sage & Selander 1975, Kornfield et al. 1982, Witte et al. 1990, Hori 1993), centrarchids (Ehlinger & Wilson 1988), characoids (Roberts 1974), and goodeids (Turner & Grosse 1980, Turner et al. 1983). The predominance of freshwater, lacustrine examples, and the lack of marine or riverine examples poses an interesting question: is there something unique to the lakes that leads to the development of polymorphisms or does the abundance of examples from lakes simply reflect the preponderance of ecomorphological studies in these lacustrine habitats.

The relative contributions of genetic versus environmental factors in producing the various forms of phenotypic plasticity remains unclear for many taxa (see review in Robinson & Wilson 1994). At one end of the spectrum, Hori (1993) has demonstrated that the handedness polymorphism in a scale-eating cichlid is clearly under tight genetic control, but the frequency of different morphs depends on frequency-dependent selection. At the other end, in pumpkinseed sunfishes the development of molariform morphs depends on the availability of durophagous prey in the environment and the incorporation of these prey into the diet (Wainwright et al. 1991, Mittelbach et al. 1992). The role of intrinsic, environmental, and use-driven factors (see Fig. 1) in producing polymorphisms will be an active area for future research.

A major unanswered question concerns the role of polymorphisms, especially in panmictic sympatric populations, in inhibiting or promoting morphological and ecological diversity. The development, fixation and ultimate reproductive isolation of distinct morphs due to disruptive selection may promote the development of morphological and ecological diversity in a community. However, the presence of a polymorphic species may inhibit invasion by other taxa because the polymorphic species is occupying a wider ecological niche and thus usurping ecological resources. For example, are the four distinct morphs of Arctic charr described by Malmquist et al. (1992) and Sandland et al. (1992) on their way to forming distinct species or do they form a stable metasppecies that excludes other species from inhabiting these lakes? The potential role of polymorphisms in generating species diversity among fishes was discussed extensively in Echelle & Kornfield (1984) and remains a controversial topic today.

Composition of ecological communities

For over seventy-five years two contrasting views have dominated the debate over the organization of communities (Jackson et al. 1992). Clements (1916) argued that communities are discrete assemblages of species with tight biotic connections; in contrast, Gleason (1926) argued that communities are chance associations of species which overlap in some abiotic requirements, but lack tight interconnections. The contentious nature of this debate can be seen in arguments over stochastic versus deterministic patterns of community structure (e.g. Grossman et al. 1982 versus Rahel et al. 1984 and Yant et al. 1984 or Gladfelter & Gladfelter 1978 versus Sale 1978) and random versus nonrandom assemblages (e.g. Gilpin & Diamond 1984 versus Connor & Simberloff 1984).

Ecomorphological studies can play a central role in these debates. Ecomorphological studies not only contribute insights into the role of biotic and abiotic factors in determining the distributional limits of individual species but also can address the integration of species within communities, especially among competitors. The resources available to

and needed by fish are to some extent predictable. Winemiller (1991) in a survey of five independently-derived fish assemblages distributed from boreal regions to the tropics has identified consistent, convergent ecomorphological patterns among these assemblages. Winemiller et al. (1995) reports similar results from a comparison of riverine cichlid assemblages in Africa, Central America, and South America. Functional morphological, ecological, and morphological studies have demonstrated convergence in the foraging biology of cichlids and centrarchids (e.g. Norton & Brainerd 1993). Schluter & McPhail (1992) present several examples of multiple invasions by sticklebacks from the marine environment into freshwater lakes that have been accompanied by consistent, predictable changes in morphology and ecology. Robinson & Sloan (1994) in their review of character release and displacement in fishes have argued that niches in part are properties of the environment into which new fish species invade or evolve. These studies would argue that deterministic elements do play an important role in the structure of these fish communities. However, the importance of deterministic elements may decline in communities dominated by frequent disturbance, broad dispersal potential, and high diversity.

Finally, insights from ecomorphological studies may be used to predict the impacts on existing communities by biotic or abiotic disturbance, including the invasion of new species. Several studies have documented dramatic shifts in community composition and the morphology of community members after invasions. Witte et al. (1990) recorded dramatic changes in the abundance of haplochromine cichlids after the introduction of Nile perch as well as shifts in several morphological characters. Similarly, Crowder (1986) documented ecological and morphological shifts in the trophic biology of bloaters, *Coregonus hoyi*, that followed dramatic increases in the populations of the introduced alewife, *Alosa pseudoharengus*, and simultaneous changes in zooplankton resources. All of these changes can be interpreted after the fact as a result of ecomorphological interactions between the invaders and the existing community. Ecomorphological studies can also be applied in a more pro-active way to predict

changes in community structure that would result from species introductions or other anthropogenic manipulations (e.g. Balon et al. 1986, Sibbing et al. 1994, Smirnov et al. 1995). For example, Balon et al. (1986) used the results from a broad ecomorphological study to predict several changes in European fish communities that would be produced from the mixture of faunas after the construction of a ship canal connecting the North Sea to the Black Sea via the Danube, Main, and Rhein rivers. Ecomorphological studies will be hard pressed to keep up with the pace of anthropogenic change.

Ecomorphological studies form part of the core of organismal biology and ecology. They provide important insights into the structure of ecological communities and at the forces driving the evolution of species. This is especially true when combined with insights derived from the other facets of comparative biology. We are confident that this active area of research will continue to grow and to contribute to our understanding of the biology of fishes.

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