Chapter 3

Ecomorphology of centrarchid fishes

D. C. Collar and P. C. Wainwright

3.1 Introduction

From the ecologist's perspective, centrarchid fishes are widely recognized as a model system for investigating the role of phenotypic variation in shaping ecological patterns. To the ichthyologist, this group is considered among the most morphologically and ecologically diverse of North America's freshwater ichthyofauna. This chapter is intended to bring these perspectives together, highlighting the contributions of studies linking resource use patterns to morphology in order to make sense of the ecological, functional, and morphological diversity exhibited within the Centrarchidae. We review literature on feeding and on locomotion.

Historically, the diversity represented within this radiation helped inspire the development of ecomorphology, a research perspective that investigates hypothesized associations between organismal design and ecology. Working independently, Werner (1974, 1977) and Keast (1978, 1985; Keast and Webb 1967) were among the first to point out a general association between head and body form and resource use in centrarchid species. Using bluegill sunfish (*Lepomis macrochirus*), green sunfish (*Lepomis cyanellus*), and largemouth bass (*Micropterus salmoides*) to represent the range of ecological and morphological diversity in centrarchids, Werner and coworkers developed the first mechanistic insights into the implications of variation in body and head morphology. The diversity of form and feeding habits represented by bluegill, largemouth bass, black crappie (*Pomoxis nigromaculatus*), and rock bass (*Ambloplites rupestris*) motivated Keast's proposal that different suites of morphological features confer varying prey capture and habitat use capabilities on these species and that these differences underlie the capacity for these species to coexist in sympatry. The rationale for ecomorphology research can be seen in both Werner's and Keast's work: an organism's morphology affects its capacity to perform an ecologically relevant task, and this performance capacity affects the resources available for its use.

This research program was made more explicit (Werner 1977; Mittelbach 1984; Wainwright 1996) by emphasizing that researchers' ability to explain ecological phenomena through organismal design requires focus on characters whose performance consequences are predictable. This stipulation established a primary role for functional morphology research, which investigates the morphological basis of performance variation. Moreover, the ecomorphology research perspective led to widespread recognition that the choice of an appropriate performance measure is vital to the success of studies that seek to understand the relationship between morphology and resource use. Performance variables range from proximate measures that focus on the mechanical capacities of isolated functional units, such as maximum pharyngeal jaw bite force, to more integrative measures that involve multiple functional units, like prey handling time, which is influenced by the fish's ability to capture and process prey. In either case, the performance measure should have predictable consequences for resource use. This is not a trivial issue, as the link between any given performance measure and resource use is more frequently assumed than demonstrated. Nevertheless, studies involving centrarchid fishes provide some of the best examples of the ecomorphology research program carried out to completion.

The morphological diversity of centrarchid fishes ranges between the forms exhibited by the predominant ecomorphs: piscivore/crayfish predator, zooplanktivore, molluscivore, and insectivore, which possess combinations of head and body characters that are associated with different patterns of resource use. Although these ecomorphs are named according to trophic habits, they are generally associated with habitat use patterns as well. Here, we highlight a set of morphological characters that have well-known consequences for performance and resource use. We focus on mouth gape, degree of hypertrophy of the pharyngeal jaw [as represented by the size of its primary adductor muscle, the levator posterior (LP)], and body depth as a set of morphological characters that separate the major ecomorphs in morphospace (Figure 3.1), and we discuss the work that has investigated the degree to which these characters explain ecological variation.

Piscivores/crayfish predators: As typified by species of *Micropterus* and warmouth (*Lepomis gulosus*) and to a lesser degree species of *Ambloplites*, these fishes have large mouths, gracile pharyngeal jaws, and relatively shallow bodies. They feed mostly on fish and crayfish in the open water, with some specializing on densely vegetated habitats (e.g., warmouth).

Zooplanktivores: This ecomorph is best represented by the bluegill, which is the most planktivorous centrarchid species. They are small-mouthed with gracile pharyngeal jaws and deep bodies, and they feed heavily on zooplankton in the open water or in vegetated areas.

Molluscivores: The molluscivorous centrarchids are the redear sunfish (*Lepomis microlophus*) and the pumpkinseed (*Lepomis gibbosus*), which are superficially similar to the bluegill, possessing relatively small mouths and deep bodies. However, they have hypertrophied pharyngeal jaws that deliver a bite forceful enough to crush snails.

Insectivores: These fishes tend to possess intermediate character values of mouth size, pharyngeal jaw robustness, and body depth. An example of an insectivore is the black crappie; however, fishes classified as insectivores display a variety of forms. They feed predominantly on aquatic immature insects in various habitats, including vegetated areas, the benthos, and the water surface.

3.2 Ecomorphology of feeding

Diets of centrarchid fishes can be explained in terms of maximizing benefits obtained from a prey item (e.g., energy) relative to costs incurred in obtaining it (e.g., time and energy involved in pursuit, capture, and processing; Werner and Hall 1974; Mittelbach 1981; Werner *et al*. 1981; Werner *et al*. 1983; Osenberg and Mittelbach 1989). As prey impose different functional demands on fish predators for their capture and processing, the costs for an individual fish will vary across prey types. Fish predators vary in morphology and performance capabilities, and the cost to consume a particular prey type should vary across individuals and species. This framework for investigating diet differences, which is known as optimal foraging theory, provides a set of clearly defined performance measures that are based on the costs predators incur when foraging and includes pursuit time, success rate of capture, and handling time. In this section, we focus on the morphological variables that underlie these integrative measures of performance as well as some of the proximate, functional performance measures that contribute to them. The feeding apparatus of centrarchid fishes is composed of two functional units: the oral jaws, which are used in prey capture, and the pharyngeal jaws, which are involved in prey processing. Due to their different functional roles, we discuss these two systems separately.

3.2.1 Oral jaws and prey capture

Prey capture in centrarchid fishes is accomplished by ingesting a volume of water containing a prey item. During a strike, rapid expansion of the buccal (i.e. mouth) cavity results from a linked series of movements of head elements, including elevation of the neurocranium (NC), depression of the lower jaw, depression of the floor of the mouth, and abduction of the suspensorium and operculum (Lauder 1985; Figure 3.2). As water is incompressible, the increase in volume of the buccal cavity causes water to flow into the mouth. The goal for a feeding fish is to use this flow of water to carry the prey item into its mouth. This mode of feeding is called suction feeding, and it imposes specific functional demands on the fish predator for successful prey capture. We will show that suction feeding performance is influenced by the size of the fish's mouth, its ability to open and close its mouth rapidly, as well as its capacity to accelerate a volume of water and generate high velocity flow.

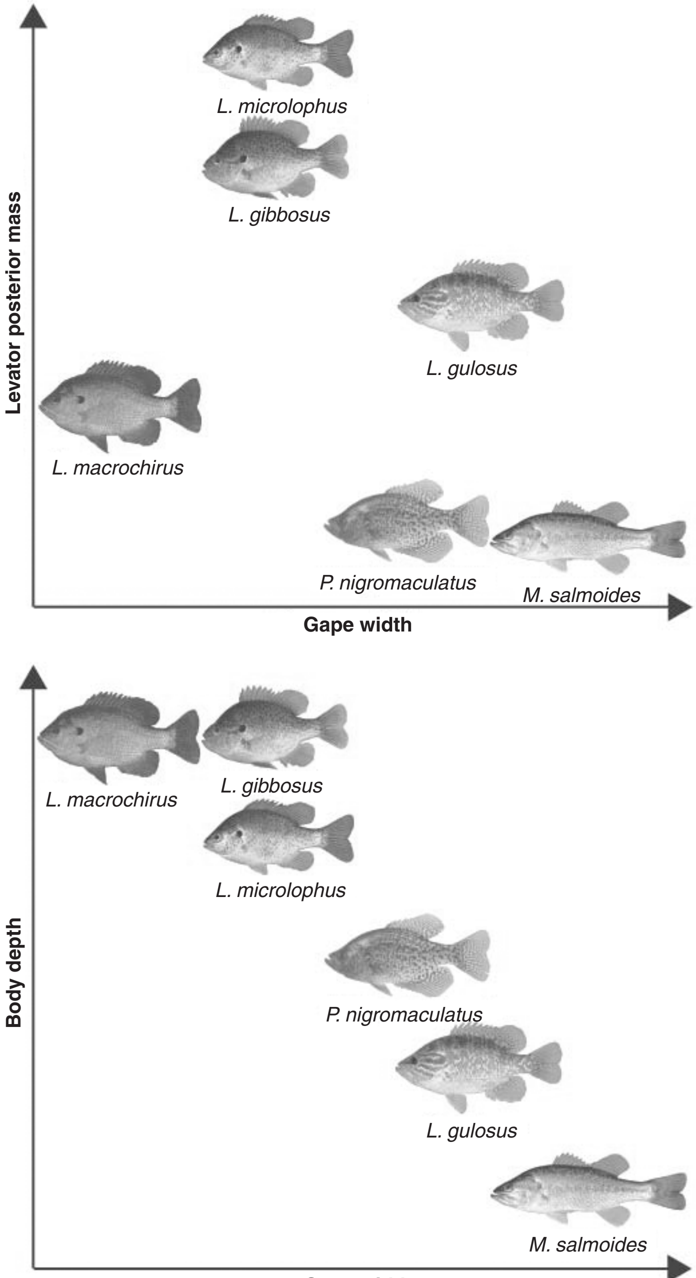

Figure 3.1 The distribution of six centrarchid species in a schematic morphospace. Axes are size-independent morphological characters whose resource-use consequences have been well studied: oral jaw gape width, levator posterior muscle mass (an indicator of pharyngeal jaw robustness), and body depth. Placement of centrarchid species in this morphospace illustrates the suites of character values that describe the predominant ecomorphs: *Lepomis macrochirus* represents the planktivore ecomorph, *Lepomis microlophus* and *Lepomis gibbosus* are molluscivores, *Pomoxis nigromaculatus* is an example of an insectivore, and *Lepomis gulosus* and *Micropterus salmoides* are piscivore/crayfish predators.

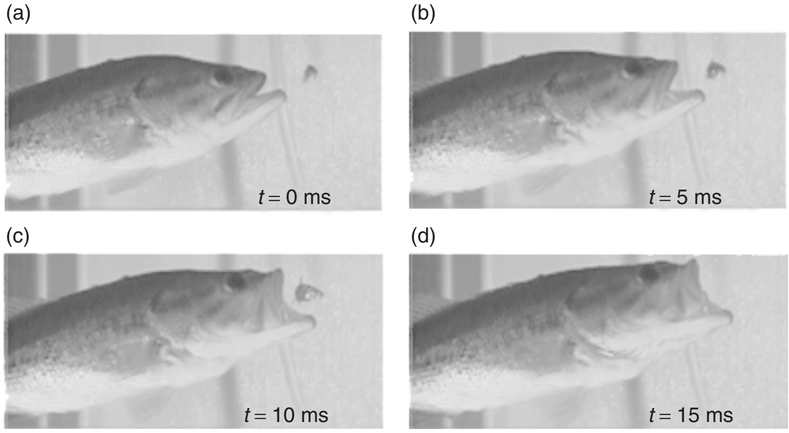

Figure 3.2 High-speed video images of a largemouth bass striking fish prey. Time is indicated in the lower, right corner of each frame. Frames represent (a) the initiation of the strike, (b) lower jaw depression, (c) hyoid depression (i.e. depression of the floor of the mouth cavity) and cranial elevation, (d) maximum buccal expansion and prey capture. These movements of cranial elements expand the buccal cavity and characterize suction feeding, the primary mode of prey capture for all centrarchid species.

3.2.1.1 Oral jaws gape width underlies variation in size of prey consumed

As prey are ingested whole, the size of the predator's mouth places an absolute size limit on prey that it can engulf (Werner 1974). Prey items vary in size, and so individual fish should exhibit variation in their success rate or efficiency of capture across prey types. Therefore, differences among individuals or species in mouth size should reflect variation in diet (e.g., Huskey and Turingan 2001). This simple hypothesized relationship has been thoroughly investigated and used to explain multiple ecological patterns in centrarchid species (Werner 1977; Wainwright and Richard 1995).

Werner (1977) showed that the maximum and optimum sized prey for a species is at least partly a function of mouth size. Using performance trials on prey of different sizes (*Daphnia* and fish), Werner measured cost as the sum of pursuit and handling times for bluegill, green sunfish, and largemouth bass. When cost is given as a function of prey size, the rank order of optimum sized prey (i.e. the prey size at minimum cost) and maximum sized prey for each species correspond to the rank order of mouth size (bluegill < green sunfish < largemouth bass) (Figure 3.3). Werner extended this analysis by quantifying the distribution of prey sizes available and successfully predicted resource utilization along this axis in each species. Furthermore, he predicted that because of its intermediate position on the niche axis, green sunfish should be excluded from habitats that contain both largemouth bass and bluegill—a pattern that is generally observed in natural systems (Hubbs and Cooper 1935; Bennett 1943; Trautman 1957; Werner *et al*. 1977).

Wainwright and Richard (1995) further demonstrated the role of mouth size in explaining variation in ontogenetic diet shifts among species. In this study, the dietary data of Keast (1985) was translated into an index of average prey size and the relationship between this variable and mouth gape was investigated in bluegill, largemouth bass, rock bass, and black crappie. Although these species exhibit extensive variation in average prey size at any given body size, this variation collapses when this diet variable is given as a function of mouth gape. Ontogenetic diet switches to larger prey items are shown to occur at approximately the same mouth gape despite occurring at different body sizes in these species. A key insight gained from this work is that the consequences of mouth gape on prey size explain ontogenetic diet shifts, a very general pattern in fish foraging ecology.

3.2.1.2 Lever mechanics of the lower jaw influence the rate of mouth opening and closing

The speed with which a fish can open and close its mouth during a strike is also partly determined by the ability of the lower jaw to transmit force and velocity generated by muscles. The lower jaw can be modeled as a simple lever system.

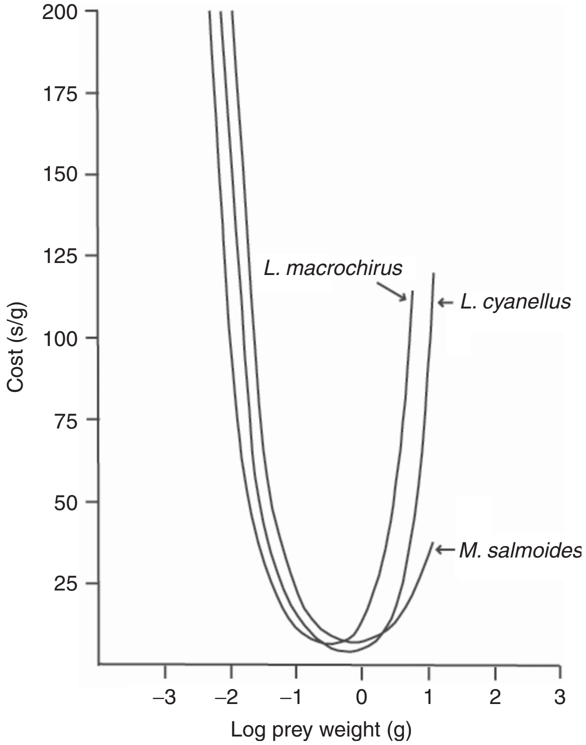

Figure 3.3 Cost of prey capture (in time per unit of prey mass) as a function of prey size in bluegill (*Lepomis macrochirus*), green sunfish (*Lepomis cyanellus*), and largemouth bass (*Micropterus salmoides*). Cost for each species is estimated for a common body size (200 g) and is a function of pursuit and handling times measured in lab performance trials. Rank order of optimum and maximum-sized prey for each species corresponds to rank order of mouth size. (Redrawn from Werner 1977, *American Naturalist,* Figure 3.7, University of Chicago Press.)

The mandible depresses when tension in the interoperculo-mandibular ligament pulls its postero-ventral margin, which acts through a lever arm to rotate the lower jaw at the joint between the articular bone of the mandible and the quadrate bone of the suspensorium (Figure 3.4). The mouth closes when the adductor mandibulae muscle, which originates in the suspensorial fossa and inserts directly on the medial face of the mandible, contracts and works through its lever arm to rotate the lower jaw at the articular-quadrate joint (Figure 3.4). Wainwright and Shaw (1999) showed that differences in these lever arms accurately predict variation in time to open and close the mouth in bluegill, spotted sunfish (*L. punctatus*), and largemouth bass. As a fish's ability to capture elusive prey is in part limited by its capacity to open and close its mouth before the prey can escape, variation in opening and closing lever arms should reflect success rate and handling time on elusive prey. Although this relationship has not been investigated in centrarchid fishes, other fish groups, such as Labridae, exhibit an association between lower jaw lever mechanics and amount of elusive prey in the diet (Westneat 1995).

3.2.1.3 Capacity to generate subambient pressure inside the mouth cavity affects forces exerted on prey

Feeding performance in a suction feeding fish is also determined by its capacity to draw a volume of water containing the prey into its mouth before the prey can escape. Expansion of the buccal cavity and resultant induced flow of water into the fish's mouth is associated with a drop in pressure inside this cavity, and the fish must be able to overcome the hydrodynamic loading exerted by the pressure gradient (Alexander 1969; Carroll *et al*. 2004). For an individual fish, more rapid expansion results in a greater magnitude of pressure drop (Sanford and Wainwright 2002; Svanbäck *et al*. 2002),

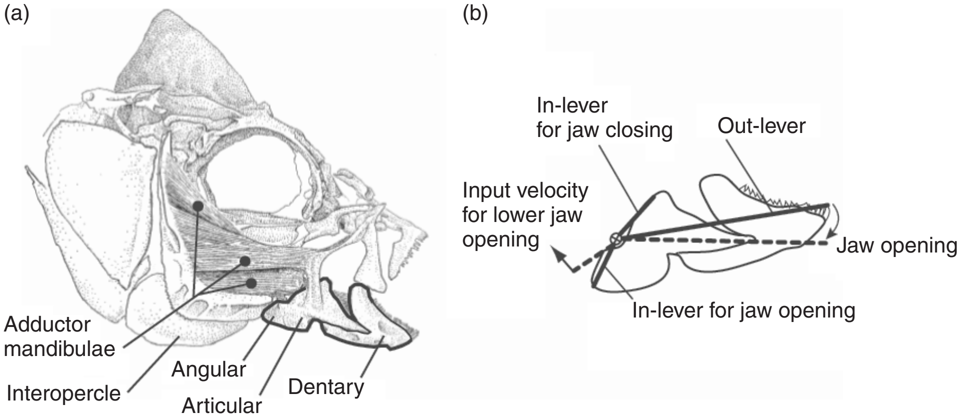

Figure 3.4 (a) Skull of a bluegill with fully opened mouth. The figure highlights structures that contribute to mouth opening and closing. The mandible (i.e. lower jaw) is composed of the dentary bone, which bears the teeth, articular bone, which articulates with the quadrate bone (deep to the adductor mandibulae muscle, not shown) to form the jaw joint, and the angular bone. The interoperculo-mandibular ligament (not shown) runs from the interopercle bone to the postero-ventral margin of the lower jaw and contributes to lower-jaw depression when the operculum retracts and abducts. The adductor mandibulae muscle originates on the suspensorium and attaches to both the upper and lower jaws; it provides power for mouth closing. (b) The lever arms of the lower jaw, modified from Wainwright and Shaw (1999, Figure 3.1). The in-lever for jaw opening is the distance between the point of rotation of the lower jaw (the articular-quadrate joint, indicated by the encircled X) and the insertion of the interoperculo-mandibular ligament. The in-lever for jaw closing is the distance between the rotation point of the jaw and the insertion point of the adductor mandibulae muscle. Force and motion are transmitted to the tip of the mandible through the out-lever, which is the length of the lower jaw. Jaw opening is illustrated by dashed lines.

and thus, rate of expansion is limited by the loading a fish can resist. In addition, differences in capacity to generate a pressure gradient in front of the striking fish's mouth are associated with differences in patterns of flow (Muller *et al*. 1982; Van Leeuwen 1984; Lauder and Clark 1984; Higham *et al*. 2006b), which affect the forces exerted on the prey. For these reasons, magnitude of the pressure drop in the buccal cavity has been used as a measure of suction feeding performance in centrarchid fishes (Norton and Brainerd 1993; Grubich and Wainwright 1997).

Carroll *et al*. (2004) developed and empirically tested a biomechanical model that uses static morphological variables to predict the maximum capacity of individual fish to generate subambient pressure inside the buccal cavity. Rotation of the NC is a major contributor to buccal expansion and is actuated by contraction of the epaxial muscles that attach to the supraoccipital crest and posterior portion of the NC (Lauder 1980). The epaxial muscles generate force that is transmitted through a moment arm to elevate the NC and expand the buccal cavity (Figure 3.5). The model predicts the magnitude of the pressure drop based on the transmission of force from the epaxial muscles to the expanding buccal volume (see Figure 3.5 for derivation) and allows the suction performance of any individual fish to be predicted from its morphology. Using a size range of bluegill, spotted sunfish, redear sunfish, largemouth bass, and black crappie, Carroll *et al*. (2004) tested this model by regressing the predicted pressure based on morphology against the largest magnitude pressure drop measured for individual fish. These species span the range of morphological and trophic diversity within the group and reveal that the model has strong predictive ability ($r^2 = 0.71$; Figure 3.5).

This model offers a mechanistic explanation for an often observed association between morphology and feeding behavior in suction feeding fishes: small-mouthed, deep-bodied fishes, such as bluegill or pumpkinseed, tend to have large magnitude pressure drops and use little body movement during a strike, whereas large-mouthed, slender-bodied fishes, such as largemouth bass, tend to have reduced pressure drops and rely more on acceleration of the body to overtake prey (Norton and Brainerd 1993). As mouth size correlates with projected area of the buccal cavity, and as body depth correlates with epaxial physiological cross sectional area (PCSA, which is proportional to its force capacity) and its moment arm, the model explains the association between these morphological characters and suction performance. Although fish with larger mouths are capable of engulfing larger prey items, they suffer a decrement in capacity to generate suction. These fishes

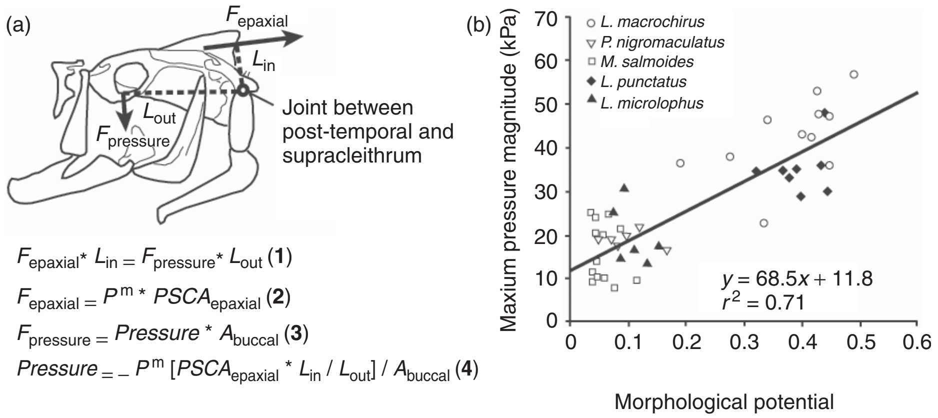

Figure 3.5 (a) Model of force transmission during buccal expansion illustrated on a largemouth bass skull redrawn from Carroll *et al*. (2004, Figure 3.2A). At the moment of minimum subambient pressure, force generated by the epaxial muscles (F_{epaxial}) acting through its moment arm (L_{in}) is equal to the force due to the intra-oral pressure drop (F_{pressure}) acting through its moment arm (L_{out}) (1). As the force generated by the epaxial muscles is equal to the product of physiological cross-sectional area of the muscle (PCSA$_{\text{epaxial}}$; m^2) and its specific tension (P^m) given in units of force per length squared (N/m^2) (2), and using the definition of pressure as force over projected area of the buccal cavity (A_{buccal}; m^2) (3), the above equation can be rewritten to give a relationship that predicts the magnitude of the pressure drop (4). (b) Regression of maximum pressure magnitude measured in lab feeding performance trials against morphological potential [(PCSA$_{\text{epaxial}}$ * ($L_{\text{in}}/L_{\text{out}}$)/$A_{\text{buccal}}$)] in various centrarchid species modified from Carroll *et al*. (2004, Figure 3.5). The model predicts a substantial amount of the variation in maximum pressure magnitude ($r^2 = 0.71$) and provides an accurate estimation of specific muscle tension ($P^m = 68.5$ kPa).

might compensate for the reduced pressure gradient by swimming to overtake their prey. On the other hand, small-mouthed fishes might be capable of using the induced flow to exert larger forces on the prey. Indeed, Collar and Wainwright (2006) found that evolutionary changes in gape width have contributed more than any other model variable to the evolution of suction performance in centrarchids. Using the centrarchid phylogeny from Near *et al*. (2005) and measurements of the model's morphological variables in 28 species, this study showed that gape width independently explains more than twice as much evolutionary change in suction capacity as any other variable even though all morphological variables underlie evolutionary change in suction capacity (Collar and Wainwright 2006). These studies provide insights into the link between morphological and functional diversity, but additional research is required to determine the consequences of variation in suction capacity for resource use. Although initially thought to increase the distance from which prey can be sucked into the mouth (Norton and Brainerd 1993), buccal pressure shows no relationship with the distance between predator and prey at the time of initiation of the strike (Wainwright *et al*. 2001; Svanbäck and Wainwright 2002).

3.2.2 Pharyngeal jaws and prey processing

Following capture, prey are processed in the pharyngeal jaw, a set of modified branchial arches immediately anterior to the esophagus. In centrarchids, prey processing includes both transport of prey from the mouth cavity to the gut as well as mastication of prey prior to transport. In fact, bite force of the pharyngeal jaw underlies the capacity for molluscivory in centrarchid fishes (Lauder 1983; Wainwright *et al*. 1991; Huckins 1997).

The pharyngeal jaw bite is accomplished by depression of the upper jaw against a stabilized and slightly elevated lower jaw. Bite force is primarily generated by the LP muscle, which actuates upper jaw depression through a simple linkage system (Wainwright 1989; Galis and Drucker 1996). The LP muscle originates on the postero-lateral face of the NC and inserts on the distal region of the dorsal side of the fourth epibranchial bone (EB 4; Figure 3.6). When this muscle contracts, it causes rotation of EB 4, which articulates with the dorsal surface of the upper jaw (third pharyngobranchial

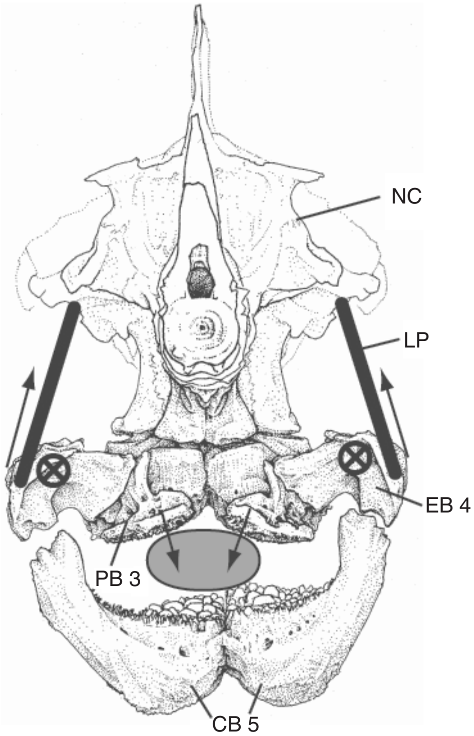

Figure 3.6 The snail crushing mechanism illustrated on a redear pharyngeal jaw in posterior view. The prey item (shown as a gray oval) is positioned between the upper and lower jaw tooth plates. Force for crushing the prey is generated by the levator posterior (LP) muscle, which originates on the neurocranium (NC) and inserts on the distal region of the arch-shaped fourth epibranchial (EB 4) bone. Contraction of the LP results in rotation of EB 4 about its center (indicated by the encircled X), actuating depression of the upper jaw (PB 3). This downward force is resisted by a stabilized and slightly elevated lower jaw (CB 5).

bone, PB 3), causing it to depress (Wainwright 1989; Figure 3.6). The lower jaw (fifth ceratobranchial bone, CB 5) resists this force and contributes somewhat to bite force by elevating as a result of its linkage with the distal region of EB 4 (through connection with the fourth CB; Galis and Drucker 1996).

The ability of a fish to crush snails is determined by its pharyngeal jaw bite force. Snails are positioned between the upper and lower tooth plates and cracked when the compression force exceeds the strength of the snail's shell. Molluscivorous centrarchid species, the pumpkinseed and the redear sunfish, possess hypertrophied pharyngeal jaws, including a more massive LP muscle, which is capable of generating a more forceful bite, larger bones, which transmit and resist this force, and molariform teeth (Lauder 1983). The relationships between sizes of these pharyngeal jaw elements, snail crushing performance (i.e. bite force), and percent of diet made up of snails contribute to a variety of ecological patterns within and between centrarchid species. We focus primarily on mass of the LP muscle as an indicator of pharyngeal jaw hypertrophy, but note that mass of the LP muscle correlates with a suite of pharyngeal characters, including robustness of bones, sizes of other muscles involved in the pharyngeal bite cycle, as well as tooth shape (Lauder 1983).

Pumpkinseed sunfish exhibit trophic polymorphism across Michigan lakes, varying in degree of hypertrophy of their pharyngeal jaws and consumption of snails (Wainwright *et al*. 1991). Typically, pumpkinseed occur in lakes with a predator, largemouth bass, and competitor, bluegill. In these lakes, largemouth bass restrict juvenile pumpkinseed and bluegill to highly vegetated habitats (Mittelbach 1981; Werner *et al*. 1983), where they compete for their primary prey resource, zooplankton (Mittelbach 1984; Osenberg *et al*. 1992). The presence of both predator and competitor limits population density of pumpkinseed thereby preventing over-exploitation of their adult prey resource, snails; however, in lakes where largemouth bass and bluegill do not occur, pumpkinseed populations have become large enough to maintain the snail population at a density so low that snails no longer contribute substantially to their diet (Osenberg *et al*. 1992). Therefore, lakes vary in snail abundance, and pumpkinseed populations inhabiting these lakes differ in pharyngeal jaw morphology and diet.

In lakes containing abundant snail populations, adult pumpkinseed attain competitive refuge from co-occurring bluegill because of their capacity to consume snails (Mittelbach 1984). Although both species consume only zooplankton as juveniles, pumpkinseed begin to switch to a diet of snails at about 40-mm standard length (SL). At smaller sizes, individuals exhibit poor performance (measured as handling time) on snails, but beyond 40-mm SL they are able to consume increasingly hard snails as they grow to adult size (Mittelbach 1984; Osenberg *et al*. 1992). This ontogenetic diet shift is associated with growth of the LP muscle. Between the size at which pumpkinseed begin to crush snails and approximately 80-mm SL, the LP muscle increases in mass, and therefore force capacity, at a greater rate than body size; however, at about 80-mm SL, pumpkinseed are capable of crushing nearly every available snail they encounter, and growth of the LP muscle slows substantially (Wainwright *et al*. 1991; Figure 3.7). This pattern differs markedly from growth of the LP muscle in pumpkinseed that occur in lakes devoid of snails. In these lakes, pumpkinseed possess smaller LP muscles at all body sizes and exhibit no shift in growth rate during ontogeny (Wainwright *et al*. 1991; Figure 3.7). As these fish do not encounter or consume snails, their pharyngeal jaws do not experience the loading regime imposed by repeated snail crushing (Wainwright *et al*. 1991), and the observed differences between lakes in degree of pharyngeal jaw hypertrophy have been shown to be a result of these environmental differences rather than genetic divergence between populations (Mittelbach *et al*. 1999).

Growth of the pharyngeal jaw and snail crushing performance also explain the consequences of human-mediated introduction of redear sunfish into the range of the pumpkinseed. Although their native ranges show almost no overlap, these species have come into secondary contact in Michigan lakes. As both are molluscivores, they are expected to compete for prey resources. Redear possess more robust pharyngeal jaws than pumpkinseed (Lauder 1983) and exhibit greater crushing strength at all body sizes (Huckins 1997; Figure 3.8). Their greater snail crushing performance permits redear to shift to a diet of snails at a smaller size (Figure 3.8) and to consume harder snails at all body sizes (Huckins 1997). Because of their superior competitive ability, the introduction of redear results in decreases in pumpkinseed snail consumption, growth rate, and abundance (Huckins *et al*. 2000).

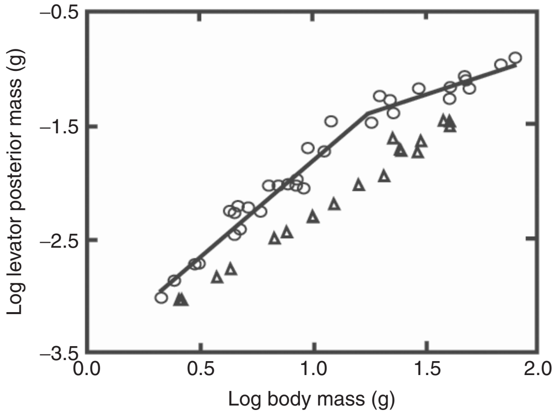

Figure 3.7 Scaling of the levator posterior (LP) muscle in pumpkinseed from a lake containing abundant snails (circles) and a lake containing effectively no snails (triangles). The LP is more massive at all body sizes examined in pumpkinseed from the lake where individuals frequently encounter and consume snails. Line segments indicate two-phase scaling of LP mass with a critical point corresponding to a body size of approximately 17 g. At body sizes smaller than 17 g, the LP grows at a greater rate than body mass, but at larger sizes, it grows at a slower rate than body mass. At body sizes larger than 17 g, pumpkinseed are capable of crushing nearly every snail they encounter. This two-phase LP scaling pattern is not evident in pumpkinseed from lakes that do not contain snails. (Redrawn from Wainwright *et al*. 1991, *Functional Ecology*, Figure 3.3, upper left panel, Blackwell Publishing.)

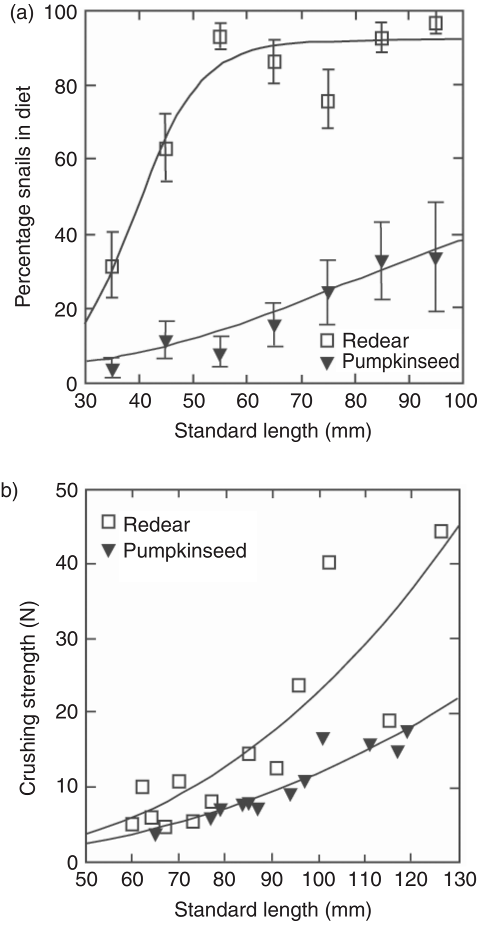

Figure 3.8 Scaling relationships of (a) percentage of diet biomass made up of snails and (b) crushing strength of co-occurring redear and pumpkinseed. Crushing strength was estimated during laboratory feeding trials as the crushing resistance of snails that have a 0.5 probability of being crushed. Redear consume more snails and crush harder snails across all body sizes. (Redrawn from Huckins 1997, *Ecology*, Figures 3.1 and 3.5, respectively. Ecological Society of America/Allen Press.)

Variation among centrarchid species in degree of pharyngeal jaw hypertrophy might be accounted for by a trade-off between capacity to generate bite force and feeding performance on soft-bodied prey. Figure 3.9 shows the scaling relationships of the LP muscle for molluscivorous centrarchids and their non-molluscivorous relatives across a range of adult body sizes. At all adult sizes, molluscivores have a larger LP muscle and nonmolluscivorous centrarchids exhibit variation in LP mass (P. C. Wainwright, unpublished data). Huckins (1997) demonstrated that redear require longer handling times than pumpkinseed when feeding on aquatic insect prey. In agreement with this result, Carroll *et al*. (2004) found that redear exhibit a weak capacity to generate subambient pressure in their buccal cavity. Poor suction performance of redear is partly due to reduced PCSA and moment arm of the epaxial muscle and increased buccal moment arm (see Figure 3.4), which might be a result of structural modifications made to accommodate the space occupied by the hypertrophied pharyngeal jaw (Carroll *et al*. 2004). Furthermore, a large, robust pharyngeal jaw might constrain the size of prey a fish can consume by preventing the passage of large prey, whereas small, gracile pharyngeal jaws (as in largemouth bass) might be flexible enough to allow passage of prey that are nearly the size of the oral jaws gape (Wainwright 1988; Wainwright and Richard 1995).

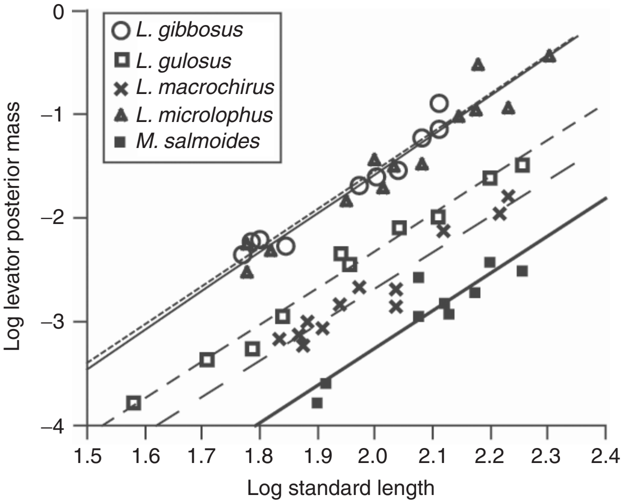

Figure 3.9 Scaling relationships of levator posterior (LP) muscle mass in the two molluscivorous species, redear (*Lepomis microlophus*) and pumpkinseed (*Lepomis gibbosus*), as well as some nonmolluscivorous species, warmouth (*Lepomis gulosus*), bluegill (*Lepomis macrochirus*), and largemouth bass (*Micropterus salmoides*). Molluscivores have more massive LP muscles than the nonmolluscivores at all body sizes, but substantial variation in LP mass exists among nonmolluscivores.

3.2.3 Comparing diversity in the feeding mechanism between lineages

Although ecomorphology studies have made explicit links between resource use patterns and morphological variation in a few centrarchid species, it is unclear whether these hypothesized relationships successfully predict associations between morphological and ecological diversity throughout the lineages of the centrarchid radiation. To this end, Collar *et al*. (2005) compared diversity in characters of the feeding apparatus in *Lepomis* and *Micropterus*. These genera are hypothesized to be sister clades with strong phylogenetic support (Near *et al*. 2005), but *Lepomis* species collectively feed on a wider range of prey resources and thus, must meet a wider range of functional demands. Using a morphological data set including species' values for maximum total length, oral jaw gape width, lever arms of the lower jaw, extent of upper jaw protrusion, mass of the primary mouth closing muscle (the adductor mandibulae), and mass of the LP muscle, Collar *et al*. found that *Lepomis* exhibits greater variation in the feeding apparatus than *Micropterus* (Figure 3.10), and therefore, the difference in diet diversity is reflected in morphological diversity. Moreover, greater variation exhibited by *Lepomis* is not accounted for by differences in time of evolution of each group, and the feeding apparatus has evolved at a faster rate in *Lepomis* (Collar *et al*. 2005). One possible explanation for the elevated rate of trophic evolution in *Lepomis* is that there has been less time between species divergence events and subsequent range overlap. If the capacity for these species to co-occur is limited by morphological and diet similarity, then less time to sympatry would be associated with an elevated rate of trophic evolution.

However, whether the feeding apparatus of *Lepomis* has evolved exceptionally fast or that of *Micropterus* has evolved slowly, remains an open question. These two clades are sister to a third clade that contains the centrarchid genera *Ambloplites, Archoplites, Centrarchus, Enneacanthus*, and *Pomoxis* (Near *et al*. 2004, 2005), and the morphological diversity within this clade will clarify whether the rate of morphological evolution has sped up in *Lepomis* or slowed down in *Micropterus*. We speculate that the species that make up this clade span the range of morphospace and diet variation of both *Lepomis* and *Micropterus. Enneacanthus* species tend to be small with relatively small, protrusible mouths, and they resemble insectivorous *Lepomis* species such as the dollar (*Lepomis marginatus*) or bantam sunfish (*Lepomis symmetricus*). *Enneachanthus* species feed on immature aquatic insects and mircrocrustacea (Schwartz 1961; Flemer and Woolcott 1966), and thus exhibit diet overlap with these *Lepomis* species as well. *Ambloplites* species as well as *Archoplites interruptus* attain relatively large body sizes and have large, speed-modified mouths that protrude little and would probably overlap

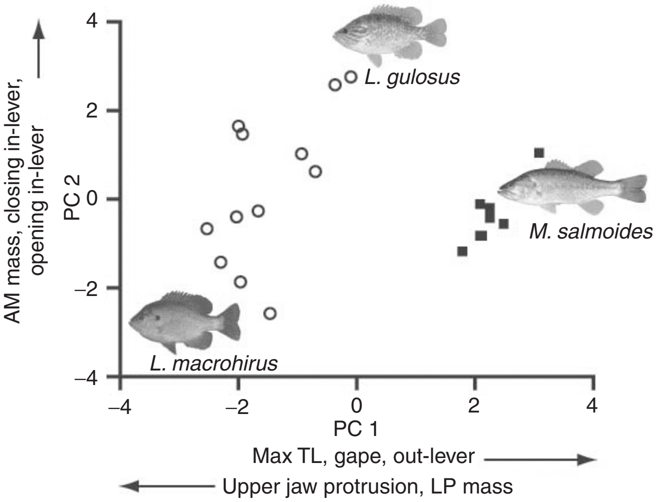

Figure 3.10 Distribution of *Lepomis* and *Micropterus* species in a feeding mechanism morphospace. Axes are principal components (PCs) derived from eight morphological characters that have predictable effects on feeding performance. Characters that correlate strongly with each PC are indicated on each axis. *Lepomis* exhibits greater variation in characters of the feeding mechanism than *Micropterus* and this difference corresponds with a difference in diet variation. (Modified from Collar *et al*. 2005, *Evolution,* Figure 3.4, Society for Study of Evolution/Allen Press.)

Micropterus in morphospace (see Figure 3.10). In addition, the diets of *Ambloplites* species (Keast 1965; Elrod 1981; Petrimoulx 1983; Angermeier 1985) and *A. interruptus* (Imler *et al*. 1975) are similar to those of *Micropterus* species and include substantial proportions of large, evasive prey like crayfish and fish. In constrast, *Pomoxis* species and *Centrarchus macropterus* differ morphologically and trophically from the rest of Centrarchidae. They have large mouths comprising gracile, highly speed-modified jaws. Although little is known about the diet of *C. macropterus, Pomoxis* species are known to feed on a unique combination of prey items that includes large proportions of fish, aquatic insects, and zooplankton (McCormick 1940; Clark 1943; Dendy 1946; Huish 1957; Mathur 1972; Liao *et al*. 2002). Therefore, we speculate that the centrarchid clade containing these genera will exhibit greater morphological and diet variations than either *Lepomis* or *Micropterus*. However, how the rate of feeding apparatus evolution in this clade compares to *Lepomis* and *Microtperus* is unclear because its lineages have been evolving independently of one another for longer than those of either *Lepomis* or *Micropterus* (Near *et al*. 2005).

3.3 Ecomorphology of locomotion

Swimming is of paramount importance in the lives of fish. It is essential for escape from predators and movement about the habitat, and is an often-overlooked component of feeding behavior. Body form of centrarchids is diverse (Figures 3.1 and 3.11) and is thought to have important implications for their locomotor abilities, activity patterns, foraging strategies, and behavioral energetics. Although the literature on the biomechanics of swimming only sparsely samples centrarchid species, it is true that centrarchids have figured prominently in research on locomotor biomechanics (Webb 1984; Lauder and Drucker 2004). As is true for feeding, the centrarchid locomotion literature is largely focused on largemouth bass and bluegill, and much of our understanding of the implications of the body form diversity in centrarchids is therefore based on inferences largely derived from research on few species. In this section, we review the current thinking about morphology–performance relationships in centrarchid locomotion, and we consider the literature on within-species polymorphisms that has been particularly influential in shaping our understanding of the implications of morphological diversity.

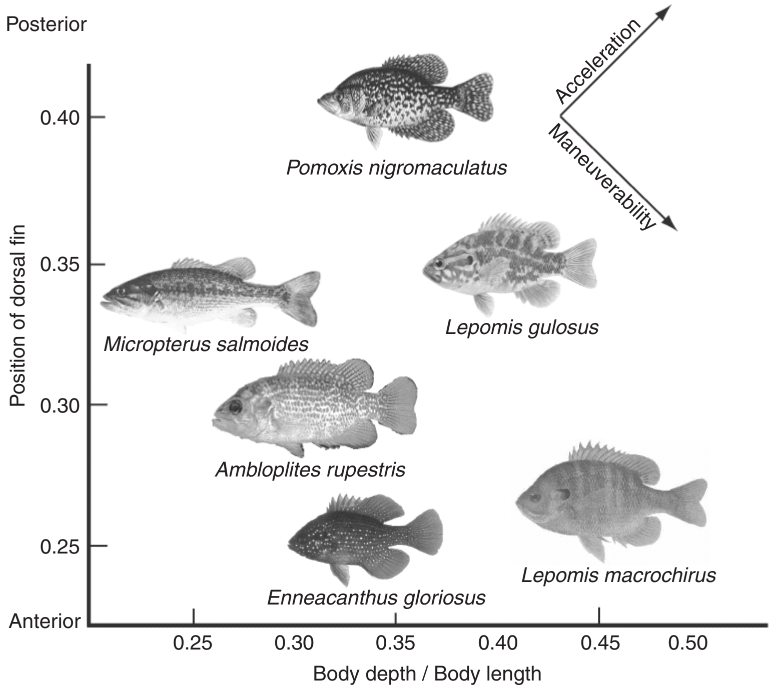

Figure 3.11 Six centrarchid species distributed in a morphospace defined by the ratio of body depth to total length (x-axis) and the distance of the first dorsal spine from the snout as a fraction of fish total length. Deep-bodied, laterally compressed phenotypes, like that exhibited by *Lepomis macrochirus*, have been identified as providing a relatively large surface area to maximize the thrust-generating surface during fast-start behaviors (Webb 1984; Domenici and Blake 1997). *L. macrochirus* has the highest accelerations in fast-starts, and *Micropterus salmoides* the poorest, of the few centrarchids that have been tested (summarized in Domenici and Blake 1997). In addition, the deep-bodied, laterally compressed phenotype is thought to be better for turning behaviors. Median fins also provide surface area for fast-start thrust and are used in turning behaviors and slow maneuvers (Standen and Lauder 2005). A dorsal fin located posteriorly on the dorsum is in a position to contribute well to fast-start thrust while a fin positioned more anteriorly should have greater effect in turning and other maneuvers. We hypothesize that this morphospace corresponds generally with a performance space that is oriented at 45 ° to the morphospace. Hence, some deep-bodied species appear better designed for maneuvering than others. Both *L. macrochirus* and *Pomoxis nigromaculatus* show features that suggest high performance in acceleration, but *L. macrochirus* appears to be better built for maneuverability. Although *Micropterus* appears in this view of locomotor space to have low performance, this body form may be relatively specialized for efficient cruising at high speeds as the shape of the body has a more optimal fineness ratio that reduces drag and the distribution of muscle on the frame may facilitate efficient swimming motion. We emphasize that most of these interpretations of swimming performance in centrarchids are hypotheses that are yet to be adequately tested.

3.3.1 Swimming performance

A powerful framework for thinking about fish locomotion was provided originally by Webb (1984, 1998) who identified three dimensions of locomotor performance: cruising, acceleration, and maneuvering. Relative to the full diversity of teleosts, most centrarchids are viewed as generalists with significant abilities in all three dimensions, but with different species showing significant variation in all three dimensions of locomotor performance. As we shall see, it is not yet possible to place most centrarchid species in Webb's performance space and herein lies a promising research program.

It is useful to consider first the relevance of these performance dimensions to the biology of centrarchid fishes. Acceleration performance is a key element of the rapid escape response of fishes when encountering would be predators (Webb 1986; Blake 2004) and has been shown to directly correlate with variation in escape success among individuals

(Walker *et al*. 2005). Acceleration is also significant for the abilities of sit-and-wait ambush predators, and it is likely that many centrarchids periodically use high acceleration strikes to capture elusive prey. For example, the warmouth lives and forages in heavily vegetated habitats where it often feeds on elusive prey. It is possible that acceleration is an important determinant of strike success in warmouths and other similar centrarchids, but this idea has not yet been tested.

Cruising performance is about being able to sustain a high rate of speed efficiently. This will be an important element in the biology of species that make extensive swimming forays during daily activity, such as species of *Micropterus* (Demers *et al*. 1996; Sammons and Maceina 2005), and is probably a major axis of diversity in centrarchids although surprisingly little is known about the typical distances covered swimming each day by different centrarchid species.

Maneuvering with the median and paired fins may have the greatest direct relevance to feeding behavior and is particularly significant for fish that feed in a spatially complex habitat, such as the vegetated littoral zone of lakes. Maneuvering performance is also likely to be a major axis of diversity in centrarchids (Webb 1984; Savino and Stein 1989).

Features that are thought to enhance fast-start performance and result in relatively high accelerations include a deep body with a large lateral surface area, including large surface area of median fins, particularly toward the tail end of the fish (Webb 1984; Domenici and Blake 1997; Blake 2004). A flexible body enhances the turning radius during fast-starts and the duration of the propulsive stroke. Finally, it is expected that a large white muscle mass, relative to body mass, will characterize strong accelerators. The laterally compressed *L. macrochirus* has shown the highest fast-start accelerations among the few centrarchids tested, performing better than *L. cyanellus*, which does better than *M. salmoides* (Webb 1975, 1978, 1986). These three species represent a range from deep-bodied to slender with bluegill being the most deep-bodied and largemouth bass the least. It seems possible that the deep-bodied form of many *Lepomis* species is an anti-predator adaptation that results in relatively high fast-start performance and a wide body profile that is difficult for predators to swallow. An interesting avenue for future research will be to compare patterns of natural selection acting on body shape in populations of species such as *L. macrochirus* in the presence and absence of gape-limited predators. Recent observations have also suggested that the spines in the dorsal fin of *Lepomis* species play a prominent role in defending against predators (Januszkiewicz and Robinson 2007).

High-performance cruisers are expected to have features that enhance locomotor thrust and minimize drag (Lighthill 1975; Webb 1984). The classic features associated with extremely high thrust do not occur in any centrarchids, such as a high aspect ratio lunate caudal fin, a thin caudal peduncle, or a stiff anterior body. However, compared to other centrarchids, *Micropterus* appears to show features that reduce drag, including a more optimal body shape (fineness ratio), and small paired fins. It is possible that *Micropterus* also has a relatively high mass of red muscle, and overall a high ratio of axial muscle mass to total body mass. Both energetic swimming efficiency and critical swimming speed during cruising in *M. salmoides* have been found to be much higher than in *Pomoxis annularis* (Beamish 1970; Parsons and Sylvester 1992).

When fish maneuver through their environment they make extensive use of both the median fins (Standen and Lauder 2005) and the pectoral fins (Drucker and Lauder 2002; Lauder and Drucker 2004). These fins are positioned away from the fish center of mass giving them high mechanical advantage when exerting forces that turn the fish (Eidietis *et al*. 2002). The centrarchid body appears to be designed to be unstable and to capitalize on the varied use of these fins particularly during slow swimming behaviors. Slow swimming in *L. macrochirus* can be powered entirely by the pectoral fins (Drucker and Lauder 2002). Among centrarchids it can be expected that fin-based maneuvers will be enhanced by relatively large dorsal, anal, pectoral, and pelvic fin surface areas, and a deep-body shape that positions the median fins away from the fish center of mass. Although not quantified in the literature, the pectoral fins of *L. macrochirus* and several other *Lepomis* species are considerably larger than similar sized individuals of *Micropterus, Ambloplites, Acantharcus*, or *Pomoxis*. Compared to other centrarchids, *Micropterus* dorsal and anal fins appear to have smaller surface area. Species of *Lepomis* have the dorsal and anal fins extending further anteriorly than in *Pomoxis*. The implications of these morphological patterns lead to the predictions that species of *Lepomis*, especially *L. macrochirus*, have better maneuverability, with members of the *Pomoxis*/*Ambloplites* clade being intermediate and *Micropterus* showing the poorest maneuverability.

3.3.2 Insights from within-species variation

Some of the most compelling arguments for the adaptive significance of morphological variation in centrarchids for their swimming ability come from studies of intra-specific variation. The power of these studies is related to a classic principle in comparative biology: studies that focus on close relatives minimize the number of confounding differences between the study groups when trying to understand the consequences of design differences. Members of the same population of fish that differ in body proportion or fin morphology are likely to be more similar to each other in additional traits, than they would be to any other population or species. One therefore has more confidence in attributing performance differences to specific morphological variation.

Researchers at the Kellogg Biological Station in Central Michigan discovered in the late 1980s that some populations of bluegill exhibited a polymorphism in body shape and fin morphology. Individuals that foraged in the vegetated littoral zone had a deeper body form and longer pectoral fins that attached more posteriorly on the body than fish in the same lake that foraged in the open water habitat (Ehlinger and Wilson 1988). These morphological differences were associated with differences in foraging behavior in the lab; littoral zone fish hovered for longer periods of time during foraging and had a higher feeding rate in a structurally complex habitat, whereas open water fish moved more constantly and had a higher feeding rate in the open water habitat when feeding on zooplankton (Ehlinger 1990). Similar patterns of variation in bluegill across these habitats have been reported by other authors (Layzer and Clady 1987; Chipps *et al*. 2004).

A second series of studies has shown a similar pattern of variation in numerous populations of pumpkinseed (Gillespie and Fox 2003; Jastrebski and Robinson 2004; Robinson *et al*. 1993, 1996, 2000). Although pumpkinseed are usually sympatric with bluegill, there are several North American drainages where pumpkinseed occur in the absence of bluegill. This has set up a situation where the well-documented competitive interaction between bluegill and pumpkinseed (Mittelbach 1984) cannot occur and pumpkinseed in these lakes frequently display an open water phenotype in addition to the usual littoral zone specialists (Robinson *et al*. 1993, 2000). Open water fish are sometimes less deep-bodied than littoral zone fish, and their caudal peduncle region is consistently enlarged. In addition, the pectoral fins are smaller in open water fish, and positioned higher on the sides of the fish (Robinson and Parsons 2002, Jastrebski and Robinson 2004). Limited data suggest similar patterns in *Lepomis humilis* and *L. cyanellus* (Hegrenes 1999, 2001) in response to specific dietary regimes. It is not clear whether these differences within species are due to phenotypic plasticity or to genetic variation for phenotype, but the evidence is strong that these patterns are the result of diversifying selection, and hence the functional implications of these morphological differences for locomotor behaviors are of central importance to our understanding of how selection acts on swimming structures.

Behavioral studies of how bluegill feed in the open water on plankton or in vegetated habitats on benthic prey help shed light on the possible significance of these morphological differences (Ehlinger 1990). Bluegill taken from the open water habitat move through the open water more quickly as they identify, strike, and consume individual planktonic prey. Littoral zone fish in the open water habitat move more periodically, hovering for extended periods, and have a slower net rate of ingesting individual prey items. The more slender body and enlarged caudal region of the open water fish may result in more efficient cruising locomotion, while their smaller pectoral fin contributes to this by creating less drag. On the other hand, feeding in the vegetation involves greater use of maneuverability and periodic hovering. The deeper body shape of littoral zone fish may allow them to make sharper turns (Walker 2004) and the enlarged pectoral fin provides a bigger surface area for the fish that probably incurs higher drag forces as it is used to perform a variety of hovering and turning maneuvers (Webb 1984; Domenici and Blake 1997). It is worth noting that although the connections between these morphological differences and more synthetic measures of performance, such as foraging rate, have been performed, there is still a need for studies that test the expected consequences of specific morphological features for more proximate measures of performance. For example, there are no studies we are aware of that test the hypothesis that more slender-bodied, open water *Lepomis* are more efficient cruisers than deeper-bodied individuals, or that larger pectoral fins result in better turning performance.

The open water–littoral zone pattern of within population differentiation is widespread among north-temperate lake fish (Robinson and Parsons 2002). Several species within six teleost families show the littoral zone and open water phenotypes, and there is strong evidence of convergent patterns of body form as described here for centrarchids. This phylogenetically broad distribution of the phenomenon is strong evidence of common selective forces that underlie the responses of many fish species to these habitat types (Robinson and Schluter 2000). One example is that of the Eurasian perch (*Perca fluviatilis*) which is known to show littoral zone and open water specialization with open water fish having a more slender body form, larger caudal peduncle, and smaller pectoral fins than littoral zone fish that have a deeper body form and larger pectoral fins (Svanbäck and Eklöv 2002, 2003).

The habitat-specific morphology found in these northern lakes appears to relate mostly to foraging patterns. Open water fish feed mostly on small mid-water crustaceans and littoral zone fish feed on a somewhat more diverse selection of benthic prey that would be plucked from their positions in the sediment or on the surface of vegetation. In addition to the overall body form patterns described earlier, open water fish tend to have a smaller mouth and show better foraging performance feeding on planktonic prey than littoral zone fish (Ehlinger 1990; Jastrebski and Robinson 2004).

Another line of investigation has compared populations of single species that live in a river to populations that live in a lake (Brinsmead and Fox 2002). This study of *A. rupestris* and *L. gibbosus* showed that for both species, individuals in the river were more slender-bodied and had smaller pectoral fins. Thus, the pattern is similar to that seen between littoral zone and open water fish. River dwelling fish appear to be better built for efficient cruising compared to lake dwellers. This may relate to a benefit to minimizing drag induced by a deep-body form and large fins in their exposure to ambient currents.

3.3.3 Integration of feeding and locomotion: a research frontier

Research on the biomechanics of feeding has generally progressed independently of research on locomotion, but fish are usually swimming as they feed and it seems likely that many of the specific adaptations for locomotion are at least partly related to performance during feeding behaviors. Although little quantitative data are available, it is known, for example, compared to bluegill, largemouth bass intercept their prey while swimming relatively fast (Norton and Brainerd 1993). The use of ram during a strike enables the fish to close the distance between itself and its prey more rapidly (Higham *et al*. 2005a, 2006a), and higher ram speed appears to be an adaptation to capturing elusive prey such as fishes. In contrast to largemouth bass, bluegill normally brake during the strike (Higham *et al*. 2005b). Probably as a result of the slower swimming speed, bluegill are more accurate than largemouth bass with their strike, as the braking bluegills show a remarkable capacity to position prey at the center of the volume of water that they ingest during the strike (Higham *et al*. 2006a). However, little is known of the diversity of these behaviors in centrarchids, and important questions remain. Is strike accuracy associated with a small mouth, or is it related to approach swimming speed, or are all three factors tightly linked?

Finally, we note that because many of the same structures used in locomotion are also part of the feeding apparatus (e.g., the anterior epaxial muscles), responses to natural selection on locomotor performance may directly affect feeding performance. For example, selection in bluegill populations that experience high predation from largemouth bass may respond by evolving a deeper-bodied form. This deep-bodied form also tends to increase the mechanical advantage of the epaxial muscles that insert on the back of the skull and power buccal expansion during suction feeding (Carroll *et al*. 2004). As a result, an increasingly deep body in response to predation may indirectly increase suction feeding capacity. The dynamics of this hypothesis have not been explored in natural populations.

3.4 Conclusions

The ecological and morphological diversity exhibited within Centrarchidae continues to inspire innovative research with relevance to the fields of ecology, evolution, and biomechanics. In this review, we have highlighted some unique insights provided by the ecomorphology research program carried out in centrarchids, but we also hope to have identified some promising avenues of future inquiry. Although much progress has been made by focusing on a few centrarchid species at the extremes of morphospace, centrarchid biologists are left to infer the consequences of morphological variation in other species from these few studies. For example, based on studies of trophic polymorphism in pumpkinseed, we speculate that the observed variation in pharyngeal jaw robustness (Figure 3.9) is a consequence of a trade-off between bite force and gape limitation, but this hypothesis remains untested. Additionally, the locomotor performance consequences of variation in body shape and fin placement in most centrarchids remains largely unexplored. We hope that further application of the ecomorphological research perspective to the full range of centrarchid forms will continue to elucidate both within- and between-species diversity in this fascinating group of fishes.

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