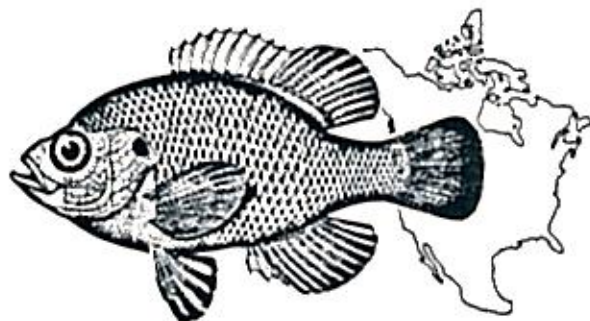


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The Evolution of Feeding Biology in Sunfishes (Centrarchidae)

Peter C. Wainwright and George V. Lauder

One of the major challenges in evolutionary morphology is to assess the extent to which ecological transformations can be attributed to changes in the functional design of organisms. Closely related species frequently differ in their ecological characteristics and it is often assumed that correlated differences in morphology or physiology underlie the ecological shifts. Though this assumption is rarely tested, major advances have recently been made in the methodologies that are useful for critically examining ecomorphological relationships (Lauder, 1982; Arnold, 1983; Greene, 1986; Huey and Bennett, 1987; Losos, 1990). Two themes have emerged as central to studies of ecomorphology and both play key roles in the present chapter. The first of these is the use of independently corroborated phylogenies as a basis for interpreting historical sequences of change in character complexes (Lauder, 1982, 1986; Greene, 1986; Huey and Bennett, 1987). Comparative research not performed within the context of a phylogenetic hypothesis is likely to arrive at incorrect conclusions about evolutionary patterns (Felsenstein, 1985). Assessing the congruence of historical change in two character sets, such as functional morphology and ecology, provides a first test of the hypothesis that a causal relationship exists between the patterns of evolution in one character set and the other (Greene, 1986). A lack of correlated changes in the two character sets falsifies the causal hypothesis. A phylogenetic framework plays a crucial role in formulating and answering questions about the temporal sequence of character acquisition because without one it may not be possible to know if changes in functional morphology and ecology occurred at the same level in the history of a clade.

The second theme concerns the significance of behavioral performance as an intermediate link between functional morphology and ecology (Huey and Stevenson, 1979; Arnold, 1983). Discovery of a strong historical correlation between functional and ecological changes provides support for the notion that one is the basis of the other. However, to establish a strong argument for causality in an

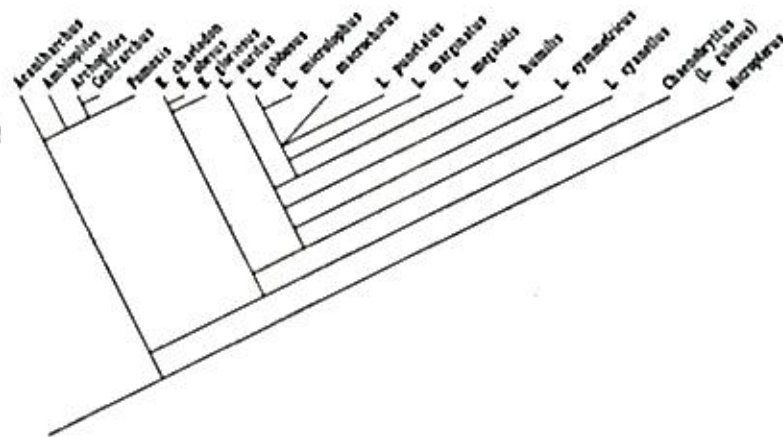
ecomorphological correlation it is necessary to elucidate the *mechanism* that permits the functional transformation to account for ecological changes (Lauder, 1991). Behavioral performance, or the ability of the organism to perform relevant tasks, provides a link within this context. In our discussion below we refer to both morphology (i.e., anatomy) and function (i.e., patterns of use of morphology) as distinct types of traits that can influence an organism's ecology. Ecomorphological correlations as they are typically portrayed involve two key assumptions (e.g., Keast and Webb, 1966; Hespelheide, 1973; Lelsler, 1980): (1) the morphological or functional feature in question confers some improvement in the capability of the organism to perform some relevant task, and (2) the improved performance can account for ecological differences. Crucial to any claim that a morphological or functional feature underlies a performance advantage is a biomechanical model that explains how the feature influences the organism's ability to perform some relevant behavior. The model provides an explanation of how the feature *causes* a performance difference and allows testable predictions to be made regarding the effects that variation in the trait will have on performance (e.g., Wainwright, 1987; Losos, 1990). Changes in functional morphology and performance that occur congruently with reference to an independently derived phylogeny can identify possible causal linkages between functional design and behavioral abilities, but the strongest support of the causal hypothesis must come from our biomechanical understanding of organismal function.

In this chapter we explore the evolution of trophic habits in fishes of the family Centrarchidae. Our primary purpose is to search for general trends in how the functional design of the feeding mechanism changes during evolution, and how these design changes account for differences among species in feeding ability and dietary habits. Two case studies are presented that focus on different stages of the prey capture process: the strike and prey handling. In each case study we use a phylogeny of the Centrarchidae to assess the extent of historical correlation among differences in diet, feeding performance, and two levels of functional morphology of the feeding mechanism (i.e., morphology and the motor patterns that drive the behavior). Correlated differences in diet, performance, and at least one level of functional morphology are sought as a first test for the causal relationship between the dietary transformation and the change in functional morphology (Greene, 1986). Three major questions are addressed: (1) Can dietary differences among species be explained by correlated differences in feeding ability? and (2) What levels of functional morphology change in conjunction with feeding performance and ecological transformations, and how might these changes provide a causal basis for shifts in diet and performance? and (3) What is the historical sequence of acquisition of the characters that make up the functional repertoire underlying novel feeding habits?

TWO CASE STUDIES

The sunfishes (Centrarchidae), an endemic North American clade of about 32 species, are exclusively carnivorous, feeding on a range of invertebrate and vertebrate prey. In the first case study we examine the prey capture mechanism in four species that exemplify the range of diets found in the family, from the piscivore *Micropterus salmoides* to the zooplankton predator *Lepomis macrochirus*. This study focuses on the

Figure 1.
Phylogeny of the
Centrarchidae used in this
chapter as a basis for inter-
preting historical patterns of
change in sunfish feeding
biology. See text for details
of the methods used in the
analysis.



mandibular jaws and their use during the strike phase of prey capture. The second case study considers the evolution of molluscivory that occurs in two species of *Lepomis*. These species crush molluscs in their pharyngeal jaws and we explore the functional basis of this novel diet. The two case studies thus contrast patterns of evolution in different components of the sunfish feeding apparatus, the mandibular jaws and the pharyngeal jaws.

METHODS FOR THE CASE STUDIES

The phylogenetic relationships of sunfishes were estimated by Humphries and Lauder (in prep) using a parsimony analysis of 53 characters. PAUP version 2.41 was used (Swofford, 1984). All characters except one were ordered, and 25 characters were multistate. This phylogeny (Fig. 1) is congruent with the topology presented by Mabee (1988) for nine centrarchid taxa.

Because of the lack of a corroborated higher-level phylogenetic hypothesis which would provide a guide to two specific outgroup taxa, Humphries and Lauder (in prep) used several outgroup taxa among the Perciformes. Polarities were established by assigning the ancestral state for each character to that of the outgroup taxa when all outgroup taxa shared a common state. Ancestral characters were coded as a "?" if variation existed among outgroups.

Our approach in using the phylogeny as a tool for determining historical sequences of change in feeding biology is to accept the phylogenetic hypothesis of the Centrarchidae as the best available estimate of the true relationships within this group. We then map the character states of diet, feeding proficiency, morphology, and motor patterns onto the phylogeny. The sequence of changes that have occurred to produce the observed pattern is inferred by assuming that a minimum number of evolutionary steps has produced the distribution of characters (i.e., the principle of parsimony). Thus, the sequence of character changes that invokes the fewest number of transformations is chosen as the most likely one. The resulting sequences for the four levels of our analyses (diet, feeding proficiency, morphology, and motor patterns) permit us to ask questions about the historical congruence of changes in different levels of feeding biology.

In this chapter we combine data from our own previous studies of functional

morphology with additional information from the ecological literature to infer patterns in the evolution of sunfish biology. Our functional research on sunfish feeding mechanisms has included morphological investigations and electromyographic studies of the patterns of muscle activity that are used during feeding behaviors. In electromyographic experiments bipolar electrodes are implanted into the muscles of anesthetized fishes (Osse, 1969; Lauder et al., 1986; Wainwright and Lauder, 1986). The separate electrode wires are then bundled into a common cable which is sutured to the fish's back. When the fish recovers from anesthesia the electrode wires are connected to amplifiers and the electrical activity of contracting muscles is recorded on a tape recorder during feeding behavior.

Electromyograms provide a direct indication of the duration and relative timing of muscle activity and a relative indication of the force generated by muscles (Basmajian and DeLuca, 1985). Prey used in EMG experiments include earthworms, snails, fish, and crickets and are often chosen to determine the response of the predator to prey of specific escape abilities.

Case Study I. The Mandibular Jaw Apparatus Suction Feeding

Suction Feeding

Like most fishes centrarchids employ suction feeding to capture prey. The functional morphology of suction feeding has been reviewed in detail elsewhere (Lauder, 1983a, 1985) and is only briefly described here. Suction feeding involves expansion of the buccal cavity to create a negative pressure pulse that draws prey and surrounding water into the mouth (e.g., Muller and Osse, 1984). Negative buccal pressure is generated by the simultaneous elevation of the neurocranium, lateral expansion of the suspensoria, and depression of the floor of the mouth via the hyoid bar (Fig. 2, a and b). During buccal expansion the gill bars at the back of the oral cavity are adducted (Fig. 2c, GBDIST), forming an effective barrier to backflow into the buccal cavity. Simultaneously the gape is increased to permit an inward flow of a volume of water containing the prey. Due to the physical properties of the medium (water is 900 times as dense and 80 times as viscous as air) prey may be unable to escape this inward flow and they are transported into the buccal cavity with the water. The jaws then close immediately, preventing escape of the prey, and the gill bars are abducted permitting water to pass out the opercular valve (Fig. 2c). Prey capture may be extremely rapid, occurring within 50 ms of the initiation of the strike in centrarchids (Nyberg, 1971; Lauder, 1983a).

Though many muscles function during the suction feeding strike (Lauder, 1983a) we focus on four in this case study. The anterior portion of the epaxialis muscle attaches to the posterior-dorsal aspect of the neurocranium and elevates the skull (Fig. 2a, EP), contributing to mouth opening and buccal expansion. The levator operculi originates on the side of the neurocranium and inserts on the dorsal margin of the opercular bone. This muscle rotates the opercle, and through couplings via the sub- and interopercle bones it contributes to increasing the gape through mandibular depression (Fig. 2a, LOP). The adductor mandibulae inserts on the coronoid process of the mandible from its origin on the lateral face of the suspensorium, and adducts the mandible when active; this is the primary jaw closing muscle (Fig. 2a, AM2). The sternohyoideus originates from the ventral region of the pectoral girdle to insert

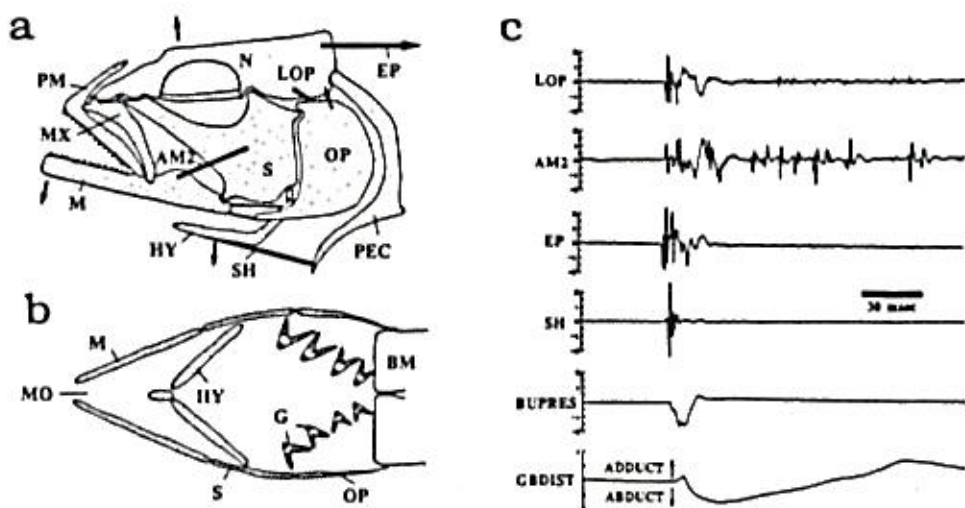


Figure 2.

a) Lateral view diagram of the major elements in the mandibular jaws of a generalized centrarchid. Small arrows indicate directions of skeletal movement during suction feeding and thick black lines represent the placement of the four muscles that were focused on in this study: AM2, division 2 of the adductor mandibulae; EP, anterior epaxialis; LOP, levator operculi; SH, sternohyoideus. b) Ventral view of a frontal section of the same region to emphasize the location of the gill bars and the hyoid bar. Note that the gill bars, if adducted, form a barrier to water movement into the buccal cavity from the opercular cavity. Other abbreviations: BM, body muscles; G, gills; HY, hyoid bar; M, mandible; MO, mouth; MX, maxilla; N, neurocranium; OP, operculum; PEC, pectoral girdle; PM, premaxilla; S, suspensorium. c) Sample recordings made during the suction feeding strike of *Ambloplites rupestris* feeding on a fish prey. Shown are the patterns of activity in four muscles, buccal pressure (BUPRES) and the distance between adjacent gill bars (GBDIST). Figure c taken from Lauder et al. (1986). Muscle abbreviations as above. Note that as the mouth opens and water begins to flow into the mouth (indicated by the rapid drop in buccal pressure), the gill bars are adducted to close off the opercular cavity. As the mouth closes, the gill bars are abducted allowing water to pass out the gill openings.

tendinously onto the hyoid bar. When active this muscle depresses the hyoid bar, and thus the floor of the mouth, producing the major expansion of the buccal cavity (Fig. 2a, SH). The motor pattern observed during a suction feeding strike involves intense bursts of activity in each of the four muscles described above, typically of 30–100 msec duration. The levator operculi commences activity first, followed by the epaxialis and the sternohyoideus and finally the adductor mandibulae.

Feeding biology

Four species are compared in this analysis of suction feeding: the largemouth bass, *Micropterus salmoides*; the rockbass, *Ambloplites rupestris*; the black crappie, *Pomoxis nigromaculatus* and the bluegill *Lepomis macrochirus* (Figs. 1 and 4). Numerous studies of the adult feeding habits of these species have been made (e.g., Huish, 1957; Ruhr, 1952; Applegate et al., 1966; Savitz, 1981; Keast, 1985 and references therein), and while some variation occurs among habitats general patterns are clear. As adults, the four species exhibit distinct patterns of prey use. At one extreme is *M. salmoides*

which is primarily a piscivore and at the other extreme is *L. macrochirus*, which feeds on zooplankton (Cladocera) and small benthic invertebrates such as chironomid larvae. Intermediate to these two species are *P. nigromaculatus* and *A. rupestris*. In lakes *P. nigromaculatus* consumes about equal volumes of small invertebrates (zooplankton, *Chaoborus* and chironomid larvae) and small fish. The diet of *A. rupestris* is dominated by large invertebrates, principally Anisoptera nymphs and crayfish, with small fish forming about one fifth of the diet in adults.

With the exception of *A. rupestris*, the feeding abilities of these species have been studied extensively, particularly the efficiency of mid-water zooplankton feeding (Werner and Hall, 1974; Confer and Blades, 1975; Vinyard and O'Brien, 1976; O'Brien, 1979) and the effects of large prey size on feeding proficiency (Lawrence, 1957; Wright, 1970; Werner, 1974, 1977). The picture that has emerged is one in which the feeding abilities of these species play a central role in limiting prey use. One of the primary dietary differences among these species is in the average size of their prey. The fish prey that are frequently eaten by *M. salmoides* are so large that they would not fit through the gape of *L. macrochirus* of the same body size (Lawrence, 1957; Werner, 1974, 1977). *L. macrochirus*, on the other hand, forages more efficiently on small prey the size of *Daphnia* (Werner, 1977), partly because it recognizes small, mid-water prey from farther away than *M. salmoides* (O'Brien, 1979). Laboratory studies of species of *Pomoxis* (O'Brien, 1979) reveal that its mixed diet of small invertebrates and fishes is correlated with the ability to proficiently capture both small and large prey (though not as large as those taken by the same sized individuals of *M. salmoides*).

The differences in morphology among these four species have important consequences for their prey capture abilities. Two aspects of cranial morphology are key; mouth size and gill raker design. In all four species mouth size grows as a constant fraction of standard length, though the fraction varies among species: *M. salmoides*, 16%; *A. rupestris*, 12%; *P. nigromaculatus*, 9%; *L. macrochirus*, 6% (Keast, 1978). Werner (1977) has shown that the effects of prey size on feeding proficiency in *L. macrochirus* and *M. salmoides* are a function of mouth diameter. That is, fishes with the same mouth size exhibit equivalent feeding performance, in spite of the fact that *L. macrochirus* and *M. salmoides* have mouths of the same size at very different body lengths. Based on cost/benefit curves, a prey size to mouth diameter ratio of 0.59 has been postulated to predict the optimal prey size in these and other sunfish species (Werner, 1974) and in other suction feeding fishes (Kislalioglu and Gibson, 1976). The importance of mouth diameter in limiting prey size has also been suggested for both *A. rupestris* and *P. nigromaculatus* (Keast and Webb, 1966; Keast, 1985).

The tendency for adult *P. nigromaculatus* to feed on very small prey in addition to much larger fish appears to present something of a paradox. However, this species is unique among these four centrarchid species in possessing a relatively large mouth in addition to many long gill rakers that are thought to be used during the handling of very small prey (Keast, 1978; O'Brien, 1979). Neither *L. macrochirus* nor *M. salmoides* possess long gill rakers, and this may be an adaptation unique, within this sample of four species, to *P. nigromaculatus*. Interestingly, in *P. annularis* there is an ontogenetic switch from a diet of zooplankton to a diet dominated by fish. This switch is correlated with a change in the growth trajectory of gill raker spacing, from negative allometry in smaller fish to positive allometry in larger fish (O'Brien, 1979).

In summary, interspecific differences among centrarchid species in mouth size and gill raker structure have been shown to play crucial roles in determining feeding

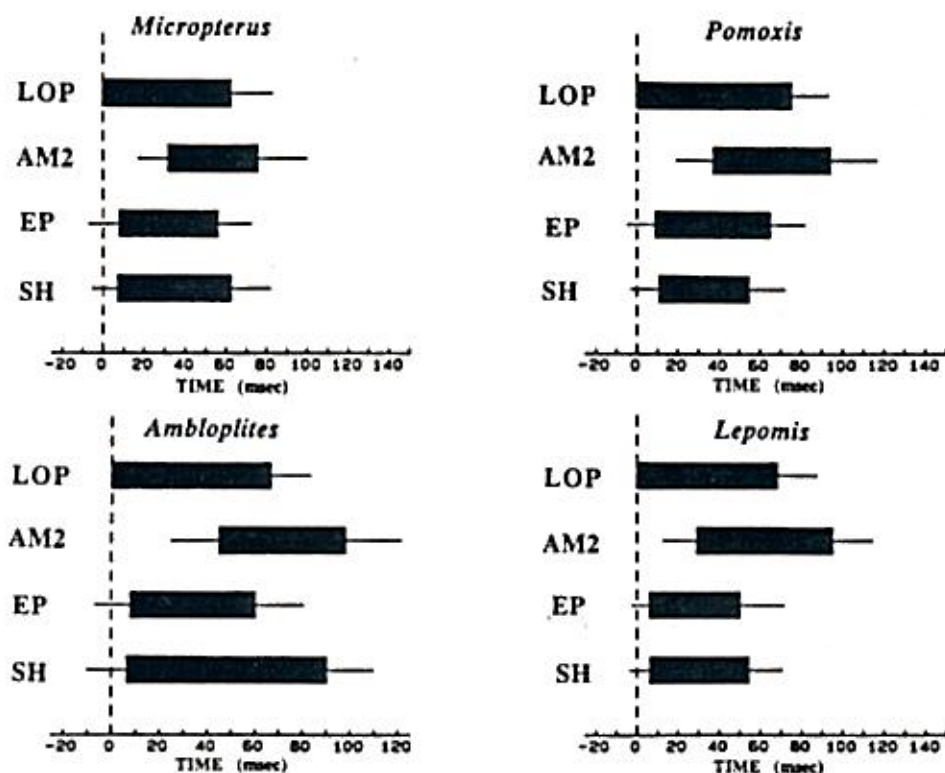


Figure 3.

Electromyographic bar diagrams illustrating the average pattern of muscle activity in four sunfish species during suction feeding on fish prey. Each panel shows the mean duration of the activity burst in each muscle (black bars), with one standard deviation indicated by the thin line on the right, and the average onset time of each muscle relative to the beginning of activity in the levator operculi (dashed line), with one standard deviation indicated on the left. Sample sizes range from two to seven individuals per species and from 21 to 63 feedings per species. Data from Wainwright and Lauder (1986). Muscle abbreviations as in Figure 2.

performance. Differences among species in prey capture abilities account for most of the major dietary distinctions among these species.

To explore the evolution of functional design at levels other than morphology we have contrasted the patterns of muscle activity used by these four species during prey capture (Wainwright and Lauder, 1986). We found the suction feeding motor pattern to be virtually the same in all four species (Fig. 3). Out of eleven variables that were measured to quantify the intensity and timing of activity in these four muscles only one, the duration of activity of the sternohyoideus muscle, was found to be significantly different among species. This was due to an especially long activity burst of the sternohyoideus in *Ambloplites* (Fig. 3, SH). Each species demonstrated an ability to modulate the motor pattern when feeding on different prey (i.e., fish, crickets, and earthworms), presumably to adapt the strike to the characteristics of the prey, but all used virtually the same motor pattern when feeding on the same prey (Fig. 3). Thus, in contrast to the conspicuous morphological differences among these divergent species there is no evidence of major transformations in the motor pattern used during prey capture.

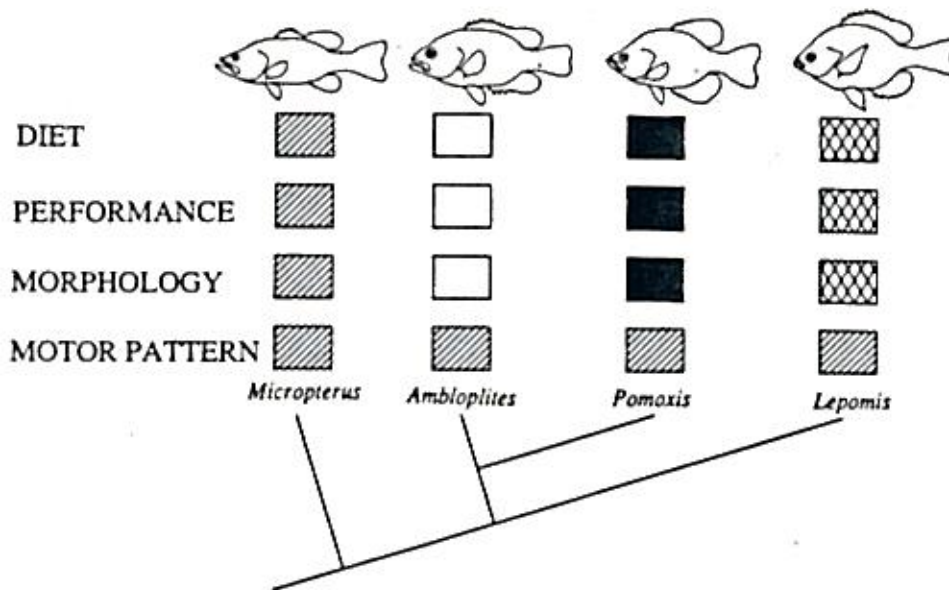


Figure 4.

Phylogenetic distribution of feeding biology characters in the case study of the mandibular jaws. Patterns filling the rectangles indicate whether that character is different from the condition found in the other species. In this case study evolutionary changes in diet, feeding performance, and feeding morphology are correlated and autapomorphic for each species, yet the pattern of muscle activity exhibited during suction feeding is strongly conserved and appears to be a symplesiomorphy for the sunfish clade, indicating that drastic changes in feeding ecology have occurred without alterations in the pattern of muscle activity used to capture prey. See text for a discussion of the nature of the differences indicated on the figure.

Historical patterns

The distribution of dietary habits on the centrarchid cladogram is congruent with the pattern of feeding abilities and morphology; all three traits are distinct in each species (Fig. 4). Most of the differences among species in patterns of prey use can be explained by differences in the range of prey that each species is able to proficiently capture (Fig. 4; performance). One striking conclusion that emerges from this analysis of the evolution of prey capture in sunfishes is the contrast in patterns of change in morphology and the motor pattern (Fig. 4). The major shifts in feeding performance and dietary habits that have occurred in this group appear to be based largely on alterations in the morphology of the prey capture apparatus but not on adaptations involving patterns of muscle activity that drive suction feeding (Fig. 4). Mouth size limits the range of prey sizes that centrarchids are able to eat and this constraint plays a central role in determining patterns of prey use in the four sunfishes examined. Similarly, the ability of species of *Pomoxis*, a relatively large mouthed form, to exploit both large and very small prey involves the novel presence of more and longer gill rakers that are believed to enhance the capture of small prey. Thus, in contrast to morphology, the suction feeding motor pattern appears to have been a generally conserved feature during speciation in centrarchids and the evolution of sunfish feeding biology.

Case Study II. The Pharyngeal Jaws

After prey are captured by centrarchids, they are passed posteriorly within the buccal cavity to the pharyngeal jaws where manipulation, chewing, and transport into the esophagus occurs. The pharyngeal jaws are a complex musculoskeletal system formed from modified gill arch elements and are functionally independent of the mandibular jaws. Two sunfish species exhibit a unique habit of crushing molluscs in their pharyngeal jaws, and this novel capability is the focus of the second case study. Below, we review the functional morphology of pharyngeal jaws in generalized perciform taxa, like sunfishes (discussed in detail in Lauder, 1983b, and Wainwright, 1989a).

Pharyngeal jaw function

Prey manipulation and chewing entail cyclical patterns of movement by the pharyngeal jaws in which the paired upper jaws (Fig. 5, PB4) are first depressed and then retracted posteriorly against the stabilized and elevated lower jaws (Fig. 5, CB5). The mechanisms of upper jaw depression and retraction involve separate mechanical couplings. Depression is caused by rotation of the arched epibranchial bone about the site of attachment of the obliquus posterior muscle (Fig. 5a, b, and c). The epibranchial articulates with the dorsal surface of the upper jaw so that when the epibranchial is rotated it pushes down and depresses the upper jaw. Rotation of the epibranchial is produced by the actions of several dorsal branchial muscles, principally the levator posterior, fourth levator externus, and the obliquus dorsalis (Fig. 5).

Upper jaw retraction occurs in conjunction with depression and is produced by a single muscle, the retractor dorsalis. This muscle originates on several anterior vertebrae and inserts on the posterior margin of the upper pharyngeal jaw (Fig 5a: RD). The lower jaw is stabilized through muscles that attach it to the pectoral girdle and interconnect the paired lower jaw bones. Some elevation of the lower jaws occurs, though the overall orbit of lower jaw movement is considerably more restricted than that of the upper jaws. The combination of upper jaw depression and retraction produces a strong pharyngeal jaw bite with a shearing component as the upper jaws move against the stabilized and slightly elevated lower jaws.

Snail predation

The trophic habits of two species, the redear sunfish, *Lepomis microlophus*, and the pumpkinseed sunfish, *Lepomis gibbosus*, are dominated by snails. No other centrarchid species are known to crush and consume significant amounts of snails. However, these are not the only sunfishes known to have the capability to crush snails. Our laboratory observations have revealed that some individuals of the green sunfish, *Lepomis cyanellus*, can crush snails, though not as proficiently as either *L. microlophus* or *L. gibbosus*. A systematic survey of the snail crushing abilities of other *Lepomis* species has never been made, so the possibility still exists that others possess the ability to crush snails.

Our analysis focuses on four species: the two snail-eating specialists *Lepomis microlophus* and *L. gibbosus*, the zooplanktivorous bluegill sunfish, *L. macrochirus*, and the previously mentioned *L. cyanellus*. The diets of *L. macrochirus*, *L. cyanellus*, and other species of *Lepomis* typically include less than 5% snails (Ruhr, 1952; Huish,

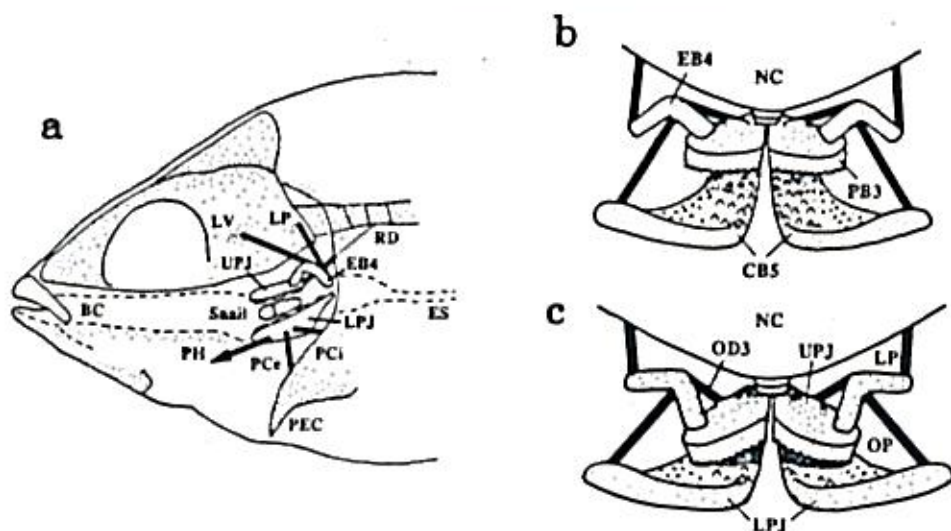


Figure 5.

a) Lateral view of the pharyngeal jaw apparatus in a typical centrarchid showing the topography of the major small crushing elements described in the text. Figures b and c illustrate the mechanism of upper pharyngeal jaw depression that is a key component of snail crushing in sunfishes. The apparatus is shown in posterior aspect before and after muscular contraction. Note that as the LP contracts it rotates the epibranchial around the latter's connection with the OP, forcing the upper jaw (UPJ or PB3) downward. In this way the upper pharyngeal jaw presses down against the lower jaw during crushing movements. Figures b and c taken from Wainwright (1989a). Thick black lines indicate the locations of muscles. Abbreviations: BC, buccal cavity; CB5, fifth ceratobranchial or lower pharyngeal jaw; EB4, fourth epibranchial; ES, esophagus; LP, levator posterior; LPJ, lower pharyngeal jaw; LV, fourth levator externus; NC, neurocranium; OD3, third obliquus dorsalis; OP, obliquus posterior; PB3, third pharyngobranchial or upper pharyngeal jaw; PCe, pharyngocleithralis externus; PCI, pharyngocleithralis internus; PEC, pectoral girdle; PH, pharyngohyoideus; RD, retractor dorsalis; UPJ, upper pharyngeal jaw.

1957; Applegate et al., 1966; Werner, 1977), and no reports are available that these species crush the snails they do consume (i.e., Mittelbach, 1984). In this case study we also examine pharyngeal jaw function in several other sunfishes which do not feed on snails (*Lepomis gulosus*, *Pomoxis nigromaculatus*, *Micropterus salmoides*, *Ambloplites rupestris*).

Both *L. microlophus* and *L. gibbosus* possess morphological specializations of the pharyngeal jaws that are correlated with the ability to crush hard-shelled prey. A comparison of the pharyngeal jaw muscles in these and other species of *Lepomis* revealed hypertrophied levator posterior and pharyngohyoideus muscles in the two mollusc-eating species. The levator posterior is the primary muscle involved in generating the crushing movement of upper pharyngeal jaw depression and its relatively high physiological cross-sectional area in the molluscivores indicates that it can generate 10–15 times as much tension as in unspecialized species (Lauder, 1986). The pharyngeal jaw bones of *L. microlophus* and *L. gibbosus* are also hypertrophied relative to the condition in other sunfishes. *L. microlophus* and *L. gibbosus* have larger, more robust jaw bones and teeth of greater diameter than other

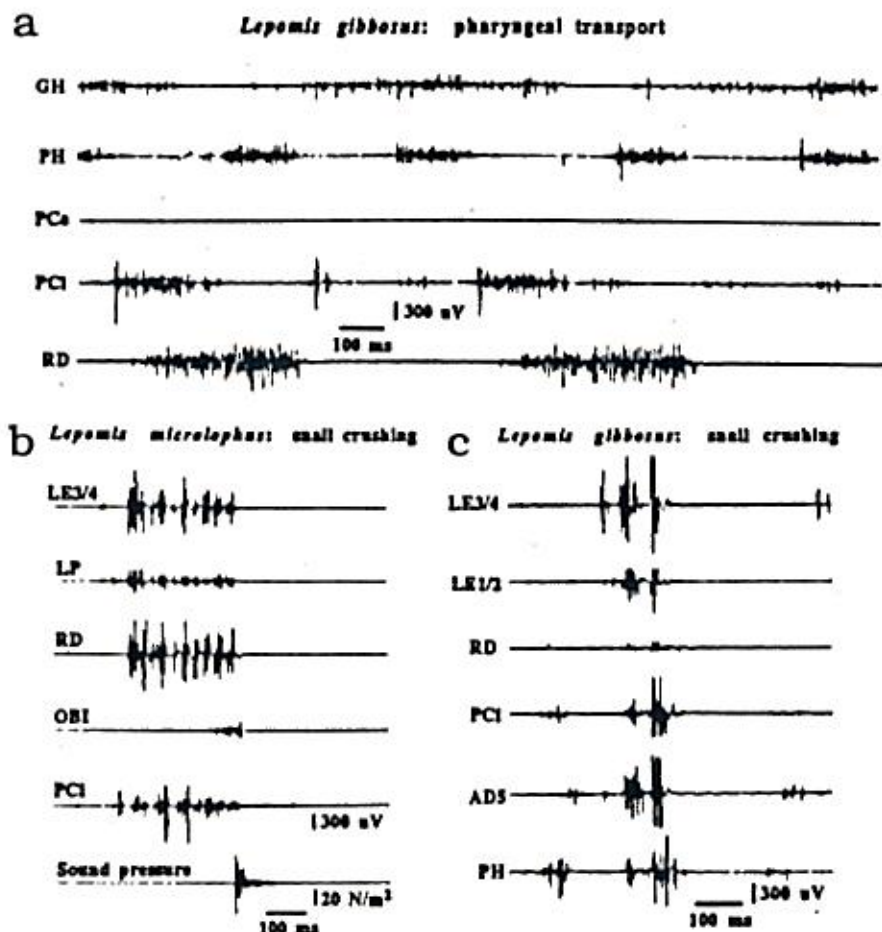


Figure 6.

Sample electromyographic recordings of pharyngeal jaw muscles taken from the two snail-eating centrarchid species. a) The typical pharyngeal transport motor pattern seen in centrarchids during handling behavior with soft prey, as exemplified by *Lepomis gibbosus* feeding on a large piece of earthworm. Note the pattern of repeated bursts that show only partial overlaps of activity among muscles. b) Recording of snail crushing by *Lepomis microlophus*, and c) *Lepomis gibbosus*. Note the almost complete overlap of activity of all muscles and the abrupt termination of activity once the snail is crushed (b, sound pressure record shows activity due to the noise made by the snail shell cracking). Muscle abbreviations as in Figure 5 and: GH, geniohyoideus; OBI, obliquus inferioris; LE1/2, first and second external levators; LE3/4, third and fourth external levators; ADS, fifth branchial adductor.

centrarchids (Lauder, 1983b). *Lepomis cyanellus*, the species that occasionally crushes snails in the laboratory, exhibits neither hypertrophied muscles nor hypertrophied pharyngeal jaw bones.

Two basic pharyngeal jaw motor patterns have been identified in sunfishes. First, during handling and swallowing of small fishes and earthworms, all species except *L. microlophus* display "pharyngeal transport", a cyclic pattern of muscle activity that may continue for over one minute as prey are chewed and simultaneously trans-

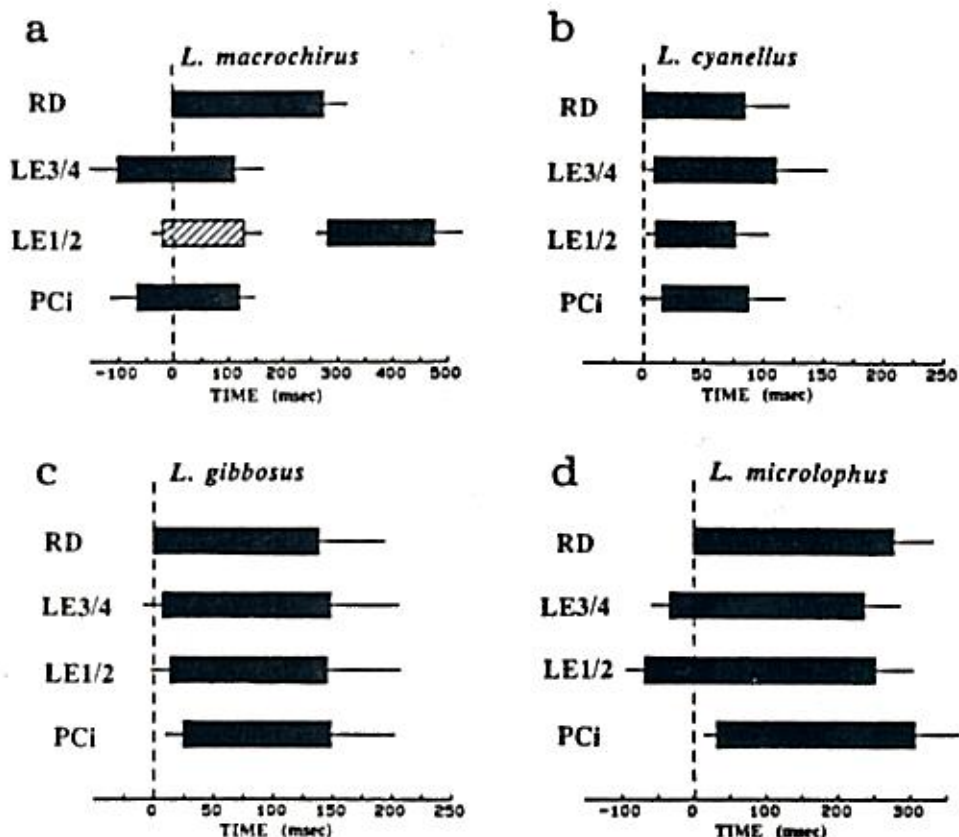


Figure 7.

Electromyographic bar diagrams showing the average motor pattern exhibited by four centrarchid species during pharyngeal jaw prey handling behaviors. *Lepomis macrochirus* only shows pharyngeal transport (here during feedings on worm and fish prey), while *L. gibbosus*, *L. microlophus*, and *L. cyanellus* exhibit the snail crushing motor pattern. Solid bars indicate activity bursts that occur in 100% of feedings and the hatched bars indicate burst of muscle activity that occur in fewer than 67% of all feedings. Other conventions as in Figure 3.

ported into the esophagus by the repeated depression and retraction of the upper jaws. A sample electromyogram of pharyngeal transport is shown from *L. gibbosus* feeding on an earthworm in Figure 6a (see Lauder, 1983b, for more detail). Figure 7a shows a bar diagram illustrating the average timing of muscle activity during pharyngeal transport in *L. macrochirus*. In this instance, we focus on activity patterns in four muscles, though several other muscles have also been studied quantitatively and show a similar pattern. During pharyngeal transport there is considerable variation among muscles in the activity onset-time (Figs. 6a and 7a). In particular, about half of the retractor dorsalis burst overlaps with the fourth levator externus and the pharyngocleithralls internus (Fig. 7a, RD, LE3/4, and PCI). Further, the second levator externus (Fig. 7a, LE1/2) is always active in a burst following the offset of activity in the other muscles, but sometimes shows a second burst that broadly overlaps the other muscles.

In addition to morphological specializations, *L. microlophus* and *L. gibbosus* also

exhibit a novel pattern of muscle activity when crushing snails (Fig. 6b and c; Fig. 7c and d). This pattern is distinct and significant in two key features. First, in contrast to the pattern seen in other sunfishes during feeding on softer prey, snail crushing involves nearly simultaneous, intense bursts of activity in all pharyngeal muscles. Thus, activity of the second levator externus almost completely overlaps activity of the other pharyngeal muscles (Fig. 7c and d). Second, the snail crushing pattern is not cyclical and ceases abruptly when the snail shell is crushed (Lauder, 1983b). This can be seen in Figure 6b where the sound pressure recording shows activity when the snail shell falls and a distinct crushing sound can be heard.

This second motor pattern is exhibited by the two snail-eating species, *L. microlophus* and *L. gibbosus*, as well as individuals of *L. cyanellus* when they eat and crush snails (Fig. 6b and c; Fig. 7b, c, and d). This pattern has not been observed in any of the other sunfish species that have been examined (*Lepomis macrochirus*, *L. gulosus*, *Pomoxis nigromaculatus*, *Micropterus salmoides*, *Ambloplites rupestris*). Both *L. cyanellus* and *L. gibbosus* will use both the pharyngeal transport and snail crushing motor pattern and modulate muscle activity depending on the type of prey being consumed. When softer prey are eaten the cyclical pattern is used, but the crushing pattern is only used when feeding on snails. In contrast, *L. microlophus* uses only the snail crushing motor pattern, even when feeding on soft-bodied prey such as earthworms or small fish.

Historical patterns

Within the Centrarchidae the novel trophic habit of crushing and consuming snails is known to occur in only two species, *L. microlophus* and *L. gibbosus*. We emphasize the distinction between the dietary habit itself and possessing the capability to crush snails. The distribution of this dietary habit on the centrarchid phylogeny is congruent with the sister-species relationship of the two snail crushers (Figs. 1 and 8). Thus, the snail-eating diet appears to have evolved only once within the Centrarchidae. Of course, all sunfishes that show this feeding habit also show an ability to crush snails, however, not all species that are able to crush snails have diets dominated by this prey type. At least one other sunfish, *L. cyanellus*, can crush snails in the laboratory but only occasionally eats them in the wild (Werner, 1977). The ability to crush snails does not seem to necessitate the ecological transition to a diet dominated by this prey type.

The key functional attribute that underlies the ability to crush snails appears to be the derived crushing motor pattern exhibited by all species capable of crushing snails (Fig. 8). The actions involved in crushing prey in the pharyngeal jaws constitute a novel behavior within sunfishes that is produced by this phylogenetically derived pattern of muscle activity (Lauder, 1986). No anatomical specializations of the muscles and bones of the pharyngeal jaws have been identified that are present in all species capable of crushing molluscs (Fig. 8). Thus, *L. cyanellus* can crush snails and it does so without the hypertrophied muscles and bones present in *L. microlophus* and *L. gibbosus*. All species capable of crushing snails, however, exhibit the novel motor pattern associated with this behavior.

When viewed in a phylogenetic context the ability to crush snails and the motor pattern associated with the behavior are distributed incongruently with the branching diagram (Fig. 8), suggesting that either these characters have evolved

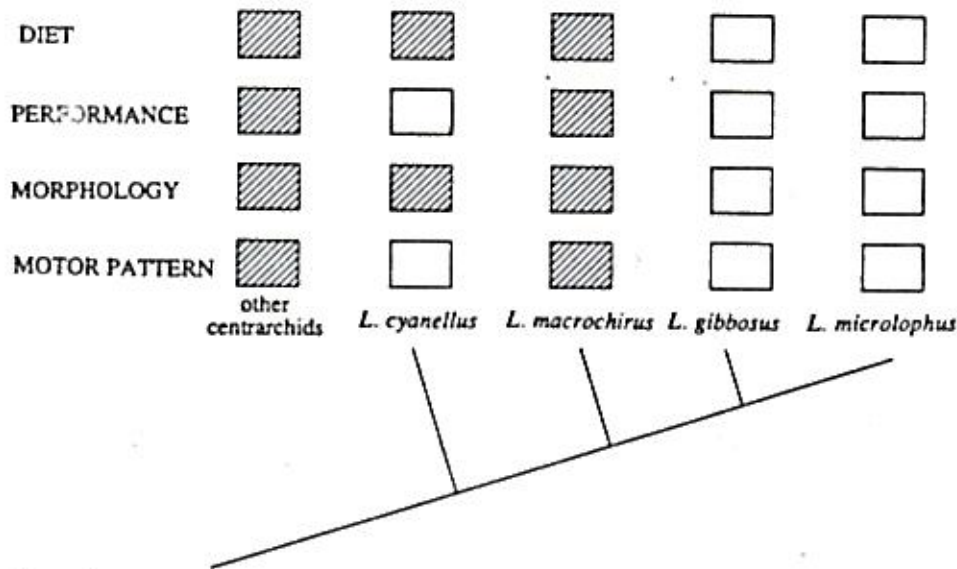


Figure 8.

Aspects of snail crushing biology mapped onto a reduced centrarchid phylogeny. The occurrence of snails in the diet is congruent with the sister species status of *L. gibbosus* and *L. microlophus*, indicating that this dietary habit has evolved only once within the Centrarchidae. Although *L. cyanellus* exhibits the snail crushing motor pattern and a limited ability to crush snails, the lack of morphological specializations appears to prevent this species from being able to use snails in its diet. The "other centrarchids" group includes species for which comparative data are available; *Lepomis gulosus*, *Pomoxis nigromaculatus*, *Micropterus salmoides*, and *Ambloplites rupestris*. Conventions as in Figure 4.

convergently in *L. cyanellus* and the two mollusc specialists or the behavior evolved once in the ancestor to a clade inclusive of these species and has been lost in *L. macrochirus*. A more thorough examination of mollusc crushing performance and motor patterns in the other seven species of *Lepomis* is required to resolve the issue of the origin of snail crushing behavior.

Based on the phylogenetic distribution of the data presented here there are two possible outcomes of future work on this problem. If additional research reveals that most or all other species of *Lepomis* exhibit the snail crushing motor pattern without the dietary or morphological specializations (suggesting that the motor pattern was lost in *L. macrochirus*) then it will be necessary to hypothesize that the origin of the snail crushing motor pattern was unrelated to the evolutionary origin of the snail diet. This would suggest that the snail crushing motor pattern, while it is necessary for the snail-eating diet, did not evolve as an adaptation for it. The other alternative, that the snail crushing motor pattern is not present in other species of *Lepomis* (or is spottily distributed within the group), would indicate that this novel motor pattern has evolved convergently at least twice in sunfishes, though the evidence suggests that it is something of an evolutionary dead end in *L. cyanellus* since this species does not appear to make use of its snail crushing ability in the wild. Regardless of the outcome, however, the framework provided by the phylogeny is crucial to any attempt to determine the number of times that the snail crushing motor pattern has evolved.

The morphological specializations of the pharyngeal jaws present in *L. microlophus* and *L. gibbosus* suggest that these species should be more proficient at snail crushing than *L. cyanellus*. The greater physiological cross-sectional area of the levator posterior muscle indicates greater force-generating capability of this muscle in the former two species. Since the levator posterior is centrally involved in generating the occlusal forces of the pharyngeal jaws, increased force capability of this muscle would be expected to lead to more effective mollusc crushing. This expectation is supported by published data as well as our laboratory observations. *Lepomis microlophus* and *L. gibbosus* are proficient molluscivores that quickly manipulate and crush snails, usually within a few seconds (Mittelbach, 1984; Osenberg and Mittelbach, 1989). Furthermore, only about 10–20% of the *L. cyanellus* individuals kept in the laboratory will crush snails (G. Lauder, unpubl. data). As yet, however, no data are available which compare snail crushing performance (i.e., handling times and the largest snails that can be crushed) among these species. The observation that only the species with morphological specializations regularly prey on snails under natural conditions suggests the hypothesis that possessing the motor pattern used in snail crushing does not, by itself, confer the ability to specialize on a snail diet, but that the additional presence of hypertrophied muscles and more robust jaw bones increases snail crushing performance sufficiently to permit this novel trophic habit.

DISCUSSION

The combined historical and functional analyses of centrarchid trophic characters permit two primary conclusions to be drawn regarding the evolution of sunfish feeding biology. First, transformations of functional morphology are strongly congruent with feeding ability, and biomechanical evaluations suggest that the morphological and/or neuromuscular changes are causally linked to the performance shifts. Second, in both case studies the evolution of feeding habits is tightly linked to the evolution of feeding ability. Dietary differences between species often involve each species eating prey that other species are incapable of successfully consuming or are less efficient at handling.

In both the mandibular jaws and the pharyngeal jaws, functional morphological transformations were found to play a primary role in determining feeding performance, and ultimately diet. In no instance were major dietary differences found without a concomitant difference in feeding performance and functional morphology. The historical perspective provided by the centrarchid phylogeny (Fig. 1) permits the observation that the major dietary differences among sunfish species can apparently be explained by evolutionary changes in feeding ability. Functional morphology sets a fundamental limit on the range of prey types that each species is able to efficiently consume. This creates a diversity of potential trophic niches within the Centrarchidae that provides one mechanism for coexistence of species by resource partitioning. Indeed, a prominent theme in studies of centrarchid feeding ecology has been that a competitive refuge is gained by species that are able to forage proficiently on prey that fall outside of the range of capability of other species (e.g., Mittelbach, 1981, 1984). As such, functional morphology is a major factor determining the feeding patterns of sunfishes. Ecological interactions, such as competi-

tion or predation pressure, are known to influence sunfish feeding habits (e.g., Werner et al., 1983; Mittelbach, 1981), but because of phylogenetic constraints in anatomy and motor patterns these factors can only operate by shifting diets within the range of prey that each species can successfully make use of.

Little evidence is provided by our data to support the notion that trophic anatomy and motor patterns are somehow constrained to evolve together. Rather, these different levels of functional design appear to evolve independently. Changes in both anatomy and motor patterns can bring about alterations of feeding ability, though simultaneous shifts at both levels need not be involved. Thus, differences among sunfishes in prey capture ability are linked to key changes in cranial anatomy, principally mouth dimensions, while the pattern of muscle activity that drives suction feeding remains largely unchanged. In contrast, the evolution of the mollusc crushing diet involved both the acquisition of a novel motor pattern and increased force generating capacity of the branchial muscles used in applying the shell-crushing forces.

A particularly striking result of the analysis of mollusc crushing is the observation that alterations in both the motor pattern and branchial morphology appear to be required for fish to achieve sufficiently high mollusc crushing performance that they may make effective use of this ecological resource. *Lepomis cyanellus* possesses the snail crushing motor pattern without specializations of pharyngeal jaw anatomy, and this species appears to show an intermediate ability to crush snails. Though the novel motor pattern makes it possible for *L. cyanellus* to show limited mollusc crushing abilities, it appears that the increased force-generating capacity of the levator posterior muscle that is shared by the two mollusc eating species, *L. microlophus* and *L. gibbosus*, is essential for improving snail crushing ability and permitting these two species to specialize on snails in the wild. Thus, during the evolution of snail crushing in the Centrarchidae ecological shifts in diet have lagged behind changes in the motor pattern and without both morphological and neuromuscular transformations, snail crushing performance appears to remain too poor to support this novel diet.

What insights into the evolution of sunfish feeding biology have been gained in these studies through the use of a phylogenetic perspective? In the analysis of the mandibular jaws we found diet, feeding ability, and morphology to differ among all four species, while the motor pattern used during suction feeding was the same in all taxa. In fact, these characters would tell the same story regardless of the relationships among the species. Diet, performance, and morphology are autapomorphies for each species. Though we have not exhaustively sampled the centrarchid clade the electromyographic data suggest that the motor pattern is plesiomorphic for the family. In this case the phylogeny did not permit us to resolve any historical questions.

In contrast, the phylogenetic perspective plays a crucial role in the interpretation of the evolution of snail crushing in the genus *Lepomis*. Without an hypothesis of centrarchid relationships it would have been impossible to determine how many times the snail diet evolved in this group. The phylogeny will also be indispensable in future attempts to determine if the snail crushing motor pattern evolved simultaneously with the snail diet and how many times the snail crushing motor pattern evolved. Issues of the historical sequence of character evolution can only be resolved within the context of a well corroborated phylogeny.

Mandibular Jaws Versus Pharyngeal Jaws

The two case studies presented in this chapter contrast separate functional systems in the feeding mechanism of sunfishes: the mandibular jaw apparatus and the pharyngeal jaw apparatus. These functional units are both necessary to the successful trophic biology of sunfishes and are involved in suction feeding and prey handling behaviors, respectively. However, one intriguing result of these analyses is that the patterns of evolution of anatomy and motor control are different in the two systems. In the mandibular jaws evolutionary changes in feeding performance and dietary habits are associated with changes in morphology only, while snail crushing behavior involves changes in both pharyngeal anatomy and the motor pattern.

Previous quantitative comparisons of the muscle activity patterns used by aquatic lower vertebrates during suction feeding have found that the motor pattern tends to be strongly conserved within closely related groups (i.e., genera and families; Shaffer and Lauder, 1985; Sanderson, 1988). Though this pattern of conservation of the suction feeding motor pattern has recently been shown to break down at a very broad phylogenetic level (Wainwright et al., 1989), there is clearly a tendency toward conservation within higher taxa, even when species with very different diets, prey capture strategies, and morphologies are compared, such as *Micropterus salmoides* and *Lepomis macrochirus* in the present study.

The generality of motor pattern conservation in the pharyngeal jaws is more difficult to assess at this time. One previous study that has compared patterns of pharyngeal muscle activity among fish species within a family (Wainwright, 1989b) found differences among haemulid species in only one out of fifteen electromyographic variables that were examined, indicating that the motor pattern has been strongly conserved within this group. Thus, the pattern of change in both morphology and motor patterns found in sunfishes may not be particularly widespread, making centrarchids a particularly important case study in the evolution of the pharyngeal jaw apparatus. Additional studies of the functional basis of novel pharyngeal jaw behaviors are needed before general patterns can be identified.

One important distinction between the two case studies, relating to the different patterns of evolution in functional morphology, is that sunfishes use only a single behavior for prey capture: suction feeding; while at least two behaviors are used by the pharyngeal jaws during prey reduction: pharyngeal transport and crushing. Thus, observed variation among species in prey capture ability and diet are brought about by modifications to the anatomy used in a common behavior, suction feeding, while the evolution of snail crushing was accomplished through the acquisition of an entirely novel behavior. Many fishes are known to capture prey using mechanisms other than suction feeding and it is possible that novel prey capture behaviors involve novel muscle activity patterns. Such a situation has been found in African cichlids (Liem, 1978, 1979) where some taxa can perform the specialized mandibular jaw behaviors of scraping algae off of hard substrata and manipulating pieces of larger prey. These novel behaviors appear to be associated with novel patterns of muscle activity (Liem, 1979), paralleling the situation we find with centrarchid pharyngeal jaws.

SUMMARY

We have presented an historical analysis of the functional morphological basis of dietary habits in North American sunfishes (Centrarchidae). General patterns were

sought in the ways that the functional design of the feeding system changes during the evolution of trophic habits in fishes. An independently derived hypothesis of centrarchid relationships was used as a basis for interpreting patterns of evolution in two aspects of feeding behavior: the strike and prey handling. In each analysis we examined the phylogenetic correlation of changes in diet, feeding performance, and two levels of functional design in the feeding mechanism (musculoskeletal morphology and patterns of muscle activity). Can changes in diet and feeding proficiency be explained by changes in morphology or in motor patterns associated with feeding behavior? The phylogenetic perspective permitted us (1) to test causal explanations by searching for congruence of character occurrence, and (2) to ask how many times specific feeding systems have evolved in the centrarchid lineage.

In the analysis of strike behavior in four species (*Micropterus salmoides*, *Ambloplites rupestris*, *Pomoxis nigromaculatus*, and *Lepomis macrochirus*) congruent changes were found in diet, feeding performance, and morphology. In contrast, the muscle activity pattern used at the strike was strongly conserved, even in fishes with feeding habits as divergent as *M. salmoides* and *L. macrochirus*, and appears to be a primitive character retained from the common ancestor of the Centrarchidae. In a separate analysis of handling behavior in four species of *Lepomis*, occurrence of molluscs in the diet was correlated with mollusc crushing abilities, morphological specializations of the pharyngeal jaw apparatus, and a novel pattern of muscle activity. In this case differences among species in dietary habits match the feeding abilities of sunfishes. In the mandibular jaws evolutionary changes in feeding performance and dietary habits are only associated with changes in morphology, while the snail diet involves changes in both pharyngeal anatomy and the motor pattern. Without the use of a phylogenetic hypothesis for the Centrarchidae it would not have been possible to determine if a snail diet evolved only once in this lineage or to show that the novel motor pattern used during snail crushing has either evolved more than once or has been secondarily lost in at least one species.

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