

# Ecomorphology of Prey Capture in Fishes

*Peter C. Wainwright*

---

## Summary

With about 24,000 living species, fishes are the most diverse group of vertebrates and offer a rich substrate for identifying general themes in the relationship between fish feeding habits and the functional design of the feeding system. All fish species appear to use one or more of the three basic feeding modes identified by Liem (1980); ram feeding, suction feeding or manipulation. Differences in the performance features that typify each mode result in different predictions for the expected design of the musculoskeletal system used to capture prey with the three modes. Manipulation is used to take prey that adhere to the substrate or remove pieces of larger prey. In this mode the force that is applied by the oral jaws to the prey or substrate is a key performance feature. In contrast, both ram and suction are enhanced by increased velocity of movements used in the rapid strikes that characterize these modes. In the design of lever systems, such as the ones involved in the jaw-opening and closing systems of teleosts, force and velocity realized at the jaw tip are traded off in alterations of the inlever-to-outlever ratio. This design trade-off suggests a major morphological distinction between ram-suction feeders and manipulators. This distinction was verified in a sample of 34 species of fishes in which no overlap between ram-suction feeders and manipulators was seen. These observations typify the recent success in the ecomorphology of fishes in identifying important general design criteria of the feeding mechanism. It is suggested that two aspects of intraspecific variation offer relatively unexplored, potentially fruitful areas of future investigation: the ontogeny of the form/diet relationship and the role of phenotypic plasticity in the evolution of fish feeding systems.

**Key words:** Musculo-skeletal system; Prey-Capture relationship; Trophic ecology; Teleost.

## 1. Introduction

The remarkable diversity of fishes (approximately 24,000 extant species; Lauder and Liem, 1983) makes this group of vertebrates a natural target for the search for generalities and repeating themes in how the functional design of organisms relates to their ecology. As a consequence of the richness of this group the field of ecomorphology has arguably made greater strides in Ichthyology than in other areas of vertebrate biology (rivaled only by the well-developed field of avian ecomorphology). Fishes occupy nearly every aquatic environment on earth and show trophic diversity that reflects the diversity in habitat and functional design of the group as a whole.

Fish diets are as diverse as the edible matter found associated with aquatic ecosystems. Food items of teleost fishes range in size from the phytoplankton eaten

by some engraulids and the bacteria taken by many deposit-feeding species up to the large tuna and cephalopod prey of marlin, swordfish and giant serranids. Prey vary in consistency from the jellyfish eaten by the ocean sunfish, *Mola mola*, to the coral skeletons that are ground up by some species of parrotfish to extract the algae and other organisms that lie within the dead or living coral skeleton. The diversity of prey eaten by fishes is truly staggering and given this diversity it is worth asking if there are general themes in the patterns of prey use by fishes and if these patterns are related to the diversity of fish feeding mechanisms. In this article I shall attempt to summarize some recent advances of ichthyological ecomorphology with a special focus on the relationship between the musculoskeletal design of the prey-capture mechanism and trophic ecology. In striving for a focused discussion I regrettably omit any treatment of other important areas of fish ecomorphology related to their trophic biology, such as the advances made in locomotion (Weihs, 1973; Webb, 1982), digestive physiology (Kapoor *et al.*, 1975), vision (Ali 1975; McFarland and Munz, 1975), and even prey-processing biomechanics (Galís, 1993).

## 2. Three Feeding Modes

In fact, there are a number of generalities to be drawn from the diverse feeding habits of fishes. In terms of understanding how this dietary diversity relates to the spectrum of functional design it is useful to consider the important observation made by Liem (1980) that the feeding modes of fishes fall into three basic categories: suction feeding, ram feeding and manipulation. Suction feeding is associated with a rapid expansion of the oral cavity that generates a pressure gradient between the inside of the buccal cavity and the ambient water, causing water to rush into the opened mouth. Prey are entrained in this current and pulled into the mouth (Lauder, 1985). Suction feeding is believed to be the primitive mode of feeding in bony fishes (Lauder, 1982).

In ram feeding, the fish overtakes the prey with a forward body movement. The key distinction between ram and suction feeding is whether the predator's mouth is thrust over the prey (ram feeding) or the predator generates a water flow that pulls the prey into the jaws (suction feeding). Ram may be accomplished by whole body movements or by rapid jaw protrusion (Motta, 1984). In some taxa rapid cranial flexion is used to quickly move the mouth over the prey (Bergert and Wainwright, 1997). In reality, ram and suction feeding appear to exist as the theoretical extremes of a continuous spectrum of the two modes (see excellent discussion in Norton and Brainerd, 1993). Thus, the majority of species employing suction also incorporate forward body or jaw movements in their strike to help traverse the last few centimeters between predator and prey.

Manipulation is a broad category that incorporates the variations on using the oral jaws to grasp prey. This includes many of the benthic-scraping coral reef taxa including butterflyfishes (Motta, 1988), surgeonfishes (Winterbottom and McLennan, 1993), many wrasses and parrotfishes (Randall, 1967), filefishes and other tetradontiform taxa (Randall, 1967). The benthic-scraping cichlids fall in this category (Fryer and Iles, 1972). In this feeding mode the oral jaws are applied to the substrate (or directly to the prey) and a biting action is used to remove the prey from the substrate or break off pieces of a larger prey.

Virtually all fish species known use one of these three feeding modes or, more typically, a combination of at least two of them (Liem, 1980). This paradigm of feeding modes in fishes provides a useful framework to consider the relationship

between the structural design of fish feeding mechanisms and the prey that fishes eat. Below, I consider two issues concerning the ecomorphology of fish feeding modes. First, what are the consequences of these three feeding modes for the types of prey that are consumed? Are the three modes associated with different types of prey? Secondly, what are the key design features of each feeding mode and how can they be modeled in a fashion that would permit researchers to assess the degree to which taxa are morphologically specialized for each mode?

## 3. Feeding Mode and Prey Type

The three feeding modes are associated with different types of prey. Here I emphasize major trends in associations. Exceptions can probably be found for all of these trends, but my aim is to attempt to summarize the major associations between feeding mode and prey type. It is important to emphasize that the focus here is on prey capture. Fish also exhibit specializations for different prey processing modes (e.g., suspension feeding, mollusk crushing, physical breakdown of plants). In general, suction and ram feeding are used to take elusive prey and prey that are found in midwater, such as plankton. Thus, piscivores, planktivores and generalized predators of mobile invertebrates can usually be placed somewhere along the ram-suction continuum. In contrast, manipulation is used to take prey that are fixed to the substrate or to remove pieces of larger prey. Many herbivores use manipulation to procure food (e.g., the Scaridae and Acanthuridae), as do predators on many immobile benthic prey such as sponges (e.g., many members of the Pomacanthidae), coral (several monacanthids and the Chaetodontidae), and molluscs (e.g., Diodontidae and some Labridae).

While ram and suction represent a continuum, there are clear tendencies for what types of prey tend to be associated with the two modes. Ram is particularly prevalent in two quite different feeding strategies. It is seen in many suspension-feeding species that swim through dense aggregations of very small prey entrapping them in gill arch structures (the Engraulidae and Clupeidae) and is also often featured in fish that eat large, elusive prey. Particularly clear examples of the latter group are the many taxa that feed in a manner similar to *Esox*, which captures prey with a rapid burst of speed, opening its mouth at the last moment before overtaking the prey. In *Esox* and similar species (e.g., *Sphyaena*) prey are firmly held by many sharp, recurved teeth, though not all ram-feeding predators are as well endowed with teeth. For example, tuna, billfish and mackerels are primarily ram feeders and most of them lack raptorial dentition. Ram-feeding specialists tend to have a large mouth.

Toward the suction end of the ram-suction continuum are many particulate planktivores that remove single zooplankters from the water column (e.g., many pomacentrids, some species of *Lepomis*). These species often have a small mouth and protrusible upper jaw. Suction feeders that prey on large elusive prey (e.g., antenariid anglerfishes, scorpaenid scorpeonfishes) have larger mouths and tend to ambush their prey utilizing stealth and camouflage to get within a short strike of their prey.

## 4. Feeding Mode and Design of Feeding Mechanism

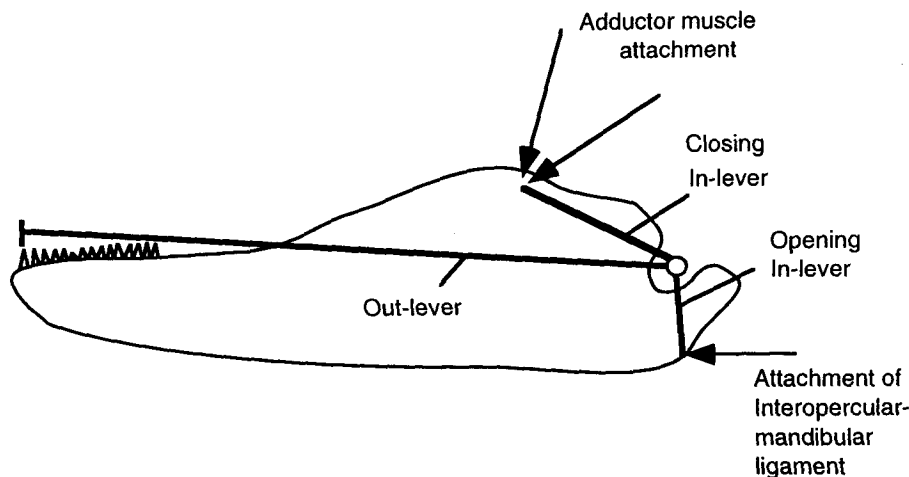
The three modes of prey capture in fishes implicate different design features. Interestingly, in many cases these features are mutually exclusive such that designing

the system to maximize performance in one mode will result in a trade-off with loss of performance in another mode. In such cases we might expect to see clear differences in the morphology of species that use different modes of prey capture. In the discussion that follows I focus on a single aspect of design of the feeding mechanism, the mechanical lever system of the jaws. Structural and physiological variation occurs at many other levels of design and can influence feeding performance, but I focus on the jaw lever system here because (1) it represents morphological variables that are easily measured by researchers and (2) has a particularly clear biomechanical consequence for feeding performance.

### Manipulation vs Ram-suction

The clearest differences in design criteria are between the manipulation and ram-suction modes. In general, the performance feature most important in manipulation is the ability to apply a large force with the jaws at the position of contact with the prey. In contrast, ram and suction ability are both enhanced by an increase in speed of movement. At many levels of design of the feeding mechanism these two performance features, force and speed, are mutually exclusive. As I hope to show in the discussion that follows, this single design trade-off reveals a number of expectations for differences in the morphology of species that fall in the two feeding modes.

Let us first consider the lever system in the jaws that are involved in depression and elevation of the mandible (Fig. 1).



**Fig. 1.** Diagram of the lever systems in the mandible of a teleost fish. For jaw closing the inlever is the distance from the centre of the joint to the attachment of the adductor mandibulae on the mandible. The outlever is the distance from the attachment of the adductor mandibulae to the tip of the tooth row. For jaw opening the inlever is the distance from the jaw joint to the attachment site of the interopercular mandibular ligament.

In a lever system, the force that is realized at the outlever, in this case the tip of the toothed jaw, is given by the equation:

$$F_0 = F_i (L_i/L_0),$$

Where  $F_0$  is force at the outlever,  $F_i$  is force at the inlever,  $L_i$  is the length of the inlever, and  $L_0$  is the length of the outlever. The important point that follows from this equation is that, assuming a constant value of force at the inlever, increasing the

ratio of the inlever to the outlever will result in a net increase in the force that is realized at the outlever.

In the same lever system the velocity of movement at the outlever is given by:

$$V_0 = V_i (L_0/L_i),$$

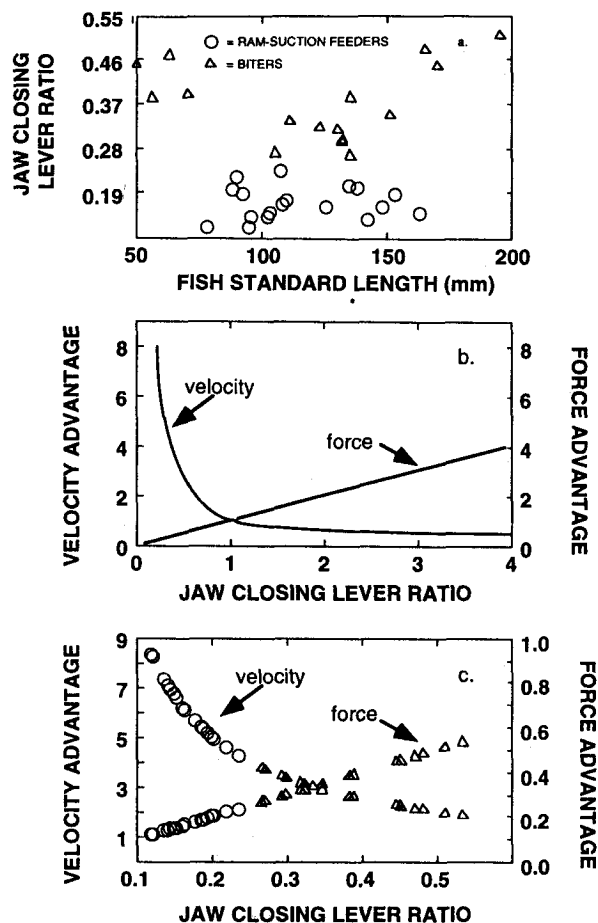
where  $V_0$  and  $V_i$  are velocity at the outlever and inlever respectively. Note that velocity at the outlever is a function of the ratio of the outlever to the inlever, while force at the outlever is a function of the inverse of this ratio. The result is that force and velocity are simultaneously altered by changes in the ratio of inlever and outlever that will trade off the two features. This trade-off is diagrammed in Figure 2b where the consequences of changing the inlever-to-outlever ratio are shown for force and velocity at the outlever.

To put this principle into action for the jaws of a fish, consider the design of the system of jaw closing (Fig. 1). The distance from the center of the jaw joint with the quadrate bone to the attachment site of the adductor mandibulae muscle is the inlever. The distance from the jaw joint to the tip of the outer tooth represents the outlever. The inforce and invelocity are provided by the adductor mandibulae muscle. The basic trade-off between force and velocity in a lever system dictates that changes in the inlever-outlever ratio of this system will improve force or velocity at the cost of the other feature (Fig. 2b).

Does this discussion of the jaw lever system actually provide any insight into the design of real fish jaws? Figure 2a shows the inlever-outlever ratio of the jaw-closing system in 34 species of fishes from 16 families. There are two points to make with this Figure. First, note that the species which use manipulation to capture prey (the triangles) all have lever ratios that are higher than any of the species that use ram-suction to capture prey. This is especially well illustrated by species of *Halichoeres*, most of which are biters. However, the ram-suction species in Figure 2a with the highest lever ratio is a suction feeder that eats zooplankton, *H. pictus*. Second, note that the values of this ratio all fall between about 0.1 and 0.5, corresponding to the region on the graph in Figure 2b in which changes in this ratio result in the biggest changes in the effect on velocity transfer. In this part of the curve, a small change in the lever ratio results in a large change in velocity transfer. Figure 2c shows the velocity and force advantage for the jaw-closing lever ratio in these same fishes. Note that the force advantage axis (right side of graph) has a very different scale than the velocity advantage. This Figure graphically illustrates the trade-off in each species between velocity and force advantage in the design of the jaw-closing lever system.

The above discussion focuses on the lever system involved in elevating or adducting the mandible. In the complex musculoskeletal system of the teleost skull there are several other locations where lever design plays an important role in determining the performance characteristics of the system. One example is the jaw-opening system in which the inlever is the distance from the jaw joint to the insertion of the interopercular-mandibular ligament on the back of the mandible. The need for rapid motion in ram-suction feeding suggests that this ratio should favor velocity in those species. This prediction has been supported in the same group of fishes shown in Figure 1a (Wainwright and Richard, 1995).

Other motions in the teleost skull involve mechanical linkages called four-bar systems. The reader is referred to the work of Muller (1987) for discussions of the various four-bar linkages that have been hypothesized for the teleost skull and the work of Westneat (1990) who has developed a methodology for testing whether four-



**Fig. 2.** (a) Plot of the jaw-closing lever ratio versus standard length in specimens of 34 species of teleost fishes. The species included in this analysis are listed in order of increasing jaw-closing ratio; rapid-strike suction feeders: *Pempheris schomburgki* (94 mm), *Chromis cyanea* (78.5 mm), *Cynoscion nebulosus* (142 mm), *Hypoplectrus indigo* (95.5 mm), *Ocyurus chrysurus* (102 mm), *Cephalopholis fulva* (103 mm), *Mycteroperca bonaci* (163 mm), *Sphyraena barracuda* (148 mm), *Paranthias furcifer* (126 mm), *Holocentrus ascensionis* (108 mm), *Lutjanus griseus* (110 mm), *Lutjanus analis* (153 mm), *Clepticus parra* (92 mm), *Epinephalus guttatus* (88 mm), *Haemulon sciurus* (138 mm), *Inermia vittata* (135 mm), *Sargocentron vexillarium* (90 mm), *Halichoeres pictus* (107); biting and crushing species: *Halichoeres garnoti* (135 mm), *Halichoeres maculipinna* (105 mm), *Halichoeres cyanocephalus* (132 mm), *Lachnolaimus maximus* (132 mm), *Halichoeres bivittatus* (130 mm), *Bodianus rufus* (111 mm), *Halichoeres radiatus* (135 mm), *Lagodon rhomboides* (70 mm), *Stegastes partitus* (50 mm), *Stegastes planifrons* (63 mm), *Melichthys niger* (195 mm), *Archosargus probatocephalus* (123 mm), *Sparisoma rubripinne* (151 mm), *Chaetodon ocellatus* (56 mm), *Balistes vetula* (170 mm), *Diodon hystrix* (165 mm). (data from Wainwright and Richard, 1995). (b) Plot of the trade-off between velocity advantage and force advantage in a lever system such as the jaw-closing system of the teleost jaw. Note that the velocity advantage is most sensitive to changes if the closing lever ratio is less than one. (c) Plot of velocity and force advantage for the 34 species in Figure 2a. Note the different scales for force and velocity advantage and that all values fall between about 0.1 and 0.5.

bar linkages actually function in fish feeding systems. The important point to be made about four-bar systems here is that, like the lever systems discussed above, they involve a trade-off of velocity and force advantage in transferring an input motion into an output motion (e.g., transferring cranial elevation into depression of the hyoid bar). Once again a dichotomy exists for the expected design features of manipulators and ram-suction feeders in most of these four-bar systems. The presence of four-bar systems in the feeding systems of cheiline labrids has been verified by Westneat (1990) who has gone on to show a significant relationship between the evolution of the velocity vs force component of two four-bar systems and dietary patterns in this group of fishes (Westneat, 1995). At least in the cheiline wrasses, the trade-off between velocity and force in the mechanical linkages of the teleost skull has been a key factor in their trophic radiation.

### Ram vs Suction

Although considerable success has been reached in identifying critical design criteria that distinguish manipulation from ram-suction, less success has been achieved in identifying the critical features of design that distinguish ram and suction feeding. In both ram and suction the speed of movements at the strike are expected to be at a premium. Thus, the elegant trade-offs between velocity and force in lever systems do not contrast ram and suction as they do the latter two categories with manipulation. The comparison is further complicated by the fact that ram-suction feeders almost always utilize a prey capture strategy that is intermediate between the two extremes. However, observations on ram and suction feeding do suggest different performance features that should be maximized. In the case of ram feeding, the feeding apparatus should be able to open rapidly and permit water to flow through the mouth and out the opercular chamber so that a bow wave is not created that might push the prey away from the predator's grasp (Lauder, 1985; Norton and Brainerd, 1993). Ram feeding is also somewhat less precise since it often relies on body lunges toward elusive prey. Hence a mouth with a large cross-sectional area is advantageous, particularly for those ram feeders eating large, elusive prey.

In suction feeding, the objective is to create a strong pressure gradient between the inside of the buccal cavity and the ambient water. This is accomplished by rapidly expanding the buccal cavity (Luder, 1985). This gradient results in a rapid flow of water into the mouth to eliminate the difference in pressure. Two factors will be particularly important in contributing to a strong flow of water during suction feeding. First, the more rapid the volume increase of the buccal cavity, the sharper will be the pressure gradient, and hence the greater the acceleration of water. Second, the smaller the mouth aperture, the higher the velocity of water entering the mouth (Alexander, 1967).

It follows from these observations that high performance suction feeders will have a relatively small mouth aperture while ram feeders will have a large mouth aperture.

Furthermore, suction feeders can be expected to have a system for expanding the buccal cavity that makes this motion as explosive as possible. Explosive buccal expansion is also expected in ram feeders so one does not expect to see a clear difference between these modes in design of the buccal expansion mechanism.

Relatively few data are available that compare the actual design of ram and suction feeders. Discussions in Norton and Brainerd (1993) and Norton (1991)

suggest that the mouth size distinction is clearly seen when comparing the more extreme ram and suction feeders, though exceptions have been noted.

## 5. Ontogeny of Feeding Design

The field of ecomorphology of the feeding systems in fishes has enjoyed considerable success in identifying general design criteria that underlie differences between species in feeding ability. However, less work has focused on the consequences of morphological variation within species. In an attempt to identify areas that should provide future researchers with fruitful material, in this and the next section I explore two issues concerning intraspecific variation that show great promise for ecomorphological Ichthyologists—ontogeny and phenotypic plasticity.

One of the universal truths about fish feeding habits is that diet changes as the fish grows. This observation led Stoner and Livingston (1984) to suggest that different size classes of a species should be considered different ecological units. Ontogenetic diet switches can be dramatic. In the pinfish, *Lagodon rhomboides* (Stoner and Livingston, 1984), individuals begin life eating copepods before moving on to amphipods and other benthic creatures. As the fish grow, they enter a phase during which they eat mostly epiphytic algae and seagrass. The largest size classes consume a significant quantity of fishes. Thus, in this species different life stages not only eat different prey but also use different feeding modes to procure their primary prey at different stages of their life. The switch from eating free-swimming invertebrates to algae involves a switch from suction feeding to manipulation.

The key question here is: are the ubiquitous ontogenetic changes in diet of fishes accompanied by changes in the design of the feeding system? This question is almost completely unexplored in the pinfish, and most other fishes (see Wainwright, 1988; Galis, 1993).

In one very important respect it is clear that the design of the feeding mechanism changes in all species. As the fish grows, so does its feeding mechanism. It is likely that many diet changes are simply a consequence of scaling up the prey to match the changing performance of a feeding mechanism that is getting larger. A general trend has been observed in generalized ram-suction predators (e.g., the Serranidae) where there is an increase in size and elusiveness of prey with increase in fish body size (Wainwright and Richard, 1995). Serranids of a similar size tend to consume similar prey.

Considering the lever systems of the jaws, might there be significant changes in lever ratios that could quantitatively influence the performance of the feeding system as a fish grows. Figure 3 shows a graph of the ontogeny of the jaw-closing lever ratio in two species of sunfishes (family Centrarchidae). Note that the jaw-closing lever ratio remains the same throughout ontogeny in the largemouth bass (*Micropterus salmoides*), but changes in bluegill sunfish (*Lepomis macrochirus*), increasing substantially as the fish grows. In the bluegill the ratio increases from about 0.12 in a 30 mm fish to about 0.22 in a 100 mm fish (equal to a decrease in the velocity advantage from 8.3 to 4.5). Note that this change in ratio covers the range of values seen among ram-suction feeding species in Figure 2a and 2c but does not cross over into the group of manipulators.

One might expect that this change in ratio would have important consequences for the way that the speed of the strike changes with increase in body size in these two species. Figure 3b illustrates the time taken to close the mouth during ram-

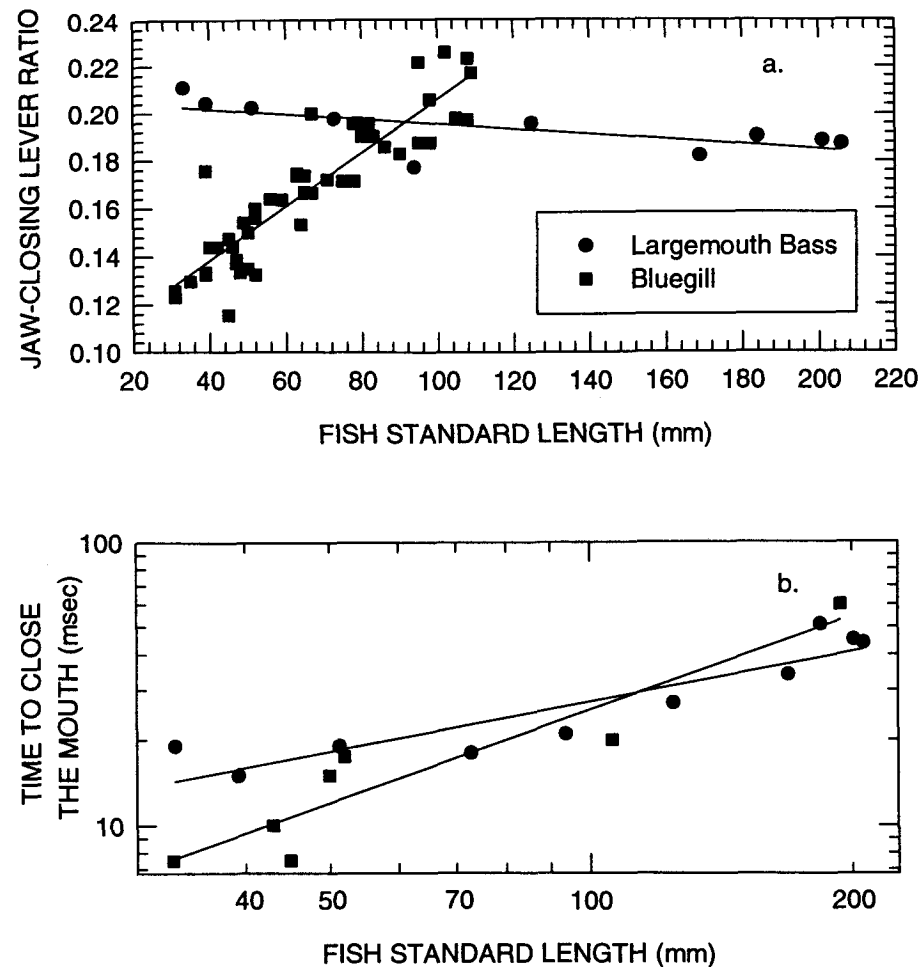


Fig. 3. (a) Plot of the jaw-closing lever ratio of largemouth bass and bluegill sunfish as a function of fish length. Note that the ratio increases considerably in the bluegill while not changing in the largemouth bass. (b) Plot of the shortest time taken to close the mouth when capturing prey during suction feeding as a function of fish size in a sample of 17 largemouth bass and bluegill sunfish. The time taken to close the mouth increases faster with increasing body size in the bluegill than it does in the largemouth bass, as suggested by the data plotted in part a. (Largemouth bass data are from Richard and Wainwright, 1995.)

suction feeding events by individuals from a size series of these two species. Data were collected by making high-speed video recordings of from 6 to 30 prey capture events from each individual, the fastest feeding sequence in which the mouth was fully opened during the strike was then selected and the time taken to close the mouth once it was fully opened was determined. Consider first the scaling pattern for the largemouth bass. In this species the jaw-closing lever ratio does not change as the fish grows. Furthermore, the entire feeding apparatus shows a striking pattern of isometric growth (retains a constant shape as it increases in size; Richard and Wainwright, 1995). However, the time taken to close the mouth

increases as fish size increases. A log-log plot of the time taken to close the mouth against fish length reveals a slope of 0.58. Because the morphology of the fish increases isometrically, we know that the increase in time with fish size is not due to changes in the lever system of the jaws. The slope of the log-log plot of time to close the jaws against fish length for the bluegill is 0.89. In other words, the bluegill is slowing down faster than the largemouth bass. This is expected from the difference between the species in the scaling of the jaw-closing lever ratio. The ratio does not change in the bass but doubles in size in the bluegill from 30 to 100 mm. Assuming that other components of the feeding system are similar in the two species, we would therefore expect the bluegill to become slower in its jaw-closing motion at a faster rate than the bass. This is what we see with the kinematic data. It is interesting to note that the bluegill undergoes a dramatic dietary switch in many lake systems at about 70–100 mm body size; it switches from feeding on elusive invertebrates found among vegetation to suction feeding on midwater zooplankton (Mittelbach, 1984, 1988). Perhaps the change in the feeding system contributes to this change in diet.

## 6. Phenotypic Plasticity

The role of phenotypic plasticity in the ecology and evolution of fish feeding systems is a topic that has produced some intriguing observations and promises to be a rich area in future. Fish have been known to exhibit developmental plasticity in response to prey type for some time, and the consequences of this flexibility for the ecology of fishes has been identified in a few cases (Skulason *et al.*, 1989). One concept, central to the theoretical literature on phenotypic plasticity, that has yet to receive attention from fish biologists, is the notion that the range of phenotypes produced in response to different prey or feeding regimes represent morphologies that are especially well suited to the particular prey involved. Theoretical work suggests that plasticity may be enhanced due to natural selection (that is, plasticity itself becomes adaptive) in cases where the alternate phenotypes result in feeding systems that perform better when feeding on the prey of local specialization (Via and Lande, 1985). Such adaptive phenotypic plasticity is thought to be particularly likely in systems where the parent individual has difficulty predicting the nature of the habitat that their young will find themselves in (Scheiner, 1993; Schiliching, 1986).

It is likely that fishes offer an excellent group in which to find evidence of adaptive phenotypic plasticity. Almost all marine teleosts have planktonic larvae and most species also have planktonic eggs. One consequence of this reproductive strategy is that parents have only a general idea of the type of habitat that their progeny will ultimately settle out of the plankton into. This may result in some variation in the range of habitats that young fish find themselves in and therefore some variation in the types of prey available as food. In this situation it might be advantageous for a species to have some flexibility in the development of its feeding mechanism so that individuals can develop a morphology that enhances feeding ability on locally abundant prey. Thus, developmental flexibility would permit a species to become morphological specialized in response to local environmental conditions.

Developmental plasticity has been demonstrated in controlled laboratory rearing experiments with several species of cichlid fishes (Greenwood, 1965; Meyer, 1987; Wimberger, 1991). In most of these cases it is clear that the plastic response improves feeding performance on one of the experimental prey; however, in none of

the laboratory studies has it been shown that the alternative ontogenetic trajectories result in two phenotypes, each well suited to the prey fed upon. A typical experimental paradigm involves rearing fishes on hard and soft prey (e.g., Greenwood, 1965). The group fed hard prey will indeed become stronger and better at eating hard prey, but there has never been strong evidence that the group fed softer prey develop a morphology well suited to their prey.

Field studies have had greater success in identifying cases where plasticity in the feeding system results in alternate adaptive peaks being reached by different individuals. In a study of four Caribbean triggerfishes, Turiangan *et al.* (1995) compared the morphology of two species that differed in diet in two Puerto Rican coral reef populations. In both species, one population ate more elusive, softer prey, while the other population consumed harder, shelled prey. In both species, the population that ate harder prey had larger biting muscles and a higher force advantage in the lever ratio for the jaw-closing system, while the population specializing on more elusive prey had a greater velocity advantage in the jaw-closing lever system. In work on the arctic char, *Salvelinus alpinus*, in Iceland (Skulason *et al.*, 1989) a polymorphism was identified that correlated with different feeding habits. In this system four distinct morphs exhibit phenotypes, each of which appears to be well suited to different feeding habits.

Clearly, the role of phenotypic plasticity in the evolution of feeding systems is a topic that has much to offer. Do lineages that live in locations characterized by the uncertain environment of the offspring tend to exhibit greater local specialization and plasticity? What are the constraints on developmental flexibility of fish feeding systems? These and other questions await future research. For now it is clear that our recent success in identifying important morphological design criteria of fish feeding systems has helped clarify the link between form and ecology in fishes, and promises to provide a foundation for future research that delves deeper into the ontogeny of functional design and the role of phenotypic plasticity in fish feeding biology.

## Acknowledgements

I thank S. Shaw who collected the kinematic data on feeding in the bluegill sunfish. Financial support was provided by National Science Foundation grant IBN 9306672.

## References

- Alexander, R.M. (1967). *Functional Design in Fishes*. Hutchinson, London.
- Ali, M.A. (1975). Retinomotor responses. In: *Vision in Fishes* (M. A. Ali, ed.) Plenum Press, New York.
- Bergert, B. and Wainwright, P.C. (1997). Morphology and kinematics of prey capture in syngnathid fishes. *Marine Biology*, **127**: 563-570.
- Fryer, G. and Iles, T.D. (1972). *The cichlid fishes of the great lakes of Africa*. T.F.H. Publications Inc., Neptune City, New Jersey.
- Galis, F. (1993). Interactions between the pharyngeal jaw apparatus, feeding behavior, and ontogeny in the cichlid fish, *Haplochromis piceatus*: a study of morphological constraints in evolutionary ecology. *J. Exp. Zool.*, **267**: 137-154.

- Greenwood, P.H. (1965). Environmental effects on the pharyngeal mill of a cichlid fish, *Astatoreochromis alluadi* and their taxonomic implications. *Proc. Linn. Soc. Lond.*, **176**: 1–10.
- Kapoor, B.G., Smit, H. and Verighina, I.A. (1975). The alimentary canal and digestion in teleosts. In: *Advances in Marine Biology* (F.S. Russell and M. Yonge, eds.), Vol. 13, pp. 109–239. Academic Press, London.
- Lauder, G.V. (1982). Patterns of evolution in the feeding mechanism of actinopterygian fishes. *Amer. Zool.*, **22**: 275–285.
- Lauder, G.V. (1985). Aquatic feeding in lower vertebrates. In: *Functional Vertebrate Morphology* (M. Hildebrand, D. Bramble, K. Liem and D. Wake, eds.), pp. 210–229. Harvard University Press, Cambridge.
- Lauder, G.V. and Liem, K.F. (1983). The evolution and interrelationships of the actinopterygian fishes. *Bull. Mus. Comp. Zool.*, **150**: 95–197.
- Liem, K.F. (1980). Acquisition of energy by teleosts: adaptive mechanisms and evolutionary patterns. In: *Environmental Physiology of Fishes* (M.M. Ali, ed.), pp. 299–334. Plenum Press, New York.
- McFarland, W.N. and Munz, F.W. (1975). The evolution of photic visual pigments in fishes: Part III. *Vision Res.*, **15**: 1071–1080.
- Meyer, A. (1987). Phenotypic plasticity and heterochrony in *Cichlasoma manguense* (Pisces, Cichlidae) and their implications for selection in cichlid fishes. *Evolution*, **41**: 1357–1369.
- Mittelbach, G.G. (1984). Predation and resource partitioning in two sunfishes. *Ecology*, **65**: 499–513.
- Mittelbach, G.G. (1988). Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. *Ecology*, **69**: 614–623.
- Motta, P.J. (1984). Mechanics and function of jaw protrusion in teleost fishes: a review. *Copeia*, **84**: 1–18.
- Motta, P.J. (1988). Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): an ecomorphological approach. *Environ. Biol. Fishes*, **22**: 39–67.
- Muller, M. (1987). Optimization principles applied to the mechanism of neurocranium elevation and mouth bottom depression in bony fishes (Halecostomi). *J. Theor. Biol.*, **126**: 343–368.
- Norton, S.F. (1991). Capture success and diet of cottid fishes: the role of predator morphology and attack kinematics. *Ecology*, **72**: 1807–1819.
- Norton, S.F. and Brainerd, E.L. (1993). Convergence in the feeding mechanism of ecomorphologically similar species. *J. Exp. Biol.*, **176**: 11–29.
- Randall, J.E. (1967). Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.*, **5**: 665–847.
- Richard, B.A. and Wainwright, P.C. (1995). Scaling the feeding mechanism of largemouth bass (*Micropterus salmoides*): I. Kinematics of prey capture. *J. Exp. Biol.*, **198**: 419–433.
- Scheiner, S.M. (1993). Genetics and evolution of phenotypic plasticity. *Ann. Rev. Ecol. Syst.* **24**: 35–68.
- Schlichting, C. (1986). The evolution of phenotypic plasticity in plants. *Ann. Rev. Ecol. Syst.*, **17**: 667–693.
- Skulason, S., Noakes, D.L.G. and Snorrason, S.S. (1989). Ontogeny of trophic morphology in four sympatric morphs of arctic charr *Salvelinus alpinus* in Thingvallavatn, Iceland. *Biol. J. Linn. Soc.*, **38**: 281–301.
- Stoner, A.W. and Livingston, R.D. (1984). Ontogenetic patterns in diet and feeding morphology in sympatric sparid fishes from seagrass meadows. *Copeia*, **1984**: 174–187.
- Turingan, R.G., Wainwright, P.C. and Hensley, D.A. (1995). Interpopulation variation in prey use and feeding biomechanics in Caribbean triggerfishes. *Oecologia*, **102**: 296–304.
- Via, S. and R. Lande. (1985). Genotype-environment interaction and the evolution of acquired characters. *Evolution*, **39**: 505–522.
- Wainwright, P.C. (1988). Morphology and ecology: the functional basis of feeding constraints in Caribbean labrid fishes. *Ecology*, **69**: 635–645.
- Wainwright, P.C. and Richard, B.A. (1995). Predicting patterns of prey use from morphology of fishes. *Env. Biol. Fish.*, **44**: 97–113.
- Webb, P.W. (1982). Locomotor patterns in the evolution of actinopterygian fishes. *Amer. Zool.*, **22**: 329–342.
- Weihls, D. (1973). The mechanics of rapid start of a slender fish. *Biorheol.*, **10**: 343–350.
- Westneat, M.W. (1990). Feeding mechanics of teleost fishes (labridae: Perciformes): a test of four-bar linkage models. *J. Morph.*, **205**: 269–295.
- Westneat, M.W. (1995). Feeding, function and phylogeny: analysis of historical biomechanics in labrid fishes using comparative methods. *Syst. Biol.*, **44**: 361–383.
- Wimberger, P.H. (1991). Plasticity of jaw and skull morphology in the neotropical cichlids *Geophagus brasiliensis* and *G. steindachneri*. *Evolution*, **45**: 1545–1563.
- Winterbottom, R. and McLennan, D.A. (1993). Cladogram versatility: evolution and biogeography of acanthuroid fishes. *Evolution*, **47**: 557–1571.