

Predicting patterns of prey use from morphology of fishes

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Synopsis

Ecomorphological analyses that search for patterns of association between morphological and prey-use data sets will have a greater chance of understanding the causal relationships between form and diet if the morphological variables used have known consequences for feeding performance. We explore the utility of fish body size, mouth gape and jaw-lever mechanics in predicting patterns of prey use in two very different communities of fishes, Caribbean coral reef fishes, and species of the Centrarchidae that live in Lake Opinicon, Ontario. In spite of major differences in the spectrum of potential prey available, the centrarchids of Lake Opinicon show dietary transitions during ontogeny that are very similar to those seen among and within species of Caribbean groupers (Serranidae). The transition from small zooplankton to intermediate sized invertebrates and ultimately to fishes appears to be very general in ram-suction feeding fishes and is probably driven largely by the constraints of mouth size on prey capture ability. The jaw-lever systems for mouth opening and closing represent direct trade-offs for speed and force of jaw movement. The ratio of in-lever to out-lever in the opening system changes during ontogeny in bluegill, indicating that the mechanics and kinematics of jaw movement may change as well. Among 34 species of Caribbean reef fishes, biting species had jaw-closing ratios that favored force translation, while species that employ rapid-strike ram-suction had closing ratios that enhanced speed of closing and mouth opening ratios that favored a more rapid expansion of the mouth during the strike. We suggest that when prey are categorized into functional groups, reflecting the specific performance features that are important in capturing and handling them, and the differences among habitats in the available prey resource are taken into account, general patterns can be found in morphology-diet relations that cross phylogenetic boundaries.

Introduction

Ecomorphological studies of fishes typically examine patterns of association between morphology and resource use. A major focus of many of these studies is the predictive relationship between fish form and patterns of prey use (e.g. Keast & Webb 1966, Chao & Musick 1977, Gatz 1979a, 1979b, Barel 1983, Kotrschal & Goldschmid 1983, Felley 1984, Grossman 1986, Wainwright 1987, 1988, Motta 1988,

Norton 1991, Winemiller 1991). An important part of the conceptual framework upon which these studies are based is the idea that fish morphology will have a major role in determining diet because variation in morphology is assumed to underlie variation in feeding ability, and variation in the latter is expected to play a central role in shaping diet. But, in spite of the primacy of this notion in ecomorphological studies, few studies have demonstrated a

causal link between specific morphological features and feeding performance in fishes.

In this paper we consider the functional significance of several morphological features and the role that they may play in shaping dietary habits. Our principal aims are to identify several morphological variables that can be easily measured in studies of fish feeding habits, to discuss their consequences for feeding performance, and to evaluate their utility in predicting ontogenetic and interspecific dietary differences in fish communities. We examine body size, mouth diameter, and the lever systems of the lower jaw. These characters were selected because we expect them to be relevant to the feeding biology of fishes representing a wide range of trophic niches and phylogenetic histories, and because the character measurements are easily made in the field or on fixed specimens in the laboratory.

Our premise is that the most informative morphological variables will be those for which a clear functional interpretation is available, based on biomechanical or physiological analyses. Such analyses would ideally indicate quantitatively the influence of variation in the feature on the ability of fishes to feed on specific prey types, or at least provide a rank-ordering for the directionality of its effects. Feeding ability may be influenced by morphology in two general ways. First, the feature may set an absolute limit on the range of prey phenotypes that a predator can capture or consume, while being relatively permissive within that limit. An example might be the biting strength of a mollusk crushing species (Wainwright 1987, 1988). Second, rather than set an absolute limit, the variable may influence the effectiveness or efficiency with which a predator captures and consumes a particular prey type. Variation in fin morphology of planktivorous bluegill sunfish, *Lepomis macrochirus*, appears to influence feeding effectiveness in such a fashion (Ehlinger 1990). Seen in another light, morphology plays a central role in determining the minimal, maximal, and optimal prey sizes.

Morphology, performance, and diet

The frequently unstated, but assumed link between morphology and diet in fishes is provided by feeding performance (Norton 1991, Wainwright 1991, Motta & Kotrschal 1992). Morphology shapes diet through its influence on fish feeding ability. This premise points to two areas of investigation in fish feeding that are important for establishing this linkage. First, functional morphological, biomechanical, and physiological analyses may be used to determine the expected consequences of morphological variation for feeding performance. These predictions can then be tested in laboratory performance experiments. Secondly, the behavioral capacity of fish represents a 'potential niche' that can be compared to the 'realized niche' or actual pattern of prey use to examine the role of feeding performance in shaping diet (Wainwright 1988).

The anatomical design of the feeding system will contribute greatly to the feeding proficiency of an individual, but predator performance is only one of several factors that determine the actual diet of an individual. Two factors may be thought of as fundamental in shaping patterns of prey use. First, the predator can only consume prey that are present in the environment. Second, the predator is limited to those prey which it is able to capture and successfully handle (i.e. feeding performance). The intersection between available prey and those that the predator is able to capture and consume sets the basic limits on potential prey-use patterns. Numerous other factors can interact to further shape diet, and in general predators only consume a small subset of available prey. Given the spectrum of prey available and the range of these prey the fish is able to consume, the choice of which prey are eaten is influenced by three major factors; encounter rates, probability of attacking encountered prey, and the probability of a successful attack (Greene 1983, Osenberg & Mittelbach 1989). Feeding ability of the predator can influence all three of these factors, as do other factors, such as the relative abundance and profitability of different prey. Additional factors that may influence prey choice are the indirect effects of competition with other species and the threat of predation (avoiding high predation hab-

itats will influence exposure to habitat-specific prey). We note that all of those factors not inherent to the fish predator (i.e., all factors other than fish feeding performance) are likely to vary among locations and communities, and this has the potential of limiting the generality of results across environments.

Materials and methods

In our discussion of the link between various morphological features, feeding performance, and diet we draw on a combination of our own original observations and previously published information. We draw mostly from work with two groups of fishes, Caribbean coral reef fishes and North American sunfishes (Centrarchidae). We selected these two groups because of the availability of an extensive literature on the trophic biology of each (Caribbean coral reef fishes: Randall 1967, Clarke 1977, Gladfelter & Johnson 1983, Wainwright 1987, 1988, Turingan & Wainwright 1993; centrarchids: Werner 1974, 1977, Keast 1978, Lauder 1983, Mittelbach 1984, 1988, Wainwright & Lauder 1986, 1993).

The relationship of diet to body size (using standard length as an estimate of 'body size') in Caribbean groupers (Serranidae) was examined using the dietary data in Randall (1967) and some data collected by the senior author on three species in Belize (*Serranus tobacarius*, *Schultzea beta*, *Lio-propoma rubre*). The fish studied by Randall (1967) were collected mostly in Puerto Rico or the Virgin Islands. Groupers were chosen for this analysis because species of this family are relatively constant in body shape. Few allometric changes in head and mouth shape are obvious when one looks across the Caribbean species of this family that span a range from about 30 mm to 1500 mm SL adult body size. This similarity in shape permits one to look at the effects of body size on diet given a relatively constant shape. All species in Randall's (1967) study were included except for the species of *Hypoplecterus*, which are different enough from the 'typical' serranid morphology (*Hypoplecterus* species have deeper body and smaller mouth) that we decided to omit them.

In order to examine the relationship between diet and morphology we constructed a single diet variable based on the average size of different prey types. This variable was constructed by ranking prey based on the typical size of individuals in each taxon using data in Sterrer (1986). The score for each fish species on this variable was determined by the major prey type in the diet (by average volumetric contribution). Smaller taxonomic units were collapsed down into major categories to facilitate general comparisons. The major prey categories included in this diet axis were, in order of increasing size: Copepoda, decapod shrimp, decapod crabs, Teleostei. We emphasize that our aim was to provide a simple index of prey-use, which reflected mostly prey size and taxonomic grouping. Although this method of quantifying diet misses many potentially significant details of prey use, we are attempting to emphasize major trends that transcend both phylogenetic and geographic boundaries.

Randall (1967) reports only the range of sizes examined for each species, so we took the geometric mean of the maximum and minimum size fish he examined as our estimate of standard length for each species. For each of the three Belizean species, the mean standard length of all specimens examined was calculated. A plot was made of the diet of each species vs. standard length.

A similar analysis was conducted for four species of the Centrarchidae, based on dietary data provided by Keast (1985), for fish in Lake Opinicon, Ontario, Canada. Keast's diet data were compared to body length and mouth gape of each species using estimates of mouth size made on fish from Lake Opinicon (Keast 1978). For this analysis the diet variable was a weighted linear combination of the proportion of the diet made up of the four prey categories used by Keast (1985):

Diet = % zooplankton (1) + % small invertebrates (2) + % large invertebrates (3) + % fish (4).

Thus, a diet of 100% fish would receive the highest possible score of '4' on this variable, a diet of 100% zooplankton would receive the lowest possible score, a '1'. As with the analysis of the groupers, this diet variable ranks prey based mostly on size, as well as taxonomic affinities, but many details of dietary patterns are lost.

Additional information on the scaling of trophic morphology was obtained by measuring both mouth gape and pharyngeal jaw gape in two centrarchid species: largemouth bass, *Micropterus salmoides* and bluegill, *Lepomis macrochirus*. Bluegill were collected in OE Lake, Dade County, Florida, and the largemouth bass were collected in Lake Annie, Highlands County, Florida. Measurements were made on anesthetized (MS-222, 1 g per liter) or fresh-dead specimens. Mouth gape was measured with dial calipers to the nearest 0.1 mm. Pharyngeal jaw gape was measured by sliding metal cylinders or rods of increasing diameter through the pharyngeal jaws, the pectoral girdle (specifically the cleithra), and into the esophagus. The diameter of the widest rod that would fit snugly through these structures and into the esophagus was taken as pharyngeal jaw gape.

Jaw-lever mechanics were investigated in (1) largemouth bass and bluegill, and (2) in a sample of 34 species of Caribbean coral reef fishes representing 13 families. Reef fish specimens were collected on the Belizean Barrier Reef. Lever arms associated with the jaw opening and closing systems were measured on specimens that had been preserved in 10% buffered formalin and stored in 70% ethanol. Data from the two centrarchid species were collected from the same individuals used in the gape analysis. Four measurements were made from each specimen. Standard length was measured to the nearest millimeter. The other measurements were made to the nearest 0.1 mm using a dial caliper or a dissecting microscope equipped with an ocular micrometer. The left lower jaw was removed from the skull of each fish. During this dissection the adductor mandibulae was cut proximal to its insertion on the lower jaw, the interopercle was cut proximal to the interoperculo-mandibular ligament, and the quadrate and articular bones were separated at their articulation (Fig. 1).

The in-lever for jaw opening was measured as the distance between the middle of the articular-quadrate joint to the insertion site of the interoperculo-mandibular ligament on the mandible (Fig. 1). In the analysis of bluegill and largemouth bass, the in-lever for jaw closing was measured as the distance between the center of the articular-quadrate joint to

the point of attachment of Meckel's cartilage in the medial depression of the dentary bone. In these fishes section A2 of the adductor mandibulae muscle attaches to Meckel's cartilage and becomes continuous with section A ω in the lower jaw. In the reef fish analysis, the in-lever for the jaw closing system was measured as the distance from the center of the jaw joint to the point of insertion of the adductor mandibulae muscle on the mandible. The location of this insertion point varied considerably among taxa, from direct attachment of fibers on the coronoid process of the articular bone (e.g. Labridae, *Sphyaena*), to a tendinous attachment to section

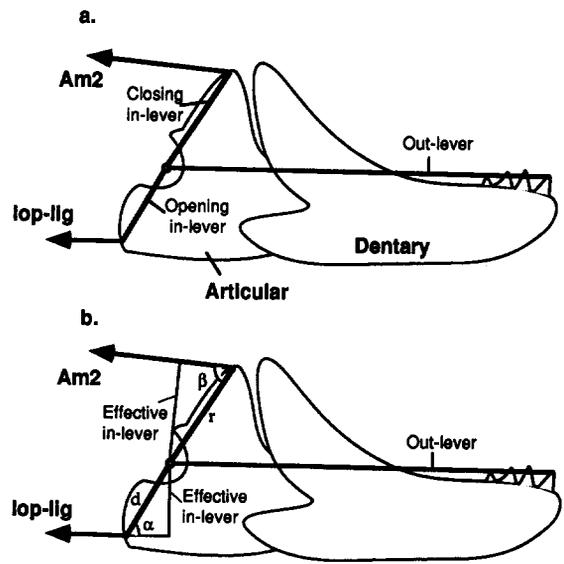


Fig. 1. Diagram of a fish lower jaw illustrating the lever arms that were measured in the analysis of lever mechanics of jaw opening and closing: a - The interoperculo-mandibular ligament (lop-lig) attaches to the articular bone ventral to the hinge between the quadrate and articular bones, yielding the distance 'd' as the opening in-lever. Section 2 of the adductor mandibulae muscle (Am2) inserts on the coronoid process of the articular in some taxa (e.g., Labridae, Balistidae), but in other taxa (e.g., Lutjanidae, Serranidae) it inserts on the medial aspect of the lower jaw via adductor mandibulae section ' ω ' (A ω). This yields distance 'r' as the in-lever for jaw closing. The out-lever in both jaw opening and jaw closing was measured as the distance from the center of the joint between the quadrate and articular and the tip of the anterior-most row of teeth on the dentary. b - In calculating the effective lever arms in the jaw opening and closing systems the angle of attachment of the lop-lig and the Am2 must be considered. For the opening system the effective lever arm will be $\sin \alpha$ times the actual lever arm, d. Similarly for the closing system, the effective in-lever is $\sin \beta$ times the actual lever arm, r.

Aw of the adductor mandibulae which lies entirely within the medial face of the mandible (e.g. Haemulidae, Lutjanidae).

For both the jaw opening and jaw closing system the out-lever was measured as the distance from the center of the jaw joint to the anterior-most tooth row. Thus, the measurements of jaw-lever mechanics were made with reference to forces and movements experienced at this one location on the lower jaw. In many oral crushing species, the actual position of prey along the mandibular tooth row during forceful biting is considerably closer to the jaw joint, so the choice of the anterior margin of the tooth row as the reference point produces a conservative estimate of the differences among trophic types.

Dimensionless ratios were calculated for the jaw opening and closing systems by dividing the in-lever by the out-lever in each case. These ratios provide a comparison of the mechanical properties of the jaw systems between taxa or among ontogenetic intervals.

The ratios that were calculated have simple and clear functional interpretations. Each ratio represents a trade-off between speed of movement of the jaw and the force exerted at the jaw tip. Thus, in the case of the jaw opening system, a value less than 1.0 for the lever ratio indicates a system that amplifies the velocity of jaw-opening muscle shortening such that the tip of the jaw moves faster than the muscle is shortening. If the jaw opening ratio is 0.1, the velocity of jaw opening will be 10 times greater than the rate of shortening of a muscle that is causing the rotation of the jaw about its joint to the quadrate bone. Thus, velocity of jaw movement is inversely proportional to the lever-ratio. This amplification of velocity occurs in direct trade-off with the force exerted at the jaw tip, as force will be directly proportional to the lever ratio. In this example of a ratio of 0.1, the mouth opening force exerted at the jaw tip will be one tenth of the force exerted by the jaw opening muscle. A jaw-opening lever ratio of 0.3 would cause the force exerted at the jaw tip to be one third of the force exerted by the jaw opening muscle.

The same trade-off between force and speed of movement will exist in the jaw closing system. Thus,

a closing ratio of 0.3 will cause the velocity of mouth closing to be about 3 times greater than the shortening velocity of the adductor mandibulae muscle, while 'biting' force at the jaw tip will be one third as high as the force being exerted by the adductor mandibulae muscle. A lower ratio will increase the jaw closing velocity and decrease the resultant force experienced at the jaw tip.

Mechanical ratios for jaw opening and closing were examined for the 34 species with reference to feeding mode. We placed each species into one of two feeding modes. Liem (1980) has identified three modes of prey capture in fishes: ram feeding, suction feeding, and manipulation. Ram and suction represent end-points of a continuum that many species fall between (Norton & Brainerd 1993) and it can be difficult to distinguish which feeding mode a particular predator uses without the aid of film or video (Norton 1991). For this reason our first feeding mode group combines ram and suction feeders. We call these species 'ram-suction feeders'. Readers interested in the distinctions between ram and suction feeders are referred to the insightful discussions in Norton & Brainerd (1993). The second group were those species that fit Liem's (1980) definition for manipulators. These species forcefully grip prey in their oral jaws during prey capture, or use the jaws to rip, shred, or crush prey during handling behaviors. We call species in this second group 'biters'. Thus, the contrast that we sought was between one group of species that rely on a rapid strike to engulf prey, and another group for which the force of jaw movements may be more significant than speed of jaw movement. Categorizations for each species were based on our personal observations of feeding fishes in the field and laboratory and on information in the literature (e.g., Böhlke & Chaplin 1968, Randall 1967, 1969, Starck & Schroeder 1971).

One final comment is warranted regarding the absence of any control for phylogenetic relationships in our study. Because existing species are derived from a specific branching pattern of evolution, interspecific analyses that treat each species as a statistically independent entity necessarily over-emphasize the independence of observations (Felsenstein 1985; and see discussions in Harvey & Pa-

gel 1991). Because no robust phylogeny for the species included in our study has been constructed (Johnson & Patterson 1993), we have chosen to explicitly ignore this problem in our analyses. Although we have attempted to gather data from congeners and confamilials with different feeding modes wherever possible, in general our analyses of Caribbean fishes should be viewed as tentative pending the availability of a phylogenetic hypothesis for percomorph teleosts. Our hope is that the patterns we observe are sufficiently strong as to be clear even in the face of phylogenetic constraints.

Results

Body size, gape, and diet

Dietary differences among Caribbean groupers show a strong relationship with body size (Fig. 2). The trend illustrated by Fig. 2 shows diet changing from copepods to shrimp around 50 to 70 mm SL, and to crabs between 100 and 200 mm SL. Species over 150 mm but less than 300 mm SL feed on either crabs or fish. Species larger than 300 mm SL eat fish. The largest Caribbean grouper, the jewfish, *Epinephalus itajara*, at 1450 mm SL is over twice as long as the next largest species and feeds predominantly on lobsters (Randall 1967). One species does not conform to the overall trend; *Paranthias furcifer*, which at 190 mm SL is much larger than the other copepod specialists.

The interspecific transformation in diet seen in Caribbean groupers is largely mirrored during the ontogeny of the grouper *Mycteroperca microlepis* from a South Carolina estuarine population of juvenile individuals (Mullaney 1994; stars in Fig. 2). Individuals below 20 mm feed on copepods and switch to amphipods through 50 mm SL. From 50 to 100 mm *M. microlepis* feeds mostly on decapod shrimp, and between 100 and 150 mm fish become the primary prey (Mullaney 1994).

The four centrarchid species from Lake Opinicon also show clear diet changes during ontogeny (Fig. 3). The transition in each species begins with the smallest fish feeding mostly on zooplankton, and changing to small invertebrates, large inverte-

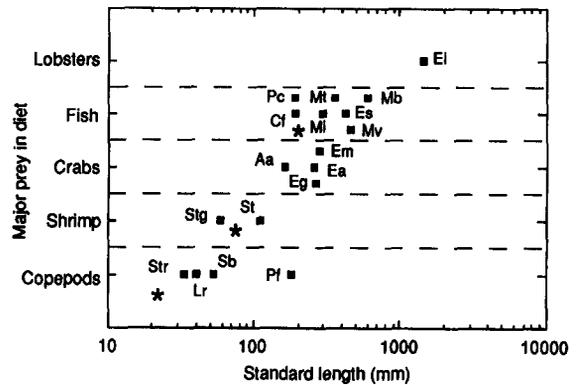


Fig. 2. Plot of the relationship between standard length and the major prey eaten (by % volumetric contribution) in 18 species of Caribbean groupers (Serranidae), based mostly on data in Randall (1967). Each species is represented by a filled square and an abbreviation. Stars indicate data from Mullaney (1993) on the ontogeny of diet in the gag, *Mycteroperca microlepis* in South Carolina. Species abbreviations: Aa = *Alphistes afer*; Cf = *Cephalopholis fulva*; Ea = *Epinephalus adscensionis*; Eg = *E. guttatus*; Ei = *E. itajara*; Em = *E. morio*; Lr = *Liopropoma rubre*; Pc = *Petrometopon cruentatum*; Pf = *Paranthias furcifer*; Mb = *Mycteroperca bonaci*; Mi = *M. interstitialis*; Mt = *M. tigris*; Mv = *M. venenosa*; Sb = *Schultzzea beta*; St = *Serranus tabacarius*; Stg = *S. tortugum*; Str = *S. tigrinus*.

brates, and ultimately fish are included in the diet of three of the four species. All four species progress through a similar sequence of diet changes. For example, no species enters an intermediate state where they feed on fish, and then switch to zooplankton at some larger body size. The differences among species in terminal diet appear to be mostly a function of mouth size in the largest size classes. At one extreme is the bluegill which never progresses beyond the diet of small invertebrates. The large-mouth bass illustrates the other extreme, becoming mostly piscivorous by about 100 mm SL. Black crappie, *Pomoxis nigromaculatus*, and rockbass, *Ambloplites rupestris*, show intermediate patterns. The crappie mixes fish and small invertebrates in its largest size classes, while the largest rockbass prey mostly on crayfish and some fish.

However, when diet is viewed as a function of mouth size the species tend to collapse toward a more universal gape-specific diet (Fig. 3). When observing diet as a function of fish length, a diet score of about 2.5 is achieved by *Micropterus* at about 50 mm SL, about 85 mm SL in *Ambloplites*, and

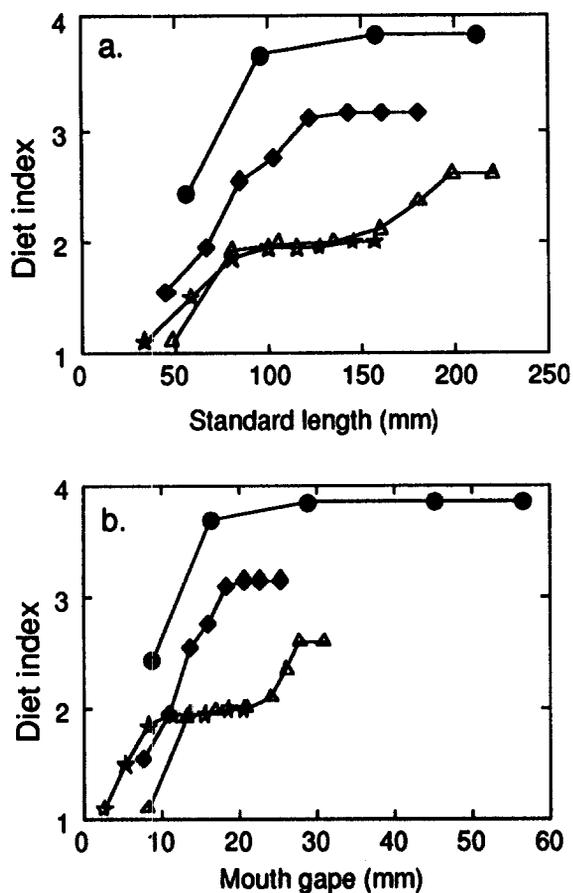


Fig. 3. PLOTS of a diet index vs. standard length and mouth gape in North American sunfishes (Centrarchidae) in Lake Opinicon, Ontario (diet data from Keast 1985, gape data from Keast 1978). The diet variable ranks prey based mostly on size: 1 = zooplankton, 2 = small invertebrates, 3 = large invertebrates, 4 = fish. See text for details of the method of calculation of the diet variable. All four species pass through similar stages during ontogeny and these stages occur at more similar mouth sizes than body sizes. Symbols: circles = largemouth bass, *Micropterus salmoides*; diamonds = rockbass, *Ambloplites rupestris*; triangles = black crappie, *Pomoxis nigromaculatus*; stars = bluegill, *Lepomis macrochirus*.

about 175 mm SL in *Pomoxis*. In contrast, the diet score of 2.5 occurs at a mouth diameter of about 10 mm in *Micropterus*, 13 mm in *Ambloplites*, and about 25 mm in *Pomoxis*. Residual differences among species are still clearly evident, but at any given mouth size these species tend to have more similar diets than they do at a given standard length.

In *Micropterus salmoides* and *Lepomis macrochirus* pharyngeal gape was smaller than mouth

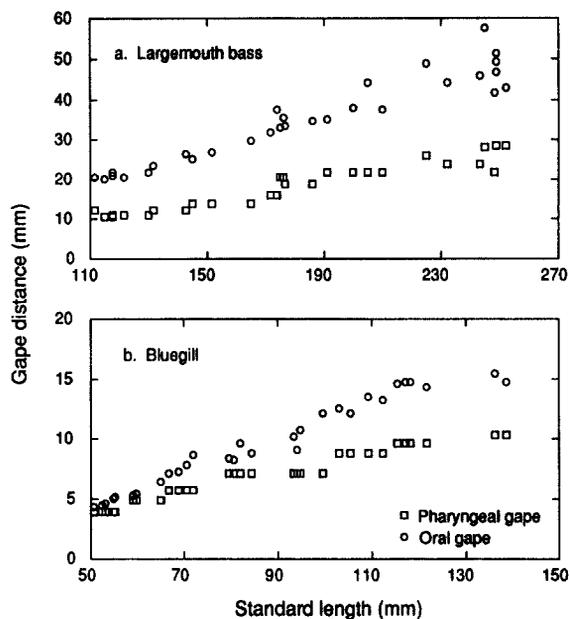


Fig. 4. Plots of mouth diameter (oral gape) and pharyngeal gape vs. standard length in (a.) largemouth bass, *Micropterus salmoides*, and (b.) bluegill, *Lepomis macrochirus*, from populations in south Florida. In both species pharyngeal gape is substantially narrower than oral gape, suggesting that oral gape may not be the ultimate constraint on maximum prey size in these fishes. Note that data plotted are untransformed, raw values. Regressions of Log_{10} transformed data against Log_{10} SL indicate scaling exponents for the two features in each fish. *Micropterus salmoides*: mouth gape, scaling exponent = 1.16 (S.E. = 0.05), y-intercept = -1.08 (0.11); pharyngeal gape, scaling exponent = 1.25 (0.07), y-intercept = -1.57 (0.15). *Lepomis macrochirus*: mouth gape, scaling exponent = 1.34 (0.05), y-intercept = -1.63 (0.09); pharyngeal gape, scaling exponent = 1.04 (0.04), y-intercept = -1.17 (0.07).

gape at all body sizes examined (Fig. 4). This difference was greatest in *Micropterus*, where the pharyngeal gape of a 120 mm fish was 10.8 mm and the oral gape was 21.0 mm. In both species the relative difference in mouth and pharyngeal gape diameter changed with body size because of differences in scaling between the two variables. ANCOVAs run to compare pharyngeal and mouth gape scaling indicated a significant interaction between body size and gape types in each species.

Jaw mechanics

The mechanical properties of the jaws changed sub-

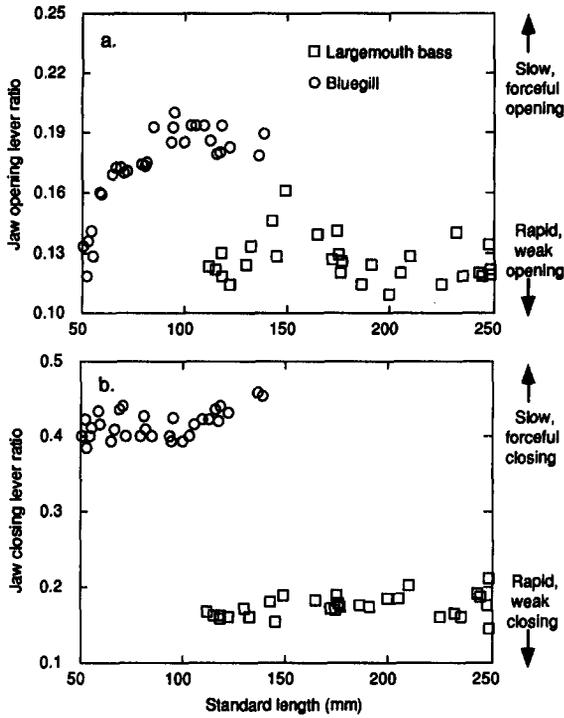


Fig. 5. PLOTS of the jaw-lever ratios for (a.) mouth opening and (b.) mouth closing in size series of largemouth bass and bluegill. Note that the jaw opening ratio changes during ontogeny for the bluegill, but remains relatively constant for the largemouth bass. These changes are likely to have important consequences for the mechanics and feeding performance of fishes. Neither species shows changes in the jaw closing system across the size ranges studied.

stantially during ontogeny in bluegill, but remained relatively constant in largemouth bass, over the size range examined (Fig. 5). In bluegill the jaw opening ratio is about 0.13 in the smallest fish examined, around 55 mm, but this ratio increases in larger bluegill to a value around 0.19. Thus, in this species there is an ontogenetic change from a mechanism with high velocity transmitting efficiency, to a system that has better force transmission at the expense of speed. In contrast, largemouth bass show no clear change in this ratio through the size range in our sample. The ratio of jaw closing lever-arms does not appear to change during ontogeny in bluegill, remaining at around 0.4 throughout the size range measured. Similarly, in largemouth bass this ratio remained at around 0.17 throughout the size series.

The sample of 34 species of Caribbean reef fishes

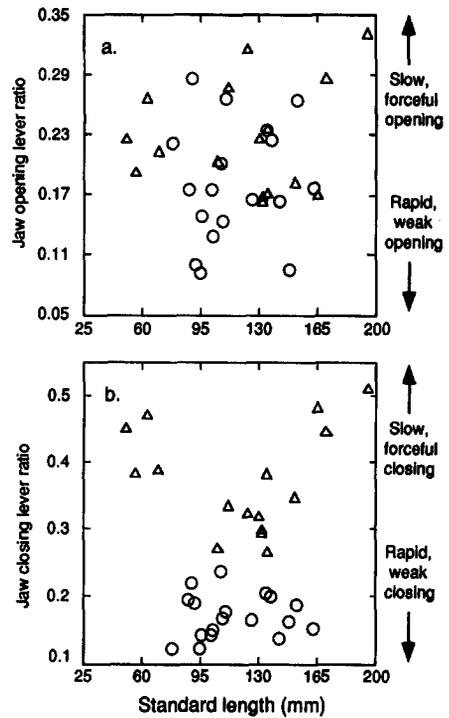


Fig. 6. Plots of the jaw-lever ratios for the (a.) mouth opening and (b.) mouth closing systems in 34 species of Caribbean coral reef fishes. Triangles represent fishes that grasp, shred, crush or otherwise manipulate prey with their oral jaws. Circles are species that use a rapid-strike, ram-suction based mode to capture prey. a - The two feeding modes separate statistically on the jaw opening ratio, with ram-suction species tending to have a lever system that enhances the relative speed of jaw opening. b - Complete separation of the two feeding modes is found on the jaw closing lever ratio axis. Biting species have lever systems that favor biting force of the jaws, while the ram-suction feeding species have jaws that would be expected to close more quickly. The species included in this analysis, 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), *Hypoplecterus indigo* (95.5 mm), *Ocyurus chrysurus* (102 mm), *Cephalopholis fulva* (103 mm), *Mycteroperca bonnaci* (163 mm), *Sphyraena barracuda* (148 mm), *Paranthias furcifer* (126 mm), *Holocentrus ascensionis* (108 mm), *Lutjanus griseus* (110 mm), *Lutjanus analis* (153 mm), *Clepticus parrai* (92 mm), *Epinephalus guttatus* (88 mm), *Haemulon sciurus* (138 mm), *Inermia vittata* (135 mm), *Sargocentron vexillarium* (90 mm), *Halichoeres pictus* (107 mm); 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).

shows a strong relationship between trophic habit and jaw mechanics. Although there was considerable overlap between the two trophic groups in the value of the jaw-opening lever ratio (Fig. 6), ANOVA indicated that the mean ratio was significantly larger in the oral-jaw biting species (F-ratio = 4.87; d.f. 1, 34; $p = 0.034$). The difference between trophic groups in the jaw closing ratio was much stronger. There was no overlap between the two groups; all oral-jaw biting species had larger closing ratios than any of the rapid-striking species.

Discussion

Body size

No morphological feature appears to play such a large role in determining diet as fish body size. As far as we are aware *all* fish species studied to date undergo changes in patterns of prey use during ontogeny. In many species, diet shifts are associated with major habitat shifts. For example, species of *Oncorhynchus* migrate from shallow rivers to the ocean during their first year of life and shift from feeding on chironomid larvae, mayflies and stoneflies to an ocean diet dominated by copepods (in the case of *Oncorhynchus gorbusha*; McDonald 1960, Bailey et al. 1975, Godin 1981). In migrating salmon and other species the change in habitat brings about drastic changes in the nature of the prey resource.

In other taxa, and even at different intervals of the life-cycle of a single species, diet shifts may occur without a concurrent habitat shift. Examples of ontogenetic diet shifts not associated with habitat shifts occur in Caribbean labrids of the genus *Halichoeres* (Wainwright 1988), the switch to piscivory in coastal South Carolina populations of juvenile gag, *Mycteroperca microlepis* (Mullaney 1994), and the switch from benthic predation to herbivory in Florida pinfish, *Lagodon rhomboides* (Carr & Adams 1973, Stoner 1980, Stoner & Livingston 1984). Most, but not all diet switches of carnivorous species involve increases in the average size of prey with increasing predator size (e.g. Randall 1967, Starck & Schroeder 1971, Gladfelter & Johnson

1983, Keast 1985, Wainwright 1987, Osenberg & Mittelbach 1989).

The universality of ontogenetic diet switches in fishes cannot be over emphasized, but *why* do fish switch diet as they grow? The most common explanation is that ontogenetic diet switches reflect the changing feeding abilities of fish. Essentially, the argument is that as fish grow they become more proficient at handling larger prey, and hence the prey size that maximizes net energy return increases (Werner 1974, 1977, Kislalioglu & Gibson 1976, Werner & Gilliam 1984, Hoyle & Keast 1987). As fish grow they are able to eat larger maximum size prey, and bigger prey become more profitable. Increasing prey size will usually lead to taxonomic changes, and we see these changes manifested as ontogenetic diet switches. Even for a single prey type, the size taken often increases with predator size (Gladfelter & Johnson 1983, Keast 1985, Wainwright 1991).

Increases in prey size do not always occur in species that change feeding mode during ontogeny. For example, the ontogenetic switch from particulate feeding to suspension feeding that occurs in many planktivorous species may involve no change or a decrease in the average size of prey (Jansen 1976, Ruelle & Hudson 1977, Rosen & Hales 1981, Drenner et al. 1982, Mummert & Drenner 1986).

While changes in feeding performance during ontogeny seem to play a central role in ontogenetic diet switches, it is a potentially misleading simplification to ascribe these changes directly to increasing body size. Body size, per se, does not underlie the changes in feeding performance that occur as fish grow, rather it is the correlated changes in key aspects of the feeding mechanism which determine feeding performance. However, virtually every morphological feature changes in size and/or shape in association with increasing body size. As a result, we observe strong, though spurious, relationships between diet or feeding performance and fish size.

How do we know which feature is responsible for changing feeding performance? For every feature that plays an important role in feeding performance, there may be hundreds that, although they are also correlated with body size, have no impact on predatory capabilities. Identifying the actual per-

formance features that underlie specific diet switches and the morphological features that determine feeding performance becomes particularly important in interspecific ecomorphological analyses because fish species may differ in trophic morphology at a common body size. Indeed it is this interspecific variation that is of primary interest in most ecomorphological analyses (Chao & Musick 1977, Gatz 1979a, Felley 1984, Wikramanayake 1990, Wine-miller 1991).

In a case where two or more competing explanations predict increases in prey size with increasing body size, two techniques may be especially valuable for separating them. First, the specific scaling relationships of the two competing limitations may make different quantitative predictions about the relationship between fish size and performance (Emerson et al. 1994). Second, comparative studies of closely related species that differ in the features of interest, while holding many other features constant, may be used to isolate the role of one factor, independent of the other (Norton 1991). The example of North American sunfishes discussed here is an example of such an opportunity.

A salient feature of the species in our analysis of the family Serranidae is that they do not show strong variation in overall body or head shape, either among species or among size classes of a single species (Randall 1969, Böhlke & Chaplin 1968). Thus, observed changes in diet are more likely to be due to changes in the effects of body size on a common functional morphology than on basic changes in how the feeding mechanism functions. Caribbean serranids show a strong relationship between body size and diet (Fig. 2). The pattern of smaller species eating copepods and other small zooplankton, intermediate sizes fish eating shrimp and crabs, and the larger species preying on fish and cephalopods indicates a general correlation between predator and prey size. It appears that body size has a tremendous effect on patterns of prey use in serranids, even in the absence of obvious changes in cranial shape and function.

Only one species in our serranid analysis, *Paranthias furcifer*, does not conform to the overall trend. This species is a zooplankton specialist, like other members of the genus (Randall 1967, Böhlke

& Chaplin 1968). The fact that it falls outside the typical pattern seen among our sample of serranids suggests that it may be a profitable species to examine for morphological, functional, and behavioral specializations related to feeding on small zooplankton (Strauss 1985). Unlike any other species over 100 mm SL considered in our analysis, *P. furcifer* is a midwater fish that spends most of its time several meters above the reef, feeding on drifting zooplankton (Randall 1967). All of the other, similar sized species are associated more directly with reef structure and feed on organisms that inhabit the reef. This species may also possess morphological specializations for planktivory, such as unusually protrusible premaxillae, a smaller than average mouth, and acute vision.

If the patterns seen among species of Caribbean serranids are dependent upon some factor that changes with body size, for example mouth size, then one would expect to see the trends that are evident in Fig. 2 during the ontogeny of individual species. We are unaware of detailed ontogenetic data for any large Caribbean serranid, but data from gag, *Mycteroperca microlepis*, in a South Carolina estuary (Mullaney 1994) show a pattern of diet ontogeny similar to the interspecific trends. Individuals less than 20 mm SL feed mostly on copepods, size classes from 30 to 125 mm SL eat primarily decapod shrimp, and individuals between 125 and 150 mm SL are mostly piscivorous. In addition, Randall (1965) reported that *Epinephalus striatus* between 160 and 686 mm SL showed a clear trend toward increasing piscivory with increasing body size.

In our sunfish example (Fig. 3), the four species undergo similar ontogenetic changes in dietary habits, but the specific transitions occur at quite different body sizes in each species. However, when diet is viewed as a function of mouth gape (a specific morphological feature that will physically limit maximum prey size) the four species show a more common pattern (Fig. 3). Consider the switch to piscivory. Fish make up at least 20% of the diet in largemouth bass at 55 mm SL, at 133 mm SL in the rockbass, and at 180 mm SL in the black crappie. However, a diet of 20% fish is achieved by all three of these species at a mouth gape of 15-20 mm (data in Keast 1985). One reason why the bluegill in

Keast's study never ate fish might be that bluegill do not have a mouth size of 20 mm until they are about 150 mm SL, about the size of the largest size class studied.

Although the relationship of diet to mouth gape shows a more consistent relationship among species than standard length, there are still considerable residual differences among species left unexplained (Fig. 3). This suggests two possibilities. First, other morphological features that influence feeding ability also vary among species, in a fashion different from mouth size. For example, it has been suggested that the general body form of these species may impact their ability to perform the locomotory behaviors used in capturing fish prey (Werner 1977), and behavioral tendencies may vary among species that lead to improved performance through experience (Wainwright 1986, Ehlinger 1990). Second, this residual variation may be unrelated to predator performance. Within the range of possible diets of a species, various factors not visible in trophic morphology (e.g., competition with other species, threat of predation during foraging in some habitats) may lead to choices that do not conform perfectly to expectations.

It is noteworthy that body size and diet show such a similar relationship in sunfishes, gag, and Caribbean groupers, given the differences in habitat and the specifics of the prey resource available to fish in these locations. We suggest that as long as the potential prey (zooplankton, intermediate-sized invertebrates, and fishes) are present in a given habitat, this ontogenetic trajectory is likely to be a very general phenomenon in actively foraging, bottom-oriented, ram-suction predators. Further, we suggest that the relationship is driven more by mouth dimensions than simple body size relationships. In other words, we propose that one can account for a substantial portion of the intra- and interspecific variation in diet within communities of bottom-oriented, ram-suction feeding fish predators by a single morphological variable, mouth size. Our aim here is to highlight the role of an easily measured morphological feature, with a clear functional interpretation. We expect this to be a frequently observed general trend, but not a 'rule' of morphology-diet patterns. Certainly, additional morphological

features will influence diet and behavioral adjustments can 'fine-tune' prey use patterns (Luczkovich 1988, Norton 1991).

Mouth size and feeding performance: a closer look

The notion that gape is an important constraint on prey use is widespread in fish biology, and it is frequently cited as the explanation for correlations between prey and predator body size (Keast & Webb 1966, Werner 1977, Hyatt 1979, Felley 1984). However, remarkably few studies of feeding habits in fishes actually measure either prey diameter or mouth diameter. Instead prey length and predator length are usually measured. This practice makes it difficult to evaluate the role of mouth size in shaping diet because the relevant features of prey and predator morphology are not considered directly. Different prey can vary tremendously in shape. For example, polychaetes tend to be very long and slender while decapod crabs have a more gibbous shape. If one considers prey length, fish may eat polychaetes that are four times their mouth diameter and twice their body length (e.g. Starck & Schroeder 1971). The dimension of a prey item that limits the fish's ability to fit the prey in its mouth should be the cross-sectional diameter.

Several authors have provided experimental evidence in ram-suction feeding fishes that mouth diameter plays a central role in determining the performance of a predator feeding on prey that vary in size (Werner 1974, 1977, Kislalioglu & Gibson 1976, Hoyle & Keast 1987). A key result from these laboratory studies is that the ratio of prey diameter to mouth diameter that maximizes the net energy return to the predator lies between about 0.4 and 0.7. At small prey sizes the prey are quickly handled but they have little caloric value, and as prey diameter approaches mouth diameter handling time increases greatly. Thus, optimal sizes are found at an intermediate prey diameter. Two important points follow from these observations. First, optimal prey sizes are a direct function of predator mouth diameter. Second, optimal prey size is always considerably less than mouth diameter.

But, is mouth diameter actually the feature that

limits prey size? As originally suggested by Lawrence (1957) for largemouth bass, the pharyngeal gapes of this species and of bluegill are significantly smaller than oral gape (Fig. 4). Indeed, the mouth gape of a 200 mm SL largemouth bass in our sample is predicted to be 38 mm while the pharyngeal gape is only 21 mm. Note however, that one cannot construct a simple ratio of mouth diameter to pharyngeal gape diameter because the scaling of these two variables differs in both bluegill and largemouth bass. As a result, the ratios change with body size. Is it possible that the repeated finding from laboratory studies that optimal prey size is always considerably less than mouth gape, arises because it is actually pharyngeal gape that limits prey size, rather than oral gape? We suggest that the answer to this question is generally no. Both laboratory studies (Werner 1974, Kislalioglu & Gibson 1976) and diet studies (Kislalioglu & Gibson 1976, Osenberg & Mittelbach 1989) show that fish do eat prey as wide as their mouth diameter, even if pharyngeal gape is actually narrower than the prey. We suggest that this is so because most prey are deformable. For example, once a fish prey is captured by a predator it can be swallowed even if it is wider than the pharyngeal gape because its shape can be altered by actions of the pharyngeal jaw apparatus as the prey is being swallowed. Pharyngeal gape is likely to be a more significant constraint when prey have a rigid, unmalleable exoskeleton or shell. For example, fish that crush mollusks in their pharyngeal jaws will be limited to feeding on those mollusks as narrow as the space between the upper and lower pharyngeal jaw bones (Osenberg & Mittelbach 1989, Wainwright 1991).

The specific morphological feature that limits pharyngeal gape appears to be the lateral distance between the right and left cleithrum bones (see also Lawrence 1957). Since the pharyngeal jaws are anterior to the pectoral girdle it is possible for hard prey that are larger than the space between the cleithra to fit between the pharyngeal jaws and be reduced to a size that fits between the more limiting space between the cleithra. Since both Lawrence's data (1957) and ours are for centrarchids it is not possible to assess how widespread this pattern is, but future studies should pay closer attention to the

possible role of the cleithra and the pharyngeal jaws in limiting prey size.

Jaw mechanics and feeding mode

Our survey of 34 species of Caribbean reef fishes indicates a striking relationship between the mechanics of the jaw closing system and mode of feeding (Fig. 5). Those species which use their oral jaws to grip, manipulate, bite, shred, or crush prey all have jaw closing lever ratios higher than the species that rely on a rapid, ram-suction based strike to capture prey. We note that this trend appears in spite of the mixture of phylogenetic proximity represented in our sample. We fully expect to see strong historical effects on such features in analyses that examine phylogenetic patterns carefully, and we acknowledge that our study has made no attempt to control for the relative independence of our observations, nevertheless the patterns observed appear to be strong enough that they may weather further scrutiny.

Our selection of species included examples from several families that have members of both feeding-mode groups. From the Pomacentridae the ram-suction feeding, mid-water zooplankton predator blue chromis, *Chromis cyanea*, has a ratio of 0.12, while the two species of *Eupomacentrus* that graze on algal mats (Randall 1967) had jaw-closing ratios above 0.3, indicating a relatively stronger bite than the ram-suction feeding species. Our sample of the Labridae included two ram-suction feeding, mid-water zooplanktivores, *Halichoeres pictus* and *Clepticus parrai*, both of which have smaller jaw-closing lever ratios (0.23 and 0.19, respectively) than the five species that represent prey grasping or biting feeding modes (range = 0.27–0.32). The latter group included four other species of *Halichoeres* that feed on mollusks, echinoderms, and polychaetes (Randall 1967, Wainwright 1988). To the extent that the feeding behaviors contrasted by this lever ratio can be associated with particular prey types, these easily measured morphological variables provide a good predictor of diet.

The jaw closing ratio represents a functional trade-off between two aspects of jaw closing: speed

and force. A large value for this ratio indicates a system that more efficiently transmits the force generated by the contracting adductor mandibulae muscle to the tooth surface. This improvement in transfer of force is gained at the direct expense of speed of movement of the jaw during closing actions. In contrast, a small value of the ratio represents a greater amplification of muscle shortening speed as experienced at the jaw tip during jaw closing. Increased velocity of jaw closing is achieved as a direct trade-off with the efficiency of force transmission. Further, these two mechanical properties, speed and force of jaw closing are likely to be important aspects of different feeding modes. Thus, one would expect that rapid opening and closing of the jaws might be an important component of the strike in ram-suction feeding predators. In contrast, a forceful bite will be an advantage in predators which rely on their oral jaws to grasp, rip and crush prey. This is the contrast that is represented by the jaw closing lever ratio in Figure 6.

The lever system of jaw opening represents a similar functional trade-off, but in this case it is less clear that the two extremes represent different 'performance peaks'. Speed of jaw opening may be anticipated as part of the repertoire in rapid-strike predators, but it is not clear what would be gained by having a relatively forceful jaw opening action. We found the lowest jaw-opening ratios in ram-suction feeding species, but there was considerable overlap, and no clear pattern emerged at high values of the jaw opening ratio (Fig. 6).

Jaw lever arms are dynamic

Our measures of the in-levers of the jaw opening and closing systems represent a simplification of the mechanics of the fish jaw. An important distinction can be made between the 'actual' and 'effective' lever arms in a mechanical system (Hildebrand 1985). The length of the effective lever arm will only be equal to the actual lever arm, which we measured, when the force being exerted on the lever is at a 90° angle to the lever. As diagrammed in Fig. 1, the force being exerted by the IOP ligament (the interopercular-mandibular ligament) on the jaw-

opening lever is not at 90° to the opening in-lever. In general, the effective lever arm is equal to the length of the actual lever arm (Fig. 1b, distance 'd') times the sine of angle α . Thus, as α decreases from 90° the effective lever arm decreases and the mechanical advantage at the pivot point of the jaw decreases. Similarly for the jaw closing system, the effective lever arm will be equal to the closing in-lever (Fig. 1b, distance 'd') times the sine of angle β . If α and β vary among species, our simplification of these systems by measuring only the distances r and d could potentially produce misleading results.

Although the incorporation of information about α and β would provide a more precise picture of jaw mechanics, we defend the use of 'actual' lever arms as a reasonable basis for interspecific comparisons of jaw mechanics based on the observation that both α and β will change substantially during the buccal expansion and compression that characterizes the strike of teleosts. In other work (Richard & Wainwright 1995), we have measured α and β from videos of feeding largemouth bass. Two important points can be summarized from those observations: both angles approach 90° at some point during the strike. Because α and β are dynamic, no single value for each would adequately characterize the mechanics of the jaws. Since both approach 90° at some point during the strike, treating the actual lever arms as indicative of the mechanical properties of the jaws does not misrepresent the situation for this species. Clearly, additional data on other species would move toward a refinement of this approach, but until comparative data are available on α and β we suggest that the convenience of measuring r and d without α and β enhances the utility of this approach to a broader range of researchers, particularly those working with preserved material (i.e. Felley 1984, Winemiller 1991).

It is interesting to note that during the mouth opening phase of the strike in largemouth bass (Richard & Wainwright 1995), α began at about 80° and decreased throughout opening to a value of 35° at the time of peak mouth opening. Thus, the lever system begins the opening phase maximizing the force translation of the jaw opening muscles but changes toward a system which improves the transmission of velocity, at the expense of force. In con-

trast, the mouth closing sequence begins at peak mouth opening, when β is about 30° , and decreases to a value of about 90° when the mouth is fully closed. Hence, the jaw closing lever system begins with an effective lever that provides high velocity transmission, and changes throughout closing toward a system that maximizes force transmission. These changes in the mechanics of the jaws appear to match the functional demands placed on the system at different stages of the strike. At the start of the strike the high force transmission maximizes the ability of the fish to accelerate the jaw in opening. As the jaw begins to depress the effective lever arm decreases, improving the efficiency of velocity transfer. During jaw adduction, the system initially provides high velocity transmission permitting rapid adduction, something that may be advantageous when the mouth is closed on an elusive prey. As the jaws approach full adduction, the adductor muscles provide an increasing efficiency of force translation, a factor that should improve the ability of the fish to exert strong biting forces on a prey that has been gripped between the jaws.

Implications for ecomorphological analyses

The expectation in ecomorphological analyses that anatomy will correlate with diet is based on the assumption that anatomy reflects performance characteristics of fishes important in predatory behaviors (Gatz 1979a, Felley 1984, Douglas 1987, Wine-miller 1991). Naturally, the potential insights gained from ecomorphological analyses will be enhanced when the morphological variables measured can be interpreted in a functional context. By selecting variables with clear functional consequences, interpretations of morphology-diet relationships can be couched in terms of the behavioral capabilities of the predator. If morphology shows no correspondence with diet it is then possible to identify specific performance characteristics that do not appear to play an important role in determining interspecific dietary differences.

The relationship between body-size and diet in centrarchids from Lake Opinicon and serranids from Caribbean coral reefs is characterized by a

transition through increasing prey sizes with increasing predator size. The smallest fishes in both communities eat small zooplankton, intermediate size fish feed on larger invertebrates (crayfish and large insect larvae in Lake Opinicon and decapod shrimp and crabs in the Caribbean), while the largest fish fed upon other fish. The trend is apparent in both interspecific and ontogenetic analyses. We suggest that this trend is widespread and reflects, above all, the influence of predator mouth size on prey-specific feeding performance. We propose that this trend can be expected to occur in other generalized, suction-feeding, benthic communities that possess an analogous prey base.

Our results on lever mechanics of the jaws parallel those of other workers who have found a significant correlation between jaw mechanics and mode of feeding in other members of the Labridae (Westneat 1990, this volume) and the Cichlidae (Barel 1983). Westneat (1990) has shown that four-bar-linkage systems operate in the jaw movements of labrids, and his models suggest morphological components of the upper-jaw movement and hyoid depression mechanisms that could be assayed to complement the variables we recommend for the mechanics of lower jaw movement. We have focused on the simpler lever ratios of the lower jaw because we feel they are easily measured and thus, could be readily included in broad-scale ecomorphological analyses that score the morphology of large numbers of individual fish.

A final point that emerges from our analyses concerns the need to quantitatively address scaling relationships of functionally significant variables. Dimensions such as mouth diameter are frequently assumed to scale isometrically with fish length and workers use simple ratios to transform measures of body length into mouth diameter (e.g. Keast 1978). Our observations on the ontogeny of mouth and pharyngeal gape in largemouth bass and bluegill indicate that mouth diameter does not scale isometrically in either species. Using a simple ratio to calculate mouth diameter from body length would be inaccurate for these populations, since the ratio changes with body size. Similarly, measuring features like maxilla length as a proxy for mouth diameter should only be done in cases where the rela-

tionship between gape and maxilla length have been quantified in a series of fish from the population under study. Such a relationship could then be used to estimate a variable such as mouth diameter in large samples of individuals that are preserved in such a fashion that prevents the direct measurement of mouth diameter.

Just as the mechanical properties of trophic structures may vary among species, they may also change during ontogeny (Fig. 5). The jaw lever systems in bluegill change during ontogeny and this may have substantial effects on the kinematics of prey capture in fish of different body size. The only work that we are aware of in which the kinematic or performance consequences expected from morphological differences in the lever systems of the jaws have been tested is that of Westneat (1990, 1991). His work demonstrates the utility of four-bar linkages in understanding interspecific jaw mechanics. No work has been done on the consequences of ontogenetic changes in jaw morphology like those we documented for largemouth bass and bluegill. Ontogenetic changes in jaw mechanics could be explored as one level that underlies diet switches between prey of different functional categories, such as the shift in *Lagodon rhomboides* from suction feeding on small mobile invertebrates to grazing epiphytes (Carr & Adams 1973, Stoner & Livingston 1984).

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