MORPHOLOGICAL BASIS OF KINETIC DIVERSITY IN FEEDING SUNFISHES

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Summary

The effects of differences among species in the scaling of lower jaw levers on the scaling of prey-capture kinematics are explored in three species of centrarchid fishes. We consider the jaw opening and closing lever systems and calculate the consequences of differences in the scaling of the in-levers for the scaling of the time taken to open the mouth \( T_o \) and the time taken to close the mouth \( T_c \) during prey capture. Predictions of \( T_o \) and \( T_c \), based on differences in the scaling of jaw in-levers, are compared with the observed scaling of \( T_o \) and \( T_c \) in three centrarchid fishes. Video recordings (200 and 400 images s\(^{-1}\)) were made of prey capture in largemouth bass Micropterus salmoides (33–206 mm standard length, SL), spotted sunfish Lepomis punctatus (24–145 mm SL) and bluegill sunfish Lepomis macrochirus (24–220 mm SL), and the fastest values of \( T_o \) and \( T_c \) were taken from the fastest recorded feeding event for each fish. The scaling exponents of \( T_o \) and \( T_c \) regressed on fish SL for largemouth bass were 0.592 and 0.572, respectively. Exponents observed for sunfishes were not significantly different from predicted values, based on scaling exponents in largemouth bass and interspecific differences in jaw lever proportions. Two conclusions are emphasized. First, between 25 and 220 mm SL, the time taken to open and close the mouth during the strike increases with body size in all three species, suggesting a general pattern for this family. Second, evolutionary changes in jaw lever mechanics are a major determinant of the diversity of prey-capture kinematics in this sample of centrarchid fishes.

Key words: feeding, kinematics, scaling, evolution, lever, sunfish, largemouth bass, Micropterus salmoides, Lepomis macrochirus, Lepomis punctatus.

Introduction

Research on the functional morphology of feeding mechanisms in fishes has enjoyed great success in characterizing the basic principles of suction feeding and how the parts of the head are manipulated to generate the subambient pressure gradient that forces water and prey into the mouth (Alexander, 1967; Osse and Muller, 1980; Muller et al., 1982; Motta, 1984; Lauder, 1985). Recent work also provides a framework for interpreting the functional consequences of the extensive morphological diversity of fish feeding systems. Four-bar linkages have been proposed to govern the movements of lower jaw depression (Anker, 1974), upper jaw protrusion (Westneat, 1990) and hyoid depression (Muller, 1987, 1989, 1996). In addition, the mechanical advantage of the lower jaw during opening and closing has been shown to vary considerably among species (Barel, 1983; Westneat, 1994; Wainwright and Richard, 1995a).

Several studies have found a strong correspondence between linkage mechanics and feeding habits (Barel, 1983; Westneat, 1995; Wainwright and Richard, 1995a; de Visser and Barel, 1996). For example, in a study of 34 species of Caribbean coral reef fishes, Wainwright and Richard (1995a) found no overlap in the mechanical advantage of jaw closing between species that eat elusive prey and those that eat slower-moving and sessile prey. Westneat (1995), using a phylogenetic hypothesis of the clade, showed a significant correlation between evolutionary changes in four-bar linkage design of the skull and diet in cheiline wrasses from the Indo-Pacific. The repeated evolution of feeding on elusive prey was associated with mechanical changes that favored velocity transfer in the jaw linkages.

The observations of a strong ecomorphological correlation between linkage mechanics and diet in fishes suggests that variation in linkage mechanics should have predictable consequences for prey-capture kinematics, but few studies have tested these predictions directly (Westneat, 1990, 1991, 1994; Muller, 1996). In this paper, we relate differences among species in prey-capture kinematics to differences in jaw linkage mechanics. We describe the ontogeny of the jaw opening and jaw closing levers in three species of the fish family Centrarchidae and use the interspecific patterns in morphology to predict differences among species in the speed of two key movements that occur during prey capture, the time taken to open the mouth during the strike and the time taken to close the mouth. The predictions are tested using data...
taken from video-recorded prey-capture sequences of the three species.

Materials and methods

Modeling the effect of jaw levers on feeding kinematics

The lever systems of lower jaw abduction and adduction in teleost fishes (Fig. 1) are key components of the mechanical linkages that underlie the buccal expansion and compression motions that are central to suction feeding in teleosts. Our approach to assessing the potential influence of species differences in lever lengths was to assume that all other elements of the jaw opening and closing systems scale similarly in the three study species (e.g. the contractile properties of the muscles, the scaling of forces that resist jaw movement) and to generate predictions of interspecific differences in jaw kinematics based only on measured differences in the scaling of the jaw levers. In other words, we ask whether knowing the differences between species in jaw lever lengths is sufficient to explain differences in key aspects of prey-capture kinematics. If interspecific differences in kinematics are not accounted for by jaw levers, the assumption of a common pattern of scaling in other parts of the system (i.e. the contractile properties of the muscles, the scaling of forces resisting jaw motion) must be re-evaluated as a possible explanation for kinematic diversity, and the dominant role of lever design must be discounted. While we expected that diversity of muscle contractile properties could potentially occur in our sample of species, our intention was first to isolate the effects of jaw lever scaling, before investigating other levels of design.

The mechanical model of jaw movement in centrarchid fishes involves rotation about the joint between the quadrato-bone of the suspensorium and the articular bone of the lower jaw (Fig. 1). Jaw depression, and hence mouth opening, is caused by tension on the interoperculo-mandibular ligament that rotates the jaw ventrally. Jaw adduction is caused by contraction of the adductor mandibulae muscles that attach to the coronoid process and the medial surface of the mandible. Consider the case of movement of the jaw during mouth opening for an individual fish (Fig. 1). An input velocity \( V_i \) is applied to the mandible through the interoperculo-mandibular ligament, and the jaw undergoes an angular excursion proportional to the length of the in-lever \( L_i \) (distance \( A \) to \( B \) in Fig. 1). As \( L_i \) increases, the input muscle must shorten a longer distance to cause the same angular rotation of the jaw. If \( V_i \) were a constant, then the time taken to depress the jaw fully \( (T_o) \) would be directly proportional to \( L_i \). Note that, in this model, \( T_o \) depends on \( L_i \) and is independent of jaw length, the out-lever of the jaw depression system.

Thus:

\[
T_o \propto L_i/V_i. \tag{1}
\]

As a fish grows, the scaling of \( V_i \) and \( L_i \) will determine the scaling of \( T_o \). A key relationship that follows from equation 1 is that the scaling exponent for \( T_o \) is equal to the scaling exponent for \( L_i \) minus the scaling exponent for \( V_i \). If \( V_i \) increases in direct proportion to the number of sarcomeres acting in series, and the muscle grows isometrically, then \( V_i \) will scale directly with body or muscle length (i.e. the slope of a log–log plot of \( V_i \) on body length would be 1.0). As time is an inverse function of velocity, if the distance the muscle shortens were to remain constant during growth, then \( T_o \) would scale with a slope of \(-1.0\) (its scaling would be determined by the scaling of \( V_i \)). However, if \( L_i \) also scales isometrically, then the distance that the muscle shortens increases directly with body length. Thus, under this set of assumptions, if \( V_i \) and \( L_i \) both scale isometrically, the net effect will be that they will cancel each other out and \( T_o \) will not change as the fish grows (equation 1).

In general, if we hold the scaling of \( V_i \) at isometry, the scaling exponent of \( T_o \) will increase above zero as the scaling exponent of \( L_i \) increases above 1.0 and will decrease below zero as the scaling exponent of \( L_i \) decreases below 1.0. For example, if \( L_i \) scales to body length with a slope of 1.3, then \( T_o \) will scale with a slope of 0.3. If \( L_i \) scales with a slope of 0.8, then \( T_o \) will scale with a slope of \(-0.2\) (equation 1). Similarly, changes in the scaling exponent of \( V_i \) will have an inverse effect on the scaling of \( T_o \). An increase in the slope of \( V_i \) will result in a decrease in the slope of \( T_o \) of the same magnitude. Deviations of \( V_i \) from isometry could potentially be caused by general scaling effects on muscle shortening rate (e.g. Marsh, 1988; Bennett et al., 1989) or by age-dependent changes in muscle biochemistry (Marsh, 1988).

To generate predictions about the scaling of jaw movements, we assumed that \( V_i \) scales similarly throughout ontogeny in each species and we calculated the consequences of variation between species in the scaling exponent of \( L_i \) for the scaling exponent of \( T_o \). On the basis of the above discussion, the scaling of \( T_o \) should change in the same direction and with the same magnitude as the scaling of \( L_i \) (equation 1). In this study,
we expressed predictions of the scaling of prey-capture kinematics in the two sunfish species relative to patterns observed in the largemouth bass. We selected the largemouth bass as the starting point for our calculations because previous work with this species indicated that growth is generally isometric (Richard and Wainwright, 1995; Wainwright and Richard, 1995a,b). Morphological variables that scale isometrically, or nearly isometrically, include the jaw opening-in-lever, the jaw closing-in-lever, jaw length, mouth diameter and the mass and shape of the sternohyoideus and adductor mandibulare muscles (see Table 1; Richard and Wainwright, 1995; Wainwright and Richard, 1995a). Predictions were made about the scaling exponents for the time to open and the time to close the mouth in the bluegill sunfish Lepomis macrochirus and the spotted sunfish Lepomis punctatus.

For the jaw depression system, we assumed that the differences between species in the scaling of $T_o$ would be a direct function of the difference in scaling of $L_i$. Thus, for each of the two sunfish species, the expected scaling exponent of $T_o$ is equal to the scaling exponent of $T_i$ in largemouth bass plus the exponent for $L_i$ in the target species minus the exponent for $L_i$ in bass. In other words, the exponent that describes scaling of $T_o$ will differ from that observed in largemouth bass by the difference in the scaling exponent of $L_i$ between the two species. The scaling of time to close the mouth ($T_c$) was calculated in a similar fashion.

**Specimens**

Observations were made on the largemouth bass (Micropterus salmoides Lacépède), the spotted sunfish (Lepomis punctatus Valenciennes) and the bluegill sunfish (Lepomis macrochirus Rafinesque), all members of the endemic North American freshwater fish family Centrarchidae. The two species of Lepomis were chosen for study because our preliminary investigations revealed diversity in the scaling of their jaw levers, suggesting that, in comparisons with the isometric largemouth bass, they could provide a useful test of the effects of jaw morphology on prey-capture kinematics. The largemouth bass and bluegill sunfish have been the focus of a number of previous studies on the functional morphology of feeding (Nyberg, 1971; Lauder, 1980, 1983; Wainwright and Lauder, 1986; Richard and Wainwright, 1995; Wainwright and Richard, 1995b; Gillis and Lauder, 1995; Grubich and Wainwright 1997). All three species adapted well to captivity (Richard, 1995b; Gillis and Lauder, 1995; Grubich and Wainwright, 1986; Richard and Wainwright, 1995; Wainwright and Richard, 1995a). Observations were made on the largemouth bass (Micropterus salmoides Lacépède) during video recording in 40 and 120 l aquaria in the laboratory at 20–23 °C and fed a mixed diet of earthworms, pieces of cut squid and sailfin mollies (Poecilia latipinna). Individuals were trained to feed on food held with forceps in the illumination of a single stroboscopic light.

**Morphology**

The following morphological characters were measured on a size series of each species: body mass (g), standard length (mm), jaw length (mm), opening-in-lever of the lower jaw (mm) and closing-in-lever of the lower jaw (mm). The latter three measurements were made on left-side structures only. Linear measurements were made using dial calipers or under a dissecting microscope equipped with an ocular micrometer. Jaw length was measured from the center of the quadrate–articulate joint (Fig. 1) to the anterior margin of the tooth row on the dentary. The opening-in-lever of the lower jaw was measured as the distance between the center of the quadrate–articulate joint and the insertion of the interoperculo-mandibular ligament (Fig. 1; distance A to B). The closing-in-lever of the lower jaw was measured from the center of the quadrate–articulate joint and the midpoint of the insertion of the adductor mandibulare muscle on the mandible (Fig. 1; distance A to C).

**Video recordings**

Prey–capture sequences were video-recorded at 200 or 400 images s$^{-1}$ using a NAC HSV-400 system operating with either one or two synchronized strobes. For the two Lepomis spp., earthworms and pieces of squid mantle were held in forceps and introduced into the filming aquarium. Prey size was scaled by cutting each piece to 30–60 % of the mouth diameter of each fish. In most cases, the prey was released and captured by the fish in the water column. In some instances, the fish took the prey from the forceps before it was released. These sequences were included in the analyses only if the fish did not make contact with the forceps and the prey broke away easily from the forceps. The protocol used for largemouth bass (Richard and Wainwright, 1995) differed from that used for the sunfishes only in that small fish (mollies) were used as prey and they were always taken directly from the forceps.

Feeding sequences were recorded from each fish over a period of 2–30 days until at least 10 sequences had been obtained in which the prey was captured, the forceps did not interfere with mouth movements of the fish and the strike appeared to be vigorous and of high intensity. Our aim was to estimate the fastest mouth opening and closing times of which each fish was capable. Unsuccessful strikes were omitted because it was noted that the mouth closing phase of the gape cycle appeared prolonged when the prey was not captured. Similarly, if contact was made with the forceps, this interfered with mouth closing. A number of factors appeared potentially to inhibit the intensity of strikes, including satiation and how ‘at ease’ the fish appeared to be with the video-recording equipment. Approximately 80 % of all feeding sequences met our criteria for inclusion in the study. We expect that the sequences we selected for study are typical of those analyzed...
in most previous studies of prey-capture kinematics in these fishes. For most individuals, 20 or more sequences were recorded before the fish was killed in tricaine methane sulfonate, and body mass and standard length were measured prior to fixing the animal in formalin. The number of sequences obtained per individual fish varied slightly among species; largemouth bass, 17.2±6.3 sequences per fish (mean ± S.D.); spotted sunfish, 27.9±13.4; bluegill sunfish, 24.1±8.8 (Fig. 2). Data were collected from 10 largemouth bass, 29 spotted sunfish and 21 bluegill sunfish. In total, 1487 prey-capture sequences were analyzed for this study.

For every prey-capture sequence, the time taken to open the mouth (T_o) and the time taken to close the mouth (T_c) were measured. T_o was measured as the time between the image prior to first jaw depression and the first image in which the jaw was maximally depressed. T_c was the time from the image prior to the onset of jaw adduction to the first image showing contact between the tips of the mandible and the premaxilla. In some sequences, the jaw was held at maximal depression for a variable time of up to 30 ms before adduction was initiated. Because our interest was in measuring the shortest time taken by each fish to open or close the jaw, the time during which the jaw was maintained at peak gape was not included in our measures of T_o or T_c. Measures of the fastest T_o and T_c for each fish were taken from the prey-capture sequence during which the total time to open and close the mouth was the shortest, not including any time in which peak gape was maintained (Fig. 2).

A subset of the data analyzed here for largemouth bass has been discussed previously (Richard and Wainwright, 1995). The present paper differs from this earlier treatment in analyzing over twice as many prey-capture sequences for each of the ten bass and in focusing on the fastest T_o and T_c for each fish, rather than the mean values of these kinematic variables, as was the focus of Richard and Wainwright (1995).

Data analysis

Scaling relationships of morphological and kinematic variables were calculated by fitting least-squares regressions to log10-transformed data. Log-transforming the data renders exponential relationships linear, thus permitting the use of parametric statistical methods such as linear regression and analysis of covariance (ANCOVA). No violations of standard parametric assumptions were found in the data. Scaling of all variables was expressed relative to standard length. Using a linear measure of body size simplifies the expression and
interpretation of scaling in the kinematic and lever variables because they are all expected to scale directly with linear measures of body size. We report the relationship between body mass and standard length to facilitate comparative use of our data by workers who prefer to express scaling relationships relative to mass.

The log-transformed values of the fastest $T_o$ and $T_c$ for each filmed fish were regressed against standard length. ANCOVAs were used to test the null hypothesis of homogeneity among species in the scaling relationships (i.e. regression slopes) for $T_o$ and $T_c$. Two methods were used to compare the observed scaling relationships of the timing variables with predicted values. First, one-sample $t$-tests were used to compare observed regression slopes with predictions. Second, ANCOVAs were calculated using the relevant jaw in-lever as the covariate. The latter approach is derived from our interpretation of scaling in the kinematic and lever variables (Table 1; Figs 3, 4). Bluegill showed the strongest departure from isometry, with the opening in-lever scaling with a slope of 1.248 and the jaw closing in-lever showing a slope of 1.397. Values for the spotted sunfish were intermediate between those for the bass and bluegill (Table 1). Largemouth bass and the spotted sunfish showed isometry between body mass and standard length (one-sample $t$-tests of the body mass exponent against 3.0: largemouth bass $t_{90}=1.5$, $P=0.15$; spotted sunfish $t_{28}=0.714$, $P=0.44$), but the bluegill sunfish showed positive allometry of body mass ($t_{100}=9.25$, $P<0.001$), with larger bluegill being relatively heavier than smaller fish.

Because the scaling exponents of $L_i$ varied among species, $T_o$ and $T_c$ were also predicted to differ across species (Table 2). For example, the difference between bluegill and bass in scaling of the jaw opening in-lever is 1.248–1.0=0.248, and hence the predicted scaling of bluegill $T_o$ is equal to the scaling of bass $T_o$ plus 0.248 (i.e. 0.592+0.248=0.84) (see above).

Observed values of $T_o$ and $T_c$ varied considerably among feedings for each fish, typically ranging over at least a factor of 2 between the fastest and slowest strike (Fig. 2). Minimum $T_o$ and $T_c$ scaled to fish standard length with slopes between 0.5 and 0.9 in all three species (Tables 1, 2; Figs 3, 4). Hereafter, ‘minimum’ $T_o$ and $T_c$ will be referred to simply as $T_o$ and $T_c$. For both bluegill and spotted sunfish, the predicted scaling exponents for $T_o$ and $T_c$ were not significantly different from the observed values (Table 2).

Analyses of covariance run on $T_o$ revealed a significant overall difference in slope among the three species (Table 3; Fig. 3). Pairwise comparisons between species indicated that

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### Table 1. Least-squares regression statistics for log_{10}-transformed morphological and kinematic variables regressed on fish standard length (mm) in three species of centrarchid

<table>
<thead>
<tr>
<th>Variable</th>
<th>Slope</th>
<th>$\log_{10} \gamma$-intercept</th>
<th>$r^2$</th>
<th>$N$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Largemouth bass</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body mass (g)</td>
<td>2.94±0.04</td>
<td>-4.61±0.08</td>
<td>0.99</td>
<td>10</td>
</tr>
<tr>
<td>Opening in-lever of lower jaw (mm)</td>
<td>1.00±0.04</td>
<td>-1.55±0.08</td>
<td>0.99</td>
<td>10</td>
</tr>
<tr>
<td>Closing in-lever of lower jaw (mm)</td>
<td>1.01±0.03</td>
<td>-1.48±0.06</td>
<td>0.99</td>
<td>10</td>
</tr>
<tr>
<td>Jaw length (mm)</td>
<td>1.07±0.02</td>
<td>-0.89±0.05</td>
<td>0.99</td>
<td>10</td>
</tr>
<tr>
<td>Time to open mouth (ms)</td>
<td>0.592±0.09</td>
<td>0.289±0.18</td>
<td>0.84</td>
<td>10</td>
</tr>
<tr>
<td>Time to close mouth (ms)</td>
<td>0.572±0.08</td>
<td>0.252±0.166</td>
<td>0.86</td>
<td>10</td>
</tr>
<tr>
<td><strong>Spotted sunfish</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body mass (g)</td>
<td>3.05±0.07</td>
<td>-4.53±0.12</td>
<td>0.99</td>
<td>29</td>
</tr>
<tr>
<td>Opening in-lever of lower jaw (mm)</td>
<td>1.118±0.04</td>
<td>-1.86±0.08</td>
<td>0.97</td>
<td>29</td>
</tr>
<tr>
<td>Closing in-lever of lower jaw (mm)</td>
<td>1.104±0.04</td>
<td>-1.75±0.08</td>
<td>0.97</td>
<td>29</td>
</tr>
<tr>
<td>Jaw length (mm)</td>
<td>0.942±0.06</td>
<td>-0.73±0.11</td>
<td>0.91</td>
<td>29</td>
</tr>
<tr>
<td>Time to open mouth</td>
<td>0.754±0.05</td>
<td>-0.18±0.09</td>
<td>0.88</td>
<td>29</td>
</tr>
<tr>
<td>Time to close mouth</td>
<td>0.648±0.1</td>
<td>0.004±0.17</td>
<td>0.63</td>
<td>29</td>
</tr>
<tr>
<td><strong>Bluegill sunfish</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body mass (g)</td>
<td>3.37±0.04</td>
<td>-5.23±0.07</td>
<td>0.99</td>
<td>101</td>
</tr>
<tr>
<td>Opening in-lever of lower jaw (mm)</td>
<td>1.248±0.03</td>
<td>-2.11±0.05</td>
<td>0.96</td>
<td>100</td>
</tr>
<tr>
<td>Closing in-lever of lower jaw (mm)</td>
<td>1.397±0.04</td>
<td>-2.34±0.07</td>
<td>0.93</td>
<td>100</td>
</tr>
<tr>
<td>Jaw length (mm)</td>
<td>0.951±0.02</td>
<td>-0.82±0.03</td>
<td>0.97</td>
<td>99</td>
</tr>
<tr>
<td>Time to open mouth</td>
<td>0.834±0.05</td>
<td>-0.32±0.1</td>
<td>0.94</td>
<td>21</td>
</tr>
<tr>
<td>Time to close mouth</td>
<td>0.907±0.08</td>
<td>-0.47±0.14</td>
<td>0.89</td>
<td>21</td>
</tr>
</tbody>
</table>

Values are means ± S.E.M. All regressions are significant at $P<0.01$. 

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bluegill and spotted sunfish did not differ significantly in the scaling exponent of $T_o$. ANCOVA results for $T_c$ showed a significant heterogeneity of slopes among the three species, and only bass and spotted sunfish did not differ significantly in pairwise comparisons (Table 3; Fig. 4).

If the differences between species in the scaling of $T_o$ and $T_c$ are a function of differences in the scaling of the in-levers for each system, then we expected that $T_o$ and $T_c$ should each have a common scaling relationship with its respective in-lever. In support of this prediction, ANCOVAs run on $T_o$ and $T_c$ using the relevant jaw in-levers as the covariate revealed no significant differences among the three species in the scaling

\[ \text{predicted exponents are based on the consequences of differences in the scaling of the in-lever} \ L_i \ \text{for these two mechanical systems (see text for details).} \]

Predicted and observed values were compared using one-sample Student’s t-tests.
Species combination of species.

Time to close mouth

Species 0.28 (2, 56) 0.76

Time to open Species 9.38 (2, 56) <0.001

variable Factor (d.f.) Dependent

A

B

Fig. 5. Log10–log10 plots of the time taken to open the mouth (A) and the time taken to close the mouth (B) against the relevant jaw in-lever. Note that, in contrast to Figs 3B and 4B, these plots suggest that the slopes are homogeneous among species. This homogeneity of slopes is consistent with the mechanical model of the mandible that suggests that the scaling of mouth opening and closing times will vary directly with the scaling exponents of the in-levers. See Table 4 for a statistical comparison of the slopes in each plot.

Discussion

Our analysis of the scaling of jaw levers and prey-capture kinematics in the three study species leads us to highlight three principal results regarding the general effects of body size and the link between morphology and kinematics. (1) All three species of centrarchids studied showed increased times to open and close the mouth with increasing body size, (2) the scaling exponent for each of these variables (Table 4; Fig. 5). The y-intercept for largemouth bass $T_o$ was significantly higher than those of the other two species, indicating that this species had a longer $T_o$ at all body sizes than the other two species, although the scaling exponent of $T_o$ did not differ significantly among species.

Table 3. Analyses of covariance (ANCOVAs) on time to open the mouth ($T_o$) and time to close the mouth ($T_c$) using fish standard length as the covariate

<table>
<thead>
<tr>
<th>Variable</th>
<th>$F$-ratio (d.f.)</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time to open mouth</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Three species</td>
<td>3.36 (2, 54)</td>
<td>0.042</td>
</tr>
<tr>
<td>Largemouth bass versus bluegill</td>
<td>6.18 (1, 27)</td>
<td>0.019</td>
</tr>
<tr>
<td>Largemouth bass versus spotted</td>
<td>4.8 (1, 39)</td>
<td>0.043</td>
</tr>
<tr>
<td>Bluegill versus spotted</td>
<td>0.534 (1, 46)</td>
<td>0.468</td>
</tr>
<tr>
<td>Time to close mouth</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Three species</td>
<td>3.87 (2, 54)</td>
<td>0.027</td>
</tr>
<tr>
<td>Bass versus bluegill</td>
<td>6.73 (1, 27)</td>
<td>0.015</td>
</tr>
<tr>
<td>Bass versus spotted</td>
<td>0.26 (1, 39)</td>
<td>0.615</td>
</tr>
<tr>
<td>Bluegill versus spotted</td>
<td>4.54 (1, 46)</td>
<td>0.038</td>
</tr>
</tbody>
</table>

Entries are the results of significance tests of the interaction term Species $\times$ Length from the ANCOVA run for the indicated combination of species.

For each variable, results are shown for all three species analyzed together and in pairwise comparisons.

Table 4. Results of analyses of covariance on time to open the mouth ($T_o$) and time to close mouth ($T_c$), using the relevant in-lever of the lower jaw as the covariate in each case

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Factor</th>
<th>$F$-ratio (d.f.)</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time to open mouth</td>
<td>Species</td>
<td>9.38 (2, 56)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Opening in-lever of lower jaw</td>
<td>577.1 (1, 56)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Species $\times$ opening in-lever of lower jaw</td>
<td>0.468 (2, 54)</td>
<td>0.629</td>
</tr>
<tr>
<td>Time to close mouth</td>
<td>Species</td>
<td>0.28 (2, 56)</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>Closing in-lever of lower jaw</td>
<td>224.4 (1, 56)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Species $\times$ closing in-lever of lower jaw</td>
<td>0.081 (2, 54)</td>
<td>0.922</td>
</tr>
</tbody>
</table>

$F$-ratios for main effects are based on models run after omitting the insignificant interaction terms.

Table 3 for a statistical comparison of the slopes in each plot.

of lever dimensions and prey-capture kinematics varied among the three species, and (3) the differences among species in the scaling of times to open and close the mouth were accounted for by differences among species in the scaling of jaw levers.

General scale effects

The movements of prey capture slowed with increasing body size in all three centarchid species. Larger fish took longer to open and close the mouth than smaller fish. These results suggest that, across the body sizes studied (24–220 mm SL), longer times to open and close the mouth during prey capture with increasing body size are probably a general feature of centarchid feeding mechanisms, and we suggest that this pattern is likely to be widespread among fishes. Comparative data for the scaling of prey-capture kinematics in other fishes are not available in the literature. However, work with larval and small juvenile fishes in several other teleost groups indicates that prey-capture times usually decrease with increasing body size in fishes ranging in length from 5 to 30 mm SL (Wanzenbock, 1992; Coughlin, 1994; Cook, 1996). Clearly, the results of the present study
should not be generalized to fishes outside the range of body sizes studied.

The broad isometric scaling of morphology in the feeding mechanism of the largemouth bass is instructive regarding the scaling of the input velocities of mouth opening and closing in this species ($V_i$ of Fig. 1). Recall that if $V_i$ and $L_i$ scale isometrically for the jaw opening and closing systems, then $T_o$ and $T_c$ will not change with increasing body size (equation 1). Given that $L_i$ for both the opening and closing systems of the largemouth bass scales isometrically and that $T_o$ scales with an exponent of 0.592 and $T_c$ with an exponent of 0.572 (Table 1), then it follows that $V_i$ must not be increasing isometrically in either system (recall that under isometry these exponents would be zero). Following equation 1, the inferred scaling exponent of $V_i$ for opening is 0.408 and for closing is 0.428. At least for the jaw adduction system, in which the adductor muscle inserts directly on the lower jaw, this value probably directly reflects the scaling of the shortening velocity of the adductor muscle. It is noteworthy that published accounts of the rates of contraction of muscle from ectothermic vertebrates report that time to peak twitch tension scales to animal length with a slope of approximately 0.45 and unloaded contraction velocity scales with an exponent of approximately 0.29 (Archer et al., 1990; Bennett et al., 1989; Marsh, 1988). This general pattern of decreasing persarcemere rates of contraction suggests that the negative allometry of $T_c$ and $T_o$ observed in the largemouth bass is due, at least in part, to the negative allometry of muscle shortening velocity.

$Lever arms and kinematic diversity$

The scaling exponents of minimum $T_o$ and minimum $T_c$ in the two *Lepomis* species closely matched the values predicted on the basis of the differences in scaling of jaw opening and closing in-levers. In each of the four cases ($T_o$ and $T_c$ for bluegill and spotted sunfish), observed scaling exponents were not significantly different from predicted values (Table 2). As is often the case in scaling studies, the general similarity of scaling exponents made it difficult to distinguish them in some pairwise comparisons. For example, bluegill and spotted sunfish scaling exponents of $T_o$ did not differ significantly (Table 3). Nevertheless, in most cases, the match between observed and expected values was strikingly close. In three of the four cases, the observed exponents were within 0.05 of the predicted value, while in the fourth case the predicted value differed by approximately 0.06 (Table 2).

A second analysis provides additional verification of the common effect that in-lever scaling had on kinematic scaling. If minimum $T_o$ and $T_c$ are regressed against the relevant in-levers, rather than fish standard length, the result is homogeneity of slopes in the three species (Fig. 5; Table 4). In other words, although the scaling of $T_o$ and $T_c$ with $SL$ differs among species, the times to open and close the mouth have common relationships when scaled against the relevant in-lever. Thus, it is not necessary to invoke the possibility of interspecific differences in the scaling exponent of $V_i$, due to factors such as changing muscle composition (Marsh, 1988), to account for the kinematic differences.

Scaling $T_o$ against the jaw opening in-lever also revealed one level of significant variation among species. Although the scaling exponent of $T_o$ versus $L_i$ did not vary among species, the largemouth bass had a longer $T_o$ at all in-lever values (Fig. 5; Table 4). The implication of this result is that $V_i$ is slower in largemouth bass, when scaled against the jaw opening in-lever (Fig. 5), than in the other two species. Does the interspecific difference in $V_i$ indicate that there is a difference between species in the shortening velocity of the jaw depression muscles? Although interspecific variation in the intrinsic rate of shortening of the jaw depression muscles is one possible basis for variation among species in $V_i$, there are other levels of design of the jaw depression system that could also explain this pattern.

The mechanism of jaw depression in centrarchids is thought to involve two separate linkage systems. First, posterior–dorsal rotation of the ventral margin of the opercle caused by contraction of the levator operculi muscle transmits motion through the subopercle and interopercle to the interoperculo-mandibular ligament. This system was modeled as a four-bar linkage by Anker (1974), although Westneat (1990) found this four-bar linkage to be inadequate in accounting for jaw depression in two labrid species. Second, jaw depression is effected by hyoid depression *via* a ligamentous connection between the hyoid bar and the interopercle bone (Osse, 1969; Liem, 1970, 1978; Lauder, 1985). The hyoid is depressed by sternohyoideus contraction and cranial elevation (Lauder, 1985; Muller, 1987; Westneat, 1990). Surprisingly, no clear synthesis of the mechanisms of jaw depression has yet emerged, but it is clear that the muscles that produce jaw depression act through a series of second-order levers. Scaling of the output velocity of movement in this system ($V_i$ of Fig. 1) only begins with the intrinsic shortening velocity of the muscles; variation among species in the scaling of the structural elements that make up these four-bar linkages or the relative timing of muscle activity could also lead to differences among species in $V_i$.

*Evolution of centrarchid feeding kinematics*

The species included in this study represent a sample of the range of feeding morphologies, strategies and ecology in the family Centrarchidae. In particular, largemouth bass and bluegill sunfish have frequently been contrasted as representing qualitatively different modes of prey capture. Largemouth bass are typically piscivorous (Werner, 1977; Keast, 1985) ram-feeding predators (Nyberg, 1971; Norton and Brainerd, 1993). In contrast, spotted and bluegill sunfish feed on zooplankton (copepods, ostracods) and small benthic arthropods such as chironomid larvae (McLane, 1955; Keast, 1978), using suction to take these prey individually (Lauder, 1980, 1983; Norton and Brainerd, 1993). Indeed, the largest pressure gradients yet reported in a suction-feeding fish (64 kPa below ambient measured in the buccal cavity) are from the bluegill (Lauder, 1980). In contrast, the largest pressure
gradients reported from largemouth bass during prey capture were 5 kPa (Norton and Brainerd, 1993) and 16.4 kPa (Grubich and Wainwright, 1997) below ambient.

This study provides evidence that jaw lever mechanics plays an important role in determining differences among these species in prey-capture kinematics. The common relationships found when scaling $T_0$ and $T_c$ against their in-levers suggest that variation among species in lever design underlies the differences in the scaling of $T_0$ and $T_c$ with body size. Although many of the differences between these species in feeding behavior were not assessed in this study, lever design adequately accounted for differences in strike speed, suggesting that evolutionary changes in the time course of the strike in these taxa can be understood at the level of changes in the ontogeny of jaw levers. In attempting to understand the consequences of the morphological diversity found in teleost fishes for prey-capture kinematics and the evolution of feeding behavior, we suggest that the mechanical linkages that have been proposed to govern movements of the hyoid (Muller, 1987, 1996), upper jaws (Westneat, 1990) and lower jaws (Anker, 1974; this study) represent an important level of design of feeding systems that has shown promise in linking morphological and functional diversity in fishes. Linkage mechanics of the skull should feature prominently in any attempt to understand the basis for the trophic radiations seen in centrarchids and many other teleost groups.

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