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MORPHOLOGICAL BASIS OF KINEMATIC 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 quadrate 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:

$$T_o \propto L_i/V_i . \quad (1)$$

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,

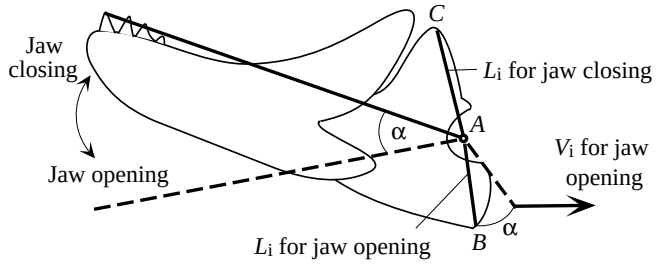

Fig. 1. Schematic diagram of the mechanical systems of jaw opening and closing in a fish lower jaw. The in-lever (L_i=*A* to *B*) for jaw opening is the distance between the center of the quadrate–articular joint (*A*) and the insertion site of the interoperculo-mandibular ligament on the posterior ventral margin of the mandible (*B*). L_i (*A* to *C*) for jaw closing is the distance between the jaw joint and the insertion of the adductor mandibulae muscle on the coronoid process of the mandible (*C*). An input velocity (V_i) is applied to the jaw opening system at point *B*. The time taken to depress the mandible through some angle (e.g. α=30 °) is proportional to the distance L_i. In the present study, we investigated the effect of differences in L_i on the kinematics of prey capture in three fish species.

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 mandibulae 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_o 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 and fed aggressively in the presence of the stroboscopic lights used during video recording. Largemouth bass (30–210 mm standard length *SL*; 0.85–166 g, *N*=10) were collected in Bevis Pond, Leon County Florida. Bluegill sunfish (24–220 mm *SL*; 0.72–364 g, *N*=122) were collected in Lake Jackson, Leon County. Spotted sunfish (24–145 mm *SL*; 0.63–65 g, *N*=61) were collected in the headwaters of the Waccisa River, Jefferson County, Florida, USA. Most fishes were killed at the collection site with an overdose of tricaine methane sulfonate and fixed in 10 % formaldehyde.

A subsample of each species was maintained for 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–articular 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–articular 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–articular joint and the midpoint of the insertion of the adductor mandibulae 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

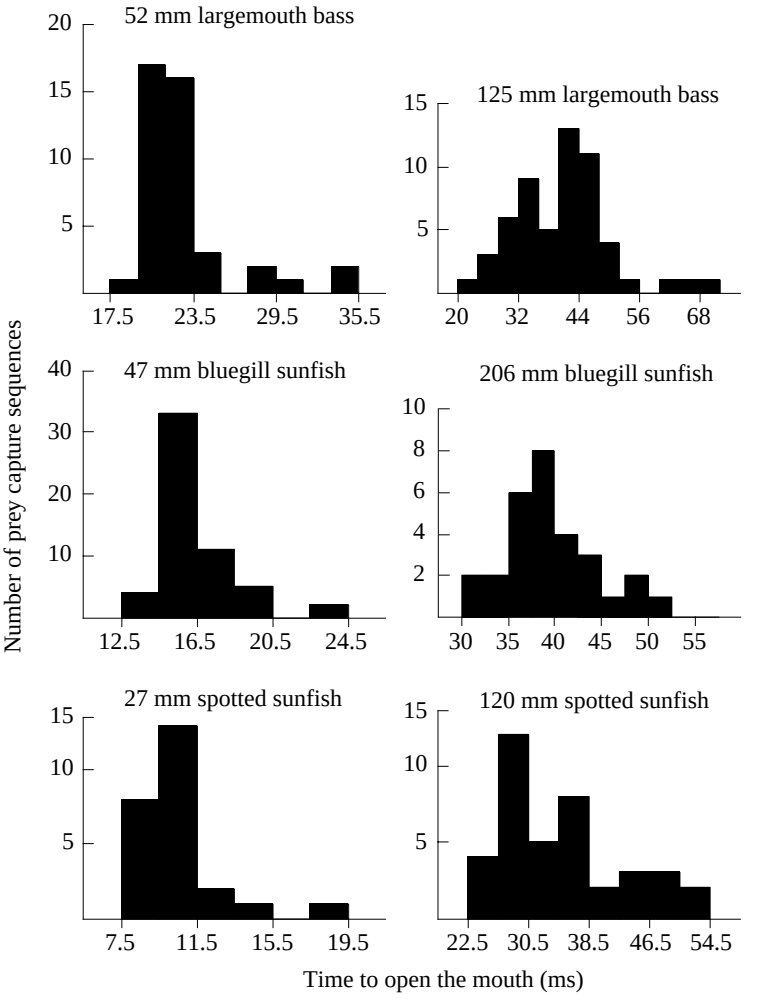

Fig. 2. Frequency histograms of the time taken to open the mouth during prey capture in six fishes. Individual fish showed extensive flexibility in the time course of the strike, typically ranging over a factor of two or more between the fastest and slowest strike recorded. We took measurements of the fastest time to open (T_o) and time to close (T_c) the mouth from the fastest overall strike for each fish.

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 $\log_{10}$-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 expectation that differences between species in the scaling of jaw levers underlie differences in the speed of jaw movement. Assuming that the speed applied to the in-levers (V_i of equation 1) scales with the same exponent in each species, we predict that T_o and T_c will scale similarly with their respective in-levers.

Results

Largemouth bass showed isometry of all jaw morphological variables (Table 1), indicating that features of the jaw maintain the same shape during the growth of this species. The other two species exhibited positive allometry of both in-levers (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_9=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

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*

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

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

Table 2. *Summary of observed and predicted scaling exponents for time to open the mouth (T_o) and time to close the mouth (T_c) in spotted and bluegill sunfish*

Variable	Slope for largemouth bass	Slope for spotted sunfish	Slope for bluegill sunfish
Opening in-lever of lower jaw	1.00	1.118	1.248
Time to open mouth	0.592	0.754 (0.71 predicted) t_{28}=0.88, P>0.2	0.834 (0.84 predicted) t_{20}=0.12, P>0.5
Closing in-lever of lower jaw	1.01	1.104	1.397
Time to close mouth	0.572	0.648 (0.675 predicted) t_{28}=0.27, P>0.5	0.907 (0.968 predicted) t_{20}=0.76, P>0.2

Predicted exponents are based on the consequences of differences in the scaling of the in-lever L_i for these two mechanical systems (see text for details).

Predicted and observed values were compared using one-sample Student's *t*-tests.

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

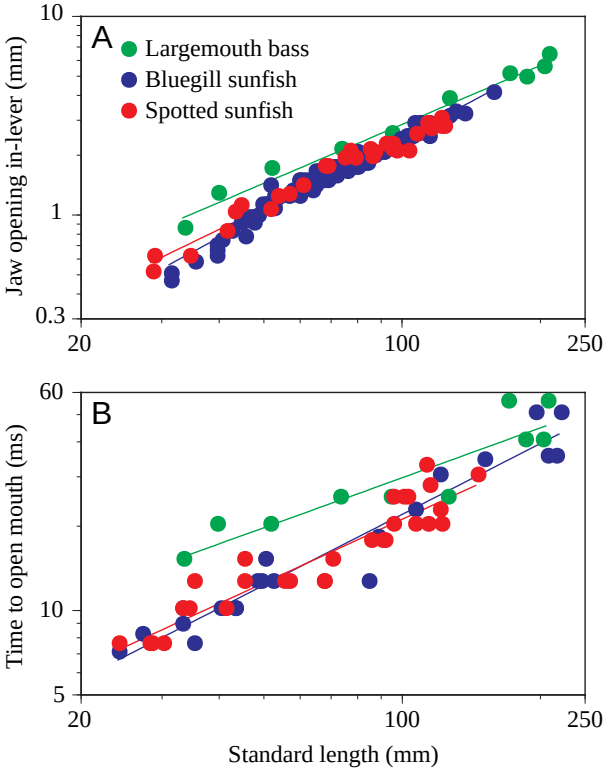

Fig. 3. Log_{10}–log_{10} plots of the jaw opening in-lever (A) and time to open the mouth (B) against fish standard length in the three centrarchid species studied. Observations were made on different specimens for the two graphs. Each point in B represents the fastest time to open the mouth recorded for an individual fish. Lines are least-squares regressions fitted to the data for each species. See Table 1 for a statistical summary of these data.

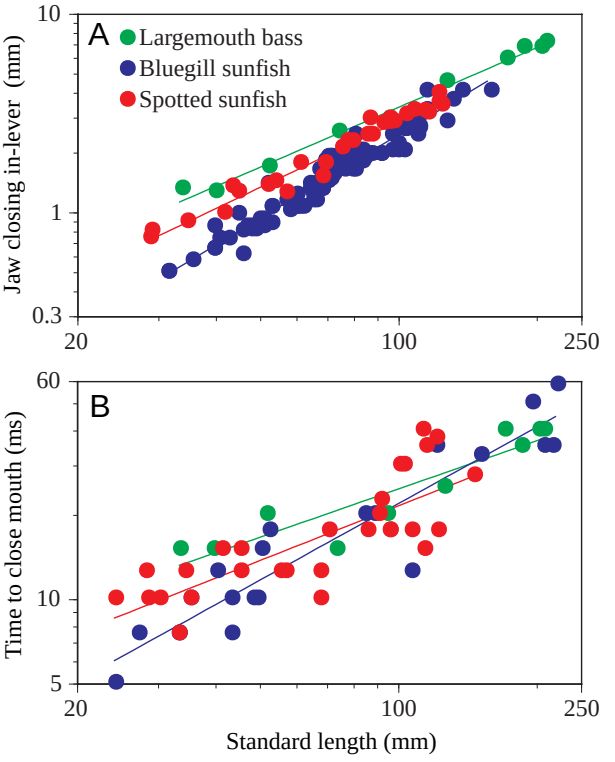

Fig. 4. Log_{10}–log_{10} plots of the jaw closing in-lever (A) and time to close the mouth (B) against fish standard length in the three centrarchid species studied. Observations were made on different specimens for the two graphs. Points in B represent the fastest measured time to close the mouth for each fish. See Table 1 for a statistical summary of these data. Note the similar pattern of differences among species in regression slopes in the two plots.

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*

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

Entries are the results of significance tests of the interaction term Species × 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.

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.

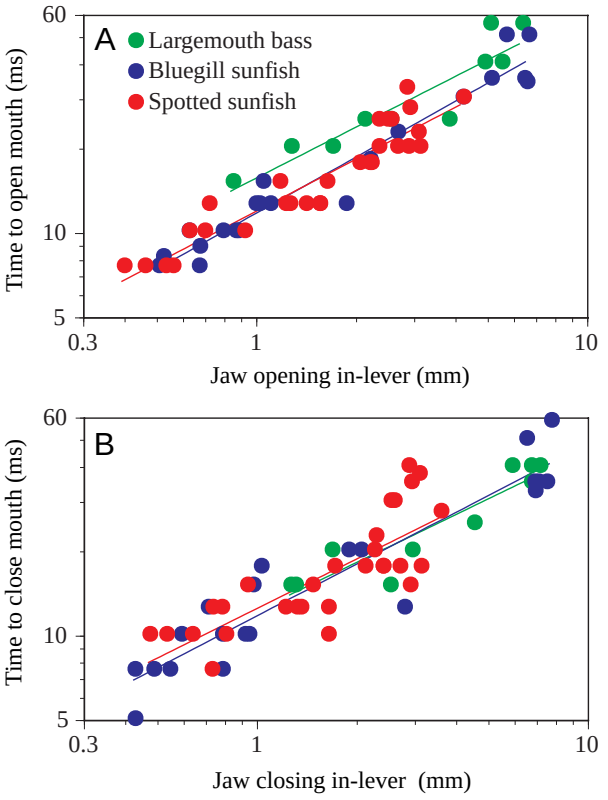

Fig. 5. Log_{10}–log_{10} plots of the time taken to open the mouth (A) and the time taken to close the mouth (B) against the relevant jaw in-lever. Note that, in contrast to Figs 3B and 4B, these plots suggest that the slopes are homogeneous among species. This homogeneity of slopes is consistent with 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 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.

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*

Dependent variable	Factor	*F*-ratio (d.f.)	*P*
Time to open mouth	Species	9.38 (2, 56)	<0.001
	Opening in-lever of lower jaw	577.1 (1, 56)	<0.001
	Species × opening in-lever of lower jaw	0.468 (2, 54)	0.629
Time to close mouth	Species	0.28 (2, 56)	0.76
	Closing in-lever of lower jaw	224.4 (1, 56)	<0.001
	Species × closing in-lever of lower jaw	0.081 (2, 54)	0.922

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

General scale effects

The movements of prey capture slowed with increasing body size in all three centrarchid 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 centrarchid 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 per-sarcomere 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_o and T_c against their in-levers suggest that variation among species in lever design underlies the differences in the scaling of T_o 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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