Morphology predicts suction feeding performance in centrarchid fishes

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Summary

Suction feeding fish differ in their capacity to generate subambient pressure while feeding, and these differences appear to relate to morphological variation. We developed a morphological model of force transmission in the fish head and parameterized it with measurements from individual fish. The model was applied to 45 individuals from five species of centrarchid fishes: *Lepomis macrochirus*, *Lepomis punctatus*, *Lepomis microlophus*, *Micropterus salmoides* and *Pomoxis nigromaculatus*. Measurements of epaxial cross-sectional area, epaxial moment arm, buccal area and buccal area moment arm were combined to estimate pressure generation capacity for individual fish. This estimation was correlated with pressure measured in fish feeding on elusive prey to test the model's ability to predict pressure generation from morphology. The model explained differences in pressure generation found among individuals ($P<0.001$, $r^2=0.71$) and produced a realistic estimate of normalized muscle stress during suction feeding (68.5 ± 6.7 kPa). Fish with smaller mouths, larger epaxial cross-sectional area and longer epaxial moments, such as *L. macrochirus* (bluegill sunfish), generated lower pressures than fish with larger mouths, smaller cross-sectional area and shorter moments, such as *M. salmoides* (largemouth bass). These results reveal a direct trade-off between morphological requirements of feeding on larger prey (larger mouth size relative to body depth) and the ability to generate subambient pressure while suction feeding on elusive prey.

Key words: Centrarchidae, suction feeding, functional morphology, performance, modeling, buccal pressure, trade-offs.

Introduction

The majority of teleost fish use suction feeding to capture prey, yet teleosts display a remarkable diversity of feeding morphology. It has been assumed that this diversity results in variation in suction feeding performance, and several attempts have been made to link morphology to behavioral performance as measured experimentally (Lauder and Clark, 1984; Norton and Brainerd, 1993; Webb, 1984; Werner, 1977) or interpreted through trophic ecology (Huskey and Turingan, 2001; Norton, 1995). However, these attempts have been largely observational in that they did not quantitatively describe the link between morphology and suction feeding performance. The lack of a general and quantitative understanding of the morphological basis of suction feeding performance limits the functional interpretation of fish morphological form, its ecological implications and its evolution. The objective of the present study was to use a biomechanical model of force transmission in the fish head to predict one aspect of suction feeding performance, subambient buccal pressure generation, from morphological parameters in five species of centrarchid fish.

Suction feeding on elusive prey involves explosive cranial kinematics that incur hydrodynamic loading, measurable as subambient pressures inside the mouth (buccal) cavity (Alexander, 1969; Van Leeuwen and Muller, 1983). The magnitude of subambient buccal pressure indicates the strength of suction generated by the fish and is expected to increase with the velocity of water flow into the mouth (Muller et al., 1982). The magnitude of buccal pressure is known to increase with increasing speed of kinematic movement (Sanford and Wainwright, 2002; Svanback et al., 2002) or in situations where increased kinematic speed would be expected, such as increased predator motivation (Lauder, 1980) or increased prey elusivity (Nemeth, 1997). Therefore, buccal pressure magnitude is considered a metric of suction feeding performance (Grubich and Wainwright, 1997; Lauder, 1983b; Lauder et al., 1986).

The only previous analysis to estimate pressure-generating capacity directly from musculoskeletal morphology was performed by Alexander (1969). In that study, which was also the first to measure buccal pressure during feeding, measured pressure was compared with estimates of pressure generation capacity to understand which muscles actuate suction feeding
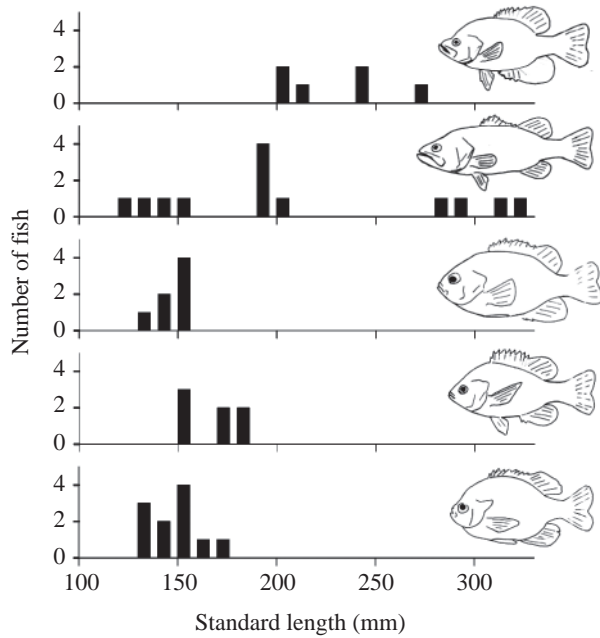
Fig. 1. Shape and size variation among individual fish used in this study. In order, from top to bottom, the species are: black crappie (*Pomoxis nigromaculatus*); largemouth bass (*Micropterus salmoides*); spotted sunfish (*Lepomis punctatus*); redear sunfish (*Lepomis microlophus*) and bluegill sunfish (*Lepomis macrochirus*). Histograms illustrate the sizes of fish used in performance experiments.

kinematics. It has since been observed that pressure magnitudes differ among species with divergent morphologies (Lauder, 1983b; Norton and Brainerd, 1993). We devised a mechanical model of force transmission, parameterized it with morphological measurements from individual fish and compared those measurements to pressures measured during suction feeding on elusive prey. We applied this model to a morphologically diverse group of centrarchid fishes (Fig. 1). It was predicted that the biomechanical model could explain

variation in pressure magnitudes among individuals, that fish would not exceed the maximum possible pressure magnitude predicted by the model and that the model would yield realistic estimates of muscle force production.

The model

Buccal pressure gradients are generated by dorsal rotation of the head, lateral expansion of the suspensoria and ventral rotation of the hyoid and lower jaw (Lauder, 1980). These kinematic events are actuated by ventral musculature (sternohyoideus and hypaxials) and dorsal musculature (epaxials) (Muller, 1989; Osse, 1969). The primary assumption of our model is that buccal pressure magnitude is limited by the ability of muscles to produce force and the ability of skeletal elements to transmit that force (cf. Alexander, 1969).

Rotation of the neurocranium involves rotation relative to the pectoral girdle and vertebral column (Thys, 1997). Manipulation of anesthetized fish revealed that pectoral rotation occurred at the joint between the supracleithrum and post-temporal bone (S-PT joint) (Gregory, 1933) and that this joint shared a common axis with intervertebral rotation. Therefore, this landmark was used as the fulcrum to estimate the torques involved in pressure production.

The buccal cavity may be modeled as an expanding cylinder with subambient buccal pressure distributed across its internal surface (Muller et al., 1982). These pressures can be resolved into a force vector oriented normal to the buccal surface of the neurocranium. The magnitude of this force is equal to the magnitude of buccal pressure multiplied by the surface area of the cylinder's projected area. The resolved force of subambient buccal pressure exerts a torque on the neurocranium. The torque generated by the epaxial muscles must be greater than the torque generated by subambient buccal pressure (Fig. 2A).

Thus, the minimum pressure a fish can generate depends on the force generated by the muscle, the moment arm of the epaxial musculature (L_{in}), the projected area of the buccal surface over which force is distributed (A_{buccal}) and the moment of area of the buccal surface (L_{out}) (Fig. 2A). L_{in} is the distance

$$F_{epaxial}=P^m (PCSA)$$
$$F_{pressure}=F_{epaxial} (L_{in}/L_{out})$$
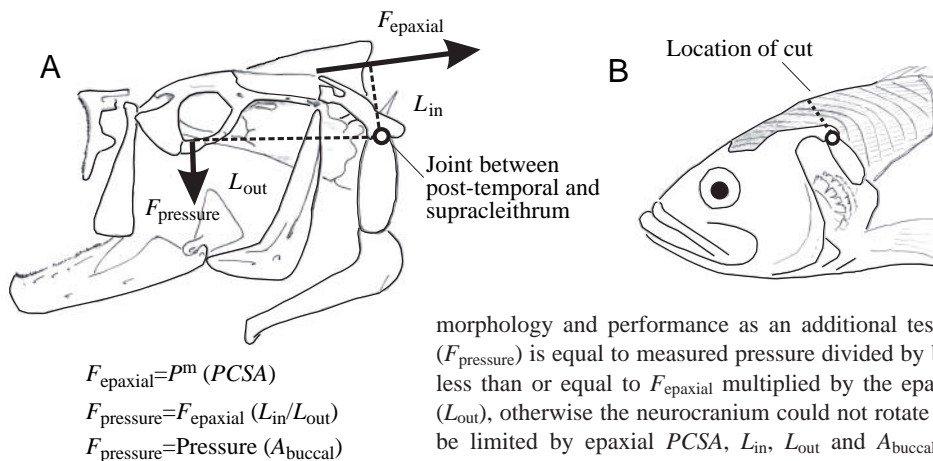$$F_{pressure}=\text{Pressure} (A_{buccal})$$

Fig. 2. (A) Model parameters and torque balance during epaxial rotation. This figure illustrates the force transmission model used in this study. Epaxial force during suction feeding ($F_{epaxial}$) is a product of epaxial physiological cross-sectional area ($PCSA$) and normalized muscle stress during suction feeding (P^m). P^m was not estimated *a priori* but was derived from the correlation between morphology and performance as an additional test of the model. The force of buccal pressure ($F_{pressure}$) is equal to measured pressure divided by buccal projected area (A_{buccal}). $F_{pressure}$ must be less than or equal to $F_{epaxial}$ multiplied by the epaxial moment (L_{in}) divided by buccal moment (L_{out}), otherwise the neurocranium could not rotate dorsally. Therefore, measured pressure should be limited by epaxial $PCSA$, L_{in}, L_{out} and A_{buccal}. The measurements or estimations of these parameters are described in the text. (B) Location of $PCSA$ measurement. $PCSA$ was measured at the minimum perpendicular distance from the line of surface fascicle orientation to the joint axis.

from the centroid of the epaxial cross section to the S-PT joint, while L_{out} is the distance from this joint to the area moment of the projected buccal area (Fig. 2A). Muscle force is the product of muscular physiological cross-sectional area (*PCSA*) and normalized stress generated by the muscle (P^m) (Lindstedt et al., 1998). Balancing the torques about the neurocranium yields the following equation for predicted pressure:

$$\text{Predicted pressure} = -P^m\{[PCSA(L_{in}/L_{out})]/A_{buccal}\} \ . \quad (1)$$

If P^m were correctly estimated, the magnitude of predicted pressure derived from morphological variables should correlate with measured pressure with a slope of one. However, any estimate of P^m would be unreliable given the lack of data on muscle force production during suction feeding. Rather than use a suspect estimate of P^m, the morphological parameters of the model were combined into a unitless morphological potential:

$$\text{Morphological pressure} = [PCSA(L_{in}/L_{out})]/A_{buccal} \ . \quad (2)$$

The slope of the regression between morphological potential and measured pressure is an empirical estimate of P^m. One of the tests of the model was that the P^m estimated by the relationship between morphological potential and measured pressure would be within the range of normalized stress predicted for skeletal muscle shortening at approximately $\frac{1}{3}V_{max}$ (Carroll, 2004) or approximately one-third of a maximum isometric force (P^o) of 150–200 kPa (James et al., 1998; Johnston and Salamonski, 1984) or 50–70 kPa (Hill, 1938). Furthermore, fish should not be able to generate pressures exceeding 200 times their morphological potential, as this would exceed the maximum isometric force that their muscles could generate.

One assumption of the model is that P^m is constant among the sizes and species of fish used in this study. Muscle force per cross-sectional area remains relatively constant across body sizes (James et al., 1998) and species differences as long as the percentage of contractile cytostructure per fiber is conserved (Lindstedt et al., 1998).

Using the model to estimate P^m was judged to be more parsimonious than using an *a priori* estimate. Furthermore, this approach does not alter the correlation between measured morphology and performance: the regression between morphological potential and measured pressure would not be affected by multiplying morphological potential by a constant, and an estimate of P^m could be chosen, *post hoc*, to produce a slope of one.

One of the advantages of this model is that it pertains only to the force balance at the time of peak pressure. The model assumes that normalized muscle force at this point (P^m) is similar across species but does not make any further assumptions about the complex relationships between muscle dynamics, skeletal kinematics and buccal pressure.

Although the ventral and dorsal musculoskeletal systems work together to generate suction feeding kinematics, they must resist buccal pressure independently. The muscles of the ventral expansion system cannot contribute force to dorsal expansion and could therefore be ignored in this study. Ventral expansion operates through a much more complex musculoskeletal system than dorsal expansion, making modeling of force transmission more difficult (Aerts, 1991; De Visser and Barel, 1998).

Materials and methods

Animals

Five species of centrarchid fish were used in this experiment: the largemouth bass, *Micropterus salmoides* (Lacepede) (*N*=13); the black crappie, *Pomoxis nigromaculatus* (Leseuer) (*N*=6); the bluegill sunfish, *Lepomis macrochirus* (Rafinesque) (*N*=12); the spotted sunfish, *Lepomis punctatus* (Valenciennes) (*N*=8) and the redear sunfish, *Lepomis microlophus* (Guenther) (*N*=6) (Fig. 1). These fish were chosen because they span much of the morphological and ecological diversity in centrarchids (Fig. 1), because pressure was known to vary among them and because most were known to perform well during pressure measurements (Lauder, 1983b; Lauder et al., 1986). We used as broad a size range of each species as we were able to collect and would withstand instrumentation (Fig. 1). Fish were collected in the wild in both Florida and California and were either kept alive for *in vivo* performance trials or were killed by overdose of MS-222 (tricaine methane sulfonate) for buccal cast measurements as described below.

In vivo *pressure performance*

Fish were housed in 100 liter tanks at 22°C in accordance with animal use and care protocols (#10168, University of California, Davis and #9901, Florida Institute of Technology). Fish were maintained on a diet of cut squid (*Loligo* sp.), goldfish (*Carassius auratus*) and freshwater shrimp (*Palaemonetes* sp.). Feeding was discontinued 3–4 days prior to experimentation.

Fish were anaesthetized by exposure to 0.3 g l^{-1} of buffered MS-222 and placed in a surgical tray containing freshwater. A large-bore needle was forced through the neurocranium caudal to the ascending process of the pre-maxilla but rostral to the braincase. The needle emerged inside the anterior buccal cavity, lateral to the vomer but medial to the pterygoids. A plastic cannula was fashioned from PE-90 tubing and threaded into the needle. The needle was then removed leaving the cannula implanted in the skull. The flared proximal end of the cannula was held flush against the roof of the buccal cavity by a small sleeve of Tygon tubing (Cole-Parmer, Vernon Hills, IL, USA) that was pushed down the protruding cannula and pressed against the fish's skin.

A Millar SPR-407 microcatheter-tipped pressure transducer (Millar Instruments, Inc., Houston, TX, USA) was threaded into the cannula and held in place by a sleeve of Tygon tubing. The pressure transducer was positioned such that it extended 1 mm into the buccal cavity of the fish, exposing the sensing element to buccal pressure. Transducer implantation took no more than 20 min, and all fish recovered from the procedure

shortly after return to their tank. Recordings commenced with all fish within 3–6 h after surgery.

The goal of the feeding trials was to elicit maximal pressure generation. Prey types were therefore selected for elusiveness and large size (Nemeth, 1997). Freshwater shrimp are highly elusive and were found to elicit largest pressure magnitudes in the *Lepomis* species but not in *M. salmoides* and *P. nigromaculatus*. These two species were fed large goldfish (3–6 cm) depending on individual size. To prevent satiation, fish were fed only a few prey items every 4–6 h over a period of 1–2 days.

In Florida, pressure traces were digitized at 1000 Hz on a DAQpad 6070E data acquisition system (National Instruments, Austin, TX, USA) and recorded on a PC running a custom LabView virtual instrument (National Instruments). In California, pressure traces were digitized at 1000 Hz with a Sonometrics II data acquisition system (Sonometrics Corp., London, Ontario) and recorded on a PC running Sonoview software. Buccal pressure was measured directly from each trace.

Measurement of maximal performance is a general problem in comparative physiology (Garland and Losos, 1994). This is especially true in feeding studies where motivational effects may heavily influence performance. Our strategy for data collection was to make every possible attempt to elicit maximal performance from individual fish including starving prior to experimentation, limiting stress during experiments and feeding large and elusive prey. Buccal pressures are known to decrease precipitously with decreasing predator motivation (Lauder, 1980), so an average minimum pressure will be heavily biased by the number of strikes recorded after a fish is no longer performing maximally. Therefore, the single lowest buccal pressure from each fish was used in the final analysis rather than the mean.

Morphological parameters

Apart from the buccal cast measurement (see below), morphological parameters were measured on the individual fish used in the study. After pressure recordings, fish were killed by overdose of MS-222. Standard length and mass were measured on the freshly killed fish. Fish were then fixed in 10% formaldehyde for two weeks before being transferred to a 75% ethanol solution for storage. Fish were dissected, and the distance from S-PT joint to the rostral and caudal extents of the buccal cavity was measured. The buccal moment arm was
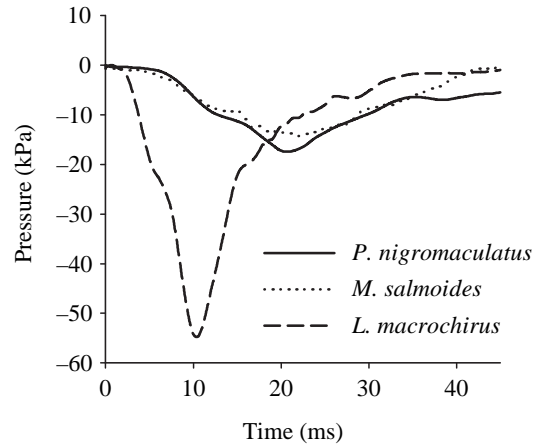

Fig. 3. Representative pressure traces from three species. Pressure magnitude and timing differed among the species used in this study. For clarity, only *L. macrochirus*, *M. salmoides* and *P. nigromaculatus* are illustrated here. Pressure profiles and magnitudes are similar to those measured in other studies of the same species (Grubich and Wainwright, 1997; Lauder, 1983b; Lauder et al., 1986; Norton and Brainerd, 1993; Sanford and Wainwright, 2002).

taken as the average of these distances, because the area moment of the buccal projected area should be halfway between the rostral and caudal extents of the buccal cavity, assuming a cylindrical cavity.

Estimates of epaxial PCSA were made from cross sections of the muscle, cut perpendicular to the orientation of muscle fibers at the minimum perpendicular distance to the S-PT joint (along the line of the moment arm; Fig. 2A). The ventral margin of each section was the axis of the S-PT joint itself, as only fibers dorsal to the joint would be capable of rotating the neurocranium. The fibers in the cut section appeared to be consistently oriented rostro-caudally, with apparent uniform orientation throughout each slice (Fig. 2B). However, the possibility that some fibers deviated from normality means the estimate represented the maximum possible PCSA for each section. Each section was digitally photographed against a ruler. IMAGEJ (NIH, Washington, DC, USA) was used to measure the area and centroid of each section. Because each section was cut perpendicular to muscle fibers, this area was an estimate of the total PCSA of the epaxial muscles. The moment arm was measured as the distance between the centroid and the ventral margin of each section, which, as

Table 1. *Scaling relationships between log 67% buccal projected area (mm^2) and log standard length (mm)*

Species	Slope	Intercept	r^2	N	Standard length (mm)
L. macrochirus	2.20±0.20	−2.47±0.39	0.91	8	56–116
L. microlophus	1.77±0.08	−1.54±0.17	0.96	22	63–175
L. punctatus	2.22±0.07	−2.36±0.13	0.99	15	59–135
P. nigromaculatus	1.68±0.12	−1.01±0.26	0.96	10	105–222
M. salmoides	2.60±0.22	−3.18±0.54	0.89	17	122–365

Means ± S.E.M. of the parameters are given.

Fig. 4. Scaling of morphological parameters from the model. 67% Buccal projected area (A), epaxial physiological cross-sectional area (*PCSA*) (B), buccal moment (C) and epaxial moment (D) are shown as a function of standard length in each of the species used in this study. Projected area measurements were made from a separate group of individuals of each species. The scaling relationships of these individuals are given in Table 1. The other three measurements were made from the individuals from whom pressure was recorded.

noted above, was cut level to the S-PT joint.

Buccal cast measurements

Measurements of buccal surface area could not be made on fixed specimens, so the buccal surface area of individuals used in this study could not be measured directly, as was done with other morphological parameters. Instead, buccal casts were made from an additional size series of each species, and the regression of buccal surface area with standard length was used to generate an estimate of individual buccal projected area (Table 1).

Buccal casts were made by injecting commercial silicon sealant into the mouths of freshly killed fish (cf. Norton, 1995). The dimensions of the buccal cavity were measured from landmarks impressed in the silicon cast.

Buccal area was measured at full buccal expansion, but maximum pressure generation is known to occur before full buccal expansion (Sanford and Wainwright, 2002). Based on data collected by Sanford and Wainwright (2002), it was determined that peak subambient pressure occurred at 67% of the maximum buccal width in the largemouth bass (*Micropterus salmoides*), the only species for which such data are

Fig. 5. Relationship between morphological potential and maximum pressure magnitude measured from individual fish. Morphological potential, as described in the text, significantly accounted for variation in pressure among the individuals used in this study (r^2=0.71). The solid line depicts this linear regression. The muscle stress estimated from this regression is 68.5 kPa. The bold, broken line indicates the theoretical maximum performance predicted by the model (200 kPa, assuming an intercept of 11.8). The lighter, broken lines indicate reasonable predictions of normalized muscle stress during suction feeding (P^m) of 50 and 75 kPa, based on *in vivo* muscle dynamics.
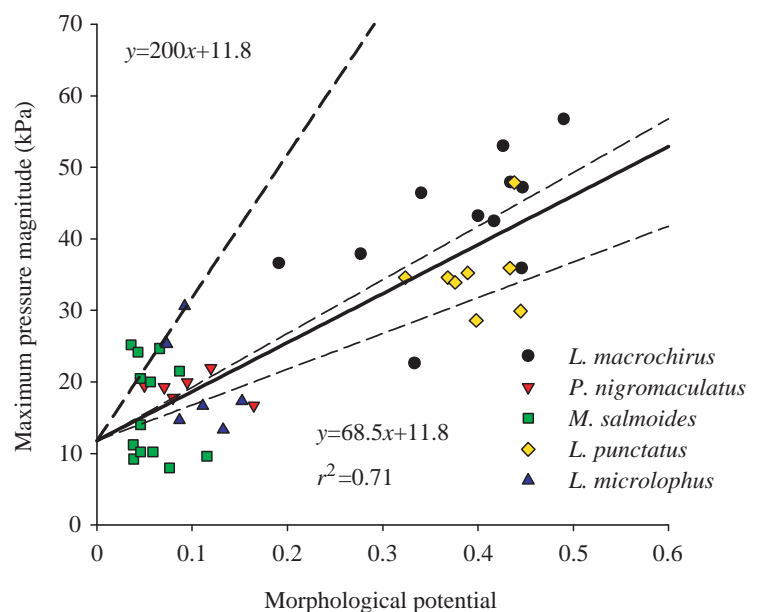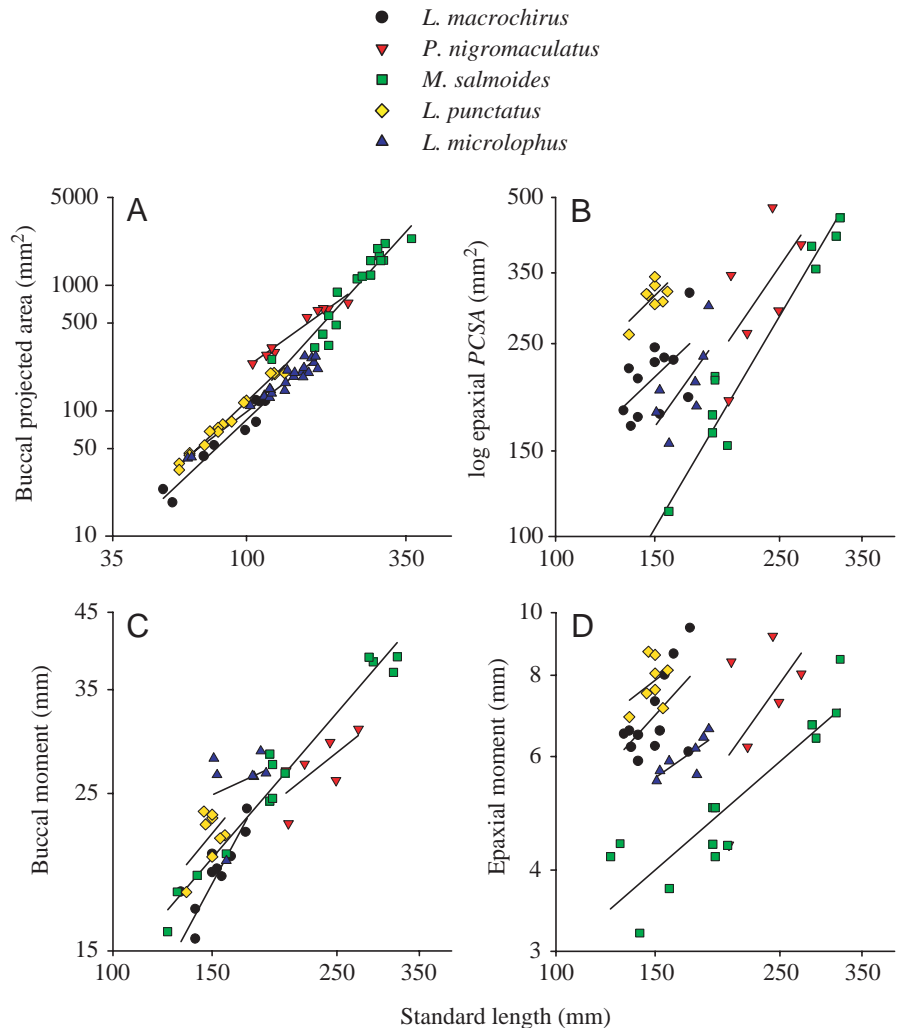
available. Therefore, the surface area term used in the model was calculated as the length of the buccal cavity multiplied by 67% of its width.

Statistical tests

Morphological variables were log-transformed and compared among species with multiple pairwise analyses of covariance (ANCOVAs; 10 comparisons). Significant differences among scaling parameters were determined by sequential Bonferroni correction with an initial α-level of 0.05. Linear regression was used to test the hypothesis that morphological potential is significantly correlated with minimum individual buccal pressure and to estimate P^m. An analysis of variance (ANOVA) was used to test species effects on the residuals. Maximum predicted pressure generation capacity was calculated by multiplying a P^m of 200 kPa by the measured morphological potential for each fish. These values were compared with measured pressures using a single t-test. Statistics were performed in SYSTAT 9 (SPSS Inc., Chicago, IL, USA) and JMP 4 (SAS Institute, Cary, NC, USA).

Results

Minimum suction pressure

Most fish fed aggressively despite instrumentation, although there was considerable intraspecific and within-individual variation in buccal pressure magnitude. The minimum buccal pressure of individuals ranged from –55.6 kPa in one *L. macrochirus* to –7.9 kPa in an individual *M. salmoides*. Pressure traces resembled those observed in other studies of these species (Fig. 3; Lauder, 1980; Sanford and Wainwright, 2002), and pressure magnitude was near the maximum of those measured in other studies (Grubich and Wainwright, 1997; Lauder, 1983b; Norton and Brainerd, 1993).

Interspecific morphological variation

Projected buccal surface area increased with standard length in all species (Table 1; Fig. 4). Significant differences in scaling intercepts were found between most species, with the exception of *L. macrochirus* and *M. salmoides* (P=0.09), and *L. punctatus* and *M. salmoides* (P=0.84). The remaining morphological variables were found to increase with standard length in all species. The relative size of epaxial PCSA and epaxial moment appeared to differ more among species than did buccal area and buccal moment (Fig. 4). In general, *L. macrochirus* and *L. punctatus* had the largest epaxial PCSA and moments while *M. salmoides* had the smallest. However, the limited sample sizes of these measurements preclude useful statistical comparisons.

Morphology and performance

Morphological potential calculated from the model successfully accounted for variation among individuals in minimum suction pressure (Fig. 5; P<0.0001, r^2=0.71). The slope of this relationship estimates a muscle force per cross-sectional area of 68.5±6.7 kPa with an intercept at 11.8±1.9 kPa. No significant species effect was found among residuals around the regression line (ANOVA, P=0.06), although *L. macrochirus* tended to out-perform its estimated performance and *L. punctatus* tended to under-perform its estimated performance (Fig. 5). Finally, measured values were significantly lower than those predicted with a P^m of 200 kPa (paired t-test, P<0.0001), with an intercept set at 11.8 kPa as derived from the regression. However, two individuals of *M. salmoides* out-performed their predicted maximum pressure generation ability (represented by the bold, broken line in Fig. 5).

A detectable within-species regression was found in *L. macrochirus* (r^2=0.38, P=0.034) but not in any of the other species. The slope of this regression was not significantly different to that of the among-species regression either including (P=0.51) or without (P=0.80) *L. macrochirus*.

Discussion

The model used in this study successfully predicted minimum suction pressures from morphological parameters (Fig. 5), supporting the hypothesis that epaxial musculoskeletal morphology limits suction pressure capacity. The muscle stress (P^m) estimated from the correlation (68.5 kPa) is within the range predicted for vertebrate white muscle contracting at shortening velocities measured *in vivo* in suction feeding muscles of *M. salmoides* (Carroll, 2004). Finally, with the two exceptions noted above, fish did not exceed their predicted performance potential as estimated by the model; these two *M. salmoides* individuals only exceeded their predicted maximum by 6.0 and 3.7 kPa, approximately 25% and 17% of their predicted pressures, respectively (Fig. 5).

Species such as *L. macrochirus* and *L. punctatus*, with smaller buccal projected areas, shorter buccal moment arms, larger epaxial muscles and longer epaxial moments, tended to produce the largest pressure magnitudes (Figs 4, 5). Species, such as *M. salmoides* and *P. nigromaculatus*, with larger buccal projected areas, longer buccal moments, smaller epaxial muscle areas and shorter epaxial moments, tended to produce smaller pressure magnitudes (Figs 4, 5). This trend has been observed in previous studies of these and other species (Lauder, 1983b; Norton and Brainerd, 1993) but was never explained in terms of musculoskeletal mechanics.

The results of the present study present two prominent difficulties. First, there is considerable residual variation around the regression line. Second, with the exception of *L. macrochirus*, the model does not account for within-species variation in pressure (Fig. 5). Residual variation may result from variation in individual performance. Some fish may not have fully activated their epaxial muscles, thus reducing buccal pressure (Lauder et al., 1986; Grubich and Wainwright, 1997). Furthermore, because morphological potential resulted from three measurements on individual fish and one regression based on standard length, there was a strong potential for error in estimated morphological potential.
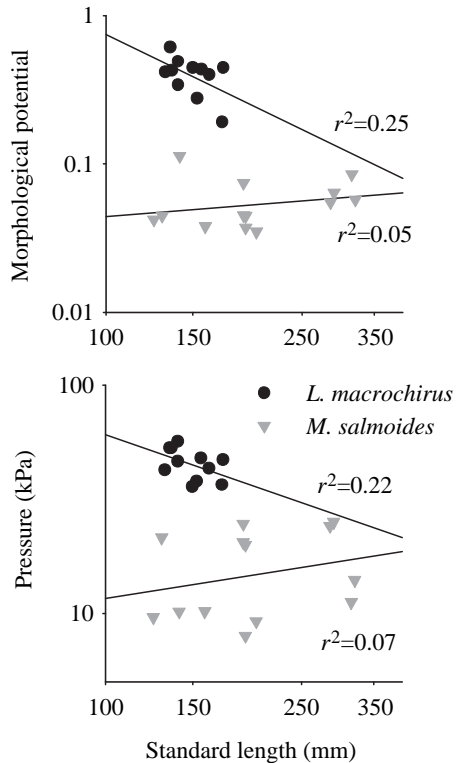
Fig. 6. Scaling relationships of morphological potential and measured pressure in *L. macrochirus* and *M. salmoides*. Differences in slope were not significant between the two species. The difference in r^2 between species indicates that pressure and morphological potential were more size dependent in *L. macrochirus* than in *M. salmoides*.

This potential for error on both axes may explain the failure to detect within-species variation in morphological potential and to account for within-species variation in pressure generation. Therefore, while the model ought to apply within and among species, measurement error may have precluded meaningful within-species comparisons in most of the species used in this study. The detectable interspecific regression in *L. macrochirus* may result from the large range of sizes used in the study and the allometric growth observed in this species with respect to morphological potential (Fig. 6). The slope of this regression is not significantly different from that of the among-species slope, suggesting that the model applies equally within *L. macrochirus* as among all included species.

Phylogenetic effects (Felsenstein, 1985) did not appear to influence the relationship between morphology and performance in the species studied. *L. microlophus* is believed to be the sister species of *L. punctatus* plus *L. miniatus* (Near et al., 2004), yet the range of pressure generation within *L. punctatus* and *L. microlophus* species spans much of the range measured in the study (Fig. 5). To a lesser extent, within-species variation in *L. macrochirus* also spans this range. Finally, *M. salmoides* is more closely related to the *Lepomis* species than to *P. nigromaculatus* (Near et al., 2004). However, *M. salmoides* and *P. nigromaculatus* are more

similar to one another in morphological potential and pressure generation than *M. salmoides* is to the *Lepomis* species. These results suggest that shared evolutionary history is not driving the overall trends observed in this study.

Scale effects

One of the most interesting results of the study was that one species (*L. macrochirus*) spanned much of the range of pressure generation and morphological potential, with smaller individuals tending to have larger morphological potential and lower buccal pressures (Fig. 6). By contrast, *M. salmoides* showed no size dependence in pressure or morphological potential despite the large range of body size used during the experiments (Fig. 6). This species is known to maintain isometry in many variables throughout ontogeny (Richard and Wainwright, 1995). These findings suggest that there are no general scaling effects on pressure, independent of relevant morphological parameters.

Kinematic speed is known to decrease with increasing body length in *M. salmoides*, *L. macrochirus* and *L. punctatus* (Wainwright and Shaw, 1999) and probably does so as well in the other species measured in this study. Muscle shortening velocity is also known to decrease with increasing body size (James et al., 1998; Rome et al., 1990). Despite the dynamic nature of pressure generation (Fig. 3), there appear to be no size effects on pressure generation independent of changes in morphology. Instead, pressure appears to depend only on muscle force production, which is not thought to scale with size (Bennett et al., 1989; James et al., 1998; Lindstedt et al., 1998).

Morphological trade-offs

Suction feeding fish are often grouped into 'ram' and 'suction' feeders (see Norton, 1995; Wainwright et al., 2001). 'Suction' feeding morphologies, represented by *L. macrochirus*, are characterized by smaller mouths, deeper bodies, increased pressure magnitudes and decreased use of body translation during prey capture (Norton and Brainerd, 1993). 'Ram' feeders, represented by *M. salmoides*, have larger mouths, shallower bodies, decreased pressure magnitudes and increased use of body translation during prey capture (Webb, 1984). These feeding strategies have been discussed as though they represent divergent suites of potentially independent morphological, performance and behavioral traits (e.g. Norton and Brainerd, 1993). Our results suggest a functional explanation for these patterns, based on the fact that the ratio of mouth size to body depth (which correlates with epaxial PCSA and moment length) appears to determine a fish's capacity for suction pressure generation.

Suction feeding requires that a predator generates a large enough buccal volume to contain its prey and draw the prey into that volume faster than the prey can escape (Muller et al., 1982). To meet these demands, fish must overcome hydrodynamic resistance, which is dominated by subambient pressure inside the buccal cavity (Alexander,

1969). A larger mouth increases the size of prey that can be taken by an individual fish (Keast, 1985; Werner, 1974) but appears to decrease the ability to generate pressure (Figs 4, 5).

In light of this result, the increased use of body translation by fish with larger mouths relative to body depth may result from a need to compensate for decreased suction performance, a direct consequence of larger mouth size. How this decreased suction performance is mediated is not clear because increased suction pressure magnitude does not appear to increase the maximum distance from which prey can be drawn into the buccal cavity (Svanback et al., 2002; Wainwright et al., 2001).

Fish with smaller mouths may compensate for their inability to take larger prey by increased effectiveness of feeding on smaller prey. In particular, the rapid drop in pressure generated by fish such as *L. macrochirus* may create acceleration forces capable of dislodging attached or clinging macroinvertebrates. Benthic macroinvertebrates are known to contribute to the diets of *L. macrochirus* and other fish with similar morphologies (Etnier and Starnes, 1993; Werner, 1977).

Trade-offs associated with molluscivory

Another interesting potential morphological trade-off is revealed within the *Lepomis* species. *L. microlophus* specializes on mollusk prey, using its hypertrophied pharyngeal jaws and muscles to crush snails (Lauder, 1983a). Its low morphological potential results from a reduced epaxial muscle PCSA and moment arm combined with increased buccal moment arm. These differences appeared to result from dorsal and caudal displacement of the pectoral girdle, possibly due to the greater space occupied by hypertrophied pharyngeal muscles and jaws. The pharyngeal jaws are often thought of as functionally independent of the oral jaws (Liem, 1974). Yet, in the case of *L. microlophus*, it appears possible that increased pharyngeal crushing ability may have compromised suction feeding performance.

Conclusions

This study successfully explains interspecific variation in suction feeding performance in terms of musculoskeletal morphology. The model may be generally used to investigate the ecological and evolutionary ramifications of morphological variation among teleost fish. Specifically, the model addresses the functional implications of variation in body depth and mouth size, both of which are known to be common axes of diversification among fishes (Keast and Webb, 1966; Winemiller, 1991; Yonekura et al., 2002). However, the relationship between suction pressure generation and prey capture ability is poorly understood at present, as is the relationship between suction pressure and other metrics of suction feeding performance, such as volume change per unit time (Muller, 1989). Therefore, we advocate caution using the model to explain patterns of trophic diversity without actual measurements of prey capture performance (e.g. Norton, 1995).

References

Aerts, P. (1991). Hyoid morphology and movements relative to abducting forces during feeding in *Astatotilapia elegans*. *J. Morphol.* **208**, 323-346.

Alexander, R. McN. (1969). Mechanics of the feeding action of a cyprinid fish. *J. Zool. Lond.* **159**, 1-15.

Bennett, A. F., Garland, T., Jr and Else, P. L. (1989). Individual correlation of morphology, muscle mechanics, and locomotion in a salamander. *Am. J. Physiol.* **256**, R1200-R1208.

Carroll, A. M. (2004). Muscle activation and strain during suction feeding in the largemouth bass *Micropterus salmoides*. *J. Exp. Biol.* **207**, 983-991.

De Visser, J. and Barel, C. D. N. (1998). The expansion apparatus in fish heads, a 3-D kinetic deduction. *Neth. J. Zool.* **48**, 361-395.

Etnier, D. A. and Starnes, W. C. (1993). *The Fishes of Tennessee*. Knoxville: University of Tennessee Press.

Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **125**, 1-15.

Garland, T. and Losos, J. B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In *Ecological Morphology* (ed. P. C. Wainwright and S. M. Reilly), pp. 240-302. Chicago: University of Chicago Press.

Gregory, W. K. (1933). Fish skulls: a study in the evolution of natural mechanisms. *Trans. Am. Phil. Soc.* **23**, 76-481.

Grubich, J. R. and Wainwright, P. C. (1997). Motor basis of suction feeding performance in largemouth bass, *Micropterus salmoides*. *J. Exp. Zool.* **277**, 1-13.

Hill, A. V. (1938). The heat of shortening and the dynamic constants of muscle. *Proc. R. Soc. Lond. B. Biol. Sci.* **126**, 136-195.

Huskey, S. H. and Turingan, R. G. (2001). Variation in prey-resource utilization and oral jaw gape between two populations of largemouth bass, *Micropterus salmoides*. *Environ. Bio. Fish.* **61**, 185-194.

James, R. S., Cole, N. J., Davies, M. L. F. and Johnston, I. A. (1998). Scaling of intrinsic contractile properties and myofibrillar protein composition of fast muscle in the fish *Myoxocephalus scorpius* L. *J. Exp. Biol.* **201**, 901-912.

Johnston, I. A. and Salamonski, J. (1984). Power output and force–velocity relationship of red and white muscle fibers from the Pacific blue marlin (*Makaira nigricans*). *J. Exp. Biol.* **111**, 171-178.

Keast, A. (1985). The piscivore feeding guild of fishes in small freshwater ecosystems. *Environ. Bio. Fish.* **12**, 119-129.

Keast, A. and Webb, D. (1966). Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. *J. Fish. Res. Bd. Can.* **23**, 1845-1874.

Lauder, G. V. (1980). The suction feeding mechanism in sunfishes (*Lepomis*) and experimental analysis. *J. Exp. Biol.* **88**, 49-72.

Lauder, G. V. (1983a). Functional and morphological bases of trophic specialization in sunfishes (Teleostei, Centrarchidae). *J. Morphol.* **178**, 1-22.

Lauder, G. V. (1983b). Prey capture hydrodynamics in fish: experimental test of two models. *J. Exp. Biol.* **104**, 1-13.

Lauder, G. V. and Clark, B. D. (1984). Water flow patterns during prey capture by teleost fishes. *J. Exp. Biol.* **113**, 143-150.

Lauder, G. V., Wainwright, P. C. and Findeis, E. (1986). Physiological mechanisms of aquatic prey capture in sunfishes: Functional determinants of buccal pressure changes. *Comp. Biochem. Physiol. A* **84**, 729-734.

Liem, K. F. (1974). Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Syst. Zool.* **22**, 425-441.

Lindstedt, S. L., McGlothlin, T., Percy, E. and Pifer, J. (1998). Task-specific design of skeletal muscle: balancing muscle structural composition. *Comp. Biochem. Physiol. B* **120**, 35-40.

Muller, M. (1989). A quantitative theory of expected volume changes of the mouth during feeding in teleost fishes. *J. Zool. Lond.* **217**, 639-662.

Muller, M., Osse, J. W. M. and Verhagen, J. H. G. (1982). A quantitative

hydrodynamical model of suction feeding in fish. *J. Theor. Biol.* **95**, 49-79.

Near, T. J., Bolnick, D. I. and Wainwright, P. C. (2004). Investigating phylogenetic relationships of sunfishes and black basses (Actinopterygii: Centrarchidae) using DNA sequences from mitochondrial and nuclear genes. *Mol. Phylogenet. Evol.* **32**, 344-357.

Nemeth, D. H. (1997). Modulation of buccal pressure during prey capture in *Hexagrammos decagrammus* (Teleostei: Hexagrammidae). *J. Exp. Biol.* **200**, 2145-2154.

Norton, S. F. (1995). A functional approach to ecomorphological patterns of feeding in cottid fishes. *Environ. Bio. Fish.* **44**, 61-78.

Norton, S. F. and Brainerd, E. L. (1993). Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *J. Exp. Biol.* **176**, 11-29.

Osse, J. W. M. (1969). Functional morphology of the head of the perch (*Perca fluviatilis* L.): an electromyographic study. *Neth. J. Zool.* **19**, 289-392.

Richard, B. A. and Wainwright, P. C. (1995). Scaling the feeding mechanism of largemouth bass (*Micropterus salmoides*): kinematics of prey capture. *J. Exp. Biol.* **198**, 419-433.

Rome, L. C., Sosnicki, A. A. and Goble, D. O. (1990). Maximum velocity of shortening of three fibre types from horse soleus muscle: implications for scaling with body size. *J. Physiol.* **431**, 173-185.

Sanford, C. P. J. and Wainwright, P. C. (2002). Use of sonomicrometry demonstrates the link between prey capture kinematics and suction pressure in largemouth bass. *J. Exp. Biol.* **205**, 3445-3457.

Svanback, R., Wainwright, P. C. and Ferry-Graham, L. A. (2002). Linking cranial kinematics, buccal pressure, and suction feeding performance in largemouth bass. *Physiol. Biochem. Zool.* **75**, 532-543.

Thys, T. (1997). Spatial variation in epaxial muscle activity during prey strike in largemouth bass (*Micropterus salmoides*). *J. Exp. Biol.* **200**, 3021-3031.

Van Leeuwen, J. L. and Muller, M. (1983). The recording and interpretation of pressures in prey sucking fish. *Neth. J. Zool.* **33**, 425-475.

Wainwright, P. C., Ferry-Graham, L. A., Waltzeck, T. B., Carroll, A. M., Hulsey, C. D. and Grubich, J. R. (2001). Evaluating the use of ram and suction during prey capture by cichlid fishes. *J. Exp. Biol.* **204**, 3039-3051.

Wainwright, P. C. and Shaw, S. S. (1999). Morphological basis of kinematic diversity in feeding sunfishes. *J. Exp. Biol.* **202**, 3101-3110.

Webb, P. W. (1984). Body and fin form and strike tactics of four teleost predators attacking fathead minnow *Pimephales promelas* prey. *Can. J. Fish. Aquat. Sci.* **41**, 157-165.

Werner, E. E. (1974). The fish size, prey size, handling time relation in several sunfishes and some implications. *J. Fish. Res. Bd. Can.* **31**, 1531-1536.

Werner, E. E. (1977). Species packing and niche complementarity in three sunfishes. *Am. Nat.* **111**, 553-578.

Winemiller, K. O. (1991). Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecol. Mon.* **61**, 343-366.

Yonekura, R., Nakai, K. and Yuma, M. (2002). Trophic polymorphism in introduced bluegill in Japan. *Ecol. Res.* **17**, 49-57.