

Cranial movements during suction feeding in teleost fishes: Are they modified to enhance suction production?

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Abstract

Suction is produced during prey capture by most teleost fishes. Here, we ask two questions about the functional basis of suction feeding. First, is there variation in the kinematic pattern produced by different species while suction feeding? Second, do species termed ‘suction specialists’ demonstrate similar modifications to their feeding behavior? We used 10 kinematic variables in a principal component analysis to identify axes of variation among 14 suction feeding teleost species (representing nine families and five orders within the Euteleostei) that demonstrate different feeding habits and habitats. MANOVA and Tukey post hoc tests were used to assess differences among species. Most species clustered together on the principal component axes, suggesting a generalized mechanism that facilitates unidirectional flow. Typically, only one species stood out as ‘extreme’ on each functional axis, and a species that stood out on one axis did not stand out on others. Only one species, the flatfish *Pleuronichthys verticalis*, an obligate benthic feeder, demonstrated modifications consistent with enhanced suction production. This species displayed a suite of changes that should enhance suction production, including large hyoid depression, large cranial rotation, and small gape. We suggest that suction performance may be greatest in such obligate benthic feeders because cranial morphology is highly modified and prey are captured from the substrate.

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Introduction

Suction feeding is the most common mechanism of prey capture in aquatic vertebrates, and probably was employed by the earliest gnathostomes (Lauder, 1985a; Moss, 1977). Suction feeding entails expanding the head and drawing the prey into the mouth along with some of the surrounding water. Because both the relative size and elusiveness of the prey can vary, the amount of

suction that is produced during feeding is expected to vary among species, and even within individuals of a species feeding on different prey types. Nonetheless, several studies have noted that the general patterns of movements, or kinematics, used by aquatic predators for capturing prey are remarkably conserved across a range of species, despite a variety of experimental prey types and feeding conditions (Bergert and Wainwright, 1997; Carroll and Wainwright, 2003; Gibb, 1997; Lauder, 1985b; Motta and Wilga, 2001).

Four phases of suction feeding were initially identified in bony fishes (Lauder, 1985a), and are now known to

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be present in elasmobranchs (e.g., Motta and Wilga, 2001), and some aquatic-feeding tetrapods (e.g., Lauder and Reilly, 1994). These are the ‘preparatory’ phase, the ‘expansive’ phase, the ‘compressive’ phase, and the ‘recovery’ phase. To produce suction, the oral or buccal cavity is first compressed during the preparatory phase, and then rapidly expanded, creating a flow of water into the buccal cavity, during the expansive phase. The rapid expansive phase is followed by the markedly slower compressive phase, where water is expelled from the opercular openings (or the mouth, if operculi are lacking), while the food item is retained in the oral jaws or buccal cavity. Finally, during the recovery phase, the elements of the head and jaws return to a relaxed, pre-feeding position. This cycle of events may be repeated cyclically to produce the flow of water necessary to transport prey into the esophagus (e.g., Gillis and Lauder, 1995).

Of central importance to suction production is the expansive phase. Both the overall change in buccal volume, and the velocity with which it occurs, affect the generation of flow into the mouth (Lauder, 1980a; van Leeuwen and Muller, 1984; Muller, 1987). Further, during the expansive phase, an anterior-to-posterior wave of expansion is generated by movement of the components of the head and jaws (Lauder, 1985a; Muller and Osse, 1984). That is, any given cranial element reaches the limit of its excursion slightly before the element immediately posterior to it. Thus, in the cranium of bony fishes (Fig. 1), the lower jaw reaches its maximal depression, then the neurocranium achieves maximum rotation, then the hyoid reaches maximum depression, and, lastly, the opercular region reaches its maximum expansion. The relative timing of the excursions of these individual elements creates unidirectional flow of water into the buccal cavity, and thereby generates ‘suction’ (Fig. 2; Ferry-Graham and Lauder, 2001). This wave-like expansive phase has also been observed in representatives from many of the major groups of aquatic-feeding vertebrates including elasmobranchs (e.g., Ferry-Graham, 1997), salamanders (e.g., Reilly, 1995), and turtles (e.g., Summers et al., 1998), underscoring its fundamental role in suction production for most aquatic-feeding vertebrates (although it is *not* seen in aquatic-feeding garter snakes that appear to generate no suction during forward strikes; Alfaro, 2002). Teleost fishes are perhaps the most derived vertebrates in this sense, having multiple mobile cranial elements (Figs. 1 and 2), and the capacity for rapid and extreme expansion (Liem, 1980).

Recent studies have attempted to correlate variations in cranial movements (or kinematics) during the expansive phase of prey capture with variations in suction pressure within individuals of a given teleost species (Svånback et al., 2002; Carroll et al., 2004). These studies reveal that the volume change of the

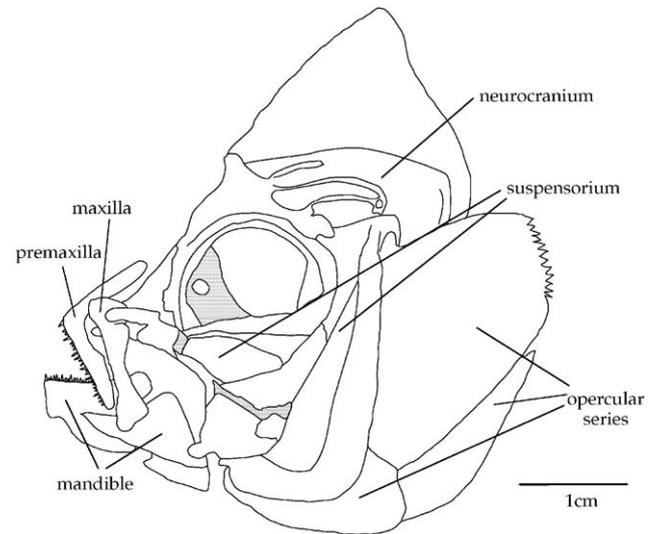


Fig. 1. Illustration of the cranium of a “typical” teleost, *Lepomis macrochirus* (after Gibb, 1997). Bones are shown as white elements; cartilages are shown as stippled elements. The cranium illustrated here possesses a protrusible premaxilla, which is present in all of the species chosen for this study. The neurocranium, or skull, houses the brain, and can be rotated dorsally relative to the axial skeleton. The oral, or anterior, jaws are comprised of the upper jaw (premaxilla and maxilla) and lower jaw (mandible). The suspensorium attaches the lower jaw to the cranium and the opercular series covers the gills. The hyoid (not shown) is medial to both the suspensorium and opercular series, and cannot be observed from a lateral view unless a fish is feeding. The buccal cavity is a medial space formed by the bones illustrated here.

buccal cavity during feeding is strongly correlated with the concomitant drop in buccal pressure, as would be expected based on simple physical principles. However, these studies were unable to pinpoint a specific kinematic variable, or even a coherent suite of variables, that explain variations in buccal expansion and resulting suction performance. For example, kinematic patterns of the oral jaws (gape), hyoid (depression), and suspensorium (abduction) all appear to play a role in determining suction production, but the relative contributions of each of these three parameters have not been defined, nor has the contribution of other cranial movements been ruled out (Svånback et al., 2002; Carroll et al., 2004). In fact, these cranial elements (the jaws, neurocranium, hyoid and opercular bones) must operate as an integrated structural complex (Sanford and Wainwright, 2002), which implies that an individual may change the amount of suction produced by manipulating the timing or maximal displacement of all four cranial elements at once.

As individuals of a species begin to specialize on a more elusive or otherwise challenging prey type, they may modify their ability to suction feed by modifying their prey-capture kinematics (as above), or by changing

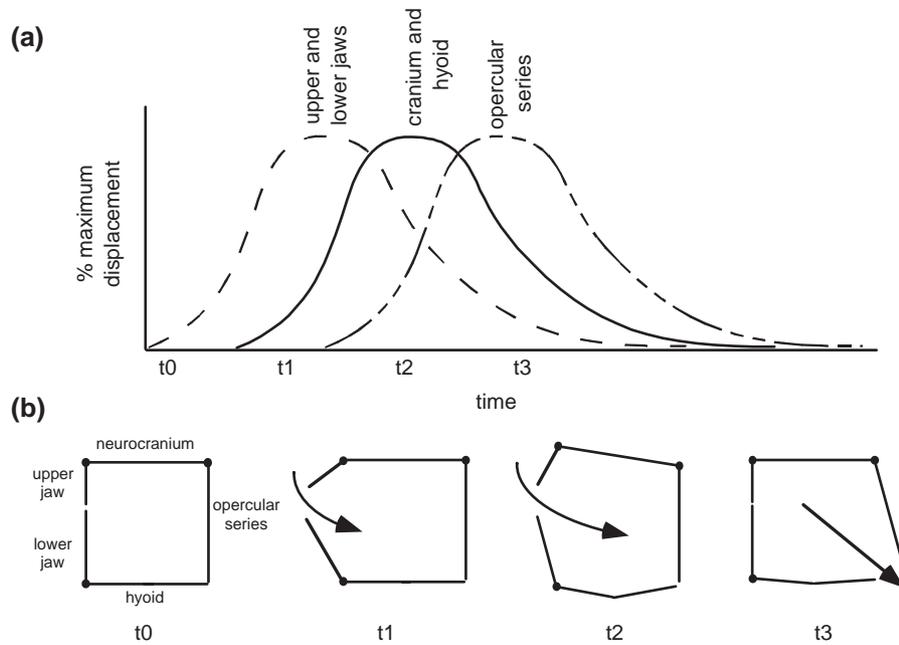


Fig. 2. Schematic illustration of the anterior-to-posterior wave of expansion that occurs during the expansive phase of suction feeding in teleost fishes. (a) Anterior elements of the cranium (e.g., the jaws) reach their maximum displacement before the medial elements (the hyoid and neurocranium), which in turn reach their maximum displacement before the posterior elements (the opercular series). (b) The result of this wave of expansion is a unidirectional flow of water (arrow) into the buccal cavity.

their feeding morphology. A recent comparative study of morphology and suction performance in centrarchids demonstrates that fish with smaller mouths and deeper bodies (which allows a greater cross-sectional area for associated musculature) consistently produce greater suction pressure during feeding (i.e., a more negative pressure inside the buccal cavity) than do fish with larger mouths and shallower bodies (Carroll et al., 2004). However, the fact that changes in morphology are highly correlated with changes in suction pressure does not preclude the possibility that changes in feeding kinematics also play a role in enhancing suction production.

In this study, we seek to determine how a range of teleost species with a variety of feeding morphologies differ in the movements produced during the expansive phase of a suction feeding event. To this end, we use kinematic data from the cranial elements of 14 teleost species to address two related questions. First, is there variation in the kinematic pattern produced by different teleost species while suction feeding? Studies of within-species variation in suction generation suggest that modification to the movements of the cranial elements could increase said suction. Alternately, changes in the morphology of the feeding apparatus may generate marked differences in suction production, while allowing the retention of a stereotypical, invariant kinematic pattern. Second, if teleost species do vary in their feeding kinematics, do the species considered to be ‘suction specialists’ all demonstrate similar modifications to the

‘basic’ suction feeding pattern? For example, all suction specialists may demonstrate increased hyoid depression, but no other consistent change in feeding kinematics. This type of result would imply that behavioral changes to the hyoid (e.g.) are critical to suction production, and thus allow us to tease apart the relative contributions of movements of the various cranial elements to suction production.

Materials and methods

The 14 teleost species used in this investigation were chosen for several reasons. First, they represent a broad phylogenetic range of teleost fishes (Fig. 3), with nine families from five orders. Second, they possess a diverse array of feeding morphologies (Fig. 4). Lastly, kinematic data for all of these species were collected using consistent methodologies by one of the two authors, which reduces the possibility of apparent variation in kinematics appearing as a result of inconsistencies in data collection or analysis procedures. Of the species available for inclusion in this analysis, we purposefully sampled repeatedly within one family, the Labridae (Fig. 4), to determine if there was an equivalent degree of variation in prey-capture kinematics among more closely related species, relative to more distantly related species. Thus, five species of Labridae of similar size were included here.

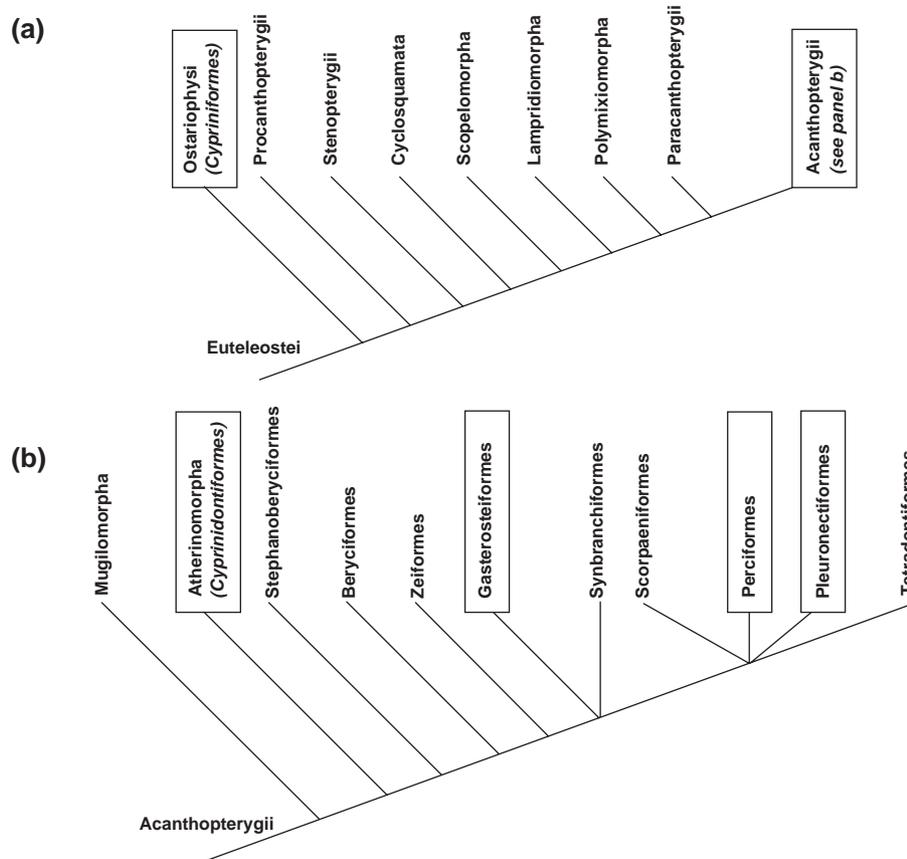


Fig. 3. The 14 species used in this study represent nine families found within five orders of the Euteleostei (i.e., the “true teleosts”). (a) One species (*Danio rerio*, Cyprinidae, Cypriniformes) examined in this study represents a basal euteleost group, the Ostariophysi, the other 13 species are all found within a derived group, the Acanthopterygii. (b) The 13 remaining species represent four distinct orders within the Acanthopterygii (see also Table 1). Hypothesized phylogenetic relationships among groups given here are based on Nelson (1994).

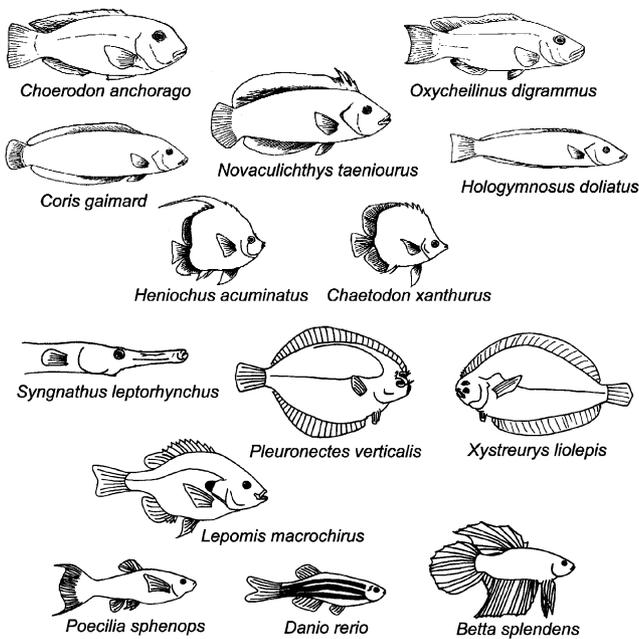


Fig. 4. Line drawings of the 14 species used in the analysis to illustrate the gross anatomical differences in the head and jaws. Images are not to scale.

Each of these species uses suction during prey capture. However, there is variation in the degree to which each species relies on this mode. The wrasse, *Choerodon anchorago*, and the butterflyfish, *Chaetodon xanthurus*, are known to employ biting behaviors for removing attached or clinging invertebrates and coral polyps, respectively (Ferry-Graham et al., 2001a, 2002). *Poecilia sphenops* is typically a scraper of periphyton (benthic autotrophs; Meffe and Snelson, 1989), although they can still employ suction to capture prey in the water column effectively. Further, at least two species have been previously identified as ‘suction specialists’ by other authors. The pipefish, *Syngnathus leptorhynchus*, has an opercular cavity capable of a large degree of lateral expansion and an elongate snout. The overall head shape is quite similar to a pipette, and it has been hypothesized to function as such (Osse and Muller, 1980). In addition, the cheeklined wrasse, *Oxycheilinus digrammus*, consumes highly mobile prey, such as large fishes, presumably capturing them using suction (Westneat, 1995). Based upon morphological data it has been hypothesized that *O. digrammus* is capable of rapid hyoid depression and lateral expansion of the buccal

Table 1. Species, family, order, size range, and experimental food used for this study

| Species (abbreviation) | Family | Order | TL (cm) | Food |
|--|-----------------|--------------------|-----------|--------------------------|
| <i>Danio rerio</i> ^a (DR) | Cyprinidae | Cypriniformes | 3.3–4.0 | Brown worm |
| <i>Poecilia sphenops</i> ^a (PS) | Poeciliidae | Cyprinodontiformes | 3.5–4.5 | Brown worm |
| <i>Betta splendens</i> ^a (BS) | Osphronemidae | Perciformes | 3.9–4.5 | Brown worm |
| <i>Heniochus acuminatus</i> ^b (HA) | Chaetodontidae | Perciformes | 5.4–9.0 | Brine shrimp |
| <i>Chaetodon xanthurus</i> ^b (CX) | Chaetodontidae | Perciformes | 6.0–6.6 | Brine shrimp |
| <i>Novaculichthys taeniourus</i> ^c (NT) | Labridae | Perciformes | 12.2–19.3 | Prawn piece ^d |
| <i>Lepomis macrochirus</i> ^c (LM) | Centrarchidae | Perciformes | 13.9–15.9 | Earthworm |
| <i>Xystreureys liolepis</i> ^f (XL) | Paralichthyidae | Pleuronectiformes | 14.9–18.2 | Earthworm |
| <i>Pleuronichthys verticalis</i> ^g (PV) | Pleuronectidae | Pleuronectiformes | 15.9–18.3 | Earthworm |
| <i>Coris gaimard</i> ^c (CG) | Labridae | Perciformes | 15.9–22.1 | Prawn piece ^d |
| <i>Choerodon anchorago</i> ^c (CA) | Labridae | Perciformes | 16.2–24.5 | Prawn piece ^d |
| <i>Oxycheilinus digrammus</i> ^c (CD) | Labridae | Perciformes | 17.0–18.4 | Prawn piece ^d |
| <i>Syngnathus leptorhynchus</i> ^h (SL) | Syngnathidae | Gasterosteiformes | 17.0–33.3 | Brine shrimp |
| <i>Hologymnosus doliiatus</i> ^c (HD) | Labridae | Perciformes | 17.7–21.8 | Prawn piece ^d |

^aGibb et al. (unpublished data); ^bFerry-Graham et al. (2001a); ^cFerry-Graham et al. (2002); ^dPrawn pieces were suspended in the water column; ^eGibb (1997); ^fGibb (1996); ^gGibb (1996); ^hFerry-Graham et al. (unpublished data).

cavity (Westneat, 1995), which would enhance suction production during prey capture. Additionally, several papers have suggested high-performance suction as the primary mechanism for obtaining highly mobile prey, with the capacity for buccal expansion being correlated with the proficiency of generating said suction (Nemeth, 1997a, b; Norton, 1991; Norton and Brainerd, 1993).

As the data used in this study come from previously published and ongoing studies, we refer the reader to the previously published studies for specific details of kinematic data collection (see Table 1); only a brief summary is provided here. In all studies, high-speed video footage was collected from fishes feeding using a lateral view. In the case of the flatfishes, the blind-side view was used (a view of the side of the fish that rests on the substrate, as filmed through a mirror placed at a 45° angle below a glass aquarium), as this is a lateral view anatomically. All of the studies used glass aquaria to house and film the fish, and a background grid or rule was placed in the field of view and used to scale the images. The field of view was illuminated with 500–600 W tungsten lamps. All prey items used were capable of some movement, due to the method of presentation or to small-scale movements produced by the prey. However, no prey item used was capable of producing large-scale or rapid evasive movements (see Table 1). Thus, all prey items here presented a similar level of challenge to their predators and can be considered to be “non-elusive” in nature. Fish were allowed to feed until satiation in a given filming bout, and filming of any one individual generally occurred over a several-day period. All images were digitized with either NIH Image or custom measurement software to quantify kinematic variables.

We selected the following variables for this study: maximum gape, the maximum distance between the tips of the upper and lower jaws (cm); maximum hyoid depression, the maximum ventral movement of the hyoid apparatus (cm); maximum upper jaw protrusion, the maximum displacement away from the neurocranium of the anterior-most region of the premaxilla (cm); maximum lower jaw rotation, the ventro-caudal angular movement of the mandible relative to the axis of the body (degrees); maximum cranial rotation, the dorso-caudal angular movement of the neurocranium relative to the axis of the body (degrees); and the timing of each of these maxima (s). We also calculated gape velocity from the gape timing and displacement variables to facilitate comparisons among taxa, but did not use this in multivariate analyses, as this is a compound variable (i.e., it is derived from two other variables already included in the analysis). The mean values for all variables for each species are provided in Table 2. We chose these variables for analysis because (1) they were measured in a consistent manner across the studies used here, (2) they are the most common variables quantified in kinematic studies of prey capture (e.g., Carroll and Wainwright, 2003; Cook, 1996; Gillis and Lauder, 1995; Lauder, 1980b; Westneat and Wainwright, 1989), and (3) they encompass the movements of several key cranial structures involved in the anterior–posterior wave of movement produced during the expansive phase of suction feeding. Although lateral movements of the suspensorium and opercular series would also be informative (sensu Grubich, 2001), they were not recorded for several of the 14 species, and thus could not be included in this analysis.

Table 2. Means of individual means (\pm SE) for kinematic displacement variables (maxima) and timing variables (time to maxima) used in the PCA

| Variables | DR | PS | BS | HA | CX | NT | LM | XL | PV | CG | CA | OD | SL | HD |
|-------------------------|--------------|--------------|--------------|--------------|---------------|--------------|--------------|--------------|---------------|---------------|----------------|--------------|--------------|--------------|
| Gape (cm) | 0.31 (0.01) | 0.31 (0.03) | 0.35 (0.01) | 0.23 (0.01) | 0.30 (0.01) | 1.28 (0.04) | 1.16 (0.03) | 1.02 (0.04) | 0.75 (0.03) | 0.85 (0.04) | 1.51 (0.11) | 1.26 (0.03) | 0.25 (0.03) | 0.68 (0.03) |
| Hyoid dep. (cm) | 0.08 (0.01) | 0.12 (0.05) | 0.09 (0.01) | 0.11 (0.01) | 0.09 (0.01) | 0.26 (0.03) | 0.38 (0.02) | 0.59 (0.03) | 0.89 (0.04) | 0.19 (0.04) | 0.36 (0.08) | 0.53 (0.08) | 0.17 (0.04) | 0.29 (0.01) |
| Upper jaw prot. (cm) | 0.13 (0.01) | 0.18 (0.01) | 0.12 (0.01) | 0.35 (0.01) | 0.25 (0.02) | 0.22 (0.03) | 0.46 (0.02) | 0.63 (0.05) | 1.03 (0.02) | 0.22 (0.02) | 0.25 (0.03) | 0.34 (0.01) | 0.17 (0.01) | 0.16 (0.01) |
| Lower jaw rot. (deg.) | 41.74 (1.39) | 20.43 (0.91) | 42.07 (1.60) | 19.56 (0.97) | 19.75 (1.44) | 41.94 (1.77) | 39.50 (1.68) | 33.12 (1.04) | 33.12 (0.60) | 24.13 (3.64) | 26.18 (0.22) | 25.09 (2.26) | 14.51 (2.57) | 16.21 (0.13) |
| Cranial rot. (deg.) | 21.92 (0.81) | 17.15 (1.21) | 21.53 (0.68) | 4.18 (0.29) | 4.27 (0.73) | 4.90 (0.85) | 9.01 (0.30) | 12.50 (0.52) | 27.59 (0.94) | 4.08 (0.67) | 4.11 (0.14) | 5.47 (0.56) | 25.08 (1.35) | 9.91 (6.33) |
| T. gape (ms) | 11.25 (1.20) | 59.33 (1.43) | 15.25 (2.52) | 23.67 (6.86) | 17.83 (3.67) | 36.0 (4.07) | 42.50 (3.64) | 32.50 (4.46) | 22.50 (2.69) | 54.89 (3.90) | 100.33 (5.82) | 45.40 (0.77) | 24.67 (9.47) | 38.66 (0.34) |
| T. hyoid dep. (ms) | 15.25 (1.47) | 82.50 (2.74) | 37.0 (11.86) | 50.67 (2.14) | 18.83 (3.05) | 50.80 (5.68) | 51.0 (3.40) | 69.80 (6.25) | 103.44 (10.3) | 55.71 (10.34) | 91.50 (32.95) | 63.17 (0.90) | 36.67 (2.34) | 68.49 (0.15) |
| T. upper jaw prot. (ms) | 27.63 (2.51) | 75.08 (4.84) | 17.75 (2.0) | 33.67 (1.87) | 18.0 (0.57) | 44.30 (4.97) | 41.75 (3.33) | 36.30 (3.73) | 43.13 (6.90) | 51.95 (8.88) | 123.08 (24.35) | 55.67 (2.90) | 28.67 (5.25) | 32.64 (3.59) |
| T. lower jaw rot. (ms) | 10.63 (0.82) | 71.83 (1.53) | 11.0 (0.94) | 27.67 (4.30) | 17.83 (0.54) | 38.67 (3.51) | 42.25 (3.84) | 31.80 (5.64) | 20.63 (2.82) | 54.62 (2.14) | 100.67 (4.94) | 46.00 (0.62) | 17.33 (5.33) | 38.25 (3.34) |
| T. cranial rot. (ms) | 16.0 (2.54) | 110.6 (0.37) | 32.25 (2.99) | 33.33 (5.81) | 27.67 (0.06) | 42.88 (1.52) | 47.75 (6.37) | 55.0 (6.05) | 40.63 (1.61) | 58.61 (12.82) | 123.33 (2.04) | 37.36 (3.43) | 17.33 (1.87) | 56.67 (6.17) |
| Gape vel. (cm/s) | 30.74 (1.09) | 7.87 (3.66) | 30.45 (2.63) | 22.32 (6.78) | 28.22 (16.11) | 39.88 (7.46) | 29.27 (2.32) | 39.69 (3.41) | 37.94 (4.69) | 16.77 (1.34) | 15.85 (0.58) | 28.74 (1.85) | 8.11 (6.71) | 21.25 (3.07) |

Note: Species abbreviations are as given in Table 1.

The 10 variables were analyzed simultaneously using principal component analysis (PCA; SPSS 11.0) to determine relationships among the variables. The PCA was performed using the correlation matrix to control for the input of variables of differing units and magnitudes. The resulting PCs formed the axes of a multi-dimensional space in which PC scores could be plotted and relationships among species visualized. Significant axes of variation in prey-capture kinematics were identified by selecting PCs with eigenvalues >1.0. Each resulting PC or axis was given a descriptive name based upon the variables that loaded strongly on it after Varimax transformation ($r > 0.5$). PC scores for each strike for each species, as well as the mean of all individual means for each species, were plotted on significant axes in a pairwise fashion to visualize where each species resided within the multivariate space. To determine if species occupied different portions of the space, a MANOVA was performed with the scores from each of the significant axes entered as dependent variables into the model. Given a significant species effect, Tukey's post hoc tests were used to determine how species differed. Possible size effects were investigated using least-squares regression of PC scores vs. body length.

Results

Least-squares regression revealed no linear relationship between total length and any of the axes of variation (all $r^2 < 0.266$); thus, the principal component factors identified here represent size-independent patterns of variation among taxa, in so much as such independence is possible. Interestingly, when total length is included in the PCA, it loads equally (0.4–0.5) on all of the axes of variation, suggesting that any effect of size is consistent across all axes. Additionally, inclusion of total length in the analysis does not change any of the other component loadings. A visual assessment of the PCA results further suggests that total length is not strongly influencing the patterns in the data; e.g., PC 1 contains a large cluster of species ranging in size from 4 to 33 cm standard length, with small species loading both above and below this cluster (Fig. 5).

In total, four axes of variation were identified which cumulatively explained 82.7% of the total variance in the data set (Table 3). Each of the variables included in the analysis loaded highly on one, and only one axis, making functional interpretation of the axes unambiguous. We term Axis 1 the 'timing' axis, as all of the timing variables loaded positively on this axis; individuals with larger scores for PC 1 took longer to produce cranial movements than those with smaller scores. Axis 2

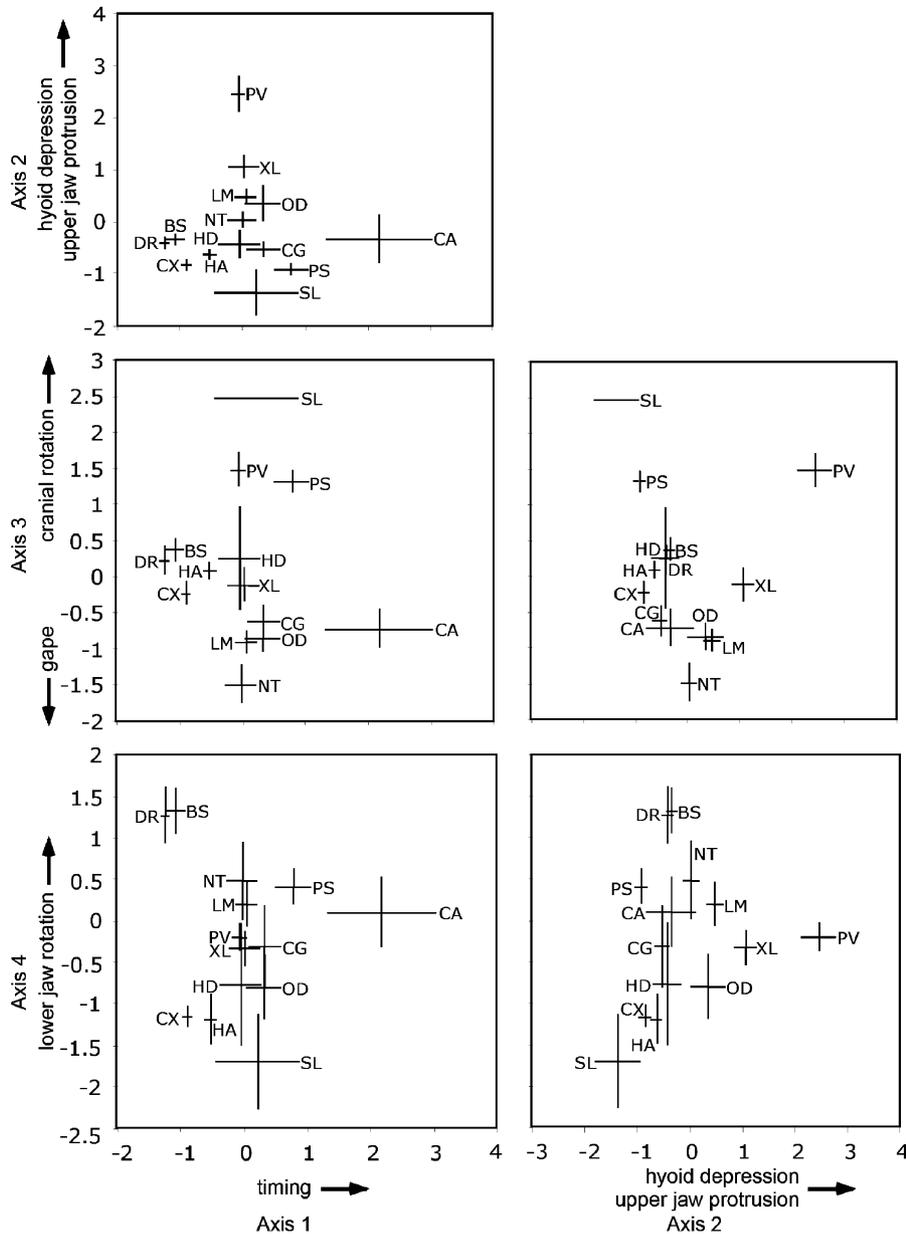


Fig. 5. Axes of kinematic variation in prey capture as revealed by PCA for 14 teleost taxa; abbreviations for species names are as given in Table 1. Five of the six possible pairwise plots are shown, the sixth (Axis 3 vs. 4) is excluded as it does not reveal novel relationships. Each point is the mean of individual means \pm SE of component loading scores on the respective axes for the species shown, as indicated by each species' initials. Each variable or combination of variables described by the axes is indicated. The arrows indicate the direction in which the variables increase along the axes. Note that timing variables load positively on Axis 1, and time to maxima, or duration of behavior, increases as you move to the right on that axis (i.e., feeding events are slower to the right). However, maximum gape loads negatively on Axis 2; thus, larger gape distances appear toward the bottom, rather than the top, of that axis.

describes variation in maximum hyoid depression and upper jaw protrusion, both of which loaded positively; individuals with larger scores on PC 2 had greater hyoid depression and premaxillary protrusion than those with smaller scores. Axis 3 encompasses maximum gape and maximum cranial rotation; on this axis, gape loads negatively and cranial elevation loads positively. Ex-

amination of the correlation matrix produced by the analysis confirmed that individuals with larger scores on PC 3 had a greater degree of cranial rotation and a smaller gape than those with smaller scores. Axis 4 describes variability in lower jaw rotation; individuals with larger scores on PC 4 had greater lower jaw depression than those with smaller scores.

Table 3. PCA variables and their loadings^a on each axis

| | Component (axis) | | | |
|-----------------------------------|------------------|--------------|---------------|--------------|
| | 1 | 2 | 3 | 4 |
| % Variance explained | 39.59 | 22.40 | 12.81 | 0.98 |
| Variables | | | | |
| Maximum gape | 0.547 | 0.408 | -0.631 | 0.076 |
| Max. hyoid depression | 0.253 | 0.894 | -0.045 | -0.210 |
| Max. upper jaw protrusion | 0.060 | 0.860 | 0.131 | -0.276 |
| Max. lower jaw rotation | -0.247 | 0.413 | -0.426 | 0.732 |
| Max. cranial rotation | -0.222 | 0.287 | 0.724 | 0.513 |
| Time of max. gape | 0.848 | -0.196 | -0.043 | -0.021 |
| Time of max. hyoid depression | 0.678 | 0.395 | 0.300 | -0.011 |
| Time of max. upper jaw protrusion | 0.886 | -0.115 | -0.023 | 0.128 |
| Time of max. lower jaw rotation | 0.924 | -0.186 | -0.047 | 0.099 |
| Time of max. cranial rotation | 0.815 | -0.199 | -0.251 | 0.156 |

^aBold face values indicate significant loading scores.

Plots of the principal component scores in pairwise comparisons of each axis reveal a cluster of species that consistently appears in all plots (Fig. 5). For clarity, only the summary means for all individuals of a given species have been plotted. This cluster is formed by approximately 11 taxa: four labrids, two chaetodontids, one paralichthyid, one centrarchid, one cyprinid, one poecilid, and one osphronemid. Three species, *Pleuronichthys verticalis* (Pleuronectidae), *C. anchorago* (Labridae), and *S. leptorhynchus* (Syngnathidae), appear at the extremes of the axes.

MANOVA confirmed that species occupied significantly different portions of the three-dimensional space (Wilk's $\lambda = 0.868$, $F_{4,244} = 9.241$, $p < 0.001$). Tukey's post hoc tests revealed a number of species as different from all other species on each axis (Fig. 6). On Axis 1, the timing axis, *C. anchorago* scored significantly higher than all other species (all $p < 0.001$). On Axis 2, the hyoid depression and jaw protrusion axis, only *P. verticalis* scored significantly higher than all other species (all $p < 0.001$), although the other flatfish, *Xystreureys liolepis*, was also different from all ($p < 0.001$) but *Lepomis macrochirus* ($p = 0.10$). On Axis 3, the cranial rotation and gape axis, *S. leptorhynchus* scored significantly higher than all other species studied (all $p < 0.001$). On Axis 4, the lower jaw rotation axis, while species effects were detected, no single species could be differentiated statistically. *Betta splendens* and *Danio rerio* had the greatest degree of jaw rotation among the taxa examined.

Gape velocity was analyzed using an additional univariate ANOVA. In this analysis, no one species stood out as significantly different from the others. Instead, several large, highly overlapping clusters of

species were observed, which was similar to the pattern shown by Axis 4.

Discussion

This analysis suggests that the timing of expansive movements of the various cranial elements is tightly regulated during suction feeding. All timing variables loaded together on the first functional axis, and no other displacement variables loaded with them. As may be expected, the correlation matrix produced by the analysis indicated that correlations between pairs of these variables were quite high (all $r > 0.52$). Studies of prey-capture kinematics in elasmobranchs have noted this same pattern (Ferry-Graham, 1998a, b). Taken together, this suggests that a predetermined series of kinematic events proceeds at predictable pace during suction feeding. Thus, no event can be excluded, nor are intervals between events modified to any significant extent. Clearly, this chain of events generates the wave of expansion that has long been noted in suction feeders, and is largely responsible for the unidirectional flow of water into the head. It appears that this chain of events is not, and perhaps cannot, be modified in any significant manner during a suction feeding event.

This study further suggests the existence of a consistent pattern of cranial movement during suction feeding among divergent teleost taxa. Eleven teleost species, in seven families and four orders (Cypriniformes, Cyprinodontiformes, Perciformes, and Pleuronectiformes) demonstrated cranial expansion with a large degree of overlap in multivariate space. This

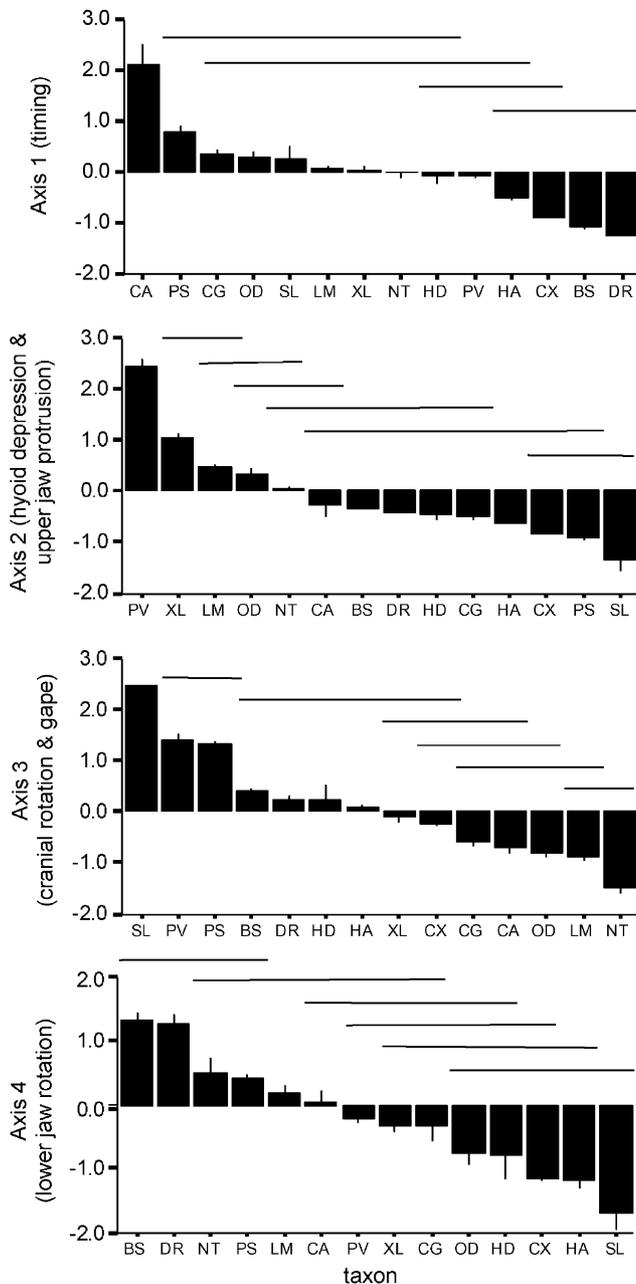


Fig. 6. Results of Tukey post hoc analyses following a significant MANOVA result for a species effect on all axes. Abbreviations for species names are as given in Table 1. Scores for each PC, or axis of variation, are plotted separately against taxon. Taxa are ranked on each X-axis according to PC score. Bars are the mean score \pm SE for that taxon. Lines above the plots indicate species that cannot be differentiated at a significance level of $p = 0.05$.

'clustering' of species suggests that these 11 fish species all produce functionally similar movements when consuming a non-elusive prey item. This pattern likely represents a stereotypical suction feeding mechanism, conserved across many teleost groups, including the phylogenetically primitive cypriniform fishes. This

cluster also encompassed most of the wrasse species; however, they did not appear to cluster any more tightly due to their phylogenetic relationship, nor were they consistently grouped together by the MANOVA post hoc tests. We suggest that when teleost fishes consume non-elusive prey that can be entrained using suction, the central nervous system employs a conserved neural pattern to produce a stereotypical pattern of movements, perhaps via a central pattern generator (Liem, 1979; Wainwright et al., 1989). This pattern may be useful in capturing a wide variety of non-challenging prey.

In contrast, the species that diverge from the cluster appear to be more specialized in their suction feeding behavior. These three most 'extreme' species were: the pipefish, *S. leptorhynchus*, the wrasse, *C. anchorago*, and the flatfish, *P. verticalis*. These species respond to a non-elusive prey item in a manner very different from most of the other species. However, only one of these, *P. verticalis*, shows modifications to the feeding kinematics that may enhance suction production.

S. leptorhynchus is unusual compared with the other species studied here in that individuals of this species produce a large degree of cranial rotation and have a very small gape. These kinematic features may enhance suction production in this species, but we also note that *S. leptorhynchus* showed the least hyoid depression of any species, and this trait has often been suggested as the key to suction production. We suggest that the large cranial rotation in this species, while contributing to an enlarged buccal cavity, plays an even more important role in placing the jaws in close proximity to the prey item. In this species, the jaws are positioned at the end of an elongate snout formed by modified neurocranial and suspensorial bones. During prey capture, pipefish orient themselves below, and slightly posterior to, the prey item, and then rapidly rotate the neurocranium bringing the snout up to the prey (pers. obs.). The snout itself expands, and movement of the prey during the capture event suggests the prey is drawn into the elongate snout at the very end of the event by suction (Ferry-Graham et al., unpublished data). However, the large contributions of snout movements and cranial rotation make pipefish unusual in the degree to which they employ 'ram' behavior, or movement toward the prey item, during prey capture.

C. anchorago was consistently the slowest species in the sample, independent of body size. This is reflected not only in the PCA results for the combined timing variables, but also in the univariate measure of jaw opening velocity (Table 2), which is the third slowest in the study, after two smaller fish species that move their jaws across a much shorter distance. For one of the largest fish in the study to be the slowest in jaw opening velocity is counter to predictions based on either physiological modeling (which predicts no change in

velocity with size, sensu Hill, 1950) or empirical studies of intraspecific scaling (where larger fish show an increase in jaw opening velocity, see Richard and Wainwright, 1995). A slow rate of expansion of the buccal cavity is unlikely to maximize suction performance, as suction production depends, at least in part, on the velocity of cranial expansion. We note that *C. anchorago* has robust jaws and a deep skull (i.e., it is elongate in the dorso-ventral plane, which likely provides a surface for the attachment of robust jaw adductor muscles), and that the diet of this wrasse includes hard invertebrate prey, such as bivalves and crabs (Tedman, 1980). Such prey are typically non-elusive, which may explain why this species produces very slow movements during prey capture. A jaw apparatus with the mechanical advantage necessary to produce very forceful movements will also tend to produce slow movements (Barel, 1983; Wainwright, 1996; Westneat, 1994). We suggest this wrasse species gains a predatory advantage over the prey not by stealth or speed, but by brute force. Additionally, we note that *C. anchorago* tends to obtain prey using ‘biting’ behaviors, even when biting is not necessary (Ferry-Graham et al., 2002).

It is perhaps noteworthy that the other slow species in this study, the black molly, *Poecilia sphenops*, also does not rely exclusively on suction feeding to capture prey. This species has a diet that consists largely of periphyton, and invertebrates resident in this material (Meffe and Snelson, 1989). Efficient scooping or scraping of such food items from the benthos is achieved with jaws capable of forming a 180° gape to maximize contact with the substrate (Gibb and Blanton, 2003), thus speed is not at a premium for this species either.

However, the ability to perform biting and related behaviors did not always yield a pattern of slow cranial movements. Our third ‘biter’, *Chaetodon xanthurus*, is one of the four fastest species in this study. Further, to test the general hypothesis that biting is an intrinsically slow behavior, we re-analyzed the data presented here in a PCA where we also included kinematic data obtained from the wrasses *Coris gaimard*, *Hologymnosus doliatus*, and *Novaulichthys taeniourus* feeding by biting attached prey. Biting events were similar in timing to suction events; thus, there was no significant separation of these species on the timing axis (nor on any other axis) using these additional data. Therefore, the ability to employ a biting strategy does not inherently reduce the speed of the feeding event. This implies that the ability to produce effective suction can be retained during biting. Alfaro et al. (2001) also observed a large degree of overlap in multivariate space when comparing electromyographic data from species using primarily suction or primarily biting for prey capture, which suggests that a similar motor pattern produces both behaviors.

The only species that demonstrated a set of movements likely to maximize suction production was *P. verticalis*. Relative to other species, *P. verticalis* had exceptionally large hyoid depression and upper jaw protrusion, and tended to have large cranial rotation and a small gape. The large degree of hyoid depression and cranial rotation produced by this species should enlarge the buccal cavity dorso-ventrally during the expansive phase (Gibb, 1995; Svänback et al., 2002; Carroll et al., 2004). Similarly, upper jaw protrusion will enlarge the buccal cavity in an anterior–posterior direction (Alexander, 1967; Gibb, 1995), and a small-diameter, round mouth should serve to increase water velocity into the mouth (Lauder, 1980a). This species also produced these behaviors rapidly, particularly when considering their size relative to the other fishes in the study. Thus, *P. verticalis* appears to produce a rapid expansion of the buccal cavity, which suggests a concomitant large drop in buccal pressure. This, in combination with a small gape, should produce an effective suction feeding behavior.

Interestingly, in addition to modifying their feeding kinematics, *P. verticalis* appear to have modified their morphology to enhance suction production. Carroll et al. (2004) found that, at least within the Centrarchidae, species that produced large suction pressures during feeding (i.e., produce the most negative buccal pressures) consistently have deep bodies and small mouths. Most flatfish have deep bodies, and *P. verticalis* is no exception. In addition, *P. verticalis* has a very small mouth and functional gape (Gibb, 2003). Thus, based on both kinematics and morphology, we predict that *P. verticalis* generates very large suction pressures during prey capture.

It is also noteworthy that *P. verticalis* produce this ‘extreme’ feeding behavior even when feeding on non-elusive prey items in the lab. Their diet in the wild consists of clam siphons and tube-dwelling polychaete worms (Allen, 1982). These prey items must be engulfed rapidly, before they can retreat into their shells or tubes and become inaccessible. Carroll et al. (2004) have suggested that a major advantage of large suction pressures may be the ability to procure attached or sessile prey; the feeding behavior and diet of *P. verticalis* provide supporting evidence for this hypothesis.

Finally, we also note that, like *C. anchorago*, *P. verticalis* appears incapable of producing a more generalized behavior when presented with non-challenging prey. This may be because the diet of *P. verticalis* is very narrow and rarely includes non-elusive prey items (Allen, 1982). Alternatively, the modifications to the morphology and/or motor pattern that facilitate this ‘extreme’ behavior may prohibit the use of alternate feeding behaviors.

Of the other species studied, only the wrasse, *O. digrammus* consistently consumes prey potentially

as elusive as the prey consumed by *P. verticalis*. Many species of wrasse include some mobile prey, such as small fishes and invertebrates, in the diet. However, *O. digrammus* is unusual among wrasses in that it consumes such prey almost exclusively, and it is also known to include highly elusive large fishes in the diet (Randall et al., 1990; Westneat, 1995). However, *O. digrammus* did not stand out as different from the other teleosts studied in this comparison. Indeed, no wrasse species is exceptional in its prey-capture kinematics when compared with other teleost species (except *C. anchorago*). In fact, prey-capture kinematics for *O. digrammus* are similar to other teleost species even when kinematic data by other authors are used (Gibb, 1997; Westneat, 1995). Our MANOVA results suggest that *O. digrammus* cannot be differentiated in any significant way from noted generalist species, such as the bluegill, *L. macrochirus* (see also Gibb, 1997). It is possible that *O. digrammus* uses a highly generalized set of kinematics to capture elusive prey, or maybe the experimental prey treatments used in these studies (especially the use of non-elusive prey items) failed to elicit more specialized kinematics. In support of the latter notion, kinematic studies of *O. digrammus* using both live and dead prey found that this species did change prey-capture kinematics when presented with more elusive prey items: live prey elicited slightly faster strikes and greater head expansion than did dead prey suspended in the water column (Ferry-Graham et al., 2001b). However, the changes in timing evoked by live prey would not be great enough to cause *O. digrammus* to stand out on the timing axis in this study (pers. obs.).

It is striking that only one species in this study showed a set of kinematic changes that suggest an increase in suction producing ability. One possible reason for this result is that we could not include variables related to lateral expansion of the cranium in this study. Thus, although our analysis revealed a species that specializes in dorso-ventral and anterior–posterior cranial expansion, lateral expansion of the head (as produced by suspensorial or opercular abduction) could not be assessed in this analysis. However, in a similar functional analysis (although much smaller in scope) conducted previously (Gibb, 1997), the relationships between the feeding kinematics of three of the species included here (*X. liolepis*, *P. verticalis*, and *L. macrochirus*) were unchanged by the addition of data for opercular abduction to the data set. We suggest that the addition of opercular data to this analysis might provide an additional axis of variation, with *P. verticalis* a likely outlier on that axis. However, the overall patterns among the taxa examined here would be unlikely to change.

In addition, while *P. verticalis* was significantly different on only one axis (Axis 2), it was near the extreme on a second axis (Axis 3), and these two axes

together described four of the five displacement variables. Thus, the only species to show modifications to feeding behavior kinematics consistent with potentially enhanced suction generation demonstrated a suite of modifications to multiple elements of the feeding apparatus. We suggest that, as a species evolves to fill a niche where suction performance is at a premium, movements of the elements of the cranium are modified in a coordinated fashion. Perhaps this is not surprising, as Sanford and Wainwright (2002) have suggested that the largemouth bass, *Micropterus salmoides*, modulates all of these kinematic parameters in concert to change suction production from one strike to the next.

It is also possible that many species have not modified their feeding behavior to maximize suction because changes that facilitate increased suction production may result in concomitant losses in other areas of feeding performance. While we have noted here that the ability to employ a biting strategy does not inherently reduce the speed of a generalized suction feeding event (see also Robinson and Wilson, 1998), we know that there is an intrinsic mechanical trade-off between the ability to produce extremely rapid movements and the ability to produce extremely forceful movements, such as those required for biting hard prey (Barel, 1983; Wainwright, 1996; Westneat, 1994). For species that are diet generalists, the ability to produce the rapid jaw movements necessary to increase suction production might compromise the ability to bite certain prey types. Thus, modifying the feeding apparatus to enhance suction production may not represent a successful strategy for dietary generalist species.

Improving upon suction production also may be quite challenging, given the density and viscosity of water. Suction is effective only over a short distance and even very radical changes to morphology appear to have produced only small effects on suction production in some families of fishes (Ferry-Graham and Wainwright, 2002; Ferry-Graham et al., 2003). It is noteworthy, therefore, that the other flatfish species included in our sample, *X. liolepis*, was similar to *P. verticalis* in exhibiting feeding kinematics that should maximize suction production: i.e., large hyoid depression and upper jaw protrusion, and a tendency toward large cranial rotation and a small gape. Like *P. verticalis*, *X. liolepis* is a benthic feeder (Allen, 1982). Obligatory benthic feeders like these flatfishes may be able to employ suction more effectively than mid-water feeders for several reasons. First, the jaw apparatus can be modified and specialized to direct suction in a specific direction. Both flatfish species have been shown to exhibit functional asymmetries that should facilitate this, and suction appears to be consistently directed toward the substrate (Gibb, 1996, 1997). Second, suction should be highly effective when it is applied to an object resting on the substrate, as the substrate itself

interacts with the water being accelerated into the expanding buccal cavity. As an analogy, envision using a pipette to capture individual brine shrimp from the water column vs. using the same pipette to capture individual brine shrimp resting on the substrate. Thirdly, feeding on substrate-based prey items should mitigate the potential problem of reduced suction effectiveness with increasing distance from the prey because preys are consistently found at a predictable and close distance. Thus, we concur with Carroll et al. (2004), who have independently suggested that suction feeding facilitates the capture of prey attached to a substrate.

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