Ontogeny of Suction Feeding Capacity in Snook, *Centropomus undecimalis*

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ABSTRACT   The ontogeny of suction feeding performance, as measured by peak suction generating capacity, was studied in the common snook, *Centropomus undecimalis*. Suction pressure inside the buccal cavity is a function of the total expansive force exerted on the buccal cavity distributed across the projected area of the buccal cavity. Thus, the scaling exponent of peak suction pressure with fish standard length was predicted to be equal to the scaling exponent of sternohyoideus muscle cross-sectional area, found to be 1.991, minus the scaling exponent for the projected buccal cavity area, found to be 2.009, equal to −0.018. No scaling was found in peak suction pressure generated by 12 snook ranging from 94 to 314 mm SL, supporting the prediction from morphology. *C. undecimalis* are able to generate similar suction pressures throughout ontogeny. *J. Exp. Zool. 305A:246–252, 2006.*   © 2006 Wiley-Liss, Inc.

Most fish use suction feeding to capture prey, a behavior that involves the rapid expansion of the mouth and buccal cavity, causing water to flow into the mouth (Fig. 1; Ferry-Graham and Lauder, 2001). The rapid cranial expansion creates a drop in pressure inside the buccal cavity (Van Leeuwen and Muller, '83), the magnitude of which has been used as a metric of suction feeding performance (Norton and Brainerd, '93; Nemeth, '97) since all of the forces that suction feeders exert on their prey increase as a function of suction pressure.

Comparative studies have confirmed that species vary considerably in their capacity to generate suction pressure, with over an order of magnitude range in peak pressure found among teleost species (Lauder, '80; Norton and Brainerd, '93; Nemeth, '97; Carroll et al., 2004). While inter-specific data are accumulating rapidly, it is less clear how suction feeding performance scales within species (Richard and Wainwright, '95; Wainwright and Shaw, '99). Do fish generate similar suction pressures throughout their lives, or does the capacity to generate suction increase as fish get larger and stronger? The answer to this question has important implications on how we view the comparative data on suction pressure and for understanding the dynamics of growth in fish

predators that typically change their feeding habits as they grow. In the present study, the scaling of suction pressure capacity was compared with morphologically based predictions of this scaling relationship in the common snook, *Centropomus undecimalis* (Bloch).

MATERIALS AND METHODS

The magnitude of suction pressure is equal to the buccal expansion forces exerted per unit of the projected buccal cavity area (Carroll et al., 2004). One estimate of the scaling of suction pressure capacity would involve measuring both the scaling of the expansive forces and the scaling of projected buccal area. Each of these variables can be related to a measure of body size, such as fish standard length using the allometric equation:

$$\text{Variable} = aL^X. \qquad (1)$$

Pressure will be equal to the force distributed across the relevant area and this relationship provides the framework for relating scaling exponents:

$$L^X_{\text{Buccal pressure}} = L^Y_{\text{Expansion force}} / L^Z_{\text{Buccal area}}. \quad (2)$$

Thus, to estimate the scaling exponent of buccal pressure, X, with body size one subtracts the scaling exponent of buccal area, Z, from the scaling exponent of expansive force, Y. Expansion of the buccal cavity involves dorsal rotation of the head, ventral rotation of the hyoid system and lateral expansion of the suspensoria. These three-dimensional movements are tightly coupled such that buccal expansion will occur with two input actions: contraction of the dorsal epaxial musculature or the ventral sternohyoideus muscle. Both the epaxialis (Carroll et al., 2004) and the sternohyoideus (De Visser and Barel, '98) act through lever systems to deliver expansion force to the buccal cavity (Figs. 1 and 2). Because these muscular inputs act antagonistically during buccal expansion, they must balance each other in order to produce a net expansive force. In the present study, we focused on estimation of the force-producing capacity of the sternohyoideus because the physiological cross-section area of this muscle is considerably simpler to estimate than the epaxial musculature. We measured the scaling of the projected area of the buccal cavity and subtracted this exponent from the scaling exponent of the physiological cross-sectional area of the sternohyoideus muscle. We then compared this estimated exponent for the scaling of suction pressure capacity with an empirical value determined from measuring peak suction pressure generated by a size series of 12 *C. undecimalis*.

All research methods described here were reviewed and approved by the Vertebrate Animal Care and Use Committees of Florida Institute of Technology and University of California, Davis. Snook were collected using seine nets in the Indian River Lagoon near Melbourne, Florida, USA. Three separate size series of *C. undecimalis* were collected. First, 27 snook, ranging from 36 mm up to 770 mm SL, were used to characterize the scaling of buccal cavity dimensions. Immediately after being euthanized by prolonged exposure to a solution of 300 mg/l MS-222, the buccal cavity of each fish was gently injected with a commercial silicon sealant until the mouth and hyoid were fully extended, but did not appear to be over-extended. The silicon cast was allowed to
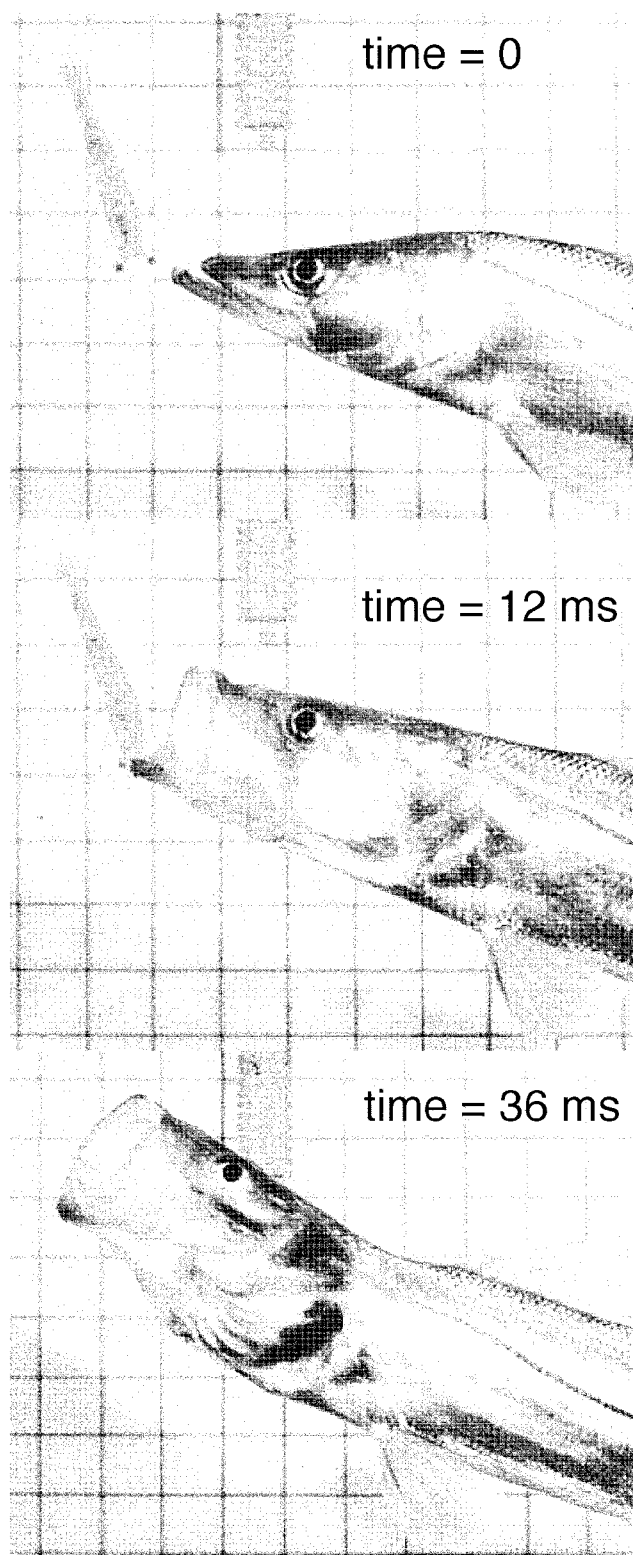

Fig. 1. Images from a video of *C. undecimalis* suction feeding to capture a penaeid shrimp. Note the rapid expansion of the mouth and buccal cavity in association with cranial elevation and hyoid depression.

cure for at least 24 hr before being removed from the fish, trimmed of excess that leaked through the gill bars and subsequently the lateral width of the cylindrical cast was measured at its anterior end where the quadrate–articular joint left a mark in the cast, at a midpoint where the proximal hyoid elements made an impression and at the posterior end of the buccal cavity just anterior to the pharyngeal jaw apparatus. The average of these three buccal diameters was calculated and used in subsequent calculations. The buccal casts were roughly cylindrical in shape; the three measures of width never differed by more than 8%. Buccal cavity length was measured as the distance along the dorsal surface of the cast from the midpoint of the impressions left by the premaxillae to a point on the midline between the tooth plates of the third pharyngobranchial bones of the pharyngeal jaw apparatus. Projected area of the expanded buccal cavity (see Carroll et al., 2004 for an explanation and discussion) was estimated by multiplying the measure of buccal length by the average of the three measures of buccal width.

Second, a series of 13 *C. undecimalis*, ranging from 62 to 660 mm SL, were collected for estimation of the physiological cross-sectional area of the sternohyoideus muscle (Fig. 2). This mid-ventral muscle is symmetrically bipinnate, running from its origin on the anterior face of the ventral extension of the pectoral girdle to its insertion on the urohyal, a sesamoid bone that develops from the central tendon of the sternohyoideus muscle and occupies the midline of the anterior portion of the muscle (Fig. 2B). Immediately after euthanizing the snook, the ventral region of these fish was first skinned so that the fiber orientation of the sternohyoideus attaching on the urohyal could be measured relative to the long axis of the urohyal. A digital photo of the ventral view of the sternohyoideus was taken with the long axis of the urohyal clearly visible. Then the urohyal was excised and a digital photo taken of the bone in lateral view with a ruler for scale. The maximum tension that a bipinnate muscle can generate will be equal to the specific tension of the muscle, times the total area of attachment of the muscle on the central tendon, times a correction for the average angle of insertion of the muscle fibers on that tendon, relative to the axis of motion of the muscle (Powell et al., '84). We assumed that specific tension did not scale with snook body size. NIH Image software was used to measure the angle of insertion of the sternohyoideus muscle

fibers from the first image and the attachment area of the sternohyoideus on the urohyal from the second image. Attachment area of the sternohyoideus on the urohyal was measured from the photographs and multiplied times two to account for the left and right sides. The sternohyoideus did not attach to the entire lateral surface of the urohyal and only the region of attachment was measured. The mechanical advantage of the sternohyoideus muscle, and hence the force that it delivers to the expanding buccal cavity, will depend upon the precise positioning of the complex hyoid system during expansion (De Visser and Barel, '96), a feature that we were unable to characterize. The assumption was made that mechanical advantage of the sternohyoideus muscle does not change with body size of snook.

Third, 12 *C. undecimalis*, ranging from 94 to 314 mm SL, were collected and transported live to the laboratory at the Florida Institute of Technology where they were maintained in various sized aquaria at room temperature (23–25°C) and habituated for 2–4 weeks prior to laboratory recordings of suction pressure during feeding. Fish larger than 314 mm were not used in this part of the study because of the spatial constraints imposed by the 150 cm pressure transducer and the difficulties in scaling up the study system while allowing fish to feed aggressively. Once these fish had acclimated to captivity and were feeding well, they were each denied food for 3 days prior to experimentation. Following anesthesia (300 mg/l MS-222), a plastic cannula was implanted through the neurocranium just anterior to the orbit through the dorsal surface of the buccal cavity, just lateral to the parasphenoid and posterior to the vomer. This position was at the anterior end of the buccal cavity just behind the moving upper jaw bones. A Millar SPF-407 catheter-tipped pressure transducer was threaded into the cannula and held in place with a sleeve of silicon sealant that was stretched over the exposed end of the cannula. This allowed the measurement surface of the pressure transducer to be held in a position just inside the roof of the buccal cavity.

Following surgery, snook were returned to their aquarium and allowed to recover from the anesthesia for 1–3 hr until they appeared willing to feed. Live adult penaeid shrimp were used as prey items during pressure recordings. Shrimp were scaled to the size of the snook by ensuring that the width of the shrimp was 20–40% of the mouth diameter of the snook. Live penaeid shrimp
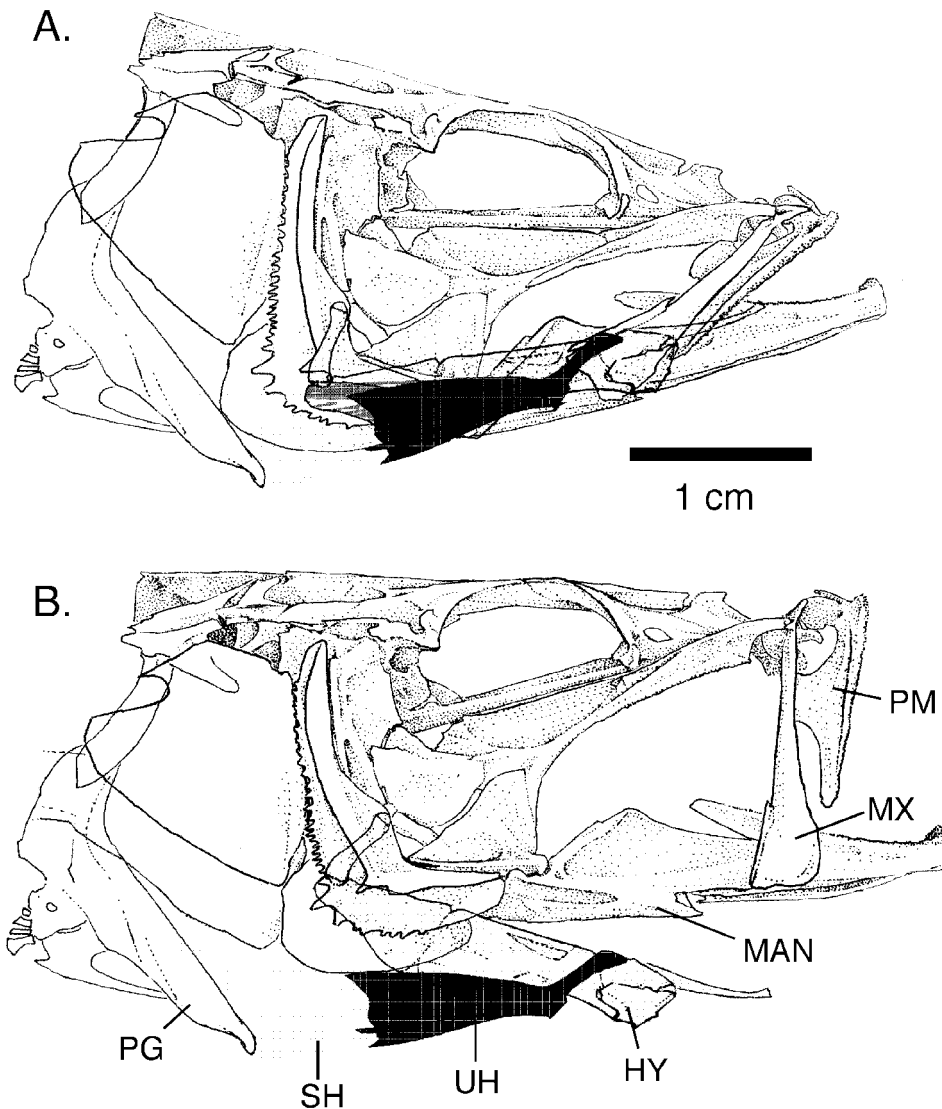
Fig. 2. Drawing of the major skeletal elements of the skull of *C. undecimalis*, shown in the closed and abducted position to illustrate the relative position of the sternohyoideus muscle (SH), the urohyal (UH), the hyoid bone (HY) and the jaws during the expansion that takes place during suction feeding. In this study, we estimated the cross-sectional area of the sternohyoideus attachment on the urohyal by measuring the area of the SH attachment on the urohyal. Other abbreviations: MAN, mandible; MX, maxilla; PG, pectoral girdle; PM, premaxilla.

are exceptionally elusive prey and snook attacked them very aggressively during the feeding trial, often requiring several strikes before successfully capturing them. Snook were fed until satiated and buccal pressure was recorded digitally at 5,000 Hz using an analog-to-digital conversion system and custom software. From the pressure recording of each strike during the feeding trials, the largest magnitude subambient pressure achieved by the fish was measured and the largest magnitude peak across all feedings for each fish was taken as the estimate of maximum suction capacity. Suction pressure is subambient and usually reported as a negative value, but here we report the absolute value of the difference between ambient and minimum pressure during the strike.

Body mass and SL were measured on all *C. undecimalis* and along with urohyal area and buccal cavity projected area, and peak suction pressure scaling relationships were determined with least-squares regression of Log_{10} transformed data, using fish standard length as the independent variable.

RESULTS

Angle of pinnation of the sternohyoideus muscle fibers converging on the urohyal bone ranged between 12.6° and 19.3° but did not change with fish size ($r^2 = 0.01$, $P = 0.98$). Attachment area of the sternohyoideus muscle on the urohyal (here-
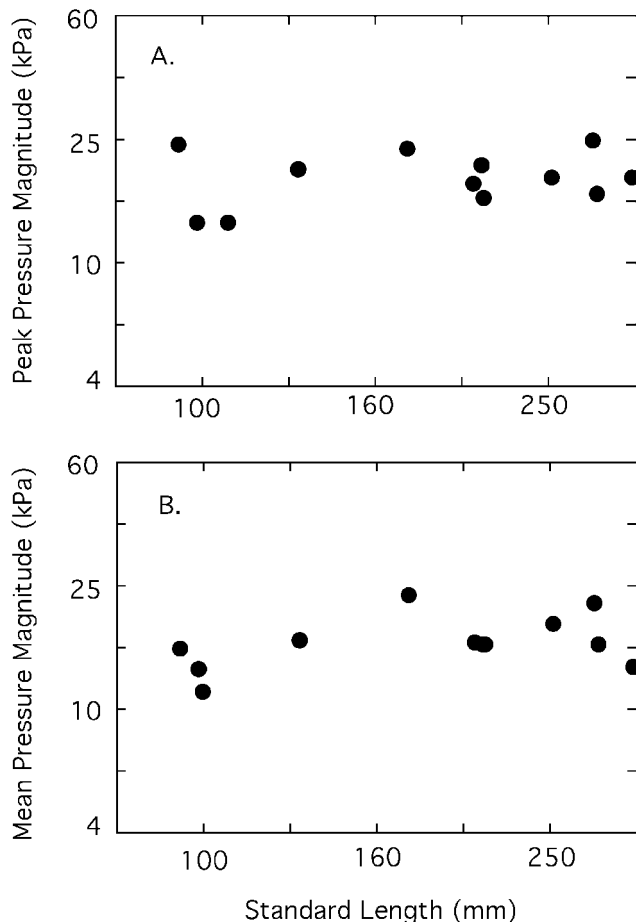

after called "urohyal area") scaled to SL with a slope of 1.991 and buccal cavity projected area with a slope of 2.009 (Table 1). Neither exponent differed from isometry. Combining these exponents results in the prediction that peak suction pressure will scale to standard length with an exponent of 1.991–2.009 = −0.018. These morphological data therefore lead to the expectation that peak suction pressure will be virtually independent of body size in *C. undecimalis*. Peak suction pressure ranged from 13.3 to 24.7 kPa with an overall average of 18.9 for the 12 snook. However, peak pressure was not significantly affected by snook size ($r^2 = 0.06$, $P = 0.44$) (Fig. 3A), and the estimated exponent ($b = 0.117$, SE = 0.15) was not significantly different from that predicted from the morphology ($t = 0.853$, d.f. = 11, $P > 0.4$). The regression of standard length on the average peak pressure across all 46 recorded feeding events also was not significant ($r^2 = 0.18$, $P = 0.17$), although there was a slight indication of a positive slope (Fig. 3B; $b = 0.19$, SE 0.13).

DISCUSSION

As they grow, snook maintain a constant capacity to generate buccal pressure during suction feeding. What are the implications of this result for the ontogeny of suction feeding performance? If one considers the buccal cavity to be a fixed-shape cylinder, then by Bernoulli's Principal, pressure is directly proportional to flow speed of the fluid entering the mouth (Denny, '93; Vogel, '94). However, buccal cavity shape and size change markedly during the course of a strike (Sanford and Wainwright, 2002) and the flows involved show changing velocity (Day et al., 2005). These factors invalidate the straightforward use of the Bernoulli relationship, underscoring the need for direct measurements of pressure and fluid speed. Nevertheless, it is likely that larger buccal pressure magnitudes are associated with faster fluid speed and possibly higher accelerations (Muller et al., '82). Drag forces experienced by prey items in this flow region will be proportional to the square of fluid velocity (Denny, '93) and

Fig. 3. (**A**) Log_{10} scaled plot of peak suction pressure and standard length in 12 *C. undecimalis*. The regression was not significant ($r^2 = 0.06$, $P = 0.44$). Values represent the single largest pressure gradient generated by each fish from several feeding sequences. (**B**) Log_{10} scaled plot of average peak pressure for all feeding events recorded in this study vs. standard length of the 12 snook. The regression was not significant ($r^2 = 0.18$, $P = 0.17$). Points represent mean values for each individual fish.

TABLE 1. Scaling relationships for urohyal surface area, and buccal cavity dimensions of snook

Dependent variable	N	Slope	y-intercept	r^2
Area of sternohyoideus attachment on urohyal (mm²)	13	1.991	−2.668	0.997
Buccal cavity projected area (mm²)	26	2.009	−3.097	0.986

Results are least-squares regressions of morphological variables regressed against Log_{10} standard length.

added mass will be proportional to fluid acceleration (Vogel, '94). Taken together, these factors indicate that the forces exerted on prey and the speed of transporting prey will increase with the magnitude of the pressure drop that occurs during suction feeding. Thus, the maintenance of a constant capacity to generate buccal pressure suggests that the potential forces exerted by snook on their prey change little during ontogeny.

One important difference in the water flow patterns generated by different sized snook is that, while peak fluid speed may not be strongly affected by body size, the volume of water that is displaced and the cross-sectional area of the flow field that enters the mouth will increase in larger fish. Thus, larger snook are likely to generate a higher volume flow rate and be more effective capturing larger prey because they displace a larger volume of water (Higham et al., 2005). The larger volume of affected water will also increase the size of prey that would be completely contained within the flow field and will increase the distance from which prey can be drawn. Suction distance, the distance from which predators suck prey into their mouth, is often used as an indication of suction ability (Wainwright et al., 2001) and can be expected to increase with snook size because of the larger volume of water that is affected by the suction event (Day et al., 2005).

The close fit between the predicted scaling exponent from the morphological model and empirical measures of snook suction capacity indicates some validation for this model of force transmission in the feeding mechanism. Another recent study (Carroll et al., 2004) modeled force transmission through the dorsal epaxial musculature in centrarchid fish. These morphological models provide a framework that can be used to evaluate the implications of morphological diversity of fish with respect to suction pressure capacity. It can be anticipated that some species will exhibit changes in their capacity to generate suction pressure as they grow, depending on the growth of the features of the suction feeding mechanism (Carroll et al., 2004). Some taxa appear to grow close to isometrically, such as the largemouth bass, *Micropterus salmoides* Lacepede, and the snook studied here. Other taxa grow allometrically, such as the nurse shark (*Ginglymostoma cirratum* Bonnaterre) (Robinson and Motta, 2002) and the African catfish (*Clarias gariepinus* Burchell) (Herrel et al., 2005), and in these taxa suction pressure capacity may change with body size. For example, among species of the Centrarchidae, bluegill (*Lepomis macrochirus* Rafinesque) exhibit weaker peak pressure capacity as they grow, a pattern that is reflected in allometric growth of the musculoskeletal components of buccal expansion (Carroll et al., 2004). An important implication of these recent studies and the present one is that one cannot assume that a species will have a specific capacity to generate suction pressure; instead, some species will show changes during ontogeny and others will not. This fact will complicate attempts to generate comparative data sets and implies that species-specific values of predicted suction pressure capacity must be expressed for a particular body size.

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