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Coupling osteological development of the feeding apparatus with feeding performance in common snook, *Centropomus undecimalis*, larvae: Identifying morphological constraints to feeding

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ABSTRACT

Identifying bottlenecks to feeding in marine finfish larvae is becoming a dominant theme as commercially important fish stocks collapse worldwide. The transition from endogenous yolk reserves to feeding exogenously is perhaps the largest constraint to developing aquaculture technologies in closed systems. Mass mortality during early larval development is generally attributed to a lack of suitable prey during the first feeding stage, however, empirical evidence identifying a causal link between morphology and performance remains scarce. In this study, we examined the link between osteological development of the feeding apparatus and feeding performance, expressed as (1) the median number of prey consumed by larvae and (2) the median size of prey consumed by larvae, during larval development of the common snook, *Centropomus undecimalis*. Cluster analysis, nMDS, and SIMPER analysis allowed us to identify functional intervals of the feeding apparatus through larval development. Results revealed that first feeding larvae exhibited rudimentary skeletal elements and selected only one or two of the prey types available relative to older larvae, which included more and larger prey types in their diet. Upon complete formation of the hyoid apparatus, around 8 dph, a dietary shift to rotifers was observed suggesting that high rates of mortality observed in closed culture systems may be attributed to the absence of a suitable small, non-elusive food organism during the first feeding stage. First feeding larvae exhibit a poorly developed feeding apparatus that may constrain their ability to consume elusive prey as an initial diet. Based on the association between stage-specific characteristics of the feeding apparatus and corresponding stage-specific metrics of feeding performance established in this study, we propose a stage-specific feeding-management scheme for snook hatchery aquaculture.

1. Introduction

Common snook, *Centropomus undecimalis* (Bloch), are a stenothermic estuarine fish whose range extends throughout the tropical and subtropical waters of North and South America; including the Gulf of Mexico, the Caribbean, and southward to Rio de Janeiro, Brazil (Gilmore et al., 1983; Muller and Taylor, 2005). In Florida, common snook play an important role in supporting one of the state's largest recreational fisheries (Muller and Taylor, 2005). Declining populations in the southern Gulf of Mexico have mounted concerns among resource managers (Muller and Taylor, 2005). Recent research has focused on commercial scale production of hatchery-reared fish for use in stock enhancement (Neidig et al., 2000).

Despite initial successes in the artificial propagation and rearing of snook species (Ager et al., 1976; Chapman et al., 1982; Lau and Shafland, 1982; Neidig et al., 2000; Alvarez-Lajonchère and Tsuzuki, 2009), reliable hatchery methods are still in their infancy. Snook have been identified as a promising candidate for aquaculture as a foodfish and for stock enhancement (Tucker, 1987; Brennan et al., 2006), although high mortality associated with early larval stages presents a significant bottleneck to their commercialization (Yanes-Roca, 2006). A significant cause of early mortality in captive snook has been attributed to starvation during the first six days of larval development (Yanes-Roca, 2006). The transition from endogenous to exogenous feeding has been identified as a significant cause of early mortality in both wild and cultured marine species (Hjort, 1914; Peterson and Ausubel, 1984; Ostrowski and Laidley, 2001) creating a distinct gap in our current understanding of larval fish biology and our approach to aquaculture rearing.

Feeding success in marine fish larvae is known to be influenced by a number of interconnected factors such as the development of the visual system and other sense organs (Job and Bellwood, 1996), digestive system (Green and McCormick, 2001), swimming ability (Fisher et al., 2000), feeding apparatus (Turingan et al., 2005), and search behavior (MacKenzie and Kiorboe, 1995). Characteristics of

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zooplankton prey organisms such as size (Krebs and Turingan, 2003), color (Checkley, 1982), density (Lasker, 1975), and swimming behavior (Beck and Turingan, 2007) are also known to influence feeding performance among marine fish larvae. Few studies have explored the relationship between feeding performance and functional morphology through the larval period of commercially important marine fishes, though it has been demonstrated that the design of the feeding mechanism limits the ability of larval stages to feed successfully (Kohno et al., 1997; Wittenrich et al., 2007).

Several studies have demonstrated that feeding success of fish larvae is influenced by the development of their suction-feeding apparatus, the primary apparatus fishes use to capture prey and the dominant feeding mode of juvenile and adult snook (Lauder, 1980; Turingan et al., 2005; Wainright et al., 2006). The suction-feeding apparatus in juvenile and adult fishes is driven by three musculoskeletal linkages in the head that act synchronously to create negative pressure within the buccal cavity (Westneat and Wainwright, 1989; Norton and Brainerd, 1993). First feeding larvae, however, lack the structural design to support complex feeding and prey-capture events are thought to employ only the hyoid linkage (Turingan et al., 2005), which may be insufficient for successful suction-feeding. The feeding apparatus changes through early ontogeny to incorporate all three musculoskeletal linkages near metamorphosis (Turingan et al., 2005). Beck and Turingan (2007) concluded that larval *Sciaenops ocellatus* could not modulate prey capture behavior until complete development of the suction-feeding apparatus around metamorphosis. Early larvae employed the same prey-capture behavior despite differences in the size or escape response of the prey encountered. Prey capture was only successful when a larva encountered a small, non-elusive prey organism that could be successfully captured with little or no suction pressure. We consider zooplankton with very little ability to escape from predation (see Beck and Turingan, 2007), such as dinoflagellates and tintinnids, as non-elusive prey in this study.

Little is known about the changes in design of the feeding apparatus and associated feeding requirements of snook larvae as they develop from hatching through metamorphosis. It has been shown that the complexity and design of the feeding apparatus at the onset of first feeding and throughout the larval period varies among marine teleosts (Turingan et al., 2005; Francis and Turingan, 2008). Differences in the initial design of the feeding apparatus are thought to have direct consequences for first feeding and mortality.

In an attempt to explore the implications of larval-feeding performance for snook aquaculture, we examined the development of the functional morphology of the feeding apparatus and feeding performance through early ontogeny in *C. undecimalis* larvae. Osteological development of *C. undecimalis* has been examined in depth by Fraser (1968) and Potthoff and Tellock (1993). We ranked morphological features in the skull that directly reflect the complexity of the feeding apparatus. Observations of feeding performance, allowed us to link patterns of morphological change with patterns of dietary shift through larval ontogeny. We address three specific questions: (1) Are discrete developmental stages of feeding apparent through larval development? (2) If so what are the key morphological features of the feeding apparatus at each stage of development? and (3) Are the expected patterns of morphological changes in the feeding apparatus associated with changes in feeding performance?

2. Materials and methods

C. undecimalis eggs were obtained from two broodstock populations housed in recirculating seawater systems at Mote Aquaculture Park. Mature adult snook, maintained under natural photo-thermal conditions, were induced to spawn using gonadotropin releasing hormone analogue (GnRHa). Eggs were maintained at a salinity of 35 ppt and shipped to Florida Institute of Technology within 14 h of spawning. Larvae were stocked into two identical recirculating systems containing five 45 L black conical rearing tanks (41 cm D × 55 cm H to bottom of cone, American Tank Company model # 0274-065) at a density of 10/L. Water quality in each rearing tank was maintained by a biological filter tower, ultraviolet sterilizer, and protein skimmer with an exchange rate of 100 mL/min. Natural seawater filtered through a 10 μm closed pore filter was maintained at 28 ± 1 °C, salinity 35 ± 2 ppt, pH 8.2, NH_3 and NO_2 < 0.02 ppm, and NO_3 < 10 ppm (Red Sea marine lab test kit). Water changes were performed every other day by replacing 10% of the total system water from the sump. Recent studies have shown that most marine fish larvae are visual feeders and that feeding success and survival rates increase with increased photoperiod (Puvanendran and Brown, 2002; Arvedlund et al., 2000). Our laboratory rearing experiences indicated that *C. undecimalis* follows this pattern, thus, in this study, we maintained photoperiod at 24 L: 0D during all trials with two 40 W fluorescent bulbs (6500 K) mounted 20 cm above the water surface. Greenwater was maintained in the rearing tanks during all trials by adding 0.5 mL of diluted *Nannochloropsis oculata* algae paste (Reed Mariculture) to the tanks each morning.

2.1. Development of the feeding apparatus

Ten larvae were haphazardly sampled from each system of rearing tanks every other day for the first 30 days. Subsequent samples were taken at 33, 40 and 46 days post hatch (dph). Specimens were fixed in 10% formalin and transferred to 70% ethanol after 24 h for later analysis. A developmental series of 144 larvae, representing a continuous size series, were cleared and stained (Potthoff, 1984) to examine ossification patterns of the feeding apparatus. Each specimen ($n = 9$ for each sampling event to 30 dph and $n = 3$ for days 33, 40 and 46) was scored for a suite of feeding-relevant characters designed to represent discrete ontogenetic functional intervals (Table 1). Key biomechanical features of the head and axial skeleton such as the oral jaws, suspensorium, hyoid arch, branchial arch, pelvic girdle, neurocranium and vertebrae were assessed based on the appearance and ossification of each structure. These elements are known to influence feeding performance in fishes (Lauder, 1980; Liem, 1991). Elements of the suspensorium, such as the hyomandibular and symplectic bones, aid in expanding the buccal cavity laterally during feeding (Otten, 1982). The opercular series and hyoid apparatus are well known to depress the lower jaw and the floor of the buccal cavity during prey-capture in fishes (Lauder, 1980; Liem, 1991). The axial skeleton (i.e., vertebral column) plays a prominent role in swimming, but also provides a framework for the axial muscles, particularly the epaxialis muscles to elevate the head during suction feeding (Lauder, 1980; Otten, 1982; Liem, 1991). However, cartilaginous precursors to these bones, may limit the movement of these elements that are essential in successful prey-capture in fish larvae (Hunt von Herbing et al., 1996). Gape height and width were also measured to reflect changes in cranial morphology. Gape height (GH) was measured as the distance between the anterior tips of the premaxilla and dentary when the included angle formed by the jaw bones was 90° using the formula:

$$GH = \sqrt{(UJL^2 + LJL^2)}$$

where: UJL = upper jaw length; LJL = lower jaw length (Wittenrich et al., 2007; Mookerji and Ramakrishna, 1994). Upper jaw length was measured from the articular-quadrate joint to the tip of the premaxilla. Lower jaw length was measured from the articular-quadrate joint to the tip of the dentary. Gape width was measured as the distance between the left and right articular-quadrate joints. Jaw length measurements were made with an ocular micrometer to the nearest 0.01 mm.

To examine intraspecific variation in the development of the feeding apparatus and test the hypothesis that discrete developmental stages of feeding are apparent through larval development we produced a

Table 1
Feeding-relevant character scores used to identify ontogenetic functional intervals related to feeding in *C. undecimalis* larvae.

Score	Character
Lower jaw	
0	Meckel's cartilage only
1	Initial ossification of dentary
2	Ossification and separation of dentary and articular
3	Loss of Meckel's cartilage
Upper jaw	
0	Cartilaginous maxilla only
1	Appearance of cartilaginous pre-maxilla
2	Ossification of maxilla and pre-maxilla
3	Supra-maxilla
Type of teeth	
0	Canines/villiformes
1	Initial growth/ossification
2	Adult arrangement complete ossification
Suspensorium	
Hyomandibulosymplectic	
0	Hyomandibulosymplectic cartilage undifferentiated
1	Initial ossification and separation of hyomandibular and quadrate
2	1/2 ossification of hyomandibular and quadrate
3	Complete ossification of hyomandibular and quadrate
Palatine/quadrate	
0	PalQ exists as undifferentiated cartilaginous bar
1	PalQ expands triangularly
2	Initial ossification and separation of palatine and quadrate
3	Appearance of metapterygoid
4	1/2 ossification of palatine and quadrate
5	Complete ossification of palatine and quadrate
Hyoid arch	
0	Undifferentiated cartilaginous hyoid bar
1	Ceratohyal and epihyal cartilage growth
2	Cartilaginous branchiostegal rays
3	Ossification and differentiation of certo and epihyals
4	Complete calcification of hyoid arch
Opercular series	
0	Opercle absent
1	Presence and ossification of opercle
2	Presence and ossification of pre-opercle
3	Presence and ossification of complete opercular series
Neurocranium	
0	Dominated by cartilaginous ethmoid plate and trabeculum
1	Epiphysial tectum, ectethmoid bar, suborbital bar and occipital process cartilage merge
2	Ossification of frontal and appearance of nasal
3	Near 1/2 ossification of neurocranium
4	Complete ossification of neurocranium
Branchial arch	
0	Cartilaginous basibranchial and 1–2 ceratobranchials
1	Articulation of hypobranchials and ceratobranchials
2	Ossification of the basi-branchial
3	Ossification of branchial arches
Pectoral girdle	
Cleithrum	
0	Cartilaginous cleithrum
1	Ossification of cleithrum
2	Appearance and ossification of supra-cleithrum
Pectoral fins	
0	Caraco-scapular cartilage only
1	Separation of proximal radials
2	Separation and ossification of scapula and caracoid
3	Presence of distal radials
Vertebrae	
0	Absent
1	Initial chondrification
2	Chondrification reaches half body length
3	Chondrification of hypurals
4	Ossification of vertebrae
5	Fin rays and epurals
6	Flexion

similarity matrix of pooled character scores using Bray–Curtis distance measures. We then performed a cluster analysis using group average linkage and Bray–Curtis distance rules to classify and map group structure (Sampey et al., 2007; Ditty et al., 2003; James and McCulloch, 1990). A minimum linkage distance of 80% was used to separate major clusters (Wittenrich, 2007). Two-dimensional ordinations were generated using non-metric multi-dimensional scaling (nMDS) to view the relationships among functional intervals using a common, dimensionless scale. Interpretation of nMDS plots was based on representative stress values and considered a good ordination with stress values <0.1 (Clark and Warwick, 2000). SIMPER (similarity percentages) was then used to determine the contribution of each skeletal character to the groups identified by cluster and nMDS analyses. Groups were labeled arbitrarily for ease of interpretation based on dominant skeletal features identified by SIMPER.

2.2. Feeding performance

Larvae were subjected to feeding trials conducted in 45 L rearing tanks. Water exchange to the rearing tank was provided each evening (5 pm–8 am) at a rate of 0.6 L/min to clear residual prey organisms and facilitate gut evacuation prior to feeding trials. Three replicates were performed every other day for the first 30 days. Subsequent samples were taken at 33, 40 and 46 days post hatch (dph). A replicate consisted of the feeding trial regime mentioned below and 20 larvae from separate broods.

The rotifer *Brachionus plicatilis* (average lorica length ranged from 180–277 μm) was maintained at 28 °C, salinity 35 ppt and fed *N. oculata* algae paste once daily. *Artemia franciscana* were cultured from cysts. Plankton tows were collected daily during flood tides at Sebastian Inlet (Sebastian, Florida) using a 50 cm diameter plankton net with 50 μm mesh screen. Suspended particulate matter was allowed to settle before zooplankton was size sorted into two experimental fractions; 35–90 and 91–270 μm. Average composition of size sorted zooplankton used in feeding trials is listed in Table 2.

Five prey types were introduced to each tank at 9 am at a density of 2 prey/mL with a total prey density of 10 organisms/mL. Prey consisted of 35–90 μm (0.11 mm median length × 0.04 mm median width) size sorted zooplankton, 91–270 μm (0.21 mm × 0.09 mm) size sorted zooplankton, rotifers (0.24 mm × 0.11 mm), newly hatched *Artemia* nauplii (less than 12 h old) (0.46 mm × 0.21 mm), and 48 h *Artemia* (0.72 mm × 0.36 mm). Larvae were allowed to feed for 2 h, after which 20 larvae were haphazardly sampled, anesthetized with MS-222 (Tricaine Methanesulfonate, Western Chemical) to prevent regurgitation of ingested prey (Wuenschel and Werner, 2004) and fixed in 10% formalin for 24 h before being transferred to 70% ethanol for later analysis.

To test the hypothesis that feeding performance varies among osteological stages of the feeding apparatus the entire digestive tract of all larvae from the feeding trials were excised and examined for

Table 2
Average density, expressed as a percentage of size sorted sample, of zooplankton collected from Sebastian inlet and used for feeding performance experiments.

Plankter	35–90 μm zooplankton	91–270 μm zooplankton
	Density (%)	Density (%)
Adult calanoid copepods	0.0	20.4
Adult cyclopoid copepods	0.0	9.5
Adult harpacticoid copepods	0.0	7.3
Copepod nauplii	12.5	27.0
Copepod copepodites	0.0	16.1
Diatoms	19.3	5.8
Dinoflagellates	10.2	2.2
Flatworms	1.3	0.0
Naked ciliates	32.9	0.0
Tintinnids	21.5	0.7
Balanus spp. nauplii	0.0	1.5
Nematodes	0.1	0.0
Polychaete larvae	0.0	2.9
Trochophores	0.0	2.9
Veligers	0.0	2.2

prey. Ingested prey organisms were quantified and measured (length and width).

Because the distribution of gape and prey dimensions, as well as relative prey consumption, did not meet the assumptions of parametric statistics, non-parametric methods were used in statistical analyses. Intraspecific variation in these metrics were determined among developmental stages using Kruskal–Wallis test. Feeding performance was expressed as (1) the median number of prey consumed by larvae and (2) the median size of prey consumed by larvae.

3. Results

3.1. Development of the feeding apparatus

Cluster and nMDS analyses produced four groups at 80% similarity (Fig. 1). The first feeding stage, which occurred at 3 dph, was labeled the 'initial hyoid' stage. The feeding apparatus at this stage exhibits primarily cartilaginous elements of the lower jaw and hyoid apparatus. The ethmoid plate is used to support the upper jaw, while the undifferentiated hyoid bar depresses the lower jaw. No premaxilla is present and the vertebrae are without neural and hemal spines. At five days after hatching, larvae transition to the 'complete hyoid' stage where the cerato- and epihyal cartilages of the hyoid apparatus expand, the epiphysial tectum of the cranium becomes more robust, the cleithrum expands to support musculoskeletal linkages of the cranium, and the upper jaw begins to differentiate (Fig. 2). The 'initial hyoid' and 'complete hyoid' stages exhibited 78% dissimilarity (Figs. 1 and 2A and B) with the hyoid arch (27%), branchial arch (27%), and neurocranium (27%) contributing most of the power to discriminate between these stages.

The 'initial opercular series' stage occurred at approximately 20 dph and was marked by initial ossification of the opercular series and overall growth and ossification of skeletal elements. The suspensorium continues to expand ventrally and initial ossification and separation of the hyomandibular, symplectic, palatine, and quadrate bones occur, allowing articulation of individual bones. The 'complete hyoid' and 'initial opercular series' stages exhibited 48% dissimilarity (Figs. 1 and 2A, B and C). Vertebrae (35%), number of teeth (25%), hyoid arch (13%) and palatine/quadrate (13%) contributed most of the power to discriminate between these stages.

The 'complete opercular series' stage occurs near 31 dph and is marked by complete separation and near total ossification of individual elements of the feeding system (Fig. 2D). Musculoskeletal linkages are now present between articulation points of the suspensorium, opercular series and hyoid apparatus allowing cranial rotation, premaxilla protrusion and lateral expansion of the suspensorium. The 'complete opercular series' stage was 49% dissimilar to the 'initial opercular series' stage with number of teeth (16%), vertebrae (12%), pectoral fins (12%), and cleithrum (8%) contributing most of the power to discriminate between these stages.

Median gape height and width were significantly different between the hyoid stages ('initial hyoid' and 'complete hyoid') and the opercular series stages ('initial opercular' and 'complete opercular'), ($H_{3,198} = 172.76$; $P<0.001$).

3.2. Development of feeding performance

Median prey length and width were significantly different between the hyoid stages ('initial hyoid' and 'complete hyoid') and the opercular series stages ('initial opercular' and 'complete opercular'); the hyoid stages consuming smaller prey ($H_{3,198} = 172.76$; $P<0.001$). Although prey size consumed increased with body size through early ontogeny, larvae did not consistently consume the largest prey possible relative to gape size. Relative to body size, gape height increased faster than prey length ($t = 3.69$; $df = 198$; $P<0.001$; Fig. 3A). Similarly, gape width increased faster than prey width $t = 4.98$; $df = 198$; $P<0.001$; Fig. 3B).

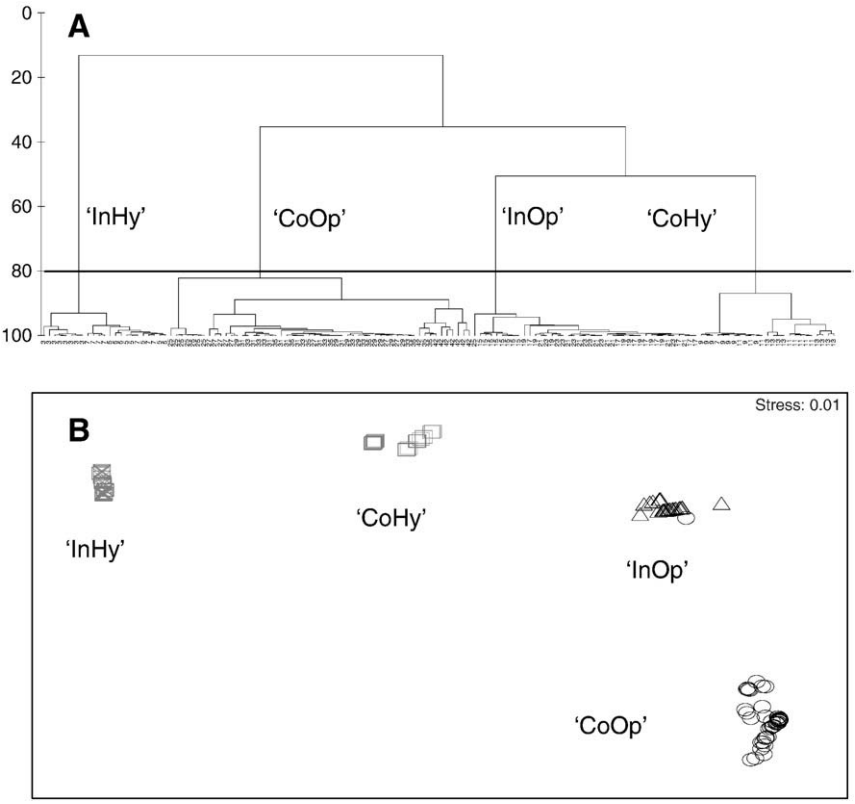

Fig. 1. (A) Cluster analysis using group average linkage and Bray–Curtis distance rules to organize and map group structure related to the development of the feeding apparatus (B) resultant clusters assigned to functional groups and separated by nMDS. 'InHy' = initial hyoid stage; 'CoHy' = complete hyoid stage; 'InOp' = initial opercular series stage' 'CoOp' = complete opercular series stage.

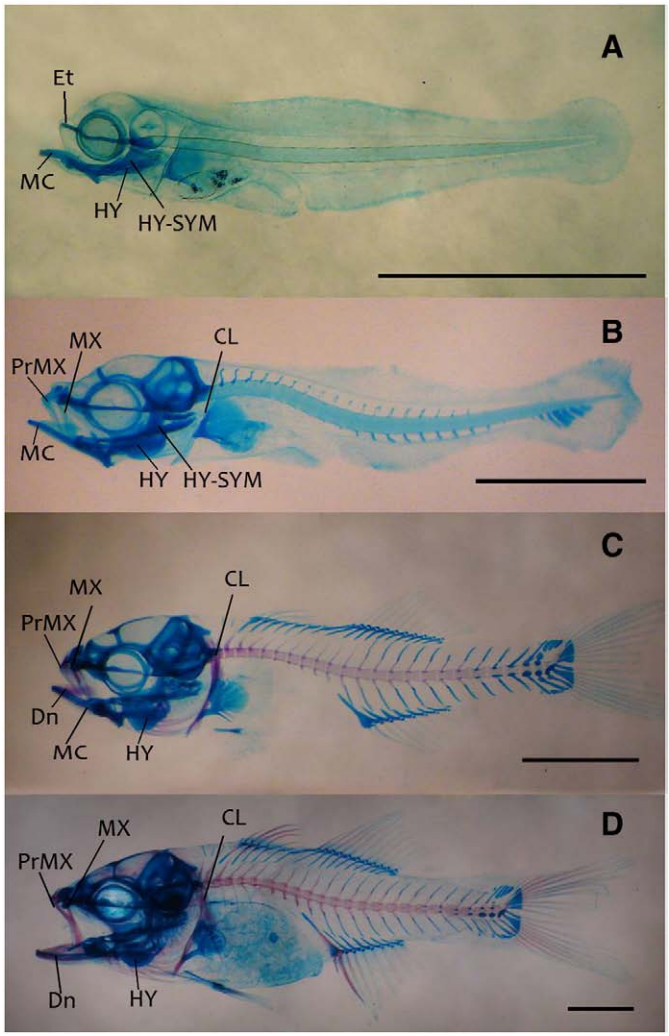

Fig. 2. Key characters quantified in cluster analysis and nMDS to analyze developmental stages of the feeding apparatus in *C. undecimalis*. (A) 'initial hyoid'; 3 dph (2.23 mm), (B) 'complete hyoid'; 11 dph (3.13 mm), (C) 'initial opercular series'; 19 dph (4.18 mm). (D) 'complete opercular series'; 33 dph (7.56 mm). Scale bar = 1 mm. HY = hyoid, MC = Meckel's cartilage, CL = cleithrum, PrMX = premaxilla, MX = maxilla, HY-SYM = hyomandibulosymplectic cartilage, DN = dentary.

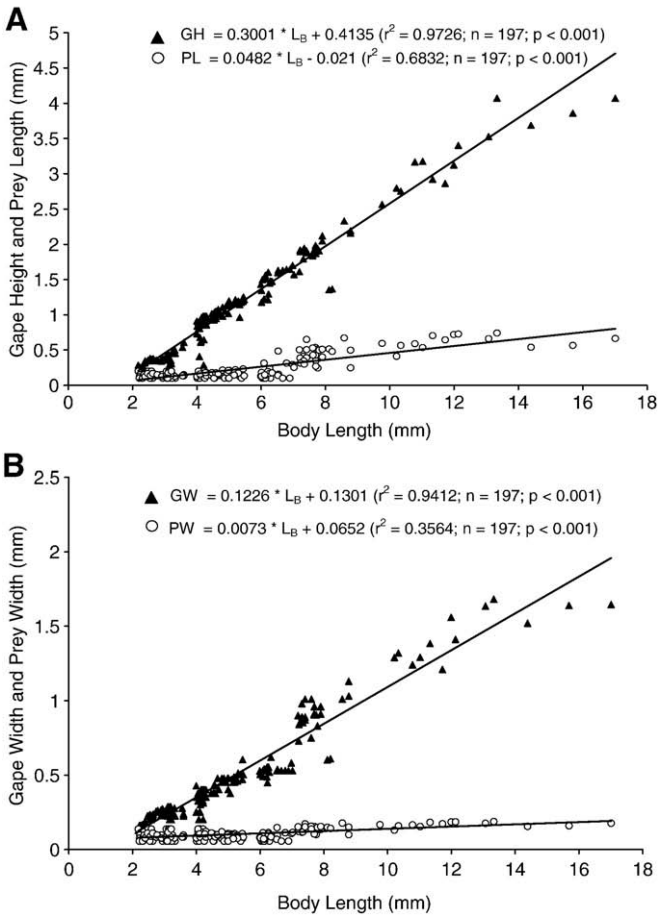

Fig. 3. Relationship between (A) gape height and prey length relative to body length and (B) gape width and prey width relative to body length. (G_H = gape height, G_W = gape width, P_L = prey length, L_B = body length.

Larvae in the 'initial hyoid' stage consumed mainly small, non-elusive 35–90 µm zooplankton such as tintinnids and dinoflagellates (66.67% of diet). Rotifers (48% of diet) and 35–90 µm zooplankton (52% of diet) accounted for near equal percentages of the diet of larvae in the 'complete hyoid' stage. Rotifer consumption was statistically higher in the 'complete hyoid' and 'initial opercular series' stages than larvae in the 'initial hyoid' and 'complete opercular series' stages ($H_{3,198} = 80.32$; $P<0.001$, Fig. 4).

Consumption of larger, more elusive 91–270 µm zooplankton was significantly higher in the opercular series stages than the hyoid stages ($H_{3,198} = 116.27$; $P<0.001$, Fig. 4). Consumption of *Artemia* (both 12 h and 48 h) was greatest in the 'complete opercular series' stage when all skeletal elements of the feeding apparatus were ossified. *Artemia* was absent in the diet of hyoid stage larvae and only four larvae in the 'initial opercular series' stage consumed 12 h *Artemia*.

4. Discussion

It is well known that shifts in food consumption occur throughout the larval-life history of fishes, in both natural and aquaculture systems (Tucker, 1998; Wuenschel and Werner, 2004; Sampey et al., 2007). Understanding the mechanisms that drive these dietary transitions is important, especially for hatchery managers whose goal is to develop and implement economically sound feeding practices for aquaculture. This study provides evidence that stage-specific changes in the selection of prey by snook larvae are associated with stage-specific changes in the functional components of the feeding apparatus. Identifying the link between functional morphology of the feeding apparatus and feeding performance in marine fish larvae is important in the design and implementation of feeding management strategies for aquaculture.

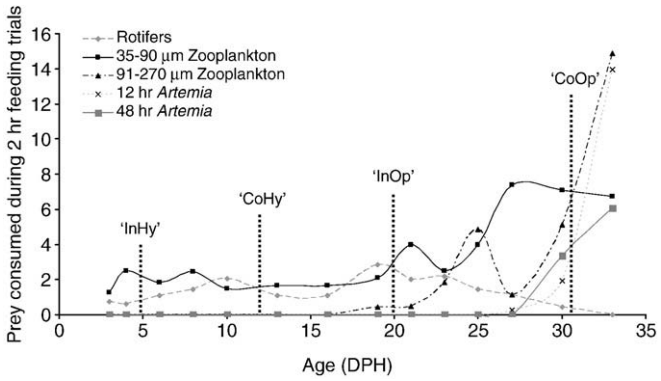

Fig. 4. Feeding performance of *C. undecimalis* larvae expressed as the average number of each of five prey types consumed during two hour feeding trials. Vertical dotted lines indicate the average age of developmental stages. InHy = initial hyoid; CoHy = complete hyoid; InOp = initial opercular series; CoOp = complete opercular series.

The first feeding stage of larvae presents a significant bottleneck to commercial aquaculture production and it is generally assumed that gape dimensions limit the ability of small fish larvae to consume commercially available *Brachionus* spp. at this feeding stage (Holt, 2003). Heath (1992) found that most species of marine fish larvae consume prey that is <20% of total gape width. Preying on common strains of rotifers first feeding larvae of *C. undecimalis* would be required to utilize approximately 85% of their total gape. Only half of first feeding *C. undecimalis* larvae in the present study consumed rotifers and those that did consumed only one prey. When rotifers were removed from the pooled data of ingested prey, first feeding larvae consumed prey that was only 30% of total gape width; ciliates, tintinnids, dinoflagellates, and small copepod nauplii dominated the diet of these larvae. Although larval-gape dimensions help explain the selection of prey in *C. undecimalis* and in other fish species (Heath, 1992; Mookerji and Ramakrishna, 1994; Holt, 2003; Krebs and Turingan, 2003), other functional properties of the feeding apparatus may underlie food consumption in fish larvae. This study postulates that the development of the suction-feeding mechanism in *C. undecimalis*, in conjunction with gape, influences prey selection in *C. undecimalis* larvae.

Our analysis of the development of the feeding apparatus and feeding performance in *C. undecimalis* revealed some key features of the early ontogeny of form and function in this fish species. The state of development of the feeding apparatus increased in complexity through ontogeny, from a simple, hyoid-driven system at the onset of exogenous feeding to a more complex feeding system just prior to metamorphosis, involving all the functional units found in adult conspecifics. First feeding larvae exhibited rudimentary elements of the chondrocranium and the feeding system was dominated by a simple, undifferentiated hyoid bar. Feeding in this stage was limited to smaller, less elusive zooplankton such as ciliates and dinoflagellates. In contrast, larvae that survived beyond the first feeding stage fed on more diverse prey types, including larger, more elusive zooplankton.

The development of the feeding apparatus in *C. undecimalis* larvae is subtle and protracted; the complete hyoid-opercular linkage system is not fully ossified until 31 days after hatching. Although not directly measured in this study, the ability of first-feeding larvae to feed on elusive zooplankton may be limited by the underdeveloped feeding apparatus at the onset of exogenous feeding. Contemporary functional morphological studies indicate that fishes that feed on relatively small, non-elusive prey rely on suction-feeding to capture prey (e.g., Wainright et al., 2006; Beck and Turingan, 2007). Suction-feeding ability is maximized when the well-coordinated, simultaneous firing of cranial muscles to depress the hyoid and lower jaws, abduct the suspensorium, and elevate the neurocranium is coupled with the fish's ability to bring the mouth as close as possible to the prey at the time of capture (Lauder, 1980; Liem, 1991; Wainright et al., 2006). In *C. undecimalis* larvae, the development of the entire suite of muskulo-skeletal linkages that are necessary for suction-feeding is not completed until 31 days after hatching. As demonstrated in red drum, *Sciaenops ocellatus*, larvae with underdeveloped opercular series are very inefficient in capturing elusive prey such as adult calanoid copepods and *Artemia* (Beck and Turingan, 2007).

The influence of the functional design of the feeding apparatus on feeding performance in *C. undecimalis* larvae may be mediated by the size and behavior, including the escape response, of zooplankton prey. Several studies have demonstrated that zooplankton prey exhibit a wide range of swimming patterns and escape responses, which affect the prey-capture ability of fish larvae (Kerfoot et al., 1980; Beck and Turingan, 2007). Elusive prey such as calanoid copepods may prove to be too energetically costly for early developmental stages of larvae to pursue, independent of prey size (Coughlin, 1991). The positive selection of small, non elusive prey by first feeding *C. undecimalis* larvae may be attributed to the larva's ability to detect predator avoidance behavior of certain prey types. However, Beck and Turingan (2007) provided evidence that early larvae attempt to capture a wide variety of zooplankton prey using a stereotypical prey-capture behavior, but with a very low capture success rate. The size and mobility of prey types that can be successfully captured by fish larvae may be influenced by the mechanical properties and musculoskeletal linkages of the feeding apparatus since they control the rate and magnitude of buccal expansion used in suction feeding (Turingan et al., 2005).

The link between the development of the feeding apparatus and feeding performance in *C. undecimalis* larvae has important implications for the successful aquaculture of this species. As noted earlier, heightened mortality associated with starvation in early larvae may be alleviated by proper design of feeding protocols in the hatchery. Based on the association between stage-specific characteristics of the feeding apparatus and corresponding stage-specific metrics of feeding performance established in this study, we propose a stage-specific feeding-management scheme for snook hatchery aquaculture. The 'initial hyoid' feeding stage lasts from first feeding (3 dph) to 5 dph. During this two day period larvae are offered small, non-elusive prey organisms such as dinoflagellates and copepod nauplii at relatively high prey densities. When the cerato- and epihyal cartilages of the hyoid apparatus are developed during the 'complete hyoid' stage (6–20 dph) rotifers are provided. The 'initial opercular series' stage (21–31 dph) should be considered a transitional period, at which time larger more elusive prey are added to the diet, concurrently with rotifers. Larger, elusive zooplankton such as calanoid copepods may be added in greater quantities with 12 h *Artemia* at the beginning of the 'initial opercular series' stage starting around 20 dph. The 'complete opercular series' stage occurs at 31 dph, at which time larvae are able to modulate prey capture and feed on a variety of organisms such as 12 and 48 h *Artemia*. Weaning periods between stages are important to accommodate differential growth rates within broods.

Understanding the interplay between predator abilities, including prey-capture and swimming, and prey characteristics, including escape response and size, contribute immensely to our ability to formulate feeding-management protocols to guarantee success in the larviculture of commercially and recreationally important fish species. The formulation of an effective feeding-management regimen benefits from studies that integrate developmental functional morphology and feeding performance.

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