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Ontogeny of the feeding apparatus and sensory modalities: Relationship to habitat differentiation among early life history stage drums (Sciaenidae) in the Chesapeake Bay

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Ontogeny of the feeding apparatus and sensory modalities: Relationship to habitat differentiation among early life history stage drums (Sciaenidae) in the Chesapeake Bay

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In Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy

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by

Alison L. Deary

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APPROVAL SHEET

This dissertation is submitted in partial fulfillment of

the requirements for the degree of

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Alison L. Deary

Approved, by the Committee, April 2015

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ABSTRACT

Although the form and function of the structure of the feeding apparatus and diet are linked in adult fishes, it is often not clear when during ontogeny the ecomorphological patterns enable early life history stage fishes (ELHS) to partition their foraging niches and reduce competition. Sciaenid (family Sciaenidae) species exhibit variability in the structure of the feeding apparatus, which allows them to exploit more foraging habitats as adults than any other family in the Chesapeake Bay. In this study, ELHS and juvenile sciaenids representing three foraging guilds (pelagic: n=92, 2.9-48.2 mm SL; generalist: n=71, 4.3-53.8 mm SL; and benthic: n=75, 1.9-43.2 mm SL) were captured during weekly, shore-based ichthyoplankton and trawl surveys throughout the lower Chesapeake Bay, York River, and tidal inlets on Eastern Shore of Virginia. Stomachs were removed, specimens were cleared and double stained, and elements of the feeding apparatus were measured. A smaller subset of specimens (n=17) were stained using a 1% phosphotungstic acid solution and then scanned using micro-computed tomography to determine sensory modality in ELHS sciaenids representing the same foraging guilds. A dietary shift occurred first in pelagic sciaenids (16 mm SL), which corresponded to an expansion of sensory modalities, particularly gustation and audition that augment vision. The dietary shift was observed next in benthic sciaenids at 20 mm SL, which corresponded to the acquisition of oral and pharyngeal specializations suited to exploiting benthic prey even though they lacked sensory specializations. Finally, generalist sciaenids experienced a dietary shift at 35 mm SL, which occurred after the expansion of sensory modality (particularly vision, olfaction, gustation, and mechanoreception) but before specializations to the feeding apparatus were observed. Phylogenetic signal, measured as Pagel's λ, was also calculated for oral jaw elements using a molecular and a morphological topology to determine if evolutionary history may constrain the configuration of these elements and to understand how topology may influence the detected phylogenetic signal. Pagel's λ was low for pelagic sciaenids in premaxilla, lower jaw, and ascending process length, regardless of the topology used in the analysis. The signal was variable for benthic sciaenids depending on the topology used in the analysis; the signal was low when a morphological topology was used but was high for lower jaw and ascending process length when a molecular topology was used. In benthic sciaenids, Pagel's λ was intermediate for premaxilla length when the molecular topology was used, suggesting that the length of the premaxilla is influenced by natural selection despite some phylogenetic constraints. Therefore, the morphological patterns detected in ELHS sciaenids are not constrained exclusively by evolutionary history and represent ecomorphological, which suggest that sciaenids are able to partition foraging in nursery habitats during these early stages.

AUTHOR'S NOTE

The chapters of this dissertation were written in the format of the journal where each chapter is expected to be submitted. Therefore, the chapters are written in the third person to represent my co-authors. The expected citations for the chapters are as follows:

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Ontogeny of the feeding apparatus and sensory modalities: Relationship to habitat differentiation among early life history stage drums (Sciaenidae) in the Chesapeake Bay

GENERAL INTRODUCTION

Efficient feeding is important for fishes, especially in the early life history stages because it can optimize growth, survival, and reduce recruitment variability (Anto et al. 2009; Houde 2009; Nunn et al. 2012). The ability to successfully locate and capture prey can increase growth, reduce larval duration, and reduce vulnerability of larvae to predation, competition, and environmental perturbations (Houde 2009; Anto and Turingan 2010; Nunn et al. 2012). However, foraging ecology is poorly understood in early life history stage fishes. To forage successfully, fishes must be able to locate and then capture prey. Depending on spawning location, the early life history stages of estuarine-dependent marine fishes may have to make migrations from offshore spawning habitats to inshore nursery habitats (Able and Fahay 2010; Ribeiro et al. 2015). During these migrations, early life history stage fishes encounter new environmental conditions, which include changes in turbidity, water depth, and structural complexity, that they must overcome to locate food, avoid predators, and ultimately survive (Poling and Fuiman 1998). An organism's ecology is influenced by its morphology because the structure of skeletal elements results in functional trade-offs in regards how such structures can be used by an organism to complete an ecological task (Clifton and Motta 1998; Ferry-Graham et al 2008). Therefore, an examination of an organism's anatomy can provide insight into how these structures are used to complete important life history tasks (Wainwright 1996; Clifton and Motta 1998; Carlson and Wainwright 2010). However, many of the ecomorphological patterns described in fishes are based on the examination of juvenile and adult fishes (Wittenrich and Turingan 2011). The types of prey that can be consumed by ELHS fishes is restricted by the developmental state of the morphological structures related to foraging activities, including the feeding apparatus and sensory structures, which undergo changes in structure, complexity, and function during ontogeny, enabling fishes to exploit different prey (Anto and Turingan 2010; Bonato and Fialho 2014). To understand how early life history stage fishes overcome new environmental conditions to forage successfully, morphological changes to sensory systems and the feeding apparatus, which include both oral and pharyngeal jaw elements, were examined.

In order for fishes to successfully locate prey in new habitats, their sensory modality (sense or combination of senses used by an organism) will shift to match the prevailing environmental conditions (Poling and Fuiman 1997, 1998, 1999; Wagner 2002; Lisney et al., 2007). However, many coastal areas such as the Chesapeake Bay have undergone dramatic changes in water quality parameters and reductions in nursery habitats due to a substantial population increases (Kemp et al. 2005; Horodysky 2008). In the Chesapeake Bay, over 50% of marshes demonstrate evidence of retreat, seagrass beds have declined by 90%, and oyster reefs have been reduced 99% from historical population levels (Kemp et al. 2005; Orth et al. 2009). To understand how these changes to water quality and nursery habitats impact foraging success in early life history stage fishes, we need to first understand the senses that fishes use to successfully locate prey and how sensory modality may shift during ontogeny.

Once fishes locate prey, they then must be able to capture and process the prey in order to gain any nutritional value from the consumed prey. For early life history stage fishes, the type of prey that can be consumed is constrained by the developmental state and structure of the feeding apparatus (Anto and Turingan 2010; Nunn et al. 2012). The pharyngeal jaws of euteleostean fishes, which are modified elements of the gill arches, are structurally and functionally independent from the more anterior oral jaws (Grubich 2003; Alfaro et al 2009). The pharyngeal jaws are noted as a driver for the diversification of feeding strategies in euteleostean fishes because they have expanded the diversity of prey that fishes can process after capture with the oral jaws (Liem 1973; Wainwright et al. 2012) whereas the oral jaws function in prey capture. Ecomorphological trends have been described in the feeding apparatus of juvenile and adult fishes (Chao and Musick 1977; Wimberger 1991; Grubich 2003; Bhagat et al. 2011). For example, adult bottom foraging fishes tend to have shorter upper and lower jaw bones and shorter gill rakers relative to pelagic foraging fishes (Chao and Musick 1977; Bentzen and McPhail 1984; Aguirre and Shervette 2005). These differences in anatomical structure enable juvenile and adult fishes to partition their niches and ultimately reduce competition (Carlson and Wainwright 2010). However, it is not known when during ontogeny these ecomorphological patterns become apparent in early life history stage fishes.

The goal of this dissertation is to identify when niche partitioning can occur during ontogeny in estuarine-dependent, early life history stage fishes from the Chesapeake Bay by describing the development of sensory modality and feeding apparatus structure in conjunction with a dietary analysis. Species of the family Sciaenidae, the drums, were used as a model group for this study. The sciaenids are an economically important family of fishes globally and they support valuable commercial and recreational fisheries, especially along the Atlantic coast of North America and the Gulf of Mexico (Flores-Coto et al., 1998; Murdy and Musick, 2013; ASMFC). In addition to their economic importance, sciaenids are also able to partition their foraging habitats as adults due to differences in feeding apparatus anatomy and sensory modality that are used to locate, capture, and process prey (Chao and Musick, 1977; Horodysky et al., 2008), especially when species have overlapping ranges. Furthermore, 14 species of sciaenids use the Chesapeake Bay at some point during their life cycle as a nursery habitat, seasonal foraging ground, or permanently as residents (Murdy and Musick 2013). Therefore, the data obtained from this study can contribute to our understanding of niche partitioning in estuarine-dependent, early life history stage sciaenids. Once ecomorphological patterns are identified, these data are predictable (Clifton and Motta 1998; Hugeny and Pouilly 1999) and can be applied to other estuarine-dependent, early life history stage fishes to understand how and when they are able to partition foraging niches due to variations in their senses and feeding apparatus structure.

CHAPTER 1: Comparative ontogeny of the feeding apparatus of sympatric drums (Perciformes: Sciaenidae) from different foraging guilds in the Chesapeake Bay

INTRODUCTION

Growth, survival, and recruitment of early life history stage (ELHS) fishes to adult populations by are influenced by the ability of individuals to forage successfully (Anto et al., 2009). In addition, the types of prey that ELHS fishes can consume may be constrained by the developmental state and structure of the feeding apparatus (includes the oral and pharyngeal jaw elements) because it is responsible for the capture and processing of prey (Anto and Turingan, 2010; Nunn et al., 2012). The evolution of pharyngeal jaws in Euteleostei effectively results in these fishes possessing two sets of jaws (i.e., pharyngeal and oral jaws) that are structurally and functionally independent of each other (Grubich, 2003; Alfaro et al., 2009). The pharyngeal jaws are regarded as a key evolutionary innovation driving the diversification of feeding strategies in euteleostean fishes and these modified gill arch elements are used to manipulate and process prey items (Liem 1973; Wainwright et al., 2012). The oral jaws function primarily to capture prey whereas the pharyngeal jaws masticate and further process prey items prior to their passage to the posterior portions of the digestive system (Clifton and Motta, 1998; Grubich and Westneat, 2006).

The anatomy of feeding apparatus elements is often correlated with the primary foraging habitat of a species. For example, fishes that forage in the water column have relatively longer upper and lower jaws whereas benthic foraging fishes tend to have short upper and lower jaws but longer ascending processes (Chao and Musick, 1977; Wimberger, 1991). The toothplates of the pharyngeal jaws are more robust in fishes that forage on hard-bodied prey, which is typical of more benthic foraging fishes compared to fishes foraging on soft-bodied prey (e.g., Grubich, 2003; Bhagat et al., 2011). Fishes with longer and more densely packed gill rakers tend to feed on smaller, pelagic prey whereas those with shorter gill rakers feed on larger, benthic prey (Chao and Musick, 1977; Bentzen and McPhail, 1984; Aguirre and Shervette, 2005). However, it is not clear when during ontogeny these patterns become apparent and fishes are able to partition foraging niches, especially in closely related fishes. Therefore, an understanding of ontogenetic changes to the structure of the feeding apparatus can provide insight into the foraging ecology, niche partitioning, and adaptation of feeding elements (Carlson and Wainwright, 2010), especially among closely related taxa.

The family Sciaenidae is an important family of fishes worldwide, with many species supporting large and valuable commercial and sport fisheries particularly along the Atlantic coast of North America and the Gulf of Mexico (Flores-Coto et al., 1998; Murdy and Musick, 2013; ASMFC). Sciaenidae is also an excellent model group to examine the development of the feeding apparatus as members exhibit a great deal of variation in the structure of the feeding apparatus. Moreover, this variation reflects the partitioning of foraging habitats as adults, especially in areas where species are sympatric (Chao and Musick, 1977; Horodysky et al., 2008). Sciaenids also have the most diverse foraging habits of any fish family in the Chesapeake Bay (Chao and Musick, 1977). There are 14 species that use the Chesapeake Bay at some point in their life cycle as a nursery habitat, a seasonal foraging habitat, or permanently as residents.

We studied four species of sciaenids common in the Chesapeake Bay that as adults partition their foraging habitats. Spotted seatrout (*Cynoscion nebulosus*) and weakfish (*Cynoscion regalis*) are both pelagic predators as adults but exploit different aspects of the pelagic environment. Adult *C. nebulosus* tend to remain in and around structured habitats like seagrass beds and forage primarily on fishes (McMichael and Peters, 1989). In contrast, *C. regalis* forage in schools in shallow, unstructured coastal areas and prey on shrimp, large zooplankton and fishes (Aguirre and Shervette, 2005; Horodysky et al., 2008; Murdy and Musick, 2013). Atlantic croaker (*Micropogonias undulatus*) is considered to be a generalist because adults forage along the water-sediment interface for invertebrates (e.g., polychaetes) but also in the water column for small fishes and crustaceans (Murdy and Musick, 2013). Spot (*Leiostomus xanthurus*) is a benthic foraging sciaenid that as an adult feeds mainly on infaunal invertebrates; as a consequence, organic detritus and sediment are frequently found in their stomachs (Chao and Musick, 1977; Hugueny and Pouilly, 1999; Horodysky et al., 2008). By examining ontogenetic changes to the feeding apparatus in these four species, we can better understand when during ontogeny these species are able to partition their niches and exploit different foraging habitats.

Our goal is to identify when during ontogeny individuals of these four sciaenid species are able to functionally partition their foraging habitats within the Chesapeake Bay. Although other factors can influence prey selection for ELHS fishes (e.g., behavior, prey availability, sensory development), the anatomy and developmental state of the feeding apparatus can help to better understand the types of prey that fishes can functionally exploit, as well as provide a baseline for comparison to other fishes (Poling and Fuiman, 1998; Anto and Turingan, 2010). Accordingly, an examination of the feeding apparatus during ontogeny can identify critical points when niche partitioning can occur and indicate a time when species are no longer directly competing for food resources.

MATERIALS AND METHODS

Specimen Collection and Processing

Larval samples were collected using a 1-m diameter, 1-mm mesh conical plankton net during a weekly shore-based ichthyoplankton sampling program in the York River, a tributary of the Chesapeake Bay. The program has been active since 2007 (Ribeiro et al., in press). Juvenile and adult sciaenids were collected from other fisheries surveys conducted by the Virginia Institute of Marine Science (VIMS) throughout the lower Chesapeake Bay, including the York River. To target species found in coastal habitats, additional larval samples were collected in the tidal creeks at the VIMS Eastern Shore Laboratory (Wachapreague, VA) during eight sampling trips over two summers. After sorting the plankton samples and identifying fishes, standard length (SL) of all specimens was measured with calipers to the nearest 0.01 mm and fixed in 10% buffered formalin (Eastern Shore samples) or 70% ethanol (York River specimens). Specimens were identified to species according to the keys and species descriptions provided by Richards (2006) and Fahay (2007).

Taxa were classified into one of three primary foraging habitats (benthic, generalist, and pelagic) based on where the adult sciaenids forage. The two species of *Cynoscion* forage in the water column and are considered pelagic foragers whereas *Leiostomus xanthurus* consumes infaunal prey and is considered to be benthic (Chao and Musick, 1977; Horodysky et al., 2008; Murdy and Musick, 2013). *Micropogonias undulatus* forages both along the benthos and in the water column and is considered a generalist forager (Chao and Musick, 1977; Murdy and Musick, 2013).

Feeding Apparatus

The structure of the feeding apparatus was examined on cleared and double stained specimens (cartilage blue, calcified structures red) prepared following a protocol based on Taylor and Van Dyke (1985). We examined 260 specimens in total (*C. nebulosus*, n=44, 3.4-118.0 mm SL; *C. regalis*, n=46, 4.1-123.0 mm SL; *M. undulatus*, n=113, 4.9-185.0 mm SL; *L. xanthurus*, n=57, 10.4-88.5 mm SL). Oral and pharyngeal jaw elements of the feeding apparatus were photographed and measured using Zeiss SteREO DiscoveryV20 microscope and ImageJ (Fig. 1). Images were post-processed (background adjusted to a uniform white) in Adobe Photoshop CS5.1 and all figures were assembled using Adobe Illustrator CS5.1. The length of the ascending process (ap); premaxilla (pmx) and lower jaw (lj; anterior tip of dentary to articulation of angulo-articular with the quadrate); and the toothed areas of the third and fourth pharyngobranchial toothplates (pbtp3 and pbtp4, respectively) and the 5th ceratobranchial (cb5) were measured to the nearest 0.001 mm. On the first and second ceratobranchials, three randomly selected gill rakers (gr) and gill filaments (gf) were measured and an average length for these elements was calculated. Oral and pharyngeal dentition was described qualitatively (e.g., re-curved, straight, stout, slender, molariform). To investigate changes in these structures within a species during ontogeny and between species of similar ontogenetic stages, all measurements were analyzed relative to head length (HL; Fig. 2). The examined characters were selected because they 1) influence the position and function of the feeding apparatus, 2) affect the types of prey a fish can effectively consume and 3) because general trends have been described in these elements for adult fishes (Chao and

Musick, 1977; Wimberger, 1991; Grubich, 2003; Aguirre and Shervette, 2005; Bhagat et al., 2011).

Data Analysis

All data analysis was completed in R using the mvpart package (R-Project). Normality was tested using a Shapiro-Wilk Normality test with an alpha of 0.05; all measured elements violated the assumption of normality and were subsequently log-transformed. Once variables were log-transformed, multivariate regression trees (De'ath, 2002) were used to examine the similarities in regards to feeding apparatus variables. Cross validations were repeated 1,000 times and the best performing tree was manually selected to balance a tree that is both complex, but still minimizes the cross-validated error (De'ath, 2002; Davidson et al., 2010). For the primary variable attributed to a split, the average HL of specimens of all species possessing that feeding apparatus element size was determined.

RESULTS

Regression Analysis

A tree with 13 leaves was selected as the best performing regression tree for the feeding apparatus data (Fig. 3). The cross validation error for the tree was 0.8 (SE = 0.055) and it explains 74% of the species data (Fig. 4). Based on the variables used to determine these species groupings, three divergences were identified that differentiate these four species during ontogeny. Average gill filament length of the second arch, premaxilla length and toothed area of cb5 were the primary variables responsible for splits at three points during ontogeny, which were mapped onto the regression tree (A, B and C, respectively; Fig. 3). Split A occurred at approximately 8.4 mm HL and corresponded to differences in the average gill filament length of cb2. The divergence B occurred at 14.1 mm HL and was attributed primarily to premaxilla length while the final divergence, C, was attributed to the toothed area of the cb5 at 19.8 mm HL.

The regression tree never recovered either species of *Cynoscion* (pelagic) with *L. xanthurus* (benthic; Fig. 3). However, *M. undulatus* (generalist) was recovered sister to *L. xanthurus* and *Cynoscion* spp., suggesting that *M. undulatus* possessed jaw structures that were intermediate between benthic and pelagic foraging sciaenids even in the early life history stages.

Oral Jaws

In specimens smaller than 8.4 mm HL, the relative lengths of the premaxilla, lower jaw and ascending process were similar and there were no noticeable differences in these structures among the four species (Fig. 5, left column). During jaw development (> 8.4 mm HL), *L. xanthurus* possessed shorter premaxillae and lower jaws but longer and more robust ascending processes relative to the other three species (Table 1). The maxillae of *L. xanthurus* were also shorter and more robust relative to the other species at this stage (Fig. 5). *Micropogonias undulatus* possessed noticeably shorter premaxillae, maxillae, and lower jaws relative to *Cynoscion* spp. during jaw differentiation (Table 1; Fig. 5). The oral jaw bones of *M. undulatus* resembled those of *L. xanthurus*, although the ascending process in *M. undulatus* was intermediate in length relative to *L. xanthurus* and *Cynoscion* spp. (Table 1). In contrast, *Cynoscion* spp. possessed relatively elongate premaxillae and lower jaws and short ascending processes throughout ontogeny; *C. nebulosus* had a greater toothed area of pbtp4 and longer ascending process relative to *C. regalis* after 8.4 mm HL (Table 1). The structure of the oral jaws was very similar in the two species of *Cynoscion*, despite *C. nebulosus* possessing more elongate and pointed teeth relative to *C. regalis* by this stage (Fig. 5).

For the four sciaenid species, teeth were first present during ontogeny on the premaxilla and then developed slightly later during ontogeny on the dentary (Fig. 5). Teeth were rounded early in ontogeny but became more slender, pointed and recurved at later stages. For *C. nebulosus*, the enlarged fang that is characteristic of the genus was first observed at 9.2 mm HL and was situated near the symphysis of the paired premaxillae (Fig. 5). In *C. regalis*, the recurved canine was not noticeable until after the second divergence of 14.1 mm HL. However, the canine was more prominent in *C. regalis* than *C. nebulosus* because *C. regalis* possessed shorter and less recurved teeth along the premaxilla. In both *C. regalis* and *C. nebulosus*, the density of teeth on the dentary appeared to decrease in specimens larger than 14.1 mm HL. By 8.4 mm HL, *M. undulatus* had relatively short, straight teeth lining both the premaxilla and the dentary, although the teeth were more densely packed along the premaxilla. By 19.5 mm HL, after the second divergence at 14.1 mm HL, the premaxilla and dentary of *M. undulatus* were lined with densely packed teeth, although there was an extremely dense patch of teeth at the symphysis of both the premaxilla and dentary (Fig. 5). The dentary teeth were relatively straight whereas the teeth near the anterior end of the premaxilla were recurved and became straighter at the posterior end of this bone. The premaxilla and dentary of *L. xanthurus* were lined with equally spaced, straight teeth by 9.4 mm HL (Fig. 5). By 19.5 mm HL, the teeth of the premaxilla were longer and more recurved anteriorly. In contrast, there was no change in shape of the teeth along the dentary, although they were sparser (Fig. 5).

Pharyngeal Jaws and Other Gill Arch Elements

The pharyngeal toothplates were calcified early during ontogeny (before 8.4 mm HL) in all four species (Fig. 6). By about 4.0 mm HL, teeth were present on all three toothplates and the shape of the teeth, which were elongate and slightly recurved, were very similar among the examined species. After 8.4 mm HL, *L. xanthurus* had a greater toothed area on cb5, pbtp3, and pbtp4 relative to the other three examined species (Table 1). Molariform teeth were present on pbtp3 by 9. 8 mm HL and along the antero-medial portion of cb5 by 14.1 mm HL for *L. xanthurus* (Fig. 6). In addition, both pbtp3 and pbtp4 were more rounded in *L. xanthurus* relative to the other species. The shape of the pharyngeal toothplates for *M. undulatus* was more similar to the *Cynoscion* spp. than to *L. xanthurus* (Fig. 6). *Micropogonias undulatus* had a greater toothed area of pbtp3, pbtp4, and cb5 by 8.4 mm HL relative to *Cynoscion* spp. although the toothed area was still smaller than those of *L. xanthurus* (Table 1). There was no visible tooth specialization on the three main pharyngeal toothplates of *M. undulatus* (Fig. 6). The teeth were elongate and recurved in *M. undulatus*, but stouter than those on the toothplates of either species of *Cynoscion*. *Cynoscion nebulosus* and *C. regalis* had the smallest toothed areas of the three pharyngeal toothplates throughout ontogeny (Table 1). Of the four species examined during ontogeny, *C. regalis* had the smallest average toothed area of cb5 after 14.1 mm HL (Table 1). By 8.4 mm HL, *C. regalis* had smaller average toothed areas for both pbtp3 and pbtp4 (Table 1).There was no observed specialization of tooth type on any of the pharyngeal toothplates (Fig. 6). However, the longest and most recurved teeth were located along the medial portion of cb5 in *C. nebulosus* and *C. regalis* (Fig. 6).

The average gill filament length and gill-raker length on the second gill arch were used in the construction of the regression tree. Among the four species, there were differences in the shape of the gill rakers and the shape of these elements changes during ontogeny in each species. Before 8.4 mm HL, the gill rakers were not densely packed on the ceratobranchial or lined with dense patches of denticles (Fig. 7). In *C. nebulosus*, there was a mix of cylindrical and pointed gill rakers at 3.9 mm HL. *Cynoscion regalis* and *M. undulatus* both possessed cylindrical gill rakers capped with denticles by 3.9 mm HL. *Leiostomus xanthurus* possessed pointed gill rakers lacking distinct denticles at 4.0 mm HL (Fig. 7).

During ontogeny, the gill rakers of *C. nebulosus* became more rounded and highly denticulated. The gill rakers positioned more proximal to the junction between the epibranchial and ceratobranchial were longer than those more distal in both *C. regalis* and *C. nebulosus* (Fig. 7). In *C. regalis*, the gill rakers became more rounded during ontogeny and by 19.1 mm HL they alternated between a wide and short base along the length of the second ceratobranchial. Unlike the two species of *Cynoscion*, there was no change in the overall shape of the gill rakers in *M. undulatus* during ontogeny, although they were capped with more denticles at later ontogenetic stages. There was also no noticeable change in gill-raker length along the second ceratobranchial in either *M. undulatus* or *L. xanthurus* (Fig. 7). In *L. xanthurus*, the gill rakers became more ridge-like, capped with long, straight denticles and more densely packed during ontogeny.

DISCUSSION

Nursery habitats are important for many early life history stage (ELHS) marine fishes because there is ample food supply and potentially more shelter from predators, which can increase the probability of survival at such a vulnerable life history stage (Beck et al., 2001; Perez-Dominguez et al., 2006). However, in fishes with similar timing of ingress and settlement in nursery habitats, niche partitioning can potentially reduce dietary overlap and interspecific competition (Zahorcsak et al., 2000). In adults, the ability to partition foraging niches is often associated with specializations to the feeding apparatus (Chao and Musick, 1977; Hugueny and Pouilly, 1999; Albertson et al., 2008; Carlson and Wainwright, 2010). Shifts in habitat for ELHS fishes are attributed to changes in structural elements or sensory systems (Poling and Fuiman, 1998; Nunn et al., 2012) but it is often not known when during ontogeny fishes acquire the structural specializations to the feeding apparatus necessary to partition their foraging niches. The regression analysis presented herein identifies points during ontogeny where feeding apparatus elements no longer maximize homogeneity (De'ath 2002), suggesting that these elements differ enough among the four sciaenid species to support niche partitioning of the foraging habitat. The presence of multiple splits suggests that development of the feeding apparatus elements that enable niche partitioning is not gradual, but rather at certain stages during growth as a salutatory process (Balon 1981; Fig. 3).

Three primary divergences have been identified during ontogeny in the four examined sciaenid species (Fig. 3). The feeding apparatus elements that supported these divergences often reflect species-specific foraging habits (Chao and Musick, 1977; Govoni, 1987; Reecht et al., 2013). Based on many of the measured oral and pharyngeal jaw elements, *L. xanthurus* was the most morphologically distinct taxon by 8.4 mm HL (Table 1), suggesting that this species was able to separate its foraging habitat from the other three sciaenids. Therefore, *L. xanthurus* may be exploiting more benthic prey even at this point in ontogeny. Adult *M. undulatus* are considered generalists because individuals are known to forage both along the benthos and in the water column (Parker, 1971; Chao and Musick, 1977). By 19.8 mm HL, the measured oral jaw elements of *M. undulatus* were intermediate between *L. xanthurus* and *Cynoscion* spp., but had pharyngeal jaws more similar to *C. nebulosus*. This variation likely supports a more versatile, generalist foraging strategy because their oral jaws are suited to capture both benthic and pelagic prey although the robustness of the benthic prey is limited by the crushing ability of the pharyngeal toothplates. Although *C. regalis* and *C. nebulosus* are both pelagic sciaenids, these species occupy different environments in the Chesapeake Bay as adults and these ecological differences are reflected in the structure of the feeding apparatus (Horodysky et al. 2008). *Cynoscion regalis* and *C. nebulosus* both possess elongate premaxillae, maxillae, and lower jaws as well as short ascending processes and smaller toothed areas of the pharyngeal toothplates. There was, however, variation between these two species in oral jaw dentition, gill-raker structure and the size of cb5. Specifically, the differences in the gill raker structure suggest that the shorter, rounded gill rakers of *C. nebulosus* enable them to forage effectively on larger prey (e.g., fishes) whereas the cylindrical, taller gill rakers of *C. regalis* are more suited to foraging on smaller prey, even in the ELHS (Aguirre and Shervette, 2005). The sciaenids examined in this study do possess structural variation in several feeding apparatus elements early during ontogeny, although it is not yet known if members of this group are actually able to exploit different foraging habitats at early stages (Poling and Fuiman, 1998; Anto et al., 2009). With this caveat, the divergences identified here suggest that there are critical points during ontogeny when elements of the feeding apparatus sequentially undergo structural differentiation that accumulate to give rise to anatomical configurations associated with the adult foraging strategy in a salutatory process (Balon 1981).

The average gill filament length on the second ceratobranchial was associated with the first divergence at 8.4 mm HL (22.4 mm SL; Table 1; Fig. 2; Fig. 7). Although not directly related to foraging niche, gill filaments are longer in more active fishes (Hughes, 1966; Wegner et al., 2010), suggesting that the pelagic *Cynoscion* spp. may be more active in foraging activities compared to the more benthic oriented *M. undulatus* and *L. xanthurus*. In specimens smaller than 8.4 mm HL, there were few differences in the oral and pharyngeal jaw structures among the four species (Table 1; Figs. 5, 6). In regards to the pharyngeal toothplates (pbtp3, pbtp4, and cb5), there were no noticeable differences in tooth type or toothplate size among the four species in specimens smaller than 8.4 mm HL (Table 1; Fig. 6). However, differences in the shape of gill rakers on the second ceratobranchial among the four species were already present by 8.4 mm HL (Fig. 7). *Leiostomus xanthurus* and *C. nebulosus* both had pointed gill rakers, although *C. nebulosus* also possessed cylindrical gill rakers. *Micropogonias undulatus* and *C. regalis* possessed only cylindrical gill rakers capped with short denticles. As adults, elements of the feeding apparatus have been linked to foraging habitat in sciaenids and in ELHS fishes the developmental state of these structures influence foraging abilities (Chao and Musick, 1977; Govoni, 1987; Anto and Turingan, 2010). Therefore, the lack of differences in many of the oral and pharyngeal jaw elements suggests that these species have not yet partitioned their foraging habitats before 8.4 mm HL because they do not yet possess the structural specializations to the feeding apparatus. Gill rakers also reflect foraging habits in fishes (Chao and Musick, 1977; Bentzen and McPhail, 1984; Aguirre and Shervette, 2005) and the variations in the gill rakers of the second ceratobranchial by 8.4 mm HL suggest that changes in foraging habitats may be starting to occur.

The second divergence in the ontogeny of these taxa (Fig. 3) occurred at approximately 14.1 mm HL (30.4 mm SL; Fig. 2) and was associated primarily with length of the premaxilla, although there are also differences in toothed area of pbtp3, eye diameter, ascending process length, and average length of the gill rakers on the second ceratobranchial. Therefore, by 14.1 mm HL, many of the adaptations of the feeding apparatus necessary to exploit different foraging habitats have been attained in these four sciaenid species (Table 1; Figs. 4-7). Teeth were more numerous, arranged in multiple rows, and were well developed along the premaxilla and dentary in all four species. *Cynoscion* spp. and the generalist *M. undulatus* possessed similarly shaped teeth, although the recurved teeth were longest in *C. nebulosus*. Teeth were still present in *L. xanthurus* at this stage but they differed in shape from the other three examined sciaenid species because these teeth were not recurved. By 14.1 mm HL, there are many differences in the oral and pharyngeal jaw elements for *L. xanthurus*, including noticeably shorter premaxillae, maxillae, and lower jaws; as well as enlarged ascending processes relative to the other species (Table 1). *Leiostomus xanthurus* also possessed more robust, rounded pharyngeal toothplates relative to the other three species. Unlike the other three species, where the toothplates were lined with elongate, slightly recurved teeth, *L. xanthurus* had molariform teeth on pbtp3 and cb5. In addition, *L. xanthurus* has ridge-like gill rakers on the second ceratobranchial capped with elongate denticles that differed in shape and density from the cylindrical gill rakers of *C. regalis* and *M.*

undulatus and the rounded gill rakers of *C. nebulosus*. The distinctive shape and structure of the oral and pharyngeal jaw elements indicates that *L. xanthurus* is anatomically able to partition their foraging habitats and adopt a more benthic foraging strategy. At this stage, *L. xanthurus* also possessed specializations in the pharyngeal jaws necessary to masticate harder-bodied prey, including greater toothed areas on the pharyngeal toothplates and molariform teeth on pbtp3 and cb5 (Chao and Musick, 1977; Govoni, 1987; Grubich, 2003; Nunn et al., 2012). *Micropogonias undulatus*, which as an adult is a generalist foraging sciaenid, possessed oral jaw elements that were more similar to the pelagic foraging *Cynoscion* spp., suggesting that at this stage, *M. undulatus* is foraging in the water column for prey similar to those of *C. nebulosus* and *C. regalis*.

The third divergence, which occurred later in the juvenile phase, was observed at approximately 19.8 mm HL (>40.0 mm SL; Fig. 2). This divergence was associated with the toothed area of cb5. By this stage, both species of *Cynoscion* possessed an enlarged canine at the symphysis of the premaxilla, although it was more distinct in *C. regalis* due to the relative stubbiness of the surrounding premaxillary teeth. However, *M. undulatus* possessed teeth more similar in shape to *L. xanthurus*, suggesting a shift in foraging habitat for *M. undulatus*. However, there were dense tooth patches at the symphysis of the premaxilla and dentary in *M. undulatus* that were not present in *L. xanthurus*. Teeth were still present at this stage for *L. xanthurus*. As in *L. xanthurus*, *M. undulatus* had shorter premaxillae, maxillae, and lower jaws, and enlarged ascending processes relative to *Cynoscion* spp (Table 1). The pharyngeal toothplates of *M. undulatus* were more robust at this stage, although the toothplates were more similar in shape to the toothplates of *C. nebulosus* and *C. regalis* (Fig. 6). The toothplates of *M. undulatus* also lacked molariform teeth, suggesting differences in ELHS foraging habits between *M. undulatus* and *L. xanthurus* (Chao and Musick, 1977). Based on the configuration of the oral and pharyngeal jaws, it is expected that *M. undulatus* exploits more benthic prey, although not exclusively because its oral and pharyngeal jaw elements were intermediate between benthic and pelagic foraging sciaenids. The gill rakers of *C. regalis* along the second ceratobranchial became more similar in shape to *C. nebulosus,* although the gill rakers were not as densely packed in *C. regalis*. The gill rakers of *C. regalis* alternated between short and tall, which was not observed in the other species (Fig. 7), and may be a specialization along the gill arches allowing a diverse assemblage of planktonic prey to be consumed effectively (Bentzen and McPhail, 1984; Bhagat et al., 2011). The toothed area of the cb5 in *C. regalis* was also greater than that of *C. nebulosus*. The differences in gill raker shape and the toothed area of the cb5 suggests that there may be niche partitioning in ELHS even in these closely related species.

Observed ontogenetic shifts in diet are associated with changes in vision and fin development, which enable larvae to more effectively sense and capture prey, as well as changes in habitat use (Nunn et al., 2012). Although there is some temporal separation regarding the ingress of these four species into the Cheseapeake Bay, ELHS of all four species are present during the summer and early fall months (Chao and Musick, 1977; Ribeiro et al., in press). Therefore, the divergences in morphological structures we described during ontogeny may enable these four species to exploit different foraging habitats in the early life history stages, thereby reducing competition in nursery habitats, including the Chesapeake Bay.

MATERIALS EXAMINED

Cynoscion nebulosus: VIMS 22223-22253 (30 C&S, 3.4-103 mm SL); VIMS 22295 (1 C&S, 31.6 mm SL)

Cynoscion regalis: VIMS 22254-22294 (29 C&S, 3.0-117); VIMS 22296 (1 C&S, 9.3 mm SL)

Leiostomus xanthurus: VIMS 22310-22365 (56 C&S, 11.6-115 mm SL); VIMS 22547 (1 C&S, 88.5 mm SL)

Micropogonias undulatus: VIMS 22384- 22489 (106 C&S, 4.0-166 mm SL); VIMS 22548-22550 (3 C&S, 44-55 mm SL)

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Table 1. Mean feeding apparatus length (mm) or area (mm^2) for *Cynoscion nebulosus*, *C. regalis*, *Micropogonias undulatus* and *Leiostomus xanthurus* once differences in the jaw elements were observed. Average measurements were calculated between the first and second split (8.4-14.1 mm HL) and the second and third split (14.1-19.8 mm HL) observed in the regression tree. Sample sizes for each split are denoted by parentheses in the first row for that split, respectively. Abbreviations: HL, head length; cb, ceratobranchial; pbtp, pharyngobranchial toothplate; gf, gill filament.

Average Feeding Apparatus Element Size	***C. nebulosus***	***C. regalis***	***M. undulatus***	***L. xanthurus***
	1st Split: 8.4-14.1 mm HL			
Premaxilla Length	4.1 (n=6)	3.5 (n=2)	2.9 (n=6)	2.4 (n=7)
Lower Jaw Length	6.0	4.8	4.5	4.5
Ascending Process Length	1.3	1.2	1.7	2.3
2nd gf length	0.7	0.7	0.6	0.6
Toothed Area pbtp3	0.3	0.2	0.5	1.8
Toothed Area pbtp4	0.2	0.1	0.3	0.9
Toothed Area cb5	0.4	0.4	0.7	1.5
	2nd Split: 14.1-19.8 mm HL			
Premaxilla Length	7.0 (n=1)	5.7 (n=2)	4.5 (n=4)	3.1 (n=2)
Lower Jaw Length	10.1	8.5	6.9	6.1
Ascending Process Length	2.3	1.8	2.7	3.3
2nd gf length	1.9	1.3	1.1	0.9
Toothed Area pbtp3	1.1	0.6	1.6	3.2
Toothed Area pbtp4	0.9	0.5	0.9	2.6
Toothed Area cb5	1.8	1.1	1.9	3.3

Fig 1. Oral and pharyngeal jaw elements measured. Black lines and outlines indicate how elements were measured (except in "Pharyngeal Jaw Elements" panel). All elements are from specimens of *M. undulatus*. Abbreviations: SL, standard length; HL, head length; ED, eye diameter; ap, ascending process; pmx, premaxilla; lj, lower jaw; gr, gill raker; cb, ceratobranchial; pbtp, pharyngobranchial toothplate; gf, gill filament; ep, epibranchial.

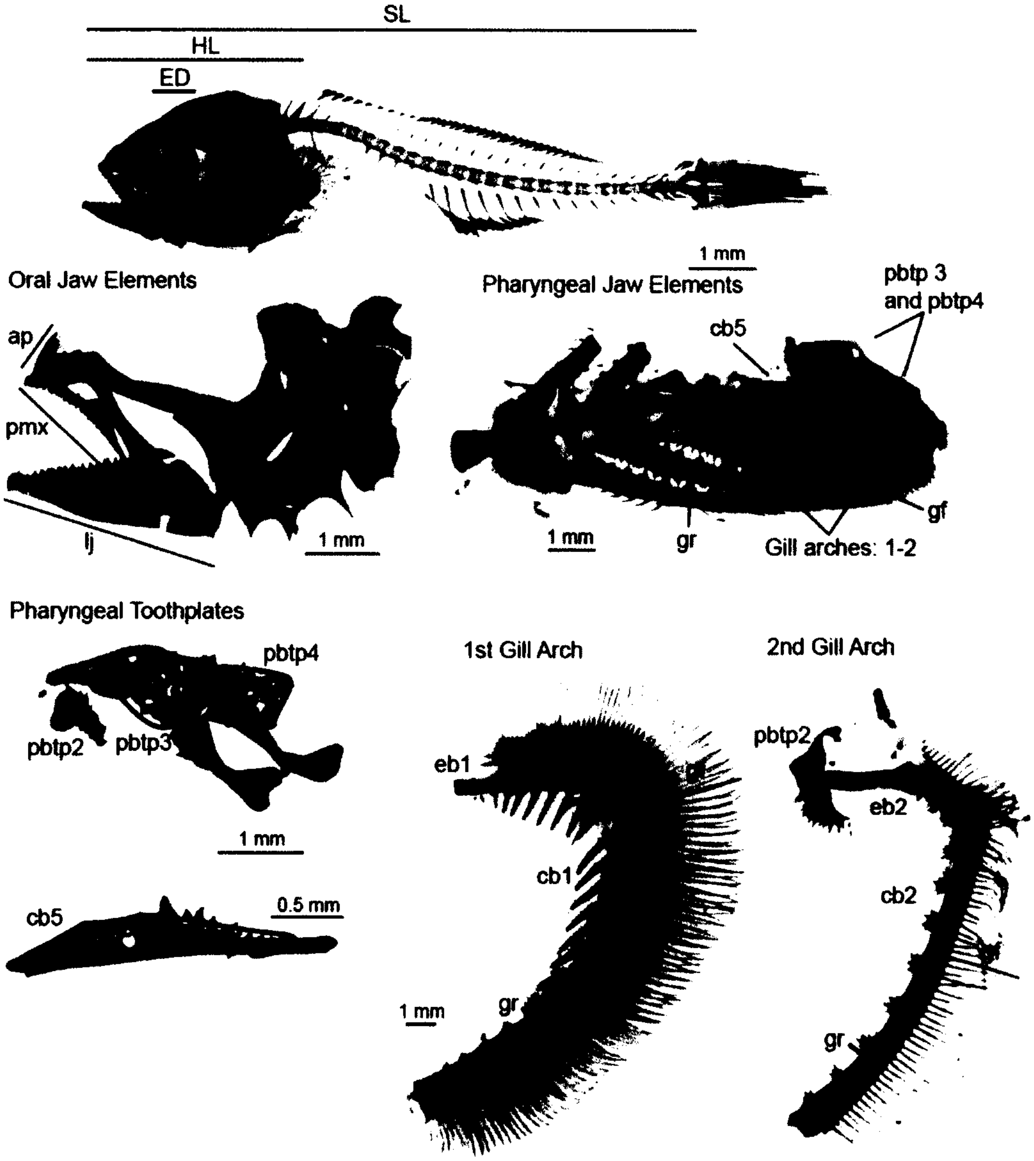

SL
HL
ED
1 mm
Oral Jaw Elements
ap
pmx
lj
1 mm
Pharyngeal Jaw Elements
pbtp 3 and pbtp4
cb5
gf
1 mm
gr
Gill arches: 1-2
Pharyngeal Toothplates
pbtp4
pbtp2
pbtp3
1 mm
cb5
0.5 mm
1st Gill Arch
eb1
gf
cb1
gr
1 mm
2nd Gill Arch
pbtp2
eb2
cb2
gr

Fig 2. Relationship of standard length (SL) to head length (HL) in mm for *Cynoscion nebulosus* (green diamonds), *C. regalis* (blue triangles), *Micropogonias undulatus* (orange circles), and *Leiostomus xanthurus* (brown squares).

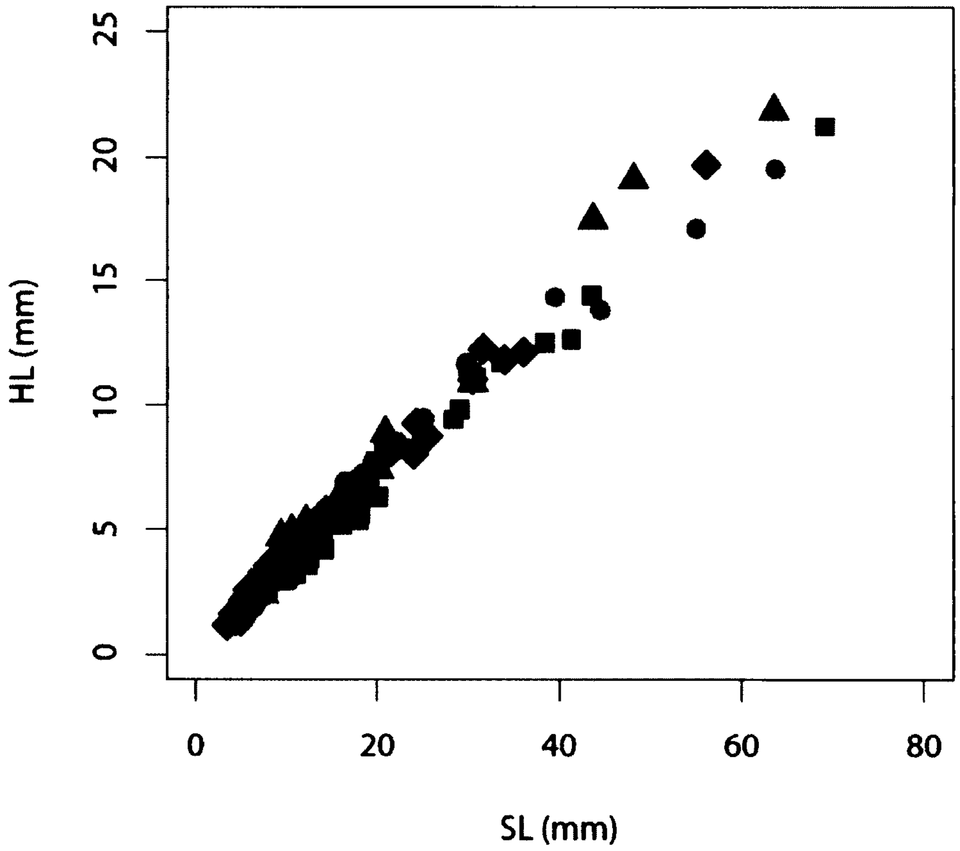
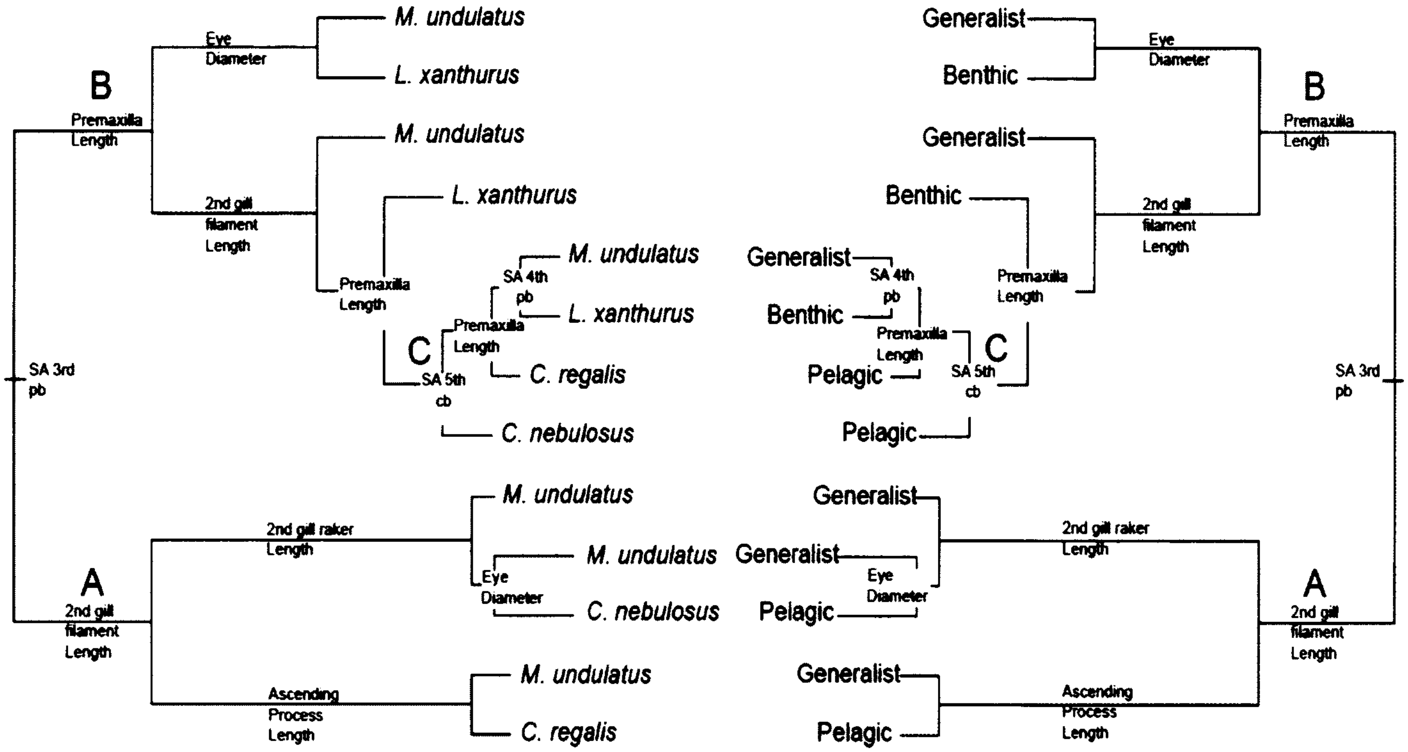

HL (mm)
0
5
10
15
20
25
0
20
40
60
80
SL (mm)

Fig 3. Pruned regression tree containing 13 leaves (cross-validation error = 0.8, Standard Error = 0.055, variance explained = 0.74). Both trees depict the same topology. The regression tree on the left is labelled with species names whereas the right tree is labelled with the foraging habitat of each species. A, B, C correspond to the location of the major splits observed in the anatomy of the elements of the feeding apparatus.



B
Premaxilla Length
Eye Diameter
M. undulatus
L. xanthurus
2nd gill filament Length
M. undulatus
L. xanthurus
Premaxilla Length
SA 4th pb
M. undulatus
L. xanthurus
Premaxilla Length
C
SA 5th cb
C. regalis
C. nebulosus
SA 3rd pb
A
2nd gill filament Length
2nd gill raker Length
M. undulatus
Eye Diameter
M. undulatus
C. nebulosus
Ascending Process Length
M. undulatus
C. regalis
Generalist
Benthic
Eye Diameter
B
Premaxilla Length
Generalist
Benthic
2nd gill filament Length
Premaxilla Length
Generalist
SA 4th pb
Benthic
Premaxilla Length
C
Pelagic
SA 5th cb
Pelagic
SA 3rd pb
Generalist
2nd gill raker Length
Generalist
Eye Diameter
Pelagic
A
2nd gill filament Length
Generalist
Ascending Process Length
Pelagic

Fig 4. The relative error (open circles, black line) and cross-validated relative error (open circles, blue line). The solid black line is one standard error above the minimum cross-validated relative error. The yellow circle denotes the best tree within one standard deviation.

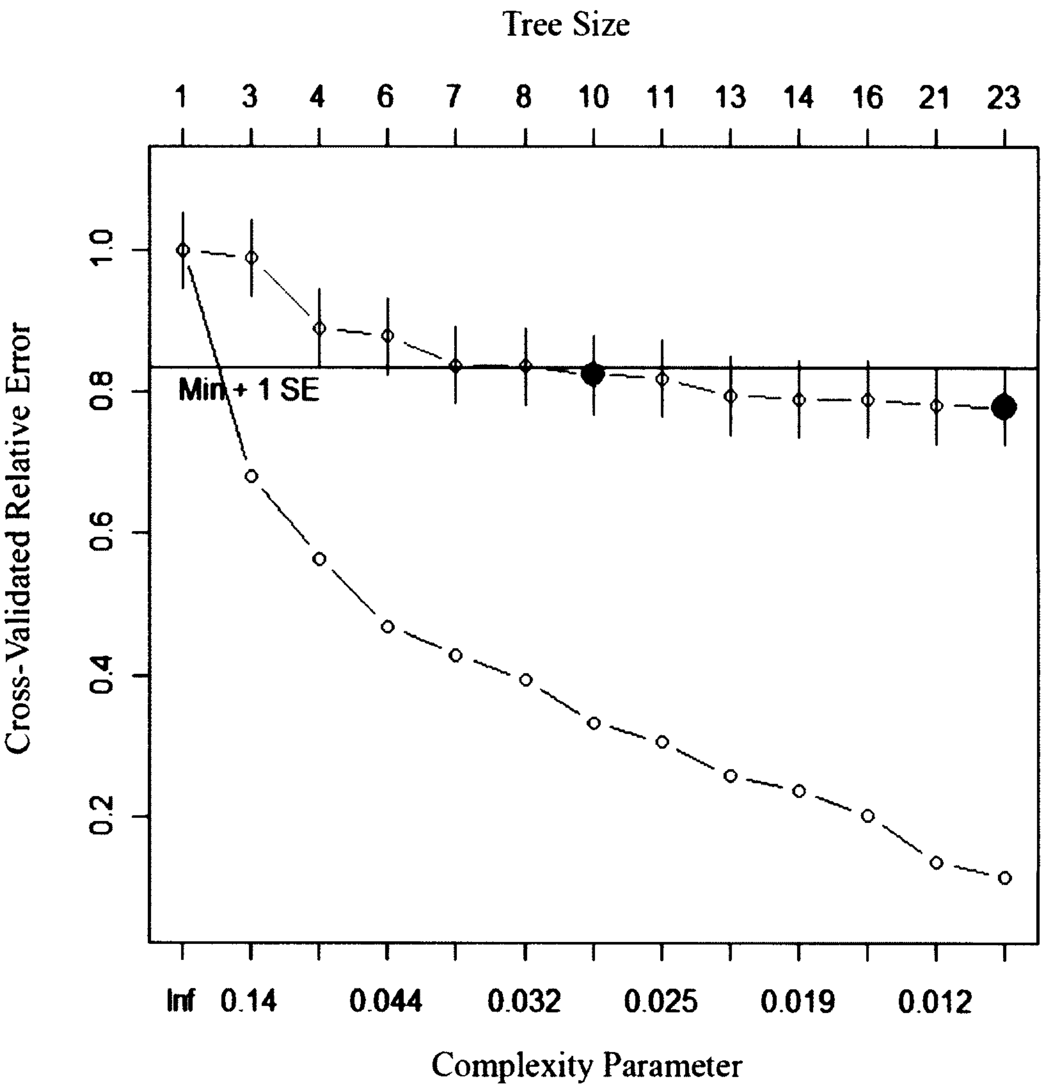

Tree Size
1
3
4
6
7
8
10
11
13
14
16
21
23
Cross-Validated Relative Error
1.0
0.8
0.6
0.4
0.2
Min + 1 SE
Inf
0.14
0.044
0.032
0.025
0.019
0.012
Complexity Parameter

Fig 5. Comparison of the oral jaws during ontogeny corresponding approximately to the three splits observed in the regression tree (left, middle, right columns respectively) for all four examined sciaenid species (A-C, *Cynoscion nebulosus*; D-F, *C. regalis*; G-I, *Micropogonias undulatus*; J-L, *Leiostomus xanthurus*). Abbreviations: ang-ar, angulo-articular; ap, ascending process; den, dentary; HL, head length; mx, maxilla; pmx, premaxilla; TL, total length.

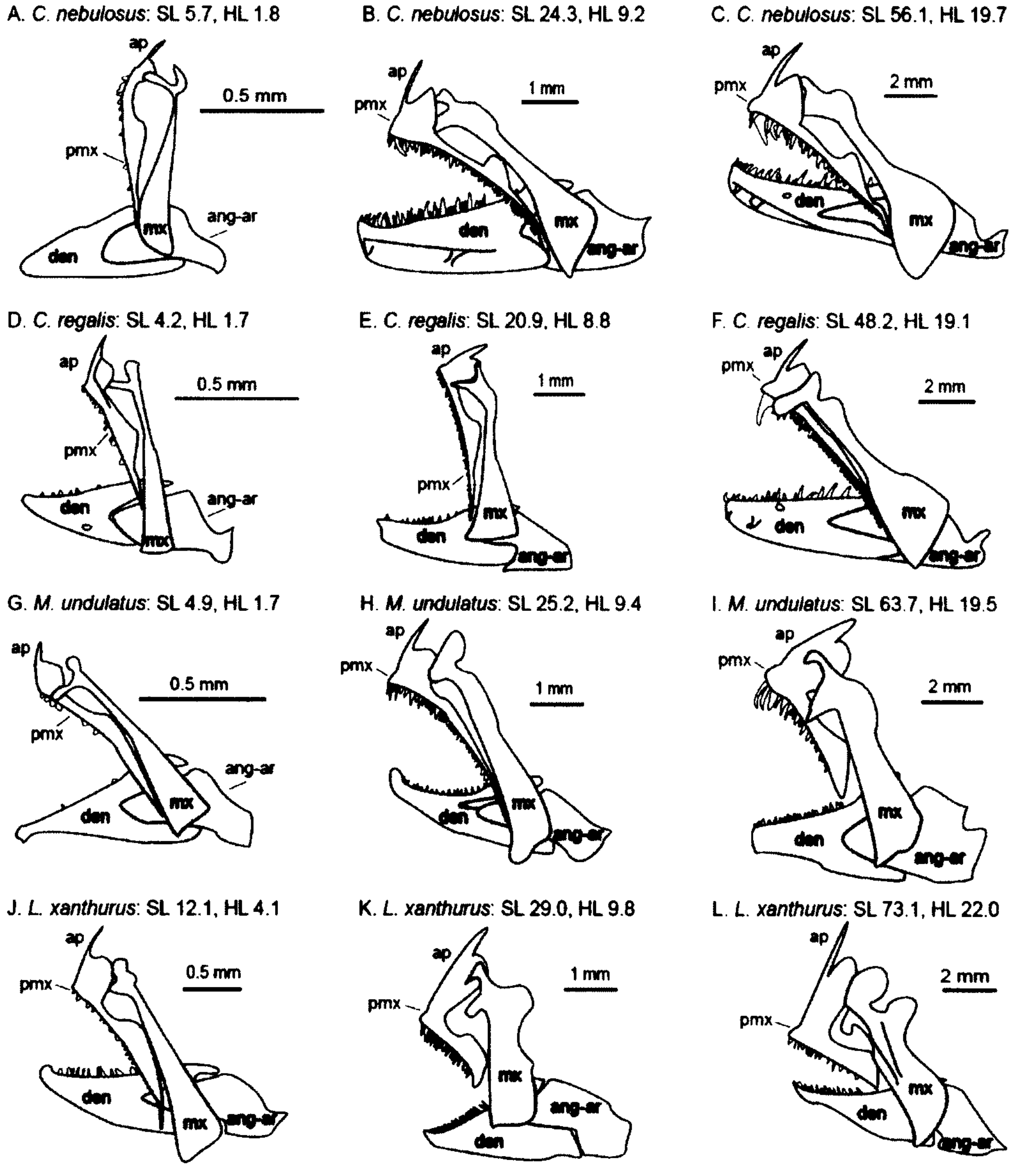
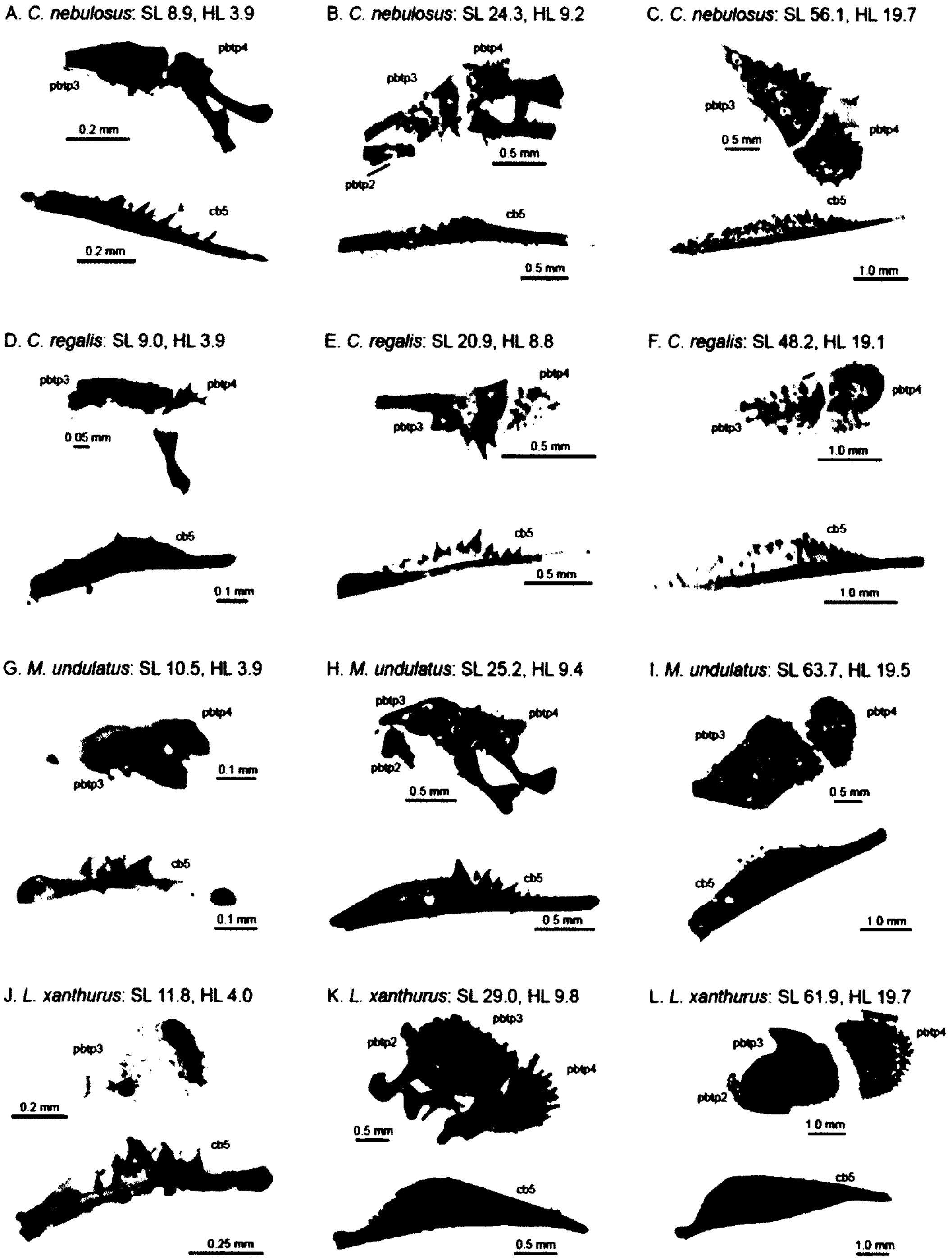


Fig 6. Comparison of the three pharyngeal toothplates during ontogeny corresponding approximately to the three splits observed in the regression tree (left, middle, right columns respectively) for all four examined sciaenid species (A-C, *Cynoscion nebulosus*; D-F, *C. regalis*; G-I, *Micropogonias undulatus*; J-L, *Leiostomus xanthurus*). Abbreviations: cb, ceratobranchial; pbtp, pharyngobranchial toothplate; HL, head length; TL, total length.



A. *C. nebulosus*: SL 8.9, HL 3.9

B. *C. nebulosus*: SL 24.3, HL 9.2

C. *C. nebulosus*: SL 56.1, HL 19.7

D. *C. regalis*: SL 9.0, HL 3.9

E. *C. regalis*: SL 20.9, HL 8.8

F. *C. regalis*: SL 48.2, HL 19.1

G. *M. undulatus*: SL 10.5, HL 3.9

H. *M. undulatus*: SL 25.2, HL 9.4

I. *M. undulatus*: SL 63.7, HL 19.5

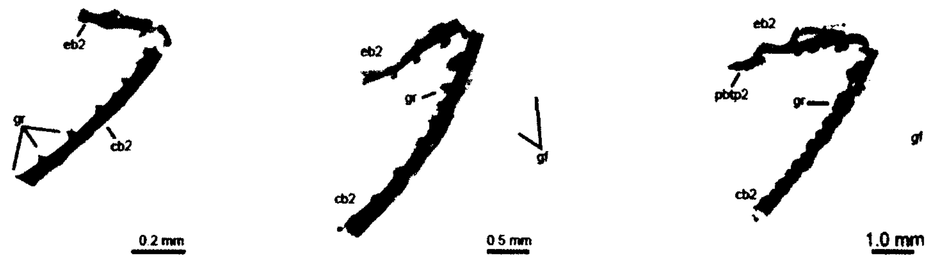
J. *L. xanthurus*: SL 11.8, HL 4.0

K. *L. xanthurus*: SL 29.0, HL 9.8

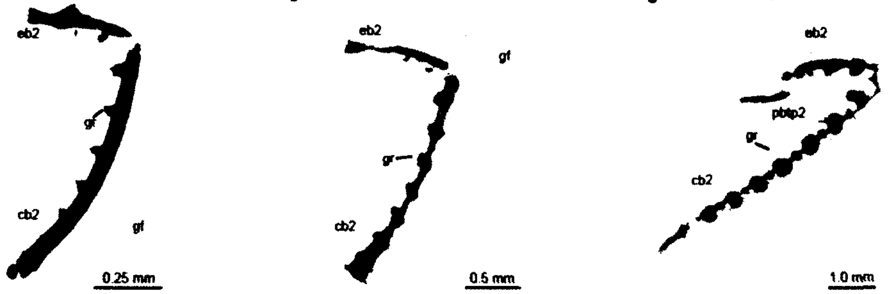
L. *L. xanthurus*: SL 61.9, HL 19.7

Fig 7. Images of the second gill arch during ontogeny corresponding approximately to the three splits observed in the regression tree (left, middle, right columns respectively) for all four examined sciaenid species (A-C, *Cynoscion nebulosus*; D-F, *C. regalis*; G-I, *Micropogonias undulatus*; J-L, *Leiostomus xanthurus*). Abbreviations: cb, ceratobranchial; ep, epibranchial; pbtp, pharyngobranchial toothplate; gr, gill raker; gf, gill filament; HL, head length; TL, total length.

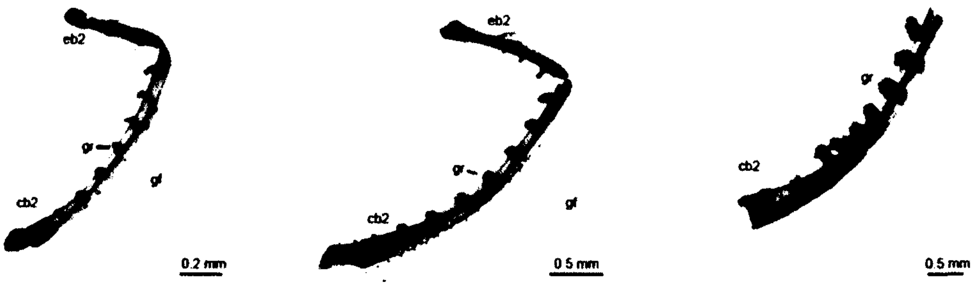
A. *C. nebulosus*: SL 8.9, HL 3.9 B. *C. nebulosus*: SL 25.6, HL 8.7 C. *C. nebulosus*: SL 56.1, HL 19.7



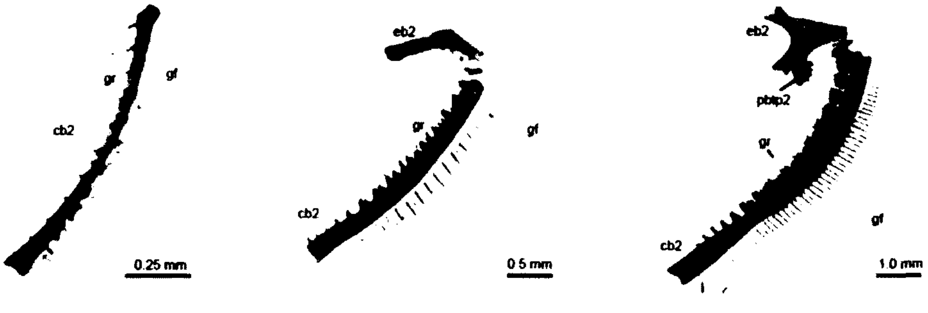
D. *C. regalis*: SL 9.0, HL 3.9 E. *C. regalis*: SL 20.9, HL 8.8 F. *C. regalis*: SL 48.2, HL 19.1



G. *M. undulatus*: SL 10.5, HL 3.9 H. *M. undulatus*: SL 25.2, HL 9.4 I. *M. undulatus*: SL 63.7, HL 19.5



J. *L. xanthurus*: SL 11.8, HL 4.0 K. *L. xanthurus*: SL 29.0, HL 9.8 L. *L. xanthurus*: SL 61.9, HL 19.7



CHAPTER 2: Development of sensory modality in early life history stage estuarine fishes (Sciaenidae) from the Chesapeake Bay using micro-computed tomography

INTRODUCTION

The substantial human population increases in coastal areas over the last century have added new pressures to estuarine and inshore areas, especially the Chesapeake Bay and its watershed. These include increased nutrient loads, decreased water clarity, depleted dissolved oxygen in the bottom water, and altered community structure of fishes [Kemp et al., 2005]. Many habitats of the Chesapeake Bay that serve as nurseries for fishes and other aquatic organisms have suffered dramatic reductions from historical populations due to these changes in water quality, particularly increasing turbidity and nutrient loads [Moore et al., 2003; Kemp et al., 2005; Orth et al., 2009]. For example, more than 50% of marshes show evidence of retreat, seagrasses have declined 90%, and oysters have been reduced 99% from population levels witnessed a century ago [Kemp et al., 2005; Orth et al., 2009]. In addition, these changes have altered the sensory environment of the Chesapeake Bay at rates faster than fishes can adapt to the new prevailing conditions [Horodysky et al., 2008a]. In this context, it is important to understand not only the senses that early life history fishes rely on to locate food and evade predators but also how a fish's reliance on a suite of senses may change during ontogeny.

Fishes in the family Sciaenidae exhibit a great deal of morphological variation in their feeding apparatus and sensory systems, allowing sympatric species to partition foraging habitats as adults [Chao and Musick, 1977; Horodysky et al., 2008a and b; Deary and Hilton, unpublished]. For example, adult *Cynoscion nebulosus* are pelagic predators of small fishes and crustaceans that reside in shallow seagrass beds [Chao and Musick, 1977; Murdy and Musick, 2013]; this species possesses eyes that are not light sensitive but have better resolution relative to the other sciaenids (low temporal summation) [Horodysky et al., 2008a]. During development, *C. nebulosus* have high visual sensitivity by the end of the larval period but also more sensitive to mechanoreceptive stimuli relative to *Micropogonias undulatus* and *Sciaenops ocellatus* [Poling and Fuiman, 1998]. *Sciaenops ocellatus* is a generalist sciaenid that as an adult, forages in the water column and along the reduced light benthic environment for invertebrates and fishes; this species has light sensitive eyes relative to other sciaenids [Horodysky et al., 2008a]. Early during ontogeny, *S. ocellatus* possess more neuromasts (free then incorporated into the cephalic canals than *C. nebulosus* and by later larval stages, their eyes become light sensitive as well, indicating strong mechanoreceptive and visual abilities suited for foraging in low-light environments [Poling and Fuiman, 1998]. *Leiostomus xanthurus* is a benthic foraging sciaenid feeding on polychaetes and bivalves as adults; this species has light sensitive eyes that balance light sensitivity, speed (flicker fusion frequency), and resolution [Horodysky et al., 2008a]. Little is known about the sensory development of *L. xanthurus*, although it is expected that they would possess light sensitive eyes by the juvenile stage because this species inhabits deeper waters along the benthos [Chao and Musick, 1977; Poling and Fuiman. 1998; Horodysky et al., 2008a]. *Sciaenops ocellatus* and *L. xanthurus* lack anterior swimbladder extensions but they are present in adult *C. nebulosus*, suggesting this species has broader auditory range than the other two species [Ramcharitar et al., 2006a; Horodysky et al., 2008b].

As fishes grow, settle, and transition into adult habitats, their sensory modalities (a sense or combination of senses used by an organism) shift in order for them to survive successfully under the new sensory conditions [Poling and Fuiman, 1998; Lisney et al., 2007]. Differences in sensory development have been described among *Cynoscion nebulosus, Micropogonias undulatus*, and *Sciaenops ocellatus*. However, ontogenetic changes to the peripheral sense organs were only observed in these species in the late larval or early juvenile period [Poling and Fuiman, 1998, 1999], which suggests there may be structural constraints on the development of the peripheral sensory organs in the early life history stages [Poling and Fuiman, 1998, 1999]. There may also be morphological changes to the sensory brain regions that precede changes to peripheral sense organs and habitat shifts [Poling and Fuiman, 1998; Lisney et al., 2007].

The development of visual and mechanoreceptive systems has been studied in some early life history stage sciaenid species, although little is known regarding olfaction, audition or gustation [Poling and Fuiman, 1997, 1998, 1999]. Therefore, we used three species of sciaenids common to the Chesapeake Bay but that represent distinct foraging habitats, to assess the relative importance of various sensory modalities. The relative size of the peripheral sense organs scales positively with the corresponding processing region of the brain for that sense, which provides a reasonable indication of the relative importance of a particular sensory system [Poling and Fuiman, 1998; Lisney et al., 2007]. We assessed ontogenetic patterns of sensory modality by using micro-computed tomography to examine the relative size of brain regions associated with olfaction, vision, gustation, audition, and mechanoreception in early life history stage sciaenids that exploit different foraging habitats as adults.

MATERIALS AND METHODS

Specimen collection- Specimens were collected using two 0.5-m opening bongo net equipped with 1-mm and 350-µm mesh outside the Virginia Institute of Marine Science's (VIMS) Eastern Shore Facility in Wachapreague, VA. Specimens were also collected from the VIMS Juvenile Fish and Blue Crab Trawl Survey using a 9.14-m semi-balloon otter trawl (38.1-mm stretched mesh and a 6.35-mm lined cod-end). Two additional trawl nets and a 50-ft seine net (1-mm mesh) were used to collect sciaenids from habitats too shallow for the VIMS Juvenile Trawl Survey vessel including a 1-m beam trawl (6.35-mm stretch mesh and 3.18-mm lined cod-end) and a 4.88-m otter trawl (38.1-mm stretched mesh and a 6.35-mm lined cod-end).Three adult foraging habitats (pelagic, generalist, benthic) were represented by a species that exemplified each foraging guild: *S. ocellatus* a generalist forager; *C. nebulosus* a pelagic forager; *Leiostomus xanthurus* and *Menticirrhus* sp. both benthic foragers. Pre-settlement specimens of *L. xanthurus* were not available. *Menticirrhus* sp. and *L. xanthurus* possess similar feeding structures (i.e., small gape, inferior mouth position, relatively short upper and lower jaw bones, villiform teeth, long intestines), are both slow swimmers, and feed on benthic prey [Chao and Musick, 1977; Murdy and Musick, 2013]. In addition, polychaetes and organic detritus were frequently encountered in the guts of *Menticirrhus* sp. and *L. xanthurus* [Chao and Musick, 1977], suggesting that these species occupy a very similar foraging habitat. Although *Menticirrhus* sp. possesses a pored barbel (absent in *L. xanthurus*) as adults, the barbel is not yet present during the early larval periods [Richards, 2006]. Some inter-specific differences in sensory development are expected, although we assume that these are likely limited in the earliest life history stage examined due to structural constraints and a lack of differentiation in the peripheral sense organs [Chao and Musick, 1977; Poling and Fuiman, 1998; Richards, 2006]. To examine ontogenetic changes in the development of sensory brain regions, specimens of these foraging habitats were grouped into three size bins of approximately equal head lengths (HL) that correspond to changes in habitat use (Table 1).

Specimen Preparation- Specimens were fixed in buffered formalin and transferred to 70% ethanol (ETOH) after fixation. Specimens were then soaked in a 1% phosphotungstic acid (PTA)-70% ETOH solution, which binds to various proteins and connective tissues [Metscher, 2009], for ~12 to 72 hours, depending on the size of the specimen (e.g., specimens less than 5.12 mm standard length (SL) soaked overnight). This provides tissue contrast in the scanned fishes [Metscher, 2009]. Specimens were then transferred back into 70% ETOH or mounted in agarose. Specimens were scanned with an Xradia MicroXCT system (Vienna, Austria) equipped with a 90 keV/8 W tungsten x-ray source and a 1,000 x 1,000 CCD camera and switchable scintillator-objective lens units [Metscher, 2009]. Because of its size, a single specimen of *S. ocellatus,* 46.92 mm SL was scanned with a SkyScan 1174 scanner (Vienna, Austria) with a 50 keV/40 W tungsten x-ray source and 1.3 megapixel CCD camera because of its size.

Illustration Preparation, Measurements, and Analysis- Images obtained from the Xradia scanner were aligned using the Xradia viewer software and exported as 8-bit TIFF image stacks. Three-dimensional reconstructions of the sensory brain regions were made using Amira (Vienna, Austria), which also allowed us to calculate the volumes of the various brain regions that were identified. The brain regions evaluated were the olfactory bulbs (olfaction), optic tectum (vision), lobus facialis and lobus vagal (gustation) and the eminentia granularis and auditory/vestibular nerve (audition/mechanoreception) [Wagner, 2002; Eastman and Lannoo, 2007; Lisney et al., 2007]. These regions were identified in the scans based on descriptions provided by Eastman and Lannoo (2007) and Kortschal (1998). In addition to marking sensory brain regions, extensions of the brain and nerve tracts were included in the volume calculations for vision, olfaction, and audition/mechanoreception because it is unknown when sensory information is processed and integrated along these tracts [Nieuwenhuys, 1982; Collin, 2012].; therefore, these regions are referred to as the optic, olfactory and auditory/mechanoreceptive tracts The brush tool in Amira was used to label the structures of interest in approximately every third or fifth image depending on the variability of the structure between slices. The interpolation function was used to highlight the structure of interest in the unmarked images. The interpolated images were then manually inspected and any errors corrected using the brush tool.

Distances between the swimbladder and inner ear were measured as the minimum distances between the anterior end of the swimbladder and the posterior edge of the most posterior otolith (lagenar) [Ramcharitar et al., 2006a]. These data were used as an additional indication of relative auditory abilities. Increased proximity of the swimbladder to the inner ear augments the auditory abilities of fishes as the mechanical displacement of the swim bladder because the pressure component of aquatic sound is better translated to displacement of the otoliths relative to the sensory hair cells [Ramcharitar et al., 2006a; Popper and Fay, 2011; Schulz-Mirbach et al., 2012].

All data were analyzed in R [R-Project]. Normality was tested using a Shapiro-Wilk Normality test ($\alpha=0.05$); data that were not normally distributed, HL and otolith volume (both saccular and lagenar), were log-transformed. Proportional data (i.e. the fractional volume of a sensory brain region) were transformed using logit in the car package [Warton and Hui, 2013]. An Analysis of Co-Variance (ANCOVA) was used to test for significant differences between the slopes of the examined sensory brain regions, otolith volumes, and swimbladder-inner ear distances with foraging habitat and head length as additive effects.

RESULTS

In the smallest specimens (HL > 1.6 mm HL) the optic tract was the largest sensory brain region relative to the other sensory regions examined in all three sciaenids. The percent of the brain devoted to processing visual information was 24.8% in *C. nebulosus*, 14.3% in *S. ocellatus* and ranged between 20.0-26.0% in *Menticirrhus* sp. (Figure 1A). With the exception of the gustatory region, there was a great deal of overlap in the relative size of the other sensory brain regions, swimbladder-inner ear distance, and otolith volume in the smallest specimens examined (Figure 1). The olfactory tract made up less than 1% of the total brain volume in the earliest stages of *C. nebulosus, S. ocellatus* and *Menticirrhus* sp. (Figure 1B). Similarly, less than 2% of the total volume of the brain was composed of the auditory/mechanoreceptive tract for these species (Figure 1C).

The relative size of the optic tract decreased with increasing body size during ontogeny, although there were no significant differences by head length or foraging habitat ($p_{HL} = 0.79$, $p_{FH} = 0.19$, respectively). There were significant increases in the relative size of the olfactory region during ontogeny, but these were not significantly different by foraging habitat ($p_{HL} < 0.05$, $p_{FH} = 0.07$). In the later ontogenetic stages, *L. xanthurus* and *S. ocellatus* possessed larger olfactory tracts (4.2% and 5.9% respectively) relative to *C. nebulosus* (2.9%; Figure 1B). The relative size of the auditory/mechanoreceptive tract increased significantly with increasing head length ($p_{HL} < 0.05$) but there were no significant differences by foraging habitat ($p_{FH} = 0.14$; Figure 1C). There was more variation in the relative size of the gustatory sensory region, and no clear ontogenetic pattern ($p_{HL} = 0.97$, $p_{FH} = 0.71$). There was, however, a slight positive trend for the benthic sciaenids (*Menticirrhus* sp. and *L. xanthurus*) during ontogeny (Figure 1D).

The swimbladder-inner ear distance increased significantly with increasing head length ($p_{HL} < 0.05$) and was significantly different by foraging habitat ($p_{FH} = 0.02$; Figure 1E). *Cynoscion nebulosus*, which had anterior projections of the swimbladder, had the smallest swimbladder-inner ear distance (0.94 mm) relative to *S. ocellatus* and *L. xanthurus*. The volume of the saccular and lagenar otoliths increased significantly during ontogeny ($p_{HL} < 0.05$; Figure 1F) with *S. ocellatus* possessing the largest otoliths. Although there were significant differences in the volume of the saccular otolith among the foraging guilds ($p_{FH} = 0.02$), there were no significant differences in the volume of the lagenar otolith among the foraging guilds ($p_{FH} = 0.10$).

In early ontogenetic stages, the optic tract was the dominant sensory region of the brain in all the examined species based on size (Figure 2). The olfactory tract was anterior to the optic tract but was small and not well-developed relative to the optic tract. The gustatory region was prominent in *C. nebulosus* (Figure 2A), but not conspicuous in

S. ocellatus (Figure 2B) or the benthic sciaenids (Figure 2C). The optic tract remained prominent and relatively unchanged during ontogeny in *C. nebulosus*, *S. ocellatus* and the benthic sciaenids. By approximately 6.0 mm HL, the olfactory tract of *C. nebulosus* and *S. ocellatus* was no longer rudimentary and had elongated (Figure 2A and B). The gustatory region also became more prominent in *S. ocellatus* by 6.0 mm HL (Figure 2B). The olfactory tract and gustatory region in the benthic sciaenids was still rudimentary at 6.0 mm HL, although the auditory/mechanoreceptive region was more developed (Figure 2C). By approximately 16.0 mm HL, the olfactory tract had elongated in all species examined, but was longest in the benthic species (Figure 2). The olfactory tract and gustatory region were now prominent in the benthic sciaenids relative to the pelagic and generalist species. The gustatory region was no longer prominent in *S. ocellatus*, although the olfactory tract dominated the anterior region of the brain (Figure 2B).

The swimbladder was present, inflated, and positioned ventral to the auditory/mechanoreceptive tract in all specimens smaller 1.7 mm HL (Figure 3A-C). The saccular and lagenar otoliths were well developed by 1.3 mm HL in *C. nebulosus* and the distance between the lagenar and swimbladder was less than 0.1 mm (Figure 3A). The saccular and lagenar otoliths were small and rudimentary in *S. ocellatus* (Figure 3B) and not yet developed in the benthic sciaenids (Figure 3C). The swimbladder-inner ear distance was approximately 0.1 mm in *S. ocellatus* and *Menticirrhus* sp., although this distance was measured from the posterior margin of the auditory/mechanoreceptive tract to the swimbladder due to the absence of otoliths in *Menticirrhus* sp. (Figure 3C). The otoliths were well developed in both *C. nebulosus* and *S. ocellatus* by 6.0 mm HL. The lagenar in *C. nebulosus* was smaller relative to *S. ocellatus* at this stage. In addition, the swimbladder was oriented posterior to the brain and on the same axis as the saccular ototliths in all the sciaenids examined. The swimbladder-ototlith distance was still small in both *C. nebulosus* and *S. ocellatus* (0.4 mm and 0.2 mm, respectively) relative to *L. xanthurus* (1.3 mm). By 16.0 mm HL, the saccular and lagenar otoliths were well developed in all species. In addition, the otoliths of *C. nebulosus* and *S. ocellatus* were oblong, whereas round in *L. xanthurus* (Figure 3). At 15.2 mm HL, the swimbladder of *C. nebulosus* possessed anterior horns that projected anteriorly towards the inner ear, maintaining a small swimbladder-inner ear distance of 0.9 mm (Figure 3A). There was no change in swimbladder or otolith shape in *S. ocellatus,* although the orientation of the saccular otoliths had changed and the swimbladder-inner ear distance was approximately 1.2 mm (Figure 3B). The swimbladder was no longer visible in the anterior portion of *L. xanthurus* so a swimbladder-inner ear measurement was not possible. However, the swimbladder-inner ear distance was estimated to be more than 2.8 mm by 15.4 mm HL (Figure 3C). At this stage, the saccular and lagenar otoliths were well developed in *L. xanthurus.*

DISCUSSION

Data on the development of sensory organs can provide insight into the senses that are used to evade predators, locate food, coordinate spawning, and find suitable settlement habitats (in larval fishes). There are some descriptions of the development and functional characteristics of the peripheral sense organs in a few early life history stage and adult sciaenids [Poling and Fuiman, 1997, 1998, 1999; Ramcharitar et al., 2006a; Horodysky et al., 2008a and b]. The development of the corresponding brain regions is, however, largely unknown for these and other estuarine fishes. In fishes, the relative size of the sensory brain region scales positively with the relative importance of a sensory system [Kotrschal et al., 1998; Lisney and Collin, 2006; Lisney et al., 2007]. This relationship has been used to successfully evaluate the relative importance of various sensory modalities in sharks [Lisney et al., 2007; Yopak and Frank, 2009], large pelagic teleosts [Lisney and Collin, 2006], and deep-sea fishes [Wagner, 2002].

Our results show that the optic tract was the largest sensory brain region during ontogeny relative to the other examined regions, although the volume of this tract relative to the other regions decreased with increasing size in taxa from all foraging guilds. This suggests that vision is the dominant sense used by pelagic, generalist, and benthic sciaenids during early ontogeny. The relative decrease in size of this region also suggests that secondary sensory systems inform the visual system. There were no significant differences among the foraging guilds in the volume of the optic tract in the early life history stages, as was found for the peripheral sense organs [Poling and Fuiman, 1998, 1999]. There was a significant increase in the relative size of the olfactory region and swimbladder-inner ear distance with respect to foraging habitat during ontogeny. Initially, the olfactory tract was not well developed and rudimentary, suggesting that early stage sciaenids may not be sensitive to olfactory cues. By 16.0 mm HL, the olfactory tract was relatively long and well developed in both *S. ocellatus* (4.2%) and the benthic sciaenids (5.9%) relative to *C. nebulosus* (2.9%; Figure 1 and 2). The swimbladder-inner ear distance was greatest throughout ontogeny for the benthic sciaenids relative to *S. ocellatus* and *C. nebulosus*, suggesting that audition is not as important for the benthic sciaenids. The relative size of the auditory/mechanoreceptive tract increased significantly during ontogeny, suggesting that these senses become more important during development and growth [Lisney et al., 2007], although there were no significant differences due to foraging habitat. The volume of the saccular and lagenar otoliths increased significantly during ontogeny, although the only significant foraging habitat differences were in the volume of the saccular (Figure 1F). Otoliths were not well developed in the benthic sciaenids until approximately 16.0 mm HL. As adults, *C. nebulosus* had an elongate oblong saccular compared to *S. ocellatus* and *L. xanthurus* in which it was more rounded. However, in the early life history stages, *C. nebulosus* and *S. ocellatus* both possessed an oblong saccular otolith (Figure 3A and B). No clear ontogenetic pattern was present for gustation, although this region is enlarged in *C. nebulosus* and *S. ocellatus* between 6.0 mm and 16.0 mm HL, suggesting improved sensitivity to chemical stimuli.

In the early life history stages, *C. nebulosus* is considered a mechanoreception specialist [Poling and Fuiman, 1998, 1999]. However, there were no significant differences in the auditory/mechanoreceptive tracts among taxa with respect to foraging habitat, although *S. ocellatus* (a generalist) possessed a slightly larger auditory/mechanoreceptive tract. Audition and mechanoreception were analyzed together for this study because hair cells of the lateral line and inner ears detect displacement, which is one of the ways sound is propagated underwater, making it difficult to assess the differential contributions of each sense [Ramcharitar et al., 2006b; Higgs and Radford, 2013]. Early in ontogeny, *S. ocellatus* was observed to possess more cephalic neuromasts relative to *C. nebulosus*, suggesting improved mechanoreceptive skills for *S. ocellatus* relative to *C. nebulosus* during the early life history stages [Poling and Fuiman, 1998]. By 16.0 mm HL, *C. nebulosus* had the smallest measured swimbladder-inner ear distance compared to *S. ocellatus* and *L. xanthurus* (Fig 1.), which suggests that audition is the dominant secondary sense in *C. nebulosus*. *Cynoscion nebulosus* also possessed a larger gustatory region relative to the other examined sciaenids at small sizes (6.0-16.0 mm HL) suggesting that gustation may also be an important secondary sense for this species at this stage.

Sciaenops ocellatus relied on both vision and mechanoreception in the early life history stages to evade predators and locate potential prey successfully [Poling and Fuiman, 1998, 1999]. By 6.0 mm HL, *S. ocellatus* had large olfactory, gustatory, and auditory/mechanoreceptive regions relative to the other sciaenids, suggesting that *S. ocellatus* is using all of these senses at this stage to inform their visual system. *Sciaenops ocellatus* also possessed a smaller swimbladder-inner ear distance, 0.2 mm, relative to *C. nebulosus* (0.3 and 0.4 mm), suggesting they are also sensitive to auditory stimuli. By approximately 16.0 mm HL, *S. ocellatus* possessed the largest olfactory and auditory/mechanoreceptive regions, suggesting that olfaction, audition, and mechanoreception are the important senses, in addition to vision, used to inform *S. ocellatus* of prey, predators, and possible favorable habitats. In addition, *S. ocellatus* is considered a generalist, foraging both in the water column and along the benthos for prey on the periphery of seagrass beds [Poling and Fuiman, 1998; Horodysky et al., 2008a]. Therefore, the use of multiple secondary senses may help individuals of *S. ocellatus* effectively move in and out of structured seagrass habitats without an extreme loss in responsiveness to sensory stimuli.

To examine sensory modality in benthic sciaenids, *Menticirrhus* sp. and *L. xanthurus* were used due to the inability to capture the earliest stages of *L. xanthurus*.

Menticirrhus sp. and *L. xanthurus* have similar feeding structures, are both slow swimmers, and forage for prey along the benthos [Chao and Musick, 1977; Murdy and Musick, 2013]. Polychaetes and organic detritus are frequently encountered in the guts of *Menticirrhus* sp. and *L. xanthurus* [Chao and Musick, 1977], suggesting that these species occupy a very similar foraging habitat and ontogenetic trends in sensory modality are expected to be similar. A caveat, however, is that as adults, *Menticirrhus* sp. possess a barbel and lack a swimbladder whereas *L. xanthurus* lacks a barbel and retains the swimbladder throughout ontogeny [Chao and Musick, 1977], suggesting that adults utilize different senses. However, these differences occur late during ontogeny (late juvenile stage). Therefore, some inter-specific differences in sensory development are expected, but not in the earliest examined life history stage due to structural constraints on peripheral sense organ development, which will translate to relatively similar-sized sensory brain regions for *Menticirrhus* sp. and *L. xanthurus* [Chao and Musick, 1977; Poling and Fuiman, 1998]. Otoliths were not observed in the smallest benthic sciaenids, suggesting that audition is not an important sense for benthic sciaenids, especially early during ontogeny (HL smaller than 2.0 mm). By about 6.0 mm HL, benthic sciaenids did not possess any noticeable specializations to the sensory brain regions. Benthic sciaenids had large swimbladder-inner ear distances, small otolith volumes, variable sizes of the brain regions associated with audition/mechanoreception, and relatively small gustatory regions. By 16.0 mm HL, the olfactory region was similar in size to that of *S. ocellatus* and *L. xanthurus* also possessed a relatively large gustatory region. This suggests that benthic, epifaunal foraging sciaenids rely on olfactory and gustatory stimuli to inform the visual cues in order to locate prey and evade predators successfully. Epifaunal benthic foragers like *Menticirrhus* sp. and *L. xanthurus* consume burrowing prey and obtain food by engulfing sediment and sifting for prey [Chao and Musick, 1977; Coull, 1990; personal observation). Therefore, increased sensitivity to gustatory cues during ontogeny would enable these sciaenids to sift through sediment to locate prey and reduce incidental sediment consumption more effectively.

Sensory modality data can be a powerful tool to understand sensory development in early life history stage fishes and to understand the potential impact of water quality change on this critical life history stage due to the predictive nature of ecomorphological data [Hugueny and Pouilly, 1999]. Due to similar selective pressures, fishes that occupy similar foraging habitats to the sciaenids we examined may display similar sensory modalities in the early life history stages [Hugueny and Pouilly, 1999]. For example, it is likely that fishes that settle and reside in seagrass beds, similar to *C. nebulosus*, rely on vision as a dominant sense, but that this sense is augmented by audition, mechanoreception, and possibly gustation. Changes to water quality have been occurring at rates faster than natural selection can act, which may influence survival of early life history stage fishes due to reduced foraging success [Horodysky et al., 2008a; Nunn et al., 2012]. Fishes such as *L. xanthurus* that lack sensory specialization in the late larval and early juvenile stages may be more susceptible to starvation at these stages under turbid conditions due to a lack of secondary systems to inform an impaired optic system. Therefore, an understanding of sensory modality together with water quality information will enable scientists and managers to more accurately predict the impact of water quality perturbations on early life history stage estuarine-dependent fishes.

MATERIALS EXAMINED

Cynoscion nebulosus: VIMS 22566-22571 (6 A, 4.7-40.4 mm SL)

Leiostomus xanthurus: VIMS 22556-22559 (4 A, 13.9-46.7 mm SL)

Menticirrhus sp.: VIMS 22560-22561 (2 A, 2.5-3.9 mm SL)

Sciaenops ocellatus: VIMS 22562-22565 (4 A, 3.7-46.9 mm SL)

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Table 1. Specimens by foraging guild examined for the assessment of sensory modality. Standard length (SL) and head length (HL) measurements in mm.

	Benthic	**Generalist**	**Pelagic**
Pelagic Larvae/Pre-Settlement	*Menticirrhus* sp. SL=2.51, HL=0.83	*Sciaenops ocellatus* SL=3.65, HL=0.89	*Cynoscion nebulosus* SL=4.74, HL=1.28
	Menticirrhus sp. SL=3.86, HL=1.63		*C. nebulosus* SL=5.12, HL=1.59
	Leiostomus xanthurus SL=13.9, HL=3.98		
Settlement Larvae	*L. xanthurus* SL=15.61, HL=5.01	*S. ocellatus* SL=14.79, HL=5.13	*C. nebulosus* SL=11.01, HL=4.63
	L. xanthurus SL=17.15, HL=5.26		*C. nebulosus* SL=14.17, HL=5.99
Juvenile	*L. xanthurus* SL=30.68, HL=10.82	*S. ocellatus* SL=34.7, HL=13.05	*C. nebulosus* SL=31.43, HL=11.6
	L. xanthurus SL=46.71, HL=15.40	*S. ocellatus* SL=46.92, HL=15.98	*C. nebulosus* SL=40.36, HL=15.2

Figure 1. Relative sizes of sensory brain regions (A-D), swimbladder-inner ear distances (E), and otolith volume (F; saccular otolith volume illustrated here but lagenar otolith follows a similar pattern) by head length (mm; log-transformed). *Cynoscion nebulosus* is shown by blue triangles, *Sciaenops ocellatus* by orange squares, and the benthic sciaenids (*Menticirrhus* sp. and *Leiostomus xanthurus*) by brown circles. Significant results of the ANCOVA are indicated by an asterisk and qualified by HL for head length and FH for foraging habitat.

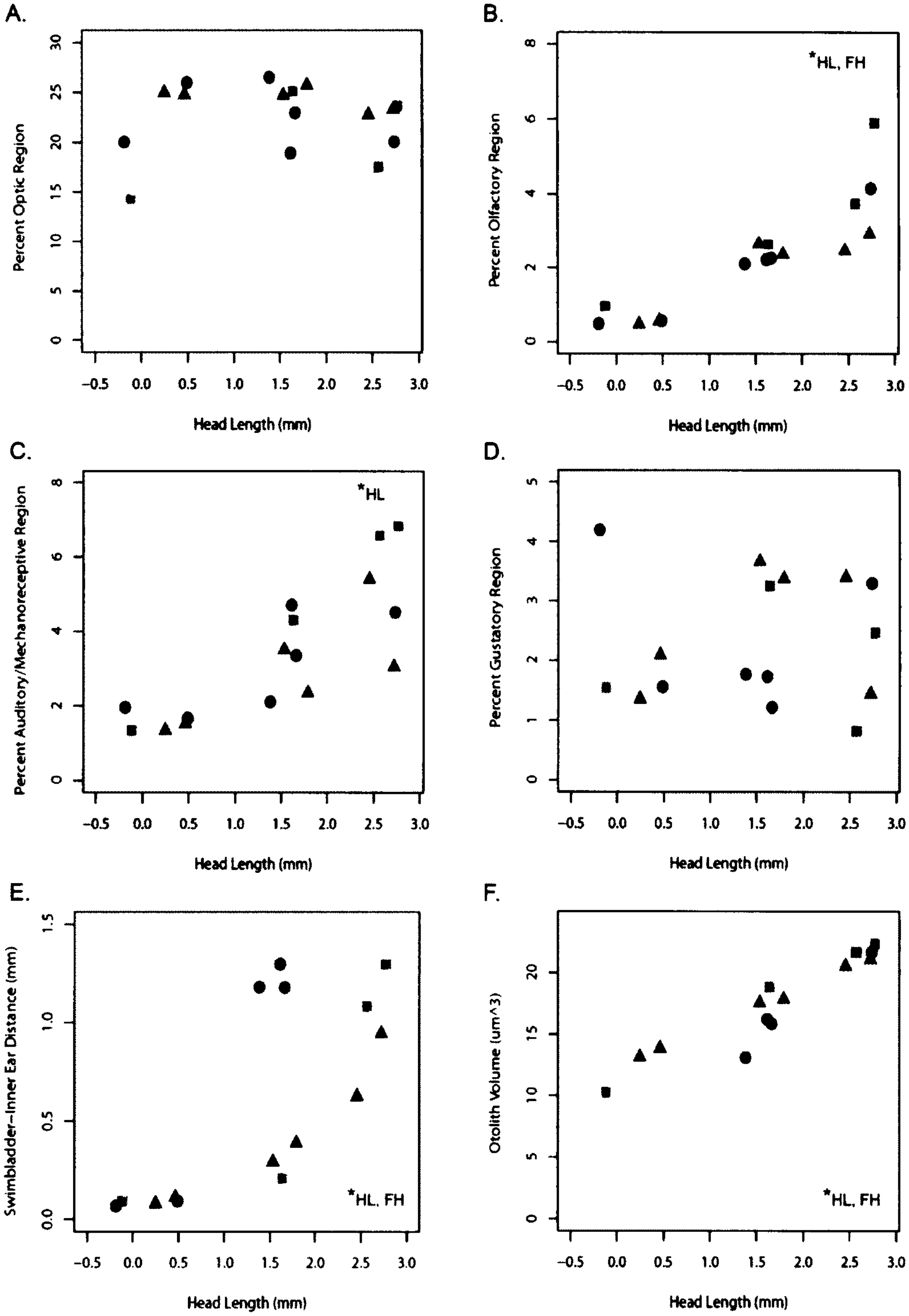

A.
Percent Optic Region
0 5 10 15 20 25 30
Head Length (mm)
-0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
B.
Percent Olfactory Region
0 2 4 6 8
*HL, FH
Head Length (mm)
-0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
C.
Percent Auditory/Mechanoreceptive Region
0 2 4 6 8
*HL
Head Length (mm)
-0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
D.
Percent Gustatory Region
0 1 2 3 4 5
Head Length (mm)
-0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
E.
Swimbladder–Inner Ear Distance (mm)
0.0 0.5 1.0 1.5
*HL, FH
Head Length (mm)
-0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0
F.
Otolith Volume (um^3)
0 5 10 15 20
*HL, FH
Head Length (mm)
-0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0

Figure 2. Sensory brain regions of (A) *Cynoscion nebulosus*, (B) *Sciaenops ocellatus*, and (C) the benthic sciaenids (*Menitcirrhus* sp. and *Leiostomus xanthurus*) with the scale indicated on each panel. The non-sensory brain regions are in purple, the optic tectum (vision) is in blue, the olfactory bulbs (olfaction) are in green, the eminentia granularis and auditory/vestibular nerve (hearing/mechanoreception) are in red, and lobus facialis and lobus vagal (gustation) are in pink. The swimbladder is in gold and any anterior projections are in dark blue. The saccular otoliths are yellow and the lagenar otoliths are teal. Specimen sizes, head length (HL) and standard length (SL) or total length (TL), are indicated above each panel.

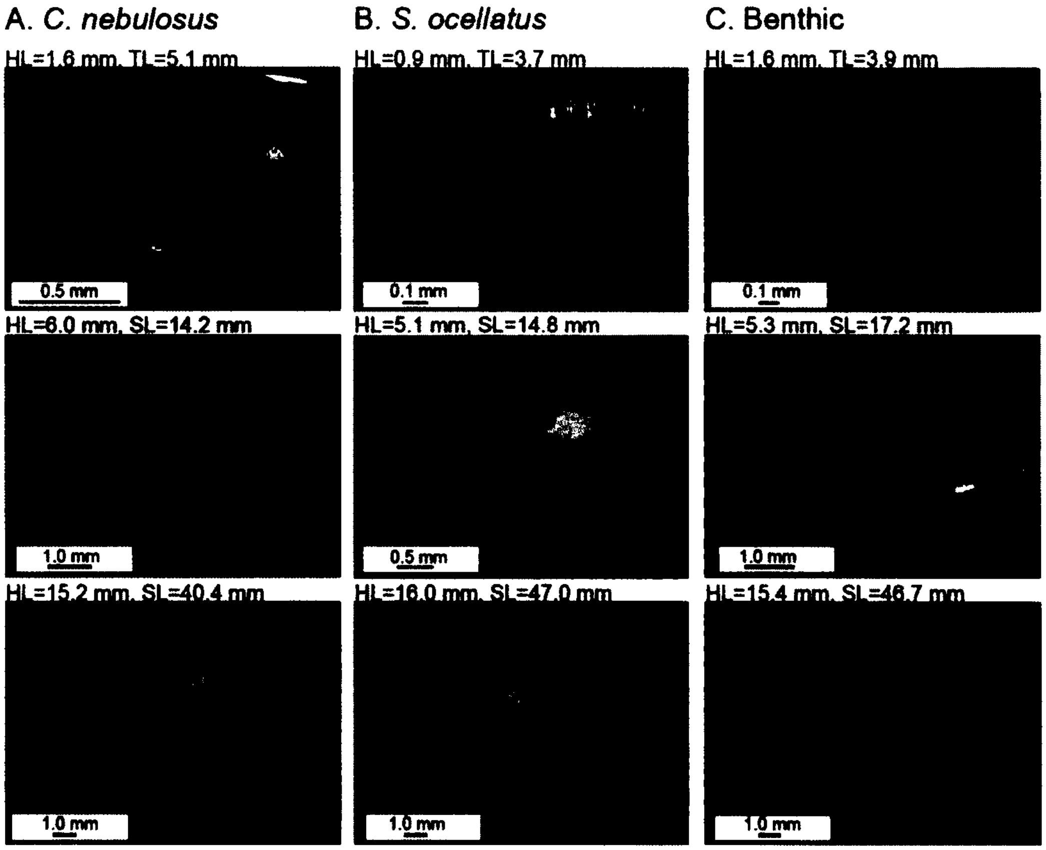
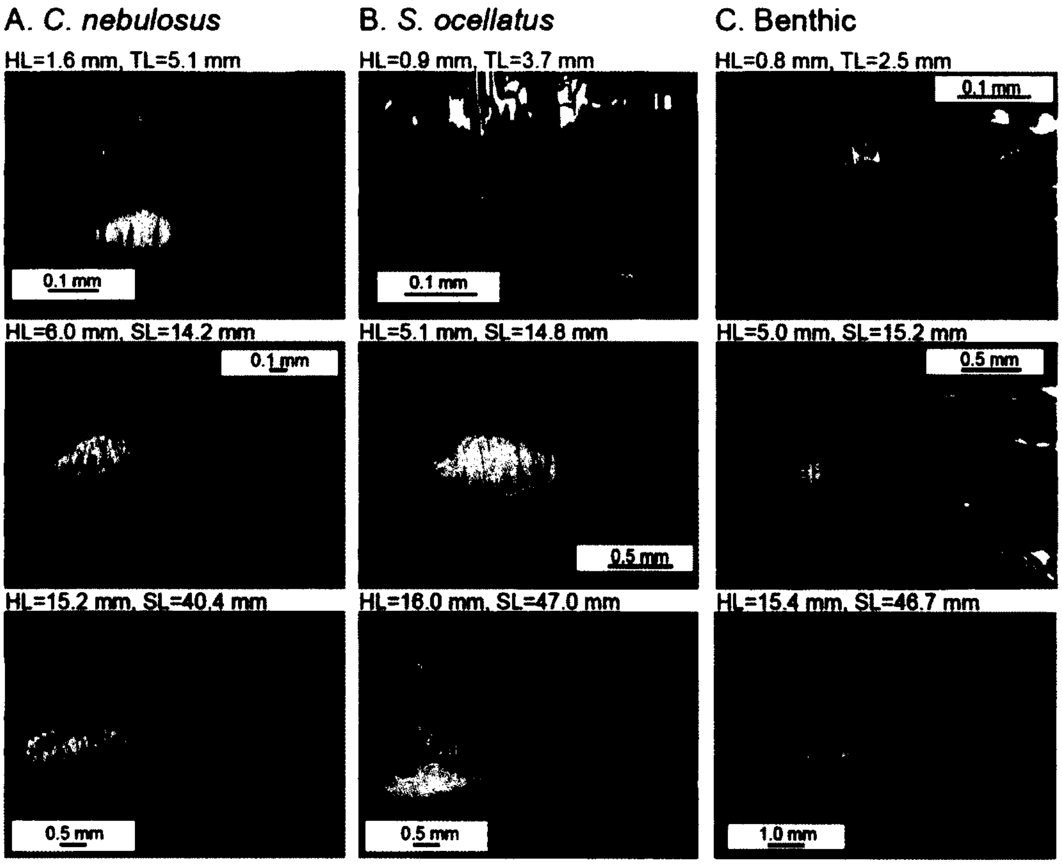

A. C. nebulosus
B. S. ocellatus
C. Benthic
HL=1.6 mm, TL=5.1 mm
0.5 mm
HL=0.9 mm, TL=3.7 mm
0.1 mm
HL=1.6 mm, TL=3.9 mm
0.1 mm
HL=6.0 mm, SL=14.2 mm
1.0 mm
HL=5.1 mm, SL=14.8 mm
0.5 mm
HL=5.3 mm, SL=17.2 mm
1.0 mm
HL=15.2 mm, SL=40.4 mm
1.0 mm
HL=16.0 mm, SL=47.0 mm
1.0 mm
HL=15.4 mm, SL=46.7 mm
1.0 mm

Figure 3. Close-up of swimbladder-inner ear proximity in (A) *Cynoscion nebulosus*, (B) *Sciaenops ocellatus*, and (C) the benthic sciaenids (*Menitcirrhus* sp. and *Leiostomus xanthurus*) with the scale indicated on each panel. The swimbladder is highlighted in gold and any anterior projections are denoted by dark blue. The saccular otoliths are yellow and the lagenar otoliths are teal. The non-sensory brain regions are in purple, the optic tectum (vision) is in blue, the eminentia granularis and auditory/vestibular nerve (hearing/mechanoreception) are in red, and lobus facialis and lobus vagal (gustation) are in pink. Specimen sizes, head length (HL) and standard length (SL) or total length (TL), are indicated above each panel.


A. C. nebulosus
B. S. ocellatus
C. Benthic
HL=1.6 mm, TL=5.1 mm
0.1 mm
HL=0.9 mm, TL=3.7 mm
0.1 mm
HL=0.8 mm, TL=2.5 mm
0.1 mm
HL=6.0 mm, SL=14.2 mm
0.1 mm
HL=5.1 mm, SL=14.8 mm
0.5 mm
HL=5.0 mm, SL=15.2 mm
0.5 mm
HL=15.2 mm, SL=40.4 mm
0.5 mm
HL=16.0 mm, SL=47.0 mm
0.5 mm
HL=15.4 mm, SL=46.7 mm
1.0 mm

CHAPTER 3: Niche partitioning in the early life history stages of estuarine-dependent fishes from the Chesapeake Bay (family Sciaenidae)

INTRODUCTION

Ecomorphology integrates anatomical, functional, ecological, behavioral, and evolutionary studies to gain better insight into not only the function of structures an organism possesses but also, how these structures are used by an organism to complete key life history tasks (Clifton & Motta 1998). Many fishes exhibit correlations between the form of structures and their function, allowing comparative morphological studies to be quite robust when inferring ecological patterns from morphological data (Cochran-Biederman & Winemiller 2010). In addition, morphological data can provide insight into the abilities, which can then be used to predict the foraging ecology of a species (Hugueny & Pouilly 1999; Hulsey et al. 2010). To effectively conserve fisheries resources, it is also necessary to understand how foraging ecology and habitat requirements changes throughout ontogeny, as well as the processes that operate at the individual, population, and community level (Krebs & Turingan 2003; Nunn et al. 2012). Foraging ecologies change with ontogeny because ELHS fishes lack sufficient development of many of the systems required to detect, capture, and process prey items (Nunn et al. 2012). By understanding when during ontogeny different systems develop, we can gain insight into when ELHS fishes are functionally able to reduce competition through habitat partitioning.

Broadly recognized ontogenetic changes in the structure of feeding apparatus elements of fishes accompany dietary shifts (Hernandez et al. 2002; Anto & Turingan 2010), yet most ecomorphological studies focus on adult stages (Mullaney & Gale 1996).

However, ELHS fishes are more susceptible to starvation than late juvenile or adult fishes (Nunn et al. 2012) and feeding success in ELHS fishes is influenced by the developmental state of the sensory systems and feeding apparatus needed to locate, capture, and process prey (Poling & Fuiman 1998, 1999; Anto et al. 2009; Anto and Turingan 2010). Therefore, a study that examines the development of sensory and feeding systems in fishes, in conjunction with diet, will provide the necessary links to examine ecomorphological patterns during ontogeny.

Members of the family Sciaenidae support important commercial and recreational fisheries in coastal and estuarine environments in the Western Atlantic Ocean (Chao & Musick 1977; Murdy & Musick 2013; Santos et al. 2013). Fourteen species either reside in the Chesapeake Bay year round, or use seagrass beds, mud, and sand bottom areas as seasonal nursery habitats (Able & Fahay 2010; Murdy & Musick 2013). As adults, sciaenids exploit more foraging habitats in the Chesapeake Bay than any other family of fishes. They are able to exploit these diverse foraging habitats because they have different sensory modalities to locate and capture prey and different configurations to the feeding apparatus to process the captured prey (Chao & Musick 1977; Poling & Fuiman 1998, 1999; Horodysky et al. 2008a&b; Deary and Hilton *in preparation*). Because the foraging niches and feeding and sensory systems are so diverse, an ecomorphological study, including an ontogenetic perspective, will provide the data needed to understand the feeding ecology of fishes in the Chesapeake Bay.

In this study, we examined the relationship between the structure of the feeding apparatus and sensory modality and the dietary habits of 11 sciaenid species that use the Chesapeake Bay to identify when during ontogeny these species can partition their foraging niches. Many of these species support substantial commercial and recreational fisheries along the western coast of the Atlantic Ocean and within the Chesapeake Bay. It is important to understand the habitat requirements and how they differ in ELHS sciaenid species to properly manage these valuable fishery resources. Further, because ecomorphological studies are predictive (Clifton & Motta 1998; Hugueny & Pouilly 1999), data presented here for ELHS sciaenids can be applied to less well-studied estuarine fishes to infer foraging habitats from an examination of their sensory systems and feeding apparatus. The primary goal of this study was to provide ecomorphological data on fishes that are closely related, yet ecologically diverse to better understand the linkages between the anatomy and function of sensory system and feeding apparatus to foraging ecology during ontogeny.

MATERIALS AND METHODS

Specimen Collection and Processing

Larval samples were collected using a 1-m diameter ring plankton net with 1-mm mesh during an ongoing, weekly shore-based ichthyoplankton sampling program that has been actively sampling in the York River estuary of the Chesapeake Bay since 2007 (Ribeiro et al. 2015). Juvenile and adult sciaenids were collected from other surveys throughout the lower Chesapeake Bay and York River, including the VIMS Juvenile Fish and Blue Crab Trawl Survey, the VIMS Juvenile Striped Bass Seine Survey, and the Chesapeake Bay Multispecies Monitoring and Assessment Program. Additional larval samples were taken in the tidal inlets near the VIMS Eastern Shore facility at Wachapreague, VA, during ten sampling trips over two summers to target sciaenids found in coastal habitats using a 1-mm and 370-µm, 0.5-m diameter opening bongo net.

After sorting the plankton samples and identifying fishes (Richards 2006; Fahay 2007), standard length (SL) of all specimens was measured with digital calipers to the nearest 0.01 mm and fixed either in 10% buffered formalin (Eastern Shore samples) or 70% ethanol (all other specimens). Taxa were classified into one of three primary foraging guilds (benthic, generalist, or pelagic) based on where the adult sciaenids forage. For example, *Cynoscion nebulosus* and *C. regalis* forage in the water column and are considered pelagic foragers whereas *Leiostomus xanthurus* consume infaunal prey and is considered to be a benthic forager (Chao & Musick, 1977; Horodysky et al. 2008b). *Micropogonias undulatus* forages both along the benthos and in the water column and is considered a generalist forager because (Chao & Musick, 1977; Murdy & Musick 2013).

Dietary Analysis

Stomachs and elements of the feeding apparatus were analyzed in the same specimens (n=238). In total, stomachs were excised from pelagic (n=92; 2.9-48.2 mm SL), generalist (n=71; 4.3-53.8 mm SL), and benthic (n=75; 1.9-43.2 mm SL) sciaenids, which included representatives from 11 sciaenids. Ecomorphological patterns were assessed at the species level for *C. nebulosus* (n= 22; 4.5-36.1 mm SL), *M. undulatus* (n= 59; 5.4-39.6 mm SL), and *L. xanthurus* (n= 42; 11.0-41.3 mm SL). Stomach contents were classified into the lowest possible taxonomic level and then pooled into broader groupings based on the prey's primary habitat (i.e., pelagic prey are in the water column and benthic prey are found in and along the benthos). Broad prey categories were used to elucidate habitat-use patterns of the different sciaenid species found in the Chesapeake Bay in ELHS. The final prey categories were: pelagic crustaceans, benthic crustaceans, pelagic shrimps (mysids), benthic shrimps, benthic worms (e.g., polychaetes), benthic fishes, pelagic fishes, mollusks, pelagic eggs, and unicellular benthic phytoplankton. The mean percent number of a given prey item was calculated to identify prey importance and to reduce the bias associated with a few stomachs containing an anomalous number of prey items and small sample sizes (Chipps & Garvey 2007; Latour et al. 2008). For this study, the sampling unit was tow number. Mean percent number of a given prey category was calculated as

$$M\%N_k = \Sigma M_i q_{ik} / \Sigma M_i \tag{1}$$

$$q_{ik} = n_{ik} / n_i \tag{2}$$

where M_i is the number of sciaenids collected at site i, n_i is the total number of all prey items found in a sciaenid species' stomach at site i, and n_{ik} is the total number of prey type k in a sciaenid species' stomach at site i. This method analyzes each stomach as an independent unit to account for autocorrelation within the diet data (Chipps & Garvey 2007).

Feeding Apparatus

Once stomachs were excised, specimens were cleared and double stained (such that cartilaginous structures appeared blue and calcified structures appeared red) following a protocol based on Taylor and Van Dyke (1985). Oral and pharyngeal jaw elements of the feeding apparatus were measured (Fig. 1) using a Zeiss SteREO DiscoveryV20 microscope. Measurements included: length of the ascending process; premaxilla, and lower jaw (anterior tip of dentary to articulation of angulo-articular with the quadrate); and the toothed areas of the third and fourth pharyngobranchial toothplates and the 5th ceratobranchial. On the first and second ceratobranchials, the mean of three randomly selected gill rakers and gill filaments was used to obtain an average length for these elements. These characters were selected because they influence the position and function of the feeding apparatus, types of prey that can effectively be consumed, and because general trends have been described in these elements for adult fishes (Chao & Musick, 1977; Wimberger 1991; Grubich 2003; Aguirre & Shervette 2005; Bhagat et al. 2011). In addition, variation in the elements of the feeding apparatus was observed among taxa of ELHS sciaenids from the Chesapeake Bay (Deary & Hilton *in preparation*). Prior to statistical analysis, all feeding apparatus elements were scaled by SL.

Data Analysis

Data analysis was conducted in R using cluster, clValid, vegan, and MASS packages (R Development Core Team, 2008). Mean percent number for each prey category were calculated for each 1 mm size bin or 5 mm size bin in specimens longer than 20 mm SL. Cluster analysis, using the calculated Euclidean dissimilarity matrix, was used to determine the structure of dietary data in ELHS sciaenids. Internal validation for hierarchial clustering was used to identify the optimal number of clusters present in the data, which also minimized connectivity. Non-metric multidimensional scaling (nMDS) techniques were used to display the dietary data in an ecologically meaningful way using the metaMDS function in R in order to identify the prey items that were attributed to any identified dietary shifts during ontogeny (Oksanen et al. 2008). The envfit function was used to correlate dietary data with feeding apparatus data to examine how changes in feeding apparatus elements may influence ontogenetic patterns in diet (Oksanen et al. 2008).

RESULTS

Interspecific Ontogenetic Dietary Patterns

Sample sizes were large enough to examine species-specific dietary trends for *C. nebulosus* (n= 22; 4.5-36.1 mm SL), *M. undulatus* (n= 59; 5.4-39.6 mm SL), and *L. xanthurus* (n= 42; 11.0-41.3 mm SL), which represented each of the three broad sciaenid foraging guilds of the Chesapeake Bay (pelagic, generalist, and benthic, respectively). Two groups were identified by the cluster analysis in the three species. For *C. nebulosus*, little dissimilarity was observed in the data, although specimens between 20-30 mm SL clustered together (connectivity= 4.24; Fig. 2A). Small specimens of *C. nebulosus* fed primarily on pelagic crustaceans, specifically calanoid copepods, whereas specimens longer than 25 mm SL fed primarily on pelagic shrimp (mysids) and pelagic fishes (stress= 0; Fig. 2B). The greatest differences in diet were observed after 25 mm SL (connectivity= 3.86; Fig. 2C) in ELHS *M. undulatus*. Although the diet of *M. undulatus* smaller than 25 mm SL was diverse, there was a great deal of overlap in these smaller size bins. Small specimens of *M. undulatus* fed on a variety of prey items whereas larger specimens fed primarily on pelagic shrimp (mysids) after 25 mm SL (stress= 3.7×10^{-4}, Fig. 2D). Two clusters were also identified for *L. xanthurus* in which specimens larger than 20 mm SL were more similar to each other than to specimens smaller than 20 mm SL (connectivity= 8.18; Fig. 2E). The diet of *L. xanthurus* was also more variable during ontogeny, with specimens smaller than 14 mm SL feeding on benthic phytoplankton (diatoms) and pelagic crustaceans (calanoid copepods); they shifted to pelagic shrimp (mysids) between 14-25 mm SL. In larger size ranges (>25 mm SL), *L. xanthurus* fed primarily on benthic crustaceans (isopods and amphipods) and benthic polychaete worms (stress= 2.3×10^{-3}; Fig. 2F).

Ontogenetic Dietary Patterns by Foraging Guild

Two clusters were identified in the diet data from the cluster analysis in all three foraging guilds. For pelagic sciaenids, diets were most dissimilar between specimens larger and smaller than 16 mm SL (connectivity= 5.3; Fig. 3A). Smaller pelagic sciaenids fed on pelagic crustaceans (calanoid copepods) whereas larger pelagic sciaenids fed primarily on pelagic shrimp (mysids), benthic crustaceans (isopods and amphipods), and pelagic fishes (stress= 2.3×10^{-3}; Fig. 3B). Generalist sciaenids exhibited less structure in the cluster analysis, suggesting that diets were not as dissimilar by size bin compared to the other two foraging guilds. Dissimilarity related to diet became most pronounced at 35 mm SL in ELHS generalist sciaenids (connectivity= 2.93; Fig. 3C). Smaller generalist sciaenids fed on a combination of pelagic eggs, pelagic crustaceans, and other pelagic prey; whereas larger generalist sciaenids fed on pelagic shrimp (mysids), benthic polychaete worms, and pelagic fishes (stress= 8.8×10^{-5}; Fig. 3D). The diet of benthic sciaenids differed between specimens larger than 20 mm SL and those smaller than 19 mm SL (connectivity= 6.2; Fig. 3E). Small benthic sciaenids fed on pelagic eggs, pelagic crustaceans, and mollusks whereas at larger sizes, benthic sciaenids fed primarily on pelagic shrimp, benthic crustaceans, and benthic worms (stress= 0.03; Fig. 3F).

Ontogenetic Patterns in Ecomorphology

For *C. nebulosus*, changes in diet were associated with several aspects of the feeding apparatus elements, although there were no significant correlations for these elements. In particular, changes in diet were associated with longer lower jaw and a greater toothed area of the third pharyngeal toothplate ($p=0.07$ and $p=0.06$, respectively) and reductions in gill raker counts along the first and second ceratobranchials ($p=0.07$; Table 1; Fig. 4A). Dietary shifts in *M. undulatus* were associated with significant increases in eye diameter and the toothed area of ceratobranchial 5 ($p=0.02$) and significant decreases in lower jaw length, premaxilla length ($p=0.03$), and the second epibranchial gill-raker count ($p=0.02$; Table 1; Fig. 4C). Changes in the diet of ELHS *L. xanthurus* were associated with significant increases in ascending process length ($p<0.05$) and toothed area of the third pharyngeal toothplate and ceratobranchial 5 ($p<0.05$); as well as significant decreases in lower jaw length, premaxilla length ($p=0.04$ and $p=0.01$) and gill-raker count along ceratobranchials 1 and 2 ($p<0.05$; Table 1; Fig. 4E). In addition, the oral jaws of *L. xanthurus* are morphologically distinct from the oral jaws of *M. undulatus* and *C. nebulosus* by approximately 20.0 mm SL (Fig. 4, left column insets).

Dietary shifts for pelagic sciaenids were not significantly associated with changes in feeding apparatus elements ($p>0.1$) except for the toothed area of ceratobranchial 5 ($p<0.05$), although this was not associated with a shift to a particular prey category (Table 2; Fig. 4B). Feeding apparatus elements were also associated with dietary shifts in generalist sciaenids (Table 2; Fig. 4D). In particular, there were significant increases in the toothed area of the third pharyngeal toothplate and ceratobranchial 5 ($p<0.05$) while lower jaw length, premaxilla length ($p>0.1$), and gill-raker count on ceratobranchials 1 and 2 ($p<0.05$) decreased (Table 2; Fig. 4D). Similar to the trend that was observed for *L. xanthurus*, exploitation of more benthic prey in benthic sciaenids was associated with a significantly longer ascending process and greater toothed areas of the third pharyngeal toothplate and ceratobranchial 5 ($p<0.05$) but significantly shorter premaxilla and lower jaw lengths ($p<0.05$; Table 2; Fig. 4F).

DISCUSSION

The ecology of fishes can be influenced by anatomical structures, especially those related to feeding because specializations to these elements control the ability to exploit certain prey items (Wainwright & Richard 1995; Clifton & Motta 1998). The feeding apparatus is also under constant selective pressures, due to competition and foraging success, which has resulted in a wide range of specializations to the feeding apparatus that enable fishes to partition foraging habitats, reduce competition, and coexist within an ecosystem (Wainwright & Richard 1995; Hernandez et al. 2002). During ontogeny, the elements of the feeding apparatus undergo significant changes in shape and configuration, which influence the functionality of the feeding apparatus, and in turn impact the ability of ELHS fishes to efficiently capture prey (Wainwright & Richard 1995; Hernandez et al. 2002; Anto and Turingan 2010). Thus interspecific variations in feeding apparatus development enable ELHS fishes to partition their foraging habitats. We note, however, that inter- and intraspecific patterns of feeding apparatus development (which may influence foraging success) is yet to be assessed in estuarine-dependent ELHS fishes (Wittenrich & Turingan 2011).

To examine how the structure of the feeding apparatus may influence niche partitioning in ELHS sciaenids, we first described the diets of ELHS sciaenids in the Chesapeake Bay. *Cynoscion nebulosus* and the other pelagic sciaenids did not experience a shift in foraging habitat during ontogeny, although the types of prey consumed did change with increasing size. Early during ontogeny *C. nebulosus* and other pelagic sciaenids fed primarily on pelagic crustaceans, mainly copepods, whereas later ontogenetic stages (greater than 16 mm SL) fed primarily on pelagic shrimp (mysids), pelagic fishes, and some benthic crustaceans (Fig. 2 and 3). For *C. nebulosus*, as fishes became a more important component of the diet, the length of lower jaw and toothed area of the third pharyngeal toothplate increased while the number of gill rakers on the first and second ceratobranchials decreased, although not significantly ($p>0.1$). The only feeding apparatus element that was significantly associated with changes to diet in the pelagic sciaenids was the toothed area of ceratobranchial 5 ($p<0.05$).

Cynoscion nebulosus spends the majority of its life in estuaries around seagrass beds where it forages in the water column for fishes and crustaceans as adults and for pelagic zooplankton as larvae (Poling & Fuiman 1999; Horodysky et al. 2008b; Murdy & Musick 2013; Wittenrich & Turingan 2011; Nunn et al. 2012). Although we did observe an expansion in the variety of prey items consumed with development for *C. nebulosus*, the overall habitat of these prey did not change, suggesting the *C. nebulosus* do not experience a shift in their foraging guild and continually feed in the water column regardless of ontogenetic stage. Since foraging habitat was not observed to shift during development, few morphological changes to their feeding apparatus would be expected (Clifton & Motta 1998) because the elements are already suited to exploit pelagic prey at the first-feeding stage (Wittenrich & Turingan 2011; Nunn et al. 2012; Deary and Hilton *in preparation*). In *C. nebulosus*, none of the examined feeding apparatus elements changed significantly with diet, suggesting that no major specializations to the feeding apparatus were required to enable efficient foraging of more diverse pelagic prey during ontogeny. Although pelagic sciaenids encounter novel aquatic ecosystems during ontogeny due to ingress and settlement, they feed on pelagic prey at all life history stages.

Dietary shifts for the generalist *M. undulatus*, were observed at approximately 25 mm SL, which was later than the pelagic sciaenids (16 mm SL). *Micropogonias undulatus* fed on a variety of pelagic zooplankton prey before 25 mm SL but then shifted to feeding on pelagic shrimp. As a guild, the diet of generalist sciaenids shifted at approximately 35 mm SL and included both pelagic and benthic prey. Unlike pelagic sciaenids, generalist sciaenids shift from a pelagic foraging habitat after hatching to a more benthic one after settlement in seagrass beds (Poling & Fuiman 1999). As juveniles, generalist sciaenids tend to forage on a variety of prey items, including benthic worms and pelagic fishes (Chao & Musick 1977); therefore the observed shift in diet would be expected to coincide with a change in feeding apparatus structure. As diets became more varied in generalist sciaenids, the toothed area of third pharyngeal toothplate and ceratobranchial 5 increased significantly ($p<0.05$) and the lengths of lower jaw and premaxilla decreased, although not significantly ($p>0.1$).

Unlike the other two foraging guilds, ELHS benthic sciaenids transition from a pelagic habitat to a benthic habitat after settlement with few foraging forays into the water column (Chao & Musick 1977; Horodysky et al. 2008b). Juvenile *L. xanthurus*, a benthic sciaenid, tends to forage primarily on benthic polychaetes (Chao & Musick 1977). Dietary shifts were observed in ELHS benthic sciaenids, including *L. xanthurus*, by 20 mm SL with larger individuals feeding on benthic worms, benthic crustaceans, pelagic shrimp, and pelagic fishes. Late juveniles and adult benthic sciaenids, however, forage exclusively along the benthos (Chao & Musick 1977; Horodysky et al. 2008b).

Therefore, functional constraints of the sensory systems and feeding apparatus, as well as opportunistic foraging, may result in benthic sciaenids foraging for prey found in the water column and along the bottom (Poling & Fuiman 1998; Govoni 1987). Significant dietary shifts were associated with changes to the structure of the feeding apparatus. In particular, ascending process length and toothed area of third pharyngeal toothplate and ceratobranchial 5 increased significantly while there were significant decreases in lower jaw and premaxilla length ($p<0.05$) in *L. xanthurus* as well as in the other benthic sciaenids, as the diet included more benthic prey. In addition, the feeding apparatus of benthic sciaenids is morphologically distinct from the other two foraging guilds earlier during ontogeny (Deary & Hilton *in preparation*).

In this study, dietary shifts and associated changes to the feeding apparatus were found to be similar at both the species and foraging-guild levels. A single dietary shift was observed in all three foraging guilds so that early ontogenetic stages had diets that were more similar to each other than to later ontogenetic stages. The feeding apparatus of pelagic sciaenids did not undergo significant changes in structure, with the exception of ceratobranchial 5, and their diet was dominated by pelagic prey, regardless of ontogenetic stage. The diets of benthic sciaenids shifted to include more benthic prey items at approximately 20 mm SL. Benthic sciaenids also experienced more significant changes in feeding apparatus elements relative to the other two foraging guilds, suggesting that benthic sciaenids undergo the greatest shift in foraging habitats and also partition their foraging habitats in the ELHS. The dietary shifts of generalist sciaenids were observed later during ontogeny than in the benthic and pelagic sciaenids, suggesting that these sciaenids are exploiting benthic and pelagic prey resulting in dietary overlap of ontogenetic stages. However, the observed dietary shift was associated with some significant changes to the feeding apparatus, particularly the pharyngeal jaw elements. In addition, cerabtobranchial 5 was the only feeding apparatus element that was significantly associated with dietary shifts in ELHS sciaenids, suggesting that the increase in the toothed area of ceratobranchial 5 is necessary for pharyngeal jaw function. The changes in the structure of the feeding apparatus and corresponding dietary shifts suggest that sciaenids are able to partition their foraging habitats in the ELHS, which can improve feeding success and reduce competition in nursery habitats (Carson & Wainwright 2010; Wittenrich & Turingan 2011). It should be noted, however, that the patterns described here are at the guild and species level and do not capture individual variability. Therefore, phenotypic plasticity of feeding apparatus elements may impact prey selection, growth rates, stage duration, and survival at the individual level (Anto & Turingan 2010; Houde 2009), which is beyond the scope of this study.

Ecomorphological patterns though well-studied in adult fishes (Wainwright 1996; Clifton & Motta 1998; Carlson & Wainwright 2010) are generally not described in an ontogenetic context, which would identify when these patterns become apparent to enable ELHS fishes to partition their foraging niches (Hernandez et al. 2002). We observed ecomorphological patterns in ELHS estuarine-dependent fishes of the family Sciaenidae, which exploit different foraging habitats as adults, and identified when during ontogeny these sciaenids begin to partition their foraging habitats. In addition, the morphological data can also be predictive since fishes with similar feeding habits tend to possess similar specializations to the feeding apparatus (Clifton & Motta 1998; Hugueny & Pouilly 1999). Sciaenids occupy the widest range of foraging habitats of any other fish family in the Chesapeake Bay (Chao & Musick 1977; Horodysky et al. 2008b). Therefore, an ontogenetic ecomorphological study on sciaenids provides the data needed to predict the ecology, ELHS habitat requirements, and the onset of niche partitioning for more cryptic fishes that may occupy similar adult foraging habitats.

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Table 1. Feeding apparatus elements significantly correlated to diets of ELHS sciaenids at the species level. Abbreviations: ap, ascending process; cb, ceratobranchial; ep, epibranchial; lj, lower jaw; pbtp, pharyngobranchial toothplate; pmx, premaxilla.

Feeding Apparatus Element	**p-value**	**R^2**
	Cynoscion nebulosus	
cb5 toothed area	0.051	0.473
	Micropogonias undulatus	
lj length	0.027	0.427
pmx length	0.025	0.405
ep1 gill raker count	0.011	0.448
ep2 gill raker count	0.018	0.355
cb5 toothed area	0.018	0.620
Eye diameter	0.019	0.568
	Leiostomus xanthurus	
lj length	0.044	0.508
pmx length	0.005	0.807
ap length	0.003	0.813
cb1 gill raker count	0.002	0.849
pbtp3 toothed area	0.002	0.887
cb5 toothed area	0.002	0.904
cb2 gill raker count	0.002	0.893

Table 2. Feeding apparatus elements significantly correlated to diets of ELHS sciaenids at the guild level. Abbreviations: ap, ascending process; cb, ceratobranchial; ep, epibranchial; lj, lower jaw; pbtp, pharyngobranchial toothplate; pmx, premaxilla.

Feeding Apparatus Element	**p-value**	**R^2**
	Pelagic Sciaenids	
cb5 toothed area	0.006	0.566
	Generalist Sciaenids	
cb1 gill raker count	0.012	0.309
ep1 gill raker count	0.013	0.317
cb2 gill raker count	0.018	0.293
cb5 toothed area	0.007	0.419
pbtp3 toothed area	0.001	0.566
	Benthic Sciaenids	
cb5 toothed area	0.001	0.857
pbtp3 toothed area	0.001	0.842
lj length	0.009	0.427
pmx length	0.002	0.602
ap length	0.001	0.641

Fig. 1. Measure oral and pharyngeal jaw elements. Black lines and outlines indicate how elements were measured (except in "Pharyngeal Jaw Elements" panel). All elements are from specimens of *M. undulatus*. Abbreviations: SL, standard length; HL, head length; ED, eye diameter; ap, ascending process; pmx, premaxilla; lj, lower jaw; gr, gill raker; cb, ceratobranchial; pbtp, pharyngobranchial toothplate; gf, gill filament; ep, epibranchial.

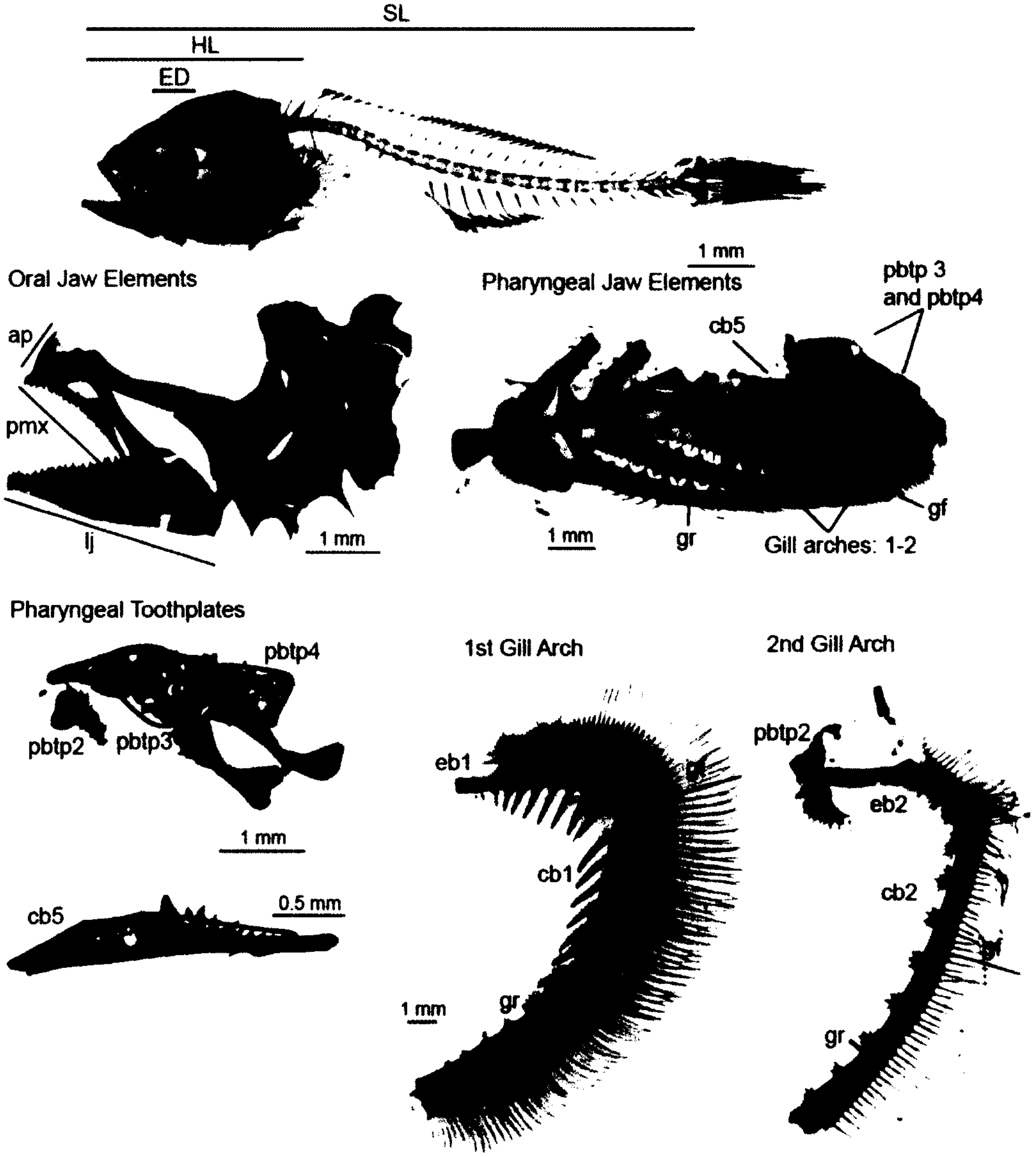

SL
HL
ED
1 mm
Oral Jaw Elements
ap
pmx
lj
1 mm
Pharyngeal Jaw Elements
pbtp 3 and pbtp4
cb5
1 mm
gr
Gill arches: 1-2
gf
Pharyngeal Toothplates
pbtp4
pbtp2
pbtp3
1 mm
cb5
0.5 mm
1st Gill Arch
eb1
cb1
gr
1 mm
2nd Gill Arch
pbtp2
eb2
cb2
gf
gr

Fig. 2. Diet of three early life history stage sciaenid species from the Chesapeake Bay: *Cynoscion nebulosus* (top row; A and B), *Micropogonias undulatus* (middle row; C and D), and *Leiostomus xanthurus* (bottom row; E and F). The cluster analysis recovered two dietary clusters (left column) for each species with blue denoting cluster one (early ontogenetic stages) and red denoting cluster two (later ontogenetic stages). The results from the nMDS (right column) shows the prey (red text) that is being exploited at each standard length size bin (blue numbers).

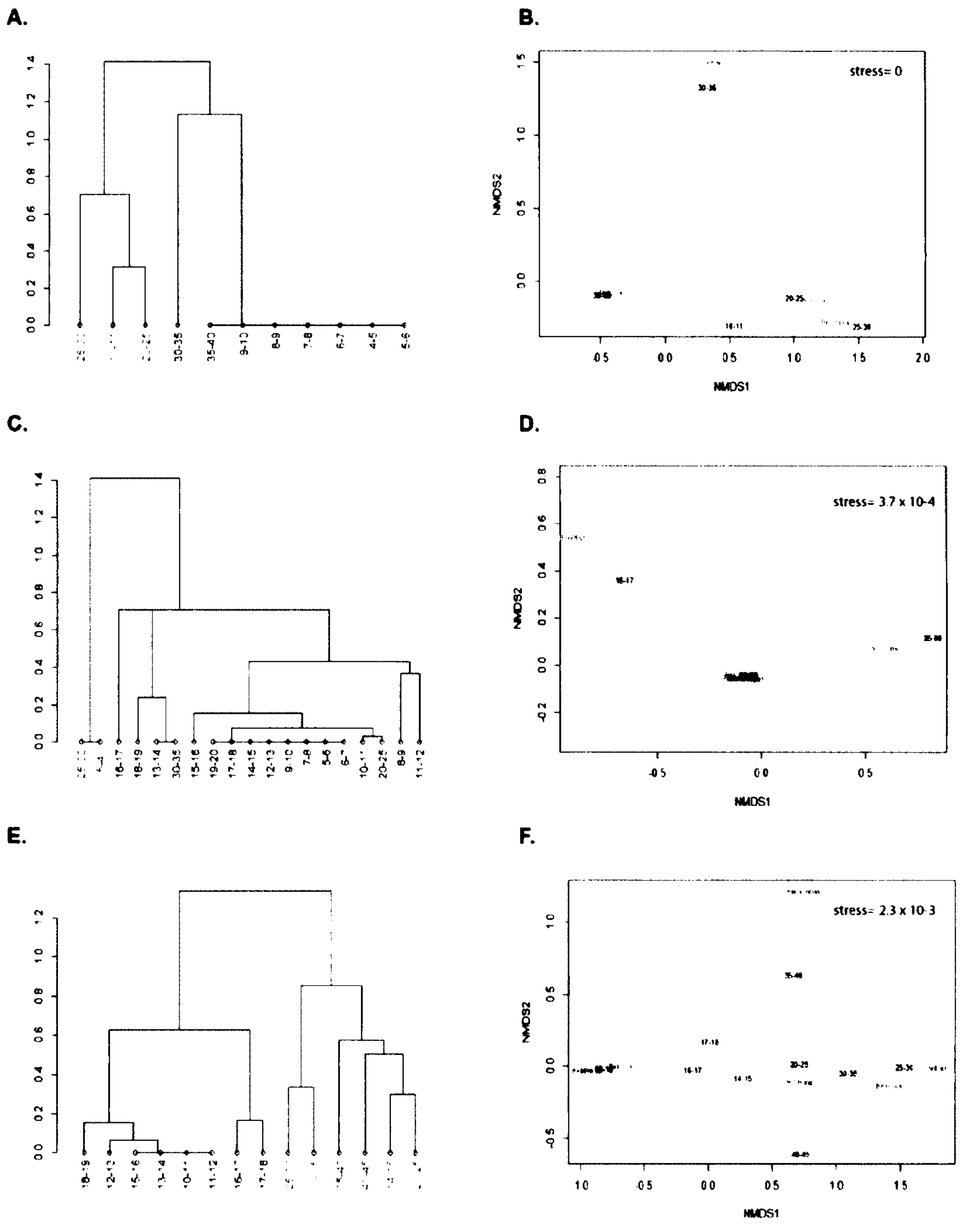

A.
B.
stress= 0
NMDS1
NMDS2
C.
D.
stress= 3.7 x 10-4
NMDS1
NMDS2
E.
F.
stress= 2.3 x 10-3
NMDS1
NMDS2
30-35
35-40
9-10
8-9
7-8
6-7
4-5
5-6
16-17
18-19
13-14
15-16
19-20
17-18
14-15
12-13
5-6
10-11
20-25
11-12
12-13
15-16
11-12

Fig. 3. Diet of three early life history stage sciaenid foraging guilds from the Chesapeake Bay: pelagic sciaenids (top row; A and B), generalist sciaenids (middle row; C and D), and benthic sciaenids (bottom row; E and F). The cluster analysis recovered two dietary clusters (left column) for each foraging guild with blue denoting cluster one (early ontogenetic stages) and red denoting cluster two (later ontogenetic stages). The results from the nMDS (right column) shows the prey (red text) that is being exploited at each standard length size bin (blue numbers).

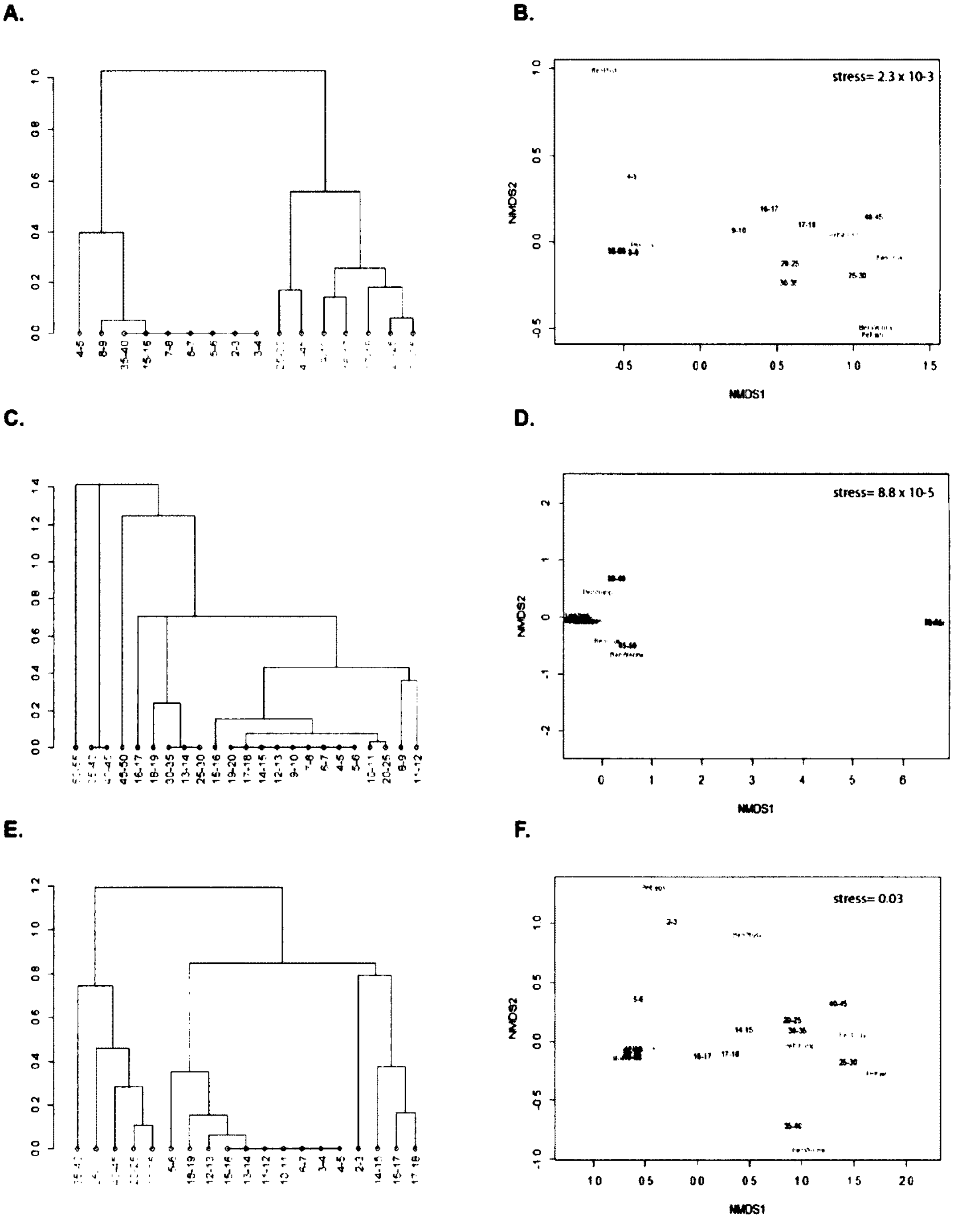
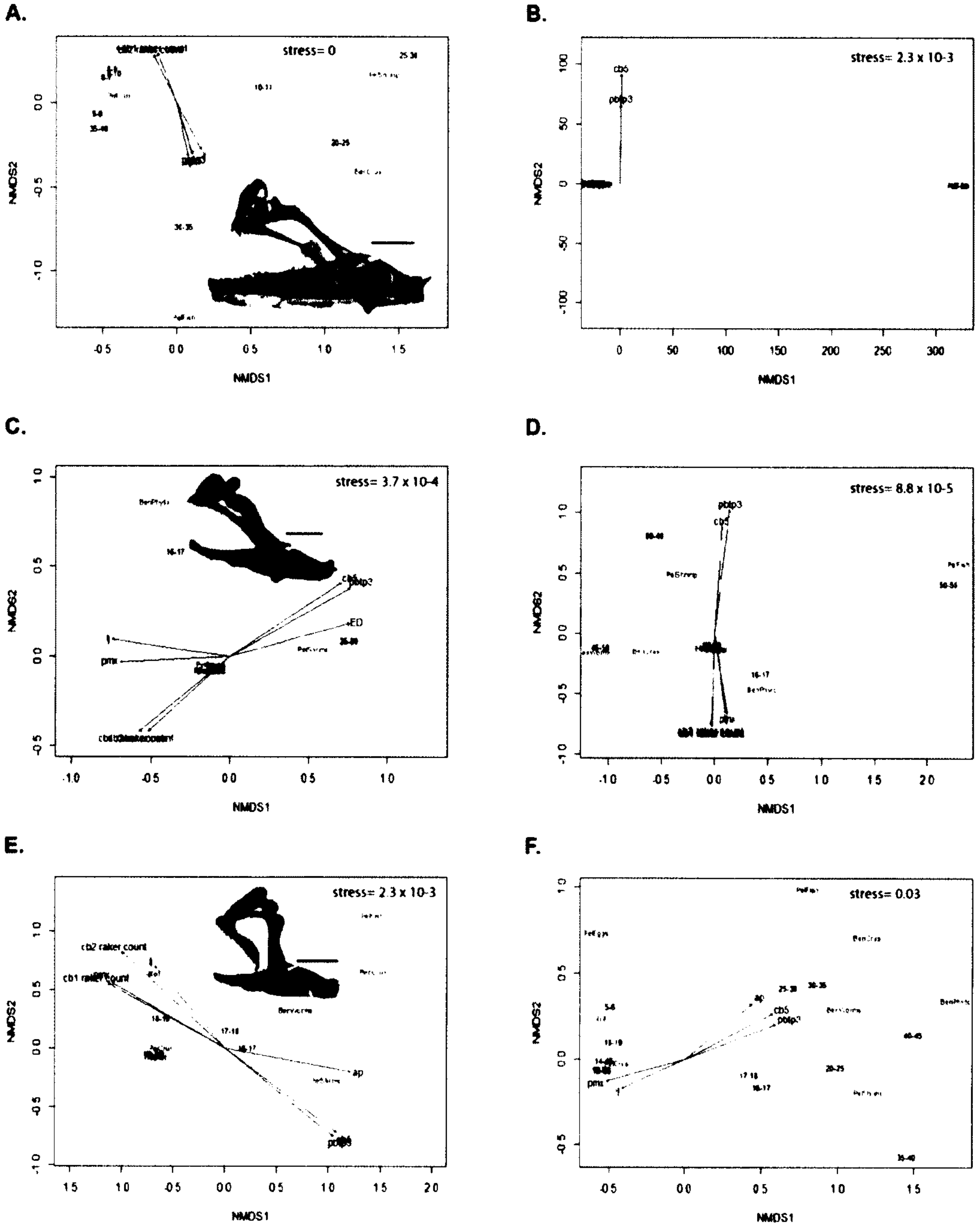

A.
B.
C.
D.
E.
F.
stress= 2.3 x 10-3
stress= 8.8 x 10-5
stress= 0.03
NMDS1
NMDS2
4-5
8-9
35-40
15-16
7-8
6-7
5-6
2-3
3-4
45-50
16-17
18-19
30-35
13-14
25-30
19-20
17-18
14-15
12-13
9-10
10-11
20-25
11-12
13-14
11-12
4-5

Fig. 4. The diet of three early life history stage sciaenid species (left column) representing three foraging guilds (right column) from the Chesapeake Bay in relation to the structure of the feeding apparatus: *Cynoscion nebulosus* and pelagic sciaenids (top row; A and B, respectively), *Micropogonias undulatus* and generalist sciaenids (middle row; C and D, respectively), and *Leiostomus xanthurus* and benthic sciaenids (bottom row; E and F, respectively). Prey categories are shown as red text and each standard length size bin is denoted by black numbers, and the variable and direction of change for feeding apparatus elements are denoted by blue arrows and text. Abbreviations: SL, standard length; HL, head length; ED, eye diameter; ap, ascending process; pmx, premaxilla; lj, lower jaw; gr, gill raker; cb, ceratobranchial; pbtp, pharyngobranchial toothplate; gf, gill filament; ep, epibranchial. Inset picture for each species-level nMDS (left column) shows the structure of the oral jaws after dietary shifts were observed in the cluster analysis. Black line with each image indicates a scale of 1 mm.


A.
stress= 0
NMDS1
NMDS2
B.
stress= 2.3 x 10-3
cb5
pblp3
NMDS1
NMDS2
C.
stress= 3.7 x 10-4
cb5
pblp3
ED
pmx
NMDS1
NMDS2
D.
stress= 8.8 x 10-5
pblp3
cb5
NMDS1
NMDS2
E.
stress= 2.3 x 10-3
cb2 raker count
cb1 raker count
ap
pblp3
NMDS1
NMDS2
F.
stress= 0.03
ap
cb5
pblp3
pmx
NMDS1
NMDS2

CHAPTER 4: Influence of phylogeny on feeding structures in early life history stage Drums (Sciaenidae) from the Chesapeake Bay

INTRODUCTION

Fishes of the family Sciaenidae are abundant in tropical to temperate coastal and estuarine areas worldwide, with approximately 66 genera and more than 270 described species that are commonly exploited in fisheries (Sasaki 1989; Chao 2002; Xu et al. 2014; Lo et al. *in review*). Sciaenids are variable in their external morphology, particularly the feeding apparatus, which sciaenids use to partition their foraging habitats as adults (Chao and Musick 1977; Sasaki 1989; Xu et al. 2014). Fourteen species of sciaenids reside in the Chesapeake Bay and use the aquatic habitats of the Bay as year-round residents or seasonally as foraging grounds and nursery habitats (Chao and Musick 1977). In the Chesapeake Bay, the morphological diversity of the feeding apparatus, which includes both the oral and pharyngeal jaw elements, permits adult sciaenids to exploit a wide spectrum of foraging habitats. It has been suggested that this morphological diversity evolved to reduce competitive exclusion (Chao and Musick 1977). In addition, adult and early life history stage (ELHS) sciaenids display ecomorphological patterns in the oral and pharyngeal jaw elements that have been described in other groups of fishes (Chao and Musick 1977; Clifton and Motta 1998; Carlson and Wainwright 2010; Hulsey et al. 2010; Deary and Hilton unpublished). Variation in feeding apparatus morphology provides insight into the foraging habits of fishes (Carlson and Wainwright 2010) but because sciaenid species are closely related, there are likely to be phylogenetic constraints acting on the feeding apparatus elements and it is unknown if phylogenetic constraints may override ecological adaptation in sciaenids (Poling & Fuiman 1998).

Evolutionary history is an important constraint on an organism's morphology (Cheverud et al. 1985). Phylogenetically related species tend to resemble each other in phenotype and ecological characteristics; therefore, observations from closely related species are not independent (Hernández et al. 2013). Because sciaenids are hierarchically related, metrics characterizing the structure of the feeding apparatus are not independent and violate the assumptions of traditional statistics (Felsenstein 1985; Garland et al. 2005). Therefore, the ecomorphological patterns described in ELHS sciaenids may be attributed more to evolutionary history than responses to natural selection pressures (Felsenstein 1985; Hernández et al. 2013; Deary and Hilton unpublished). Phylogenetic comparative methods can be applied to the data to account for the phylogenetic signal before traditional statistics can be used (Garland et al. 1999; Garland et al. 2005; Hernández et al. 2013To investigate whether evolutionary history is driving the patterns in the development of the oral jaws of sciaenids, we applied phylogenetic comparative methods to measurements of oral jaw elements to account for, and to determine, the phylogenetic signal in the feeding apparatus. We also incorporated and two topologies in our analyses to better understand how topology influences the phylogenetic signal detected in the feeding apparatus data.

MATERIALS AND METHODS

Specimen Collection and Processing

Larval samples were collected using a 1-mm mesh plankton net during a weekly shore-based ichthyoplankton sampling program in the York River, a tributary of the

Chesapeake Bay, that has been active since 2007 (Ribeiro et al. 2015). Juvenile and adult sciaenids were obtained from other surveys conducted by the Virginia Institute of Marine Science (VIMS) throughout the lower Chesapeake Bay and York River. To target species found in coastal habitats (i.e., bays, inlets, and ocean shore), additional samples were collected at the VIMS Eastern Shore Laboratory (Wachapreague, VA), during eight sampling trips over two summers. After sorting the plankton samples and identifying larval sciaenids using guides of Richards (2006) and Fahay (2007), standard length (SL) of all specimens was measured with digital calipers to the nearest 0.01 mm and fixed in 10% buffered formalin (Eastern Shore samples) or 70% ethanol (York River specimens).

Feeding Apparatus

The structure of the feeding apparatus was examined on cleared and double stained (cartilage blue, calcified structures red) sciaenid genera from the Chesapeake Bay prepared following a protocol based on Taylor and Van Dyke (1985). The examined sciaenid genera that reside in the Chesapeake Bay were: *Bairdiella* (1 species; n=24), *Cynoscion* (2 species; n=90), *Larimus* (1 species; n=8), *Leiostomus* (1 species; n=53), *Micropogonias* (1 species; n=110), *Menticirrhus* sp. (3 species; n=16), *Pogonias* (1 species; n=12), *Sciaenops* (1 species; n=35), *Stellifer* (1 species; n=2). An additional sciaenid genus was also examined that does not reside in the Chesapeake Bay watershed but is native to the freshwater rivers of central North America (*Aplodinotus*, 1 species; n=12).

The structure of oral jaws of fishes is correlated with its foraging guild; fishes that forage in the water column have relatively longer upper and lower jaws, whereas benthic foraging fishes typically have a longer ascending process (Clifton & Motta 1998; Carlson

& Wainwright 2010; Hulsey et al. 2010). Therefore, the lengths of the ascending process, premaxilla, and lower jaw (anterior tip of dentary to articulation of angulo-articular with the quadrate) were the measured oral jaw elements (Fig. 1) because they influence the position and function of the feeding apparatus, types of a prey a fish can effectively consume, and general trends have been described in these elements for adult fishes (Chao and Musick, 1977; Wimberger, 1991; Aguirre and Shervette, 2005). Of the 11 examined sciaenid species, five are considered to be pelagic (*Cynoscion nebulosus, C. regalis, Bairdiella chrysoura, Stellifer lanceolatus, Larimus fasciatus*) and six are considered to be benthic (*Aplodinotus grunniens, Leiostomus xanthurus, Menticirrhus* sp., *Micropogonias undulatus, Sciaenops ocellatus, Pogonias cromis*). All measurements were taken using a stereo microscope (Zeiss SteREO DiscoveryV20) and ImageJ (available for download: http://imagej.nih.gov/ij/index.html).

Measurements of oral jaw elements were also taken on alcohol-stored museum specimens. Specimens were examined from 65 of the 66 currently described sciaenid genera (see "Materials Examined") and were comparable to those taken for the cleared and double stained specimens from Chesapeake Bay (Fig. 1). All specimens were imaged with a digital camera (Canon Powershot A590) and measurements were taken with digital calipers to the nearest 0.01 mm. The primary foraging habitat of taxa was determined by the position of the mouth since it has been observed in other groups that fishes with terminal mouths primarily forage in the water column (pelagic foragers) whereas those with subterminal mouths primarily forage along the benthos (benthic foragers; Chao and Musick 1977; Carlson and Wainwright 2010; Ruehl et al. 2011). The pelagic foraging sciaenid genera are: *Argyrosomus, Atractoscion, Atrobucca, Austronibea, Bahaba,* *Bairdiella, Chrysochir, Cilus, Collichthys, Corvula, Cynoscion, Daysciaena, Elattarchus, Isopisthus, Kathala, Larimichthys, Larimus, Macrodon, Miichthys, Miracorvina, Nebris, Nibea, Odontoscion, Otolithes, Otolithoides, Panna, Pennahia, Pentheroscion, Plagioscion, Protonibea, Pseudotolithus, Pteroscion, Pterotolithus, Sciaena, Seriphus, Stellifer,* and *Totoaba* (Fig. 2). The benthic foraging sciaenid genera are: *Aplodinotus, Boesemania, Cheilotrema, Ctenosciaena, Dendrophysa, Equetus, Genyonemus, Johnius, Leiostomus, Lonchurus, Menticirrhus, Micropogonias, Ophioscion, Pachypops, Pachyurus, Paralonchurus, Pareques, Pogonias, Roncador, Sciaenops,* and *Umbrina* (Fig. 2).

Phylogenetic Comparative Methods

Two phylogenies were used in this study: one based on morphology proposed by Sasaki (1989) and a second based on molecular data proposed by Lo et al. (*in review*). For the phylogenetic comparative analyses, both phylogenies were collapsed to genus level and pruned to match the genera available from our sampling program (Fig 2). All analyses were conducted in R (The R Project for Statistical Computing, available at: http://www.r-project.org/) using the caper and ape packages with the assumption of Brownian motion as the model of trait evolution. Two methods were used to test for the signal of relatedness: phylogenetic independent contrasts (PIC) and phylogenetic generalized least squares (PGLS; Felsenstein 1985; Pagel 1999). All measurements were standardized by head length. Normality of the size-corrected measurements was tested and any non-normal measurements were log-transformed. The only measurements that was not normally distributed was standard length (SL), which was log-transformed for the analysis. Once the phylogeny was accounted for, linear models were constructed for SL with the eye diameter and the ascending process, premaxilla, and lower jaw lengths as response variables, both with the phylogeny accounted for (PIC and PGLS) and without the phylogenetic signal taken into account. The best model for the data was selected using Akaike Information Criterion (AIC) with an alpha of 0.05 to determine significance of the measured elements. Phylogenetic signal of the examined oral jaw elements was determined with Pagel's λ, which was estimated from the PGLS model using maximum likelihood (Pagel 1999; Hernández et al. 2013).

RESULTS

Ontogenetic patterns of oral jaws in Chesapeake Bay sciaenids

During ontogeny, benthic and pelagic Chesapeake Bay sciaenids had significantly different premaxilla, lower jaw, and ascending process lengths as well as eye diameters ($p<0.05$; Fig. 3). In addition, all of these elements, except for eye diameter, changed significantly with increasing SL. There was overlap in the relative size of each examined oral jaw element and eye diameter for benthic and pelagic sciaenids during early ontogeny (Fig. 3). After approximately 20 mm SL, pelagic sciaenids had longer premaxillae and lower jaws but shorter ascending processes relative to benthic sciaenids (Fig. 3). Although eye diameter differed significantly between benthic and pelagic Chesapeake Bay sciaenids (i.e., by foraging habitat), there was overlap even in the larger ontogenetic stages (Fig. 3).

Oral jaw patterns in Sciaenids

Although significant ontogenetic patterns were detected in sciaenids from the Chesapeake Bay, it is unknown if these patterns were due to relatedness or selective processes. Similarly, pelagic sciaenids outside of the Chesapeake Bay had longer premaxillae and lower jaws as well as larger eye diameters relative to benthic sciaenids, regardless of the topology used in the phylogenetic comparative analyses. Pelagic sciaenids also had shorter ascending processes at relative to benthic sciaenids (Fig. 4 and 5). They also attained larger SL. The linear model that best explained the patterns in the oral jaw data differed depending on the topology used in the analysis. When a morphological topology was used, the best performing model was PGLS, although it performed only slightly better than the linear model, which does not account for evolutionary history (Sasaki 1989; Table 1). However, PIC performed better when a molecular topology was used (Lo et al. *in review*; Table 1). The size of the premaxilla and lower jaw changed very little relative to size while eye diameter decreased relative to size for pelagic sciaenids when Sasaki's morphological phylogeny (1989) was used (Fig. 4). When a molecular phylogeny was used, the length of the premaxilla and lower jaw increased relative to size for pelagic sciaenids while eye diameter and ascending process length decreased (Fig. 5; Lo et a. *in review*). In addition, for benthic sciaenids eye diameter decreased with increasing size when the morphological topology was used but increased when the molecular topology was used (Figs. 4 and 5). This was similar to the pattern of eye diameter size observed during development for the Chesapeake Bay benthic sciaenids (Fig. 3).

Phylogenetic signal (i.e., Pagel's λ) also differed depending on the topology used during the analysis. When using the morphological topology, the phylogenetic signal was low (λ= 0) regardless of foraging guild for all elements examined (Table 2; Sasaki 1989). When using a molecular phylogeny, Pagel's λ was low for premaxilla, lower jaw, and ascending process length for pelagic sciaenids ($\lambda= 0$) but was high ($\lambda= 1$) for eye diameter, indicating a strong phylogenetic signal (Table 2; Lo et al. *in review*). When using the molecular topology, we observed the opposite trend in benthic sciaenids (Table 2; Lo et al. *in review*). For example, Pagel's λ was high for premaxilla, lower jaw, and ascending process length but low for eye diameter ($\lambda= 0$; Table 2).

DISCUSSION

Phylogenetically related species possess similar phenotypes and often inhabit similar ecological niches (Hernández et al. 2013; Münkemüller et al. 2012). Therefore, phylogenetic history can act as a constraint on the potential configuration a structure can take and may complicate the links between morphology and ecology (Clifton and Motta 1998; Poling and Fuiman 1998). Closely related species are also hierarchically related and violate the basic statistical assumption of independence (Garland et al. 1999; Garland et al. 2005; Hernández et al. 2013). We have identified morphological patterns in ELHS sciaenids from the Chesapeake Bay, which correlate to dietary shifts (Deary and Hilton unpublished). However, the examined sciaenids are closely related to each other (Fig. 2), so the observed patterns may be due to phylogenetic constraints rather than a response to selective forces related to foraging.

Ontogenetic patterns were observed in the development of the oral jaws in benthic and pelagic Chesapeake Bay sciaenids. There were significant differences in these elements by foraging habitat. ELHS pelagic sciaenids had longer premaxillae and lower jaws but shorter ascending processes relative to benthic sciaenids There was, however, overlap in the relative sizes of the premaxilla, lower jaw, and ascending process length and eye diameter early during ontogeny, prior to 20 mm SL. Significant differences were detected in eye diameter between benthic and pelagic sciaenids, but overlap in the relative size of the eye was observed even in the later stages. The morphological differences observed in the oral jaw elements suggest that ELHS sciaenids from the Chesapeake Bay possess the oral jaw elements necessary to partition their foraging habitats (Chao and Musick 1977; Carlson and Wainwright 2010). However, it is unknown if the observed ontogenetic patterns are due to phylogenetic relatedness or natural selection.

Similar to the ontogenetic patterns described in sciaenids from the Chesapeake Bay, pelagic sciaenids found outside of the Chesapeake Bay possessed longer premaxillae and lower jaws relative to benthic sciaenids regardless of the phylogeny used in the analysis. The relative size of eye diameter and lower jaw decreased as body size increased in benthic sciaenids but changed very little in pelagic sciaenids. This suggests that regardless of body size, pelagic sciaenids possessed relatively long upper and lower jaw bones. In addition, benthic sciaenids possessed longer ascending processes relative to pelagic sciaenids, suggesting that benthic sciaenids have more protrusible jaws relative to pelagic sciaenids (Hulsey et al. 2010). Pagel's λ for each element is low for both foraging guilds when the morphological topology from Sasaki's (1989) phylogeny was used in the analysis, which suggests that the trends observed in the data are independent of the phylogenetic relationship (Hernández et al. 2013). A caveat of Sasaki's phylogeny is that it is based on morphological data, which introduces some circularity into the analyses since the phylogeny was constructed with morphological data and the oral jaw measurements are also morphological data (Felsenstein 1985; Garland et al. 2005). Sasaki's (1989) morphological phylogeny was constructed using 129 derived characters, including six characters related to the structure of the oral jaws. This, in turn, suggests that circularity may be an issue when integrating phylogeny into statistical analyses of oral jaw elements.

If possible, a phylogeny constructed from data other than the data collected during the comparative study should be selected to reduce any bias associated with circularity (Felsenstein 1985; Garland et al. 2005). To account for circularity, the molecular phylogeny by Lo et al. (*in review*) was included in our analyses to determine if any differences could be detected in the phylogenetic signal of the measured oral jaw elements. Similar to the analyses based on Sasaki's (1989) phylogeny, Pagel's λ was low for pelagic sciaenids, except for eye diameter based on the molecular topology. Therefore, variations in the size of the ascending process, lower jaw, and premaxilla are not predicted by the phylogenetic relationships, but are likely controlled by selective pressures related to foraging and prey capture (Clifton and Motta 1998; Hernandez et al. 2002). In contrast, a strong phylogenetic signal was detected for benthic sciaenids for ascending process, lower jaw, and premaxilla length when the molecular topology was used (Lo et al. *in review*). This suggests that phylogenetic relationships predict the similarity in these structures among benthic sciaenids (Hernández et al. 2013). Pagel's λ is intermediate ($\lambda = 0.58$) for premaxilla length in benthic sciaenids. Therefore, phylogenetic relatedness does not account for all of the variation observed in premaxilla length. Even though the relative size of the premaxilla is likely driven by evolutionary history as indicated by an intermediate Pagel's λ, selective forces are still able to act on the premaxilla, giving rise to different configurations. These, in turn, allow varying degrees of relative jaw protrusion in conjunction with a longer ascending process (Hulsey et al. 2010; Hernández et al. 2013). Phylogenetic signal was low for pelagic sciaenids regardless of the topology used in the analysis but differed for benthic sciaenids depending on the topology used for the analysis. This may indicate some circularity associated with the morphological phylogeny because of the type of data collected for our study.

Morphological patterns that were identified in ELHS sciaenids from the Chesapeake Bay were still observed even after accounting for phylogenetic relatedness, suggesting that these patterns are not constrained by evolutionary history even though the examined sciaenids are hierarchically related to each other (Deary and Hilton unpublished). Due to the morphological data collected for this study, the molecular topology (Lo et al. *in review*) is preferred because it does not introduce any circularity into the analyses and this phylogeny is the most recent, taxonomically rich genus-level phylogeny available for sciaenids. Therefore, the morphological patterns of the feeding apparatus are shaped by selective forces related to foraging rather than phylogeny, especially for pelagic sciaenids. Some phylogenetic constraints are present in the structure of the oral jaws in benthic sciaenids, especially for ascending process and lower jaw length when using the molecular topology. Natural selection is still acting on premaxilla length, which can ultimately influence the relative protrusion of the oral jaws (Hulsey et al. 2010; Hernández et al. 2013). Evolutionary history can constrain morphological structures (Poling and Fuiman 1998) but for ELHS sciaenids, the phylogenetic signal was found to be low for oral jaw elements, especially for pelagic sciaenids. This suggests that phylogeny does not constrain the anatomy of oral jaw elements and that the morphological patterns observed in Chesapeake Bay sciaenids represent ecomorphological patterns, which are relatively unconstrained by evolutionary history.

MATERIALS EXAMINED

Aplodinotus grunniens: Bell Museum at UM 29819 (1 A, 28 mm SL); Bell Museum at UM 44648 (4 A, 30-53 mm SL); Bell Museum at UM 44904 (3 A, 45-118 mm SL); Bell Museum at UM 44659 (4 A,); VIMS 22155-22163 (9 C&S, 3.4-7.32 mm SL

Argyrosomus coronus: SAIAB 87296 (1 A, 340 mm SL)

Argyrosomus hololepidotus: SAIAB 10695 (3 A, 110-195 mm SL)

Argyrosomus inodorus: SAIAB 10265 (2 A, 335-384 mm SL); VIMS 22177-22182 (6 C&S, 2.5-4.8 mm SL)

Argyrosomus japoniucs: SAIAB 38081 (1 A, 151 mm SL); VIMS 22183-22190 (8 C&S, 3.0-5.4 mm SL)

Argyrosomus thorpei: SAIAB 675 (1 A, 359 mm SL); SAIAB 677 (1 A, 455 mm SL)

Aspericorvina jubata: CAS 79498 (1 A, 72 mm SL)

Atractoscion aequidens: SAIAB 11599 (2 A, 177-194 mm SL); SAIAB 16402 (1 A, 217 mm SL)

Atrobucca geniae: SAIAB 42672 (1 A, 181 mm SL)

Atrobucca nibe: SAIAB 36854 (3 A, 78-119 mm SL); SAIAB 36885 (3 A, 73-250 mm SL); SAIAB 80050 (1 A, 85 mm SL)

Atrobucca trewavasae: SAIAB 122 (1 A, 139 mm SL)

Austronibea oedogenys: USNM 402013 (1 A, 140 mm SL)

Bahaba polykladiskos: USNM 325508 (1 A, 182 mm SL)

Bairdiella sanctaeluciae: VIMS 3368 (2 A, 160-174 mm SL)

Bairdiella chrysoura: VIMS 22191-22222 (32 C&S, 1.2-118 mm SL); VIMS 22544-22546 (3 C&S, 42-69 mm SL)

Boesemania microplepis: USNM 305697 (1 A, 230 mm SL)

Buccone praedatoria: USNM 50385 (1 A, 260 mm SL)

Cheilotrema saturnum: CAS 17896 (1 A, 240 mm SL); CAS 68534 (1 A, 112 mm SL)

Cheilotrema fasciatum: CAS 18370 (1 A, 162 mm SL)

Chrysochir aureus: USNM 324184 (3 A, 76-270 mm SL)

Cilus gilbert: USNM 53464 (1 A, 379 mm SL); USNM 77308 (4 A, 45-125 mm SL)

Collichthys lucidus: USNM 130429 (1 A, 125 mm SL)

Corvina saturna: USNM 39823 (1 A, 222 mm SL)

Corvula macrops: USNM 321546 (2 A, 80-134 mm SL)

Ctenosciaena gracilicirrhus: BMNH 1931.12.5.102 (1 A, 109 mm SL); VIMS 3370 (1 A, 148 mm SL)

Cynoscion nebulosus: VIMS 22223-22253 (30 C&S, 3.4-103 mm SL); VIMS 22295 (1 C&S, 31.6 mm SL)

Cynoscion nothus: VIMS 4178 (1 A, 190 mm SL)

Cynoscion regalis: VIMS 22254-22294 (29 C&S, 3.0-117); VIMS 22296 (1 C&S, 9.3 mm SL)

Daysciaena albida: USNM 324579 (1 A, 217 mm SL); USNM 325089 (1 A, 38 mm SL)

Dendrophysa russelli: VIMS 7592 (1 A, 176 mm SL)

Elattarchus archidium: USNM 321549 (2 A, 88-124 mm SL)

Equetus lanceolatus: VIMS 7231 (1 A, 128 mm SL)

Equetus umbrosus: VIMS 7721 (2 A, 125-155 mm SL)

Genyonemus lineatus: SAIAB 49010 (1 A, 215 mm SL)

Isopisthus parvipinnis: VIMS 5654 (1 A, 120 mm SL)

Johnieops sina: VIMS 7513 (1 A, 123 mm SL)

Johnius amblycephalus: SAIAB 7727 (3 A, 79-174 mm SL); SAIAB 39870 (3 A, 115-139 mm SL)

Johnius dorsalis: SAIAB 1391 (2 A, 121-125 mm SL); SAIAB 3025 (1 A, 99 mm SL); SAIAB 7809 (4 A, 57-137 mm SL)

Johnius fuscolineatus: SAIAB 877337 (2 A, 132-155 mm SL)

Kathala axillaris: CAS 122854 (1 A, 120 mm SL); USNM 324174 (2 A, 52-84 mm SL)

Larimus fasciatus: VIMS 22297-22309 (13 C&S, 25.2-86.1 mm SL)

Larimichthys crocea: USNM 130379 (2 A, 147-253 mm SL)

Leiostomus xanthurus: VIMS 22310-22365 (56 C&S, 11.6-115 mm SL); VIMS 22547 (1 C&S, 88.5 mm SL)

Lonchurus lanceolatus: USNM 367724 (2 A, 111-134 mm SL); VIMS 7229 (2 A, 135-146 mm SL)

Macrodon ancyclodon: VIMS 7227 (1 A, 233 mm SL)

Macrospinosa cuja: ANSP 76806 (2 A, 145-163 mm SL); ANSP 87574 (1 A, 151 mm SL); BMNH 60.3.19.13 (1 A, 105 mm SL)

Menticirrhus sp.: VIMS 22366-22383 (18 C&S, 2.8-62.2 mm SL)

Micropogonias furnieri: USNM 133715 (1 A, 217 mm SL)

Micropogonias undulatus: VIMS 22384- 22489 (106 C&S, 4.0-166 mm SL); VIMS 22548-22550 (3 C&S, 44-55 mm SL)

Miichthys miiuy: USNM 130411 (1 A, 200 mm SL)

Miracorvina angolensis: USNM 325095 (2 A, 187-300 mm SL)

Nebris microps: VIMS 5676 (2 A, 80-116 mm SL); VIMS 7241 (1 A, 275 mm SL)

Nibea microgenys: SAIAB 70525 (1 A, 140 mm SL)

Nibea soldado: SAIAB (1 A, 152 mm SL)

Odontoscion dentex: VIMS 3371 (2 A, 101-110 mm SL)

Ophioscion scierus: USNM 80771 (1 A, 191 mm SL)

Otolithes ruber: SAIAB 1382 (1 A, 153 mm SL); SAIAB 5367 (1 A, 222 mm SL); SAIAB 11616 (2 A, 103-225 mm SL)

Otolithoides pama: USNM 324217 (2 A, 112-142 mm SL)

Pachypops adspersus: USNM 318137 (2 A, 97-157 mm SL)

Pachyurus bonariensis: USNM 181555 (1 A, 140 mm SL)

Panna microdon: USNM 324571 (2 A, 145-200 mm SL)

Paralonchurus brasiliensis: USNM 87746 (2 A, 108-176 mm SL); VIMS 7240 (1 A, 208 mm SL)

Paralonchurus elegans: VIMS 5656 (1 A, 220 mm SL)

Paranebris bauchotae: USNM 360918 (1 A, 173 mm SL)

Paranibea semiluctuosa: USNM 325069 (2 A, 169-223 mm SL)

Pareques acuminatus: VIMS 4144 (1 A, 112 mm SL)

Pennahia argentata: VIMS 15254 (1 A, 176 mm SL)

Pennahia macrophthalmus: VIMS 7504 (1 A, 145 mm SL)

Pentheroscion mbizi: CAS 235134 (1 A, 176 mm SL)

Petilipinnis grunniens: USNM 401561 (1 A, 61 mm SL)

Plagioscion auratus: USNM 52584 (1 A, 195 mm SL)

Plagioscion squamosissimus: USNM 260103 (1 A, 152 mm SL)

Pogonias cromis: VIMS 22490-22506 (17 C&S, 2.2-5.7 mm SL)

Polycirrhus rathbuni: USNM 41170 (1 A, 135 mm SL)

Protonibea diacanthus: USNM 324687 (1 A, 214 mm SL)

Protosciaena trewavasae: USNM 407380 (1 A, 127 mm SL)

Pseudolithus moorii: SAIAB 25635 (1 A, 245 mm SL)

Pseudotolithus elongatus: SAIAB 25589 (1 A, 245 mm SL)

Pseudotolithus epipercus: SAIAB 26532 (1 A, 130 mm SL)

Pseudotolithus senegalensis: SAIAB 25654 (4 A, 84-190 mm SL); SAIAB 64973 (1 A, 250 mm SL)

Pseudotolithus typus: SAIAB 26523 (1 A, 123 mm SL)

Pteroscion peli: SAIAB 26524 (2 A, 54-70 mm SL); SAIAB 64643 (1 A, 77 mm SL); SAIAB 67758 (4 A, 45-199 mm SL)

Pterotolithus maculatus: BMNH 1895.2.28.40 (1 A, 145 mm SL); CAS 114622 (2 A, 41 mm SL)

Roncador stearnsii: USNM 26757 (2 A, 155-315 mm SL)

Sagenichthys ancylodon: USNM 220144 (1 A, 171 mm SL)

Sciaena bathytatos: VIMS 3150 (1 A, 170 mm SL)

Sciaena trewavasae: VIMS 3149 (2 A, 115-164 mm SL)

Sciaena umbra: VIMS 3148 (2 A, 210-238 mm SL)

Sciaenops ocellatus: VIMS 22507-22534 (28 C&S, 4-102 mm SL); VIMS 22552-22555 (4 C&S, 30-60 mm SL)

Seriphus politus: CAS 19423 (2 A, 37-95 mm SL); CAS 213275 (1 A, 185 mm SL)

Sonorolux fluminis: BMNH 1895.2.28.47 (1 A, 75 mm SL); BMNH 1905.11.14.14.9 (1 A, 79 mm SL)

Stellifer brasiliensis: CAS 52208 (1 A, 112 mm SL)

Stellifer lanceolatus: VIMS 22535-22543 (9 C&S, 3.1-6.8 mm SL)

Totoaba macdonaldi: CAS 60768 (1 A, 279 mm SL)

Umbrina canariensis: SAIAB 3043 (1 A, 20 mm SL); SAIAB 5760 (1 A, 300 mm SL); SAIAB 12332 (3 A, 72-107 mm SL); SAIAB 26206 (1 A, 194 mm SL)

Umbrina coroides: VIMS 257 (1 A, 185 mm SL)

Umbrina robinsoni: SAIAB 67480 (1 A, 340 mm SL); SAIAB 67490 (1 A, 415 mm SL)

Umbrina ronchus: SAIAB 9148 (1 A, 185 mm SL)

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Table 1. Akaike Information Criterion (AIC) for each jaw element by traditional linear models, phylogenetic generalized least squares (PGLS), and phylogenetic independent contrasts (PIC) for pelagic and benthic sciaenids.

Sasaki Phylogeny (1989)

	Pelagic Sciaenids			**Benthic Sciaenids**		
Element	**Linear Model**	**PGLS**	**PIC**	**Linear Model**	**PGLS**	**PIC**
Premaxilla	-121.1	-123.1	-10.1	-69.3	-71.3	5.3
Lower Jaw	-107.7	-109.7	-5.4	-54.4	-56.4	9.3
Ascending Process	-129.7	-131.5	-26.3	-68.9	-70.9	-0.8
Eye Diameter	-89.3	-92.2	12.6	-63.7	-65.7	-1.0

Lo et al. Phylogeny (*in review*)

	Pelagic Sciaenids			**Benthic Sciaenids**		
Element	**Linear Model**	**PGLS**	**PIC**	**Linear Model**	**PGLS**	**PIC**
Premaxilla	-113.7	-115.8	-181.8	-70.3	-72.9	-123.7
Lower Jaw	-91.2	-93.2	-149.1	-54.4	-60.8	-110.3
Ascending Process	-122.4	-124.2	-196.6	-70.3	-72.9	-123.7
Eye Diameter	-92.8	-97.4	-172.4	-73.8	-75.8	-123.9

Table 2. Pagel's λ by foraging guild for each oral jaw element.

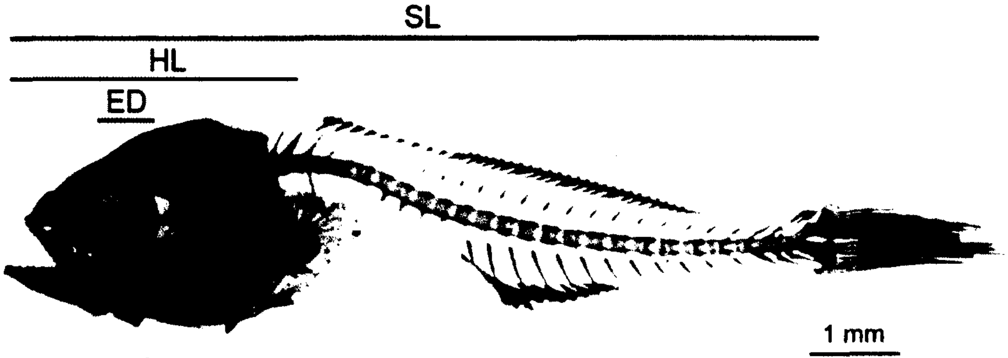
Sasaki Phylogeny (1989)

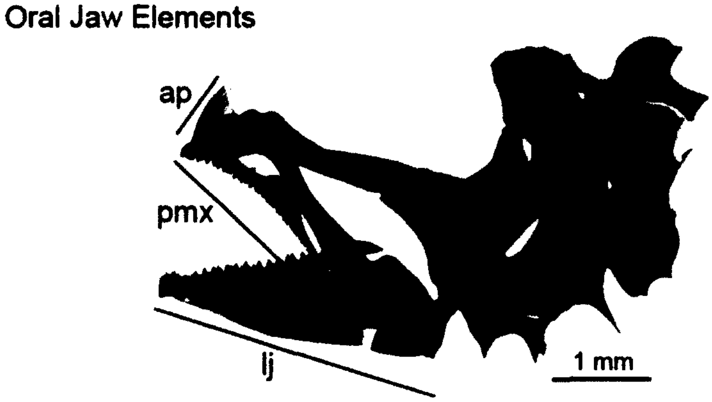
Element	Pagel's λ: Pelagic Sciaenids	Pagel's λ: Benthic Sciaenids
Premaxilla	0	0
Lower Jaw	0	0
Ascending Process	0	0
Eye Diameter	0.19	0.03

Lo et al. Phylogeny (*in review*)

Element	Pagel's λ: Pelagic Sciaenids	Pagel's λ: Benthic Sciaenids
Premaxilla	0	0.58
Lower Jaw	0	1
Ascending Process	0	1
Eye Diameter	1	0

Fig. 1. Oral jaw elements measured on a cleared and stained specimen (e.g., *Micropogonias undulatus*) and an alcohol-stored specimen (e.g., *Chrysochir aureutus*). Black lines indicate how elements were measured. Abbreviations: SL, standard length; HL, head length; ED, eye diameter; ap, ascending process; pmx, premaxilla; lj, lower jaw; POL, pre-orbital length.


SL
HL
ED
1 mm


Oral Jaw Elements
ap
pmx
lj
1 mm

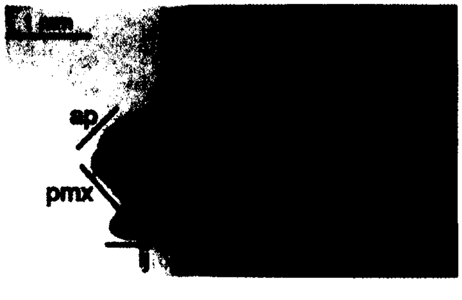

1 mm
ap
pmx

Fig. 2. Phylogenetic relationships hypothesized for sciaenid genera by A. Sasaki (1989) based on morphological data and by B. Lo et al. (*in review*) constructed from molecular data. Terminal nodes are colored based on the predominant foraging guild of the genera with blue denoting pelagic foraging sciaenids and brown denoting benthic foraging sciaenids. Chesapeake Bay sciaenid genera and *Aplodinotus* (native to freshwater regions within North America) are denoted with black asterisks.

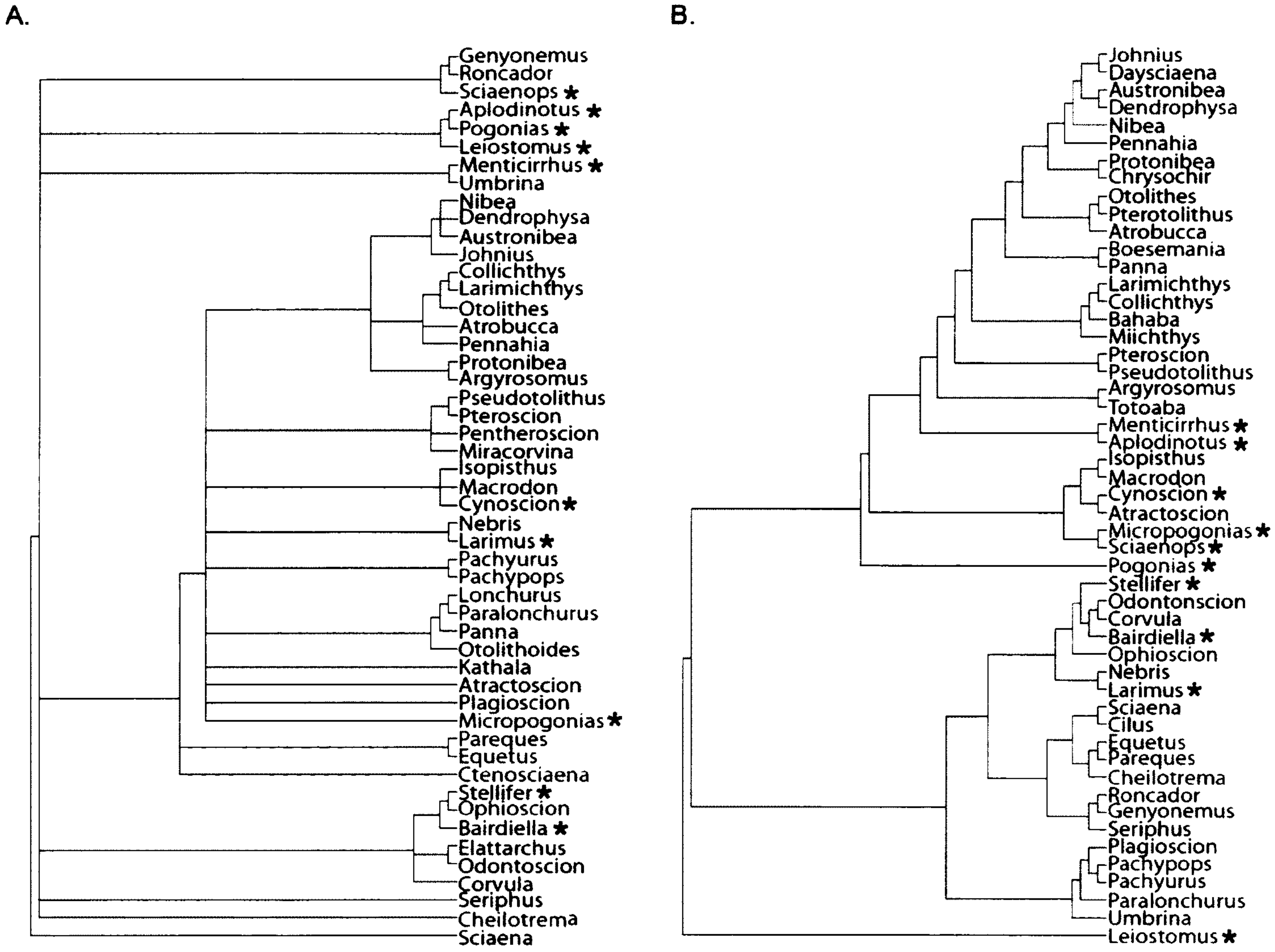

A.
Genyonemus
Roncador
Sciaenops ★
Aplodinotus ★
Pogonias ★
Leiostomus ★
Menticirrhus ★
Umbrina
Nibea
Dendrophysa
Austronibea
Johnius
Collichthys
Larimichthys
Otolithes
Atrobucca
Pennahia
Protonibea
Argyrosomus
Pseudotolithus
Pteroscion
Pentheroscion
Miracorvina
Isopisthus
Macrodon
Cynoscion ★
Nebris
Larimus ★
Pachyurus
Pachypops
Lonchurus
Paralonchurus
Panna
Otolithoides
Kathala
Atractoscion
Plagioscion
Micropogonias ★
Pareques
Equetus
Ctenosciaena
Stellifer ★
Ophioscion
Bairdiella ★
Elattarchus
Odontoscion
Corvula
Seriphus
Cheilotrema
Sciaena
B.
Johnius
Daysciaena
Austronibea
Dendrophysa
Nibea
Pennahia
Protonibea
Chrysochir
Otolithes
Pterotolithus
Atrobucca
Boesemania
Panna
Larimichthys
Collichthys
Bahaba
Miichthys
Pteroscion
Pseudotolithus
Argyrosomus
Totoaba
Menticirrhus ★
Aplodinotus ★
Isopisthus
Macrodon
Cynoscion ★
Atractoscion
Micropogonias ★
Sciaenops ★
Pogonias ★
Stellifer ★
Odontonscion
Corvula
Bairdiella ★
Ophioscion
Nebris
Larimus ★
Sciaena
Cilus
Equetus
Pareques
Cheilotrema
Roncador
Genyonemus
Seriphus
Plagioscion
Pachypops
Pachyurus
Paralonchurus
Umbrina
Leiostomus ★

Fig. 3. Development of oral jaw elements in Chesapeake Bay sciaenids using linear models when the phylogeny is not taken into account for premaxilla length (A), lower jaw length (B), ascending process length (C), and eye diameter (D). Pelagic sciaenids are denoted by blue triangles, benthic sciaenids by brown circles, and significant differences ($p < 0.05$) by foraging habitat (FH) and standard length (SL) by an asterisk. The slope for each analysis is indicated on each graph. All measurements except SL have been standardized by head length (see "Materials and Methods").

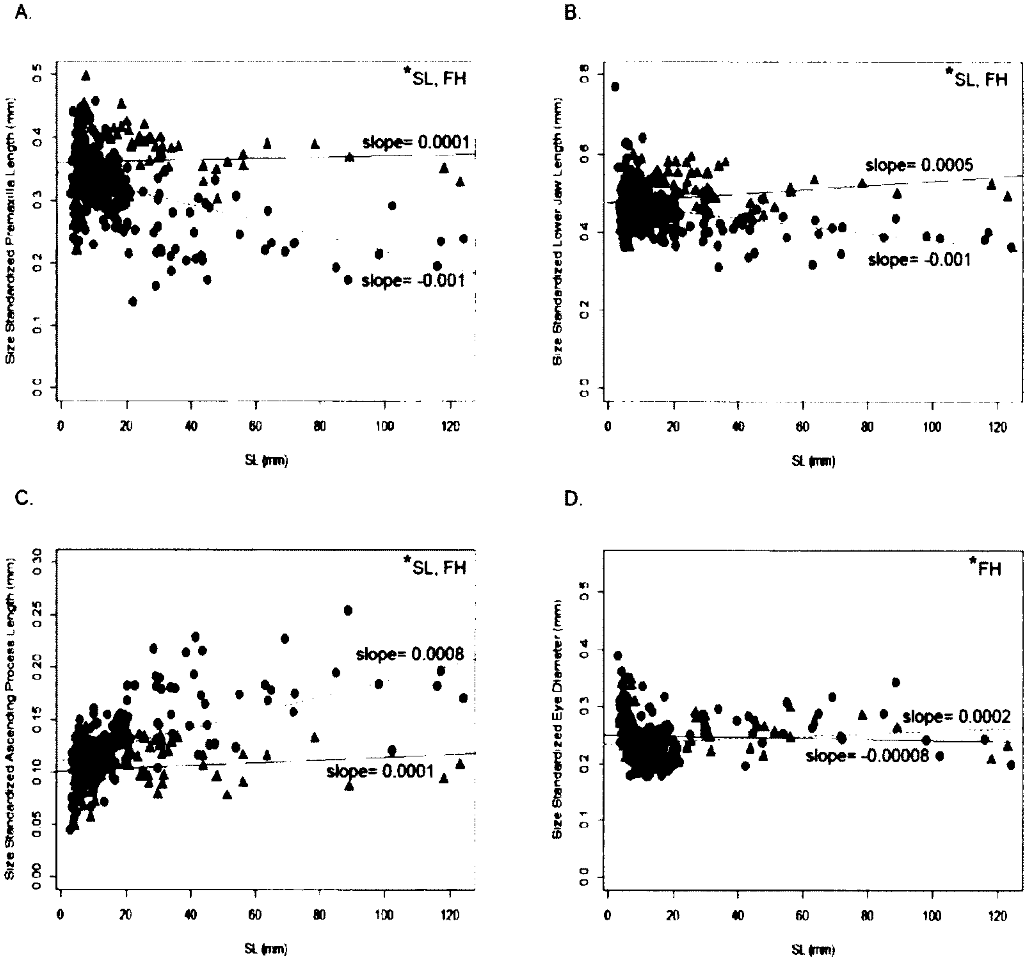
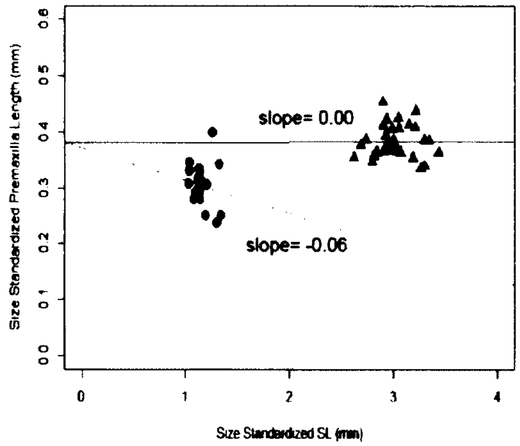
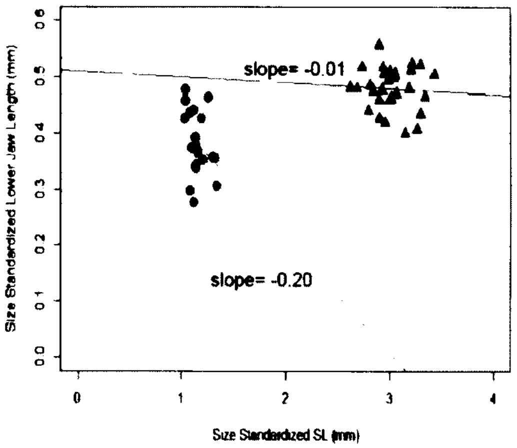

A.
*SL, FH
slope= 0.0001
slope= -0.001
Size Standardized Premaxilla Length (mm)
0.0
0.1
0.2
0.3
0.4
0.5
0
20
40
60
80
100
120
SL (mm)
B.
*SL, FH
slope= 0.0005
slope= -0.001
Size Standardized Lower Jaw Length (mm)
0.0
0.2
0.4
0.6
0.8
SL (mm)
C.
*SL, FH
slope= 0.0008
slope= 0.0001
Size Standardized Ascending Process Length (mm)
0.00
0.05
0.10
0.15
0.20
0.25
0.30
SL (mm)
D.
*FH
slope= 0.0002
slope= -0.00008
Size Standardized Eye Diameter (mm)
0.0
0.1
0.2
0.3
0.4
0.5
SL (mm)

Fig. 4. Results of phylogenetic generalized least squares (PGLS) using the topology proposed by Sasaki (1989) for premaxilla length (A), lower jaw length (B), ascending process length (C), and eye diameter (D). Pelagic sciaenids are denoted by blue triangles and benthic sciaenids by brown circles. The slope for each analysis is indicated on each graph. All measurements have been standardized by head length (see "Materials and Methods").

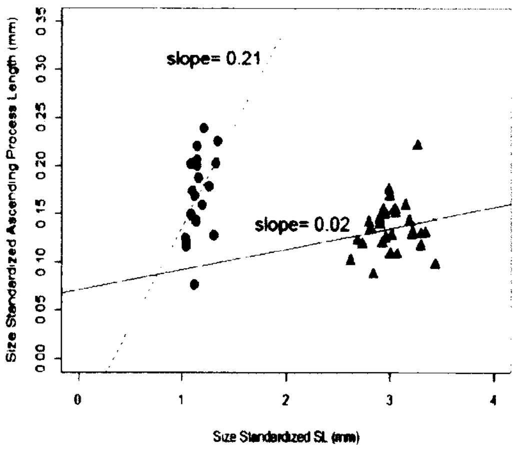
A.


Size Standardized Premaxilla Length (mm)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
slope= 0.00
slope= -0.06
0
1
2
3
4
Size Standardized SL (mm)

B.


Size Standardized Lower Jaw Length (mm)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
slope= -0.01
slope= -0.20
0
1
2
3
4
Size Standardized SL (mm)

C.


Size Standardized Ascending Process Length (mm)
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
slope= 0.21
slope= 0.02
0
1
2
3
4
Size Standardized SL (mm)

D.

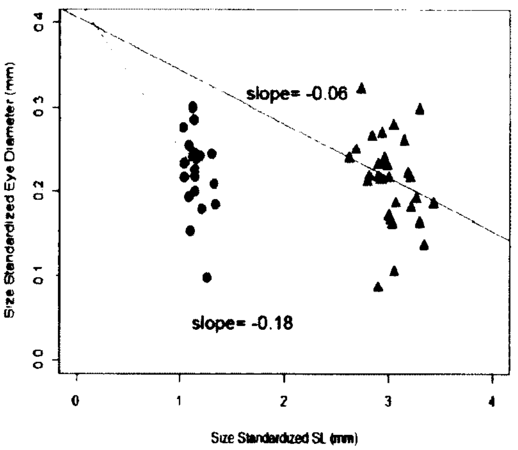
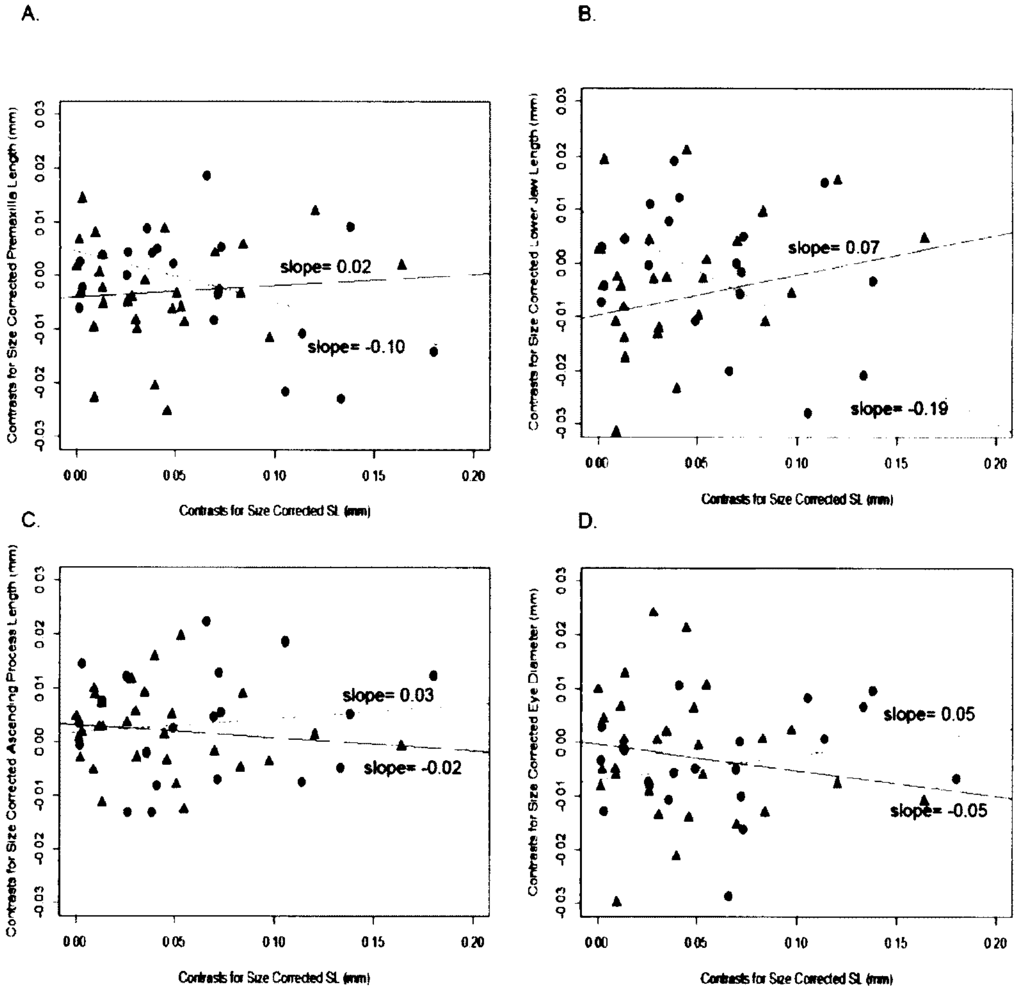

Size Standardized Eye Diameter (mm)
0.0
0.1
0.2
0.3
0.4
slope= -0.06
slope= -0.18
0
1
2
3
4
Size Standardized SL (mm)

Fig. 5. Results of phylogenetic independent contrasts (PIC) using the topology proposed by Lo et al. (*in review*) for premaxilla length (A), lower jaw length (B), ascending process length (C), and eye diameter (D). Pelagic sciaenids are denoted by blue triangles and benthic sciaenids by brown circles. The slope for each analysis is indicated on each graph. All measurements have been standardized by head length (see "Materials and Methods").


A.
B.
C.
D.
Contrasts for Size Corrected Premaxilla Length (mm)
Contrasts for Size Corrected Lower Jaw Length (mm)
Contrasts for Size Corrected Ascending Process Length (mm)
Contrasts for Size Corrected Eye Diameter (mm)
Contrasts for Size Corrected SL (mm)
-0.03
-0.02
-0.01
0.00
0.01
0.02
0.03
0.00
0.05
0.10
0.15
0.20
slope= 0.02
slope= -0.10
slope= 0.07
slope= -0.19
slope= 0.03
slope= -0.02
slope= 0.05
slope= -0.05

GENERAL CONCLUSION

The goal of this dissertation was to identify when niche partitioning can occur during ontogeny in estuarine-dependent, early life history stage fishes from the Chesapeake Bay by describing the development of sensory modality and the structure of the feeding apparatus along with dietary data. Species of the family Sciaenidae, the drums, were used as a model group for this study because they are commercially and recreationally important especially along the Atlantic coast of North America and the Gulf of Mexico, and they possess variations in the structure of feeding apparatus and sensory systems enabling adult sciaenids to partition their foraging habitats (Chao and Musick, 1977; Flores-Coto et al., 1998; Horodysky et al., 2008; Murdy and Musick, 2013; ASMFC). To identify when during ontogeny niche partitioning can occur in ELHS sciaenids, the development of the senses that are used to locate prey were described, followed by the development of the feeding apparatus, which is used to capture and process prey, and finally describe the diet of ELHS sciaenids from the Chesapeake Bay. In order to place these data into an ecomorphological context, the influence of phylogeny on the structure of the feeding apparatus must first be taken into account. If the feeding apparatus is constrained by the evolutionary history of sciaenids, the links between form and function are not due entirely to responses to selective processes related to foraging (Wainwright and Richards 1995; Clifton and Motta 1998).

Sensory modality was found to shift during ontogeny in ELHS sciaenids. The optic tract was found to be the largest sensory brain region during ontogeny, although the volume of this tract relative to the other regions decreased with increasing size in taxa from all foraging guilds. This suggests that vision is the dominant sense used by all sciaenids early during ontogeny. The relative decrease in size of the visual region suggests that secondary sensory systems inform the visual system at later ontogenetic stages. The ontogenetic pattern observed in sciaenids has also been noted in elasmobranchs and cyprinids, suggesting that vision is a more important sense earlier during ontogeny in fishes but that as foraging habitat and diet shift, other senses become more important and sensory modality shifts (Brändstatter and Kotrschal 1989, 1990; Lisney et al. 2007).

Cynoscion nebulosus had the smallest swimbladder-inner ear distance measured between 40.4-47.0 mm SL compared to *S. ocellatus* and *L. xanthurus*, suggesting that hearing is the dominant secondary sense at this stage in *C. nebulosus*. *Sciaenops ocellatus* had large olfactory, gustatory, and hearing/mechanoreceptive regions relative to the other sciaenids by 14.8 mm SL, which infers that *S. ocellatus* is using all of the other examined senses at this stage to inform their visual system. By approximately 47.0 mm SL, *S. ocellatus* possessed the largest olfactory and hearing/mechanoreceptive regions, suggesting that smell, hearing, and mechanoreception are important senses, in addition to vision, and are used to inform *S. ocellatus* of prey, predators, and possible favorable habitats. As a generalist, *S. ocellatus* forage both in the water column and along the benthos for prey on the periphery of seagrass beds (Poling and Fuiman, 1998; Horodysky et al., 2008a) and the use of multiple secondary senses may help individuals of *S. ocellatus* effectively move in and out of structured seagrass habitats without an extreme loss in responsiveness to sensory stimuli. The swimbladder-inner ear distance was greatest throughout ontogeny for benthic sciaenids relative to generalist and pelagic sciaenids, suggesting that hearing is not as important for benthic sciaenids. In addition, otoliths were not well developed in benthic sciaenids until approximately 46.7 mm SL. The olfactory region of *L. xanthurus* (benthic sciaenid) was similar in size to that of *S. ocellatus*, but it also possessed a relatively large gustatory region by 46.7 mm SL. This suggests that benthic, epifaunal foraging sciaenids are relying on olfactory and gustatory stimuli to inform the visual cues in order to successfully locate prey and evade predators. Epifaunal benthic foragers like *Menticirrhus* sp. and *L. xanthurus* consume burrowing prey and obtain food by engulfing sediment and sifting for prey (Chao and Musick, 1977; Coull, 1990; personal observation). Therefore, increased sensitivity to gustatory cues during ontogeny may enable these sciaenids to more effectively sift through sediment to locate prey and reduce incidental sediment consumption.

In addition to shifts in sensory modality, three primary divergences in the structure of the feeding apparatus were identified during ontogeny in four examined sciaenid species (*C. nebulosus*, *C. regalis*, *Micropogonias undulatus*, and *L. xanthurus*) representing three different foraging guilds (pelagic, generalist, and benthic). The feeding apparatus elements that supported these divergences often reflect the foraging habits of fishes (Chao and Musick, 1977; Govoni, 1987; Reecht et al., 2013). *Leiostomus xanthurus* (benthic) was the most morphologically distinct taxon in many of the measured oral and pharyngeal jaw elements by 22.4 mm SL, suggesting that this species possesses the necessary specializations to the feeding apparatus to partition its foraging habitat from the other three sciaenids and may be exploiting more benthic prey. The second divergence in the ontogeny of these taxa occurred at approximately 30.4 mm SL and was associated primarily with length of the premaxilla, although there were also differences in toothed area of third pharyngeal toothplate, eye diameter, ascending process length, and average length of the gill rakers on ceratobranchial 2. Therefore, by 30.4 mm SL, many of the adaptations of the feeding apparatus necessary to exploit different foraging habitats have been attained in these four sciaenid species (Chao and Musick, 1977; Govoni, 1987; Reecht et al., 2013). By 88.0 mm SL, the measured oral jaw elements of *M. undulatus* (generalist) were intermediate between *L. xanthurus* and *Cynoscion* spp. (pelagic) but had pharyngeal jaws more similar to *C. nebulosus*. This variation likely supports a more versatile, generalist foraging strategy.

The sciaenids examined in this study do possess structural variation in several feeding apparatus elements early during ontogeny, as well as different sensory modalities, although it is not yet known if sciaenids are actually able to exploit different foraging habitats at these early stages. A single dietary shift was observed in ELHS sciaenids from the Chesapeake Bay and the size observed for the shift differed for each foraging guild. The dietary shifts that were observed at the guild-level were also observed at the species-level at similar sizes, with the exception of generalist sciaenids. *Cynoscion nebulosus* and the other pelagic sciaenids did not experience a shift in foraging habitat during ontogeny, although the types of prey consumed did change with increasing size. Early during ontogeny *C. nebulosus* and other pelagic sciaenids fed primarily on pelagic crustaceans, mainly copepods, whereas later ontogenetic stages (greater than 16 mm SL) fed primarily on pelagic shrimp (mysids), pelagic fishes, and some benthic crustaceans. Dietary shifts for *M. undulatus*, a generalist, were observed at approximately 25 mm SL, which was larger than the pelagic sciaenids (16 mm SL). *Micropogonias undulatus* was feeding on a variety of pelagic zooplankton prey before 25 mm SL but then shifted to feeding on pelagic shrimp. As a guild, the diet of generalist sciaenids shifted at approximately 35 mm SL and included both pelagic and benthic prey. Dietary shifts were observed in ELHS benthic sciaenids, including *L. xanthurus*, by 20 mm SL with larger individuals feeding on benthic worms, benthic crustaceans, pelagic shrimp, and pelagic fishes. Even though changes in the feeding apparatus structure, sensory modality, and diets occurred in ELHS sciaenids, there may be phylogenetic constraints on these structures so that the configuration of these structures may be related more to evolutionary history than responses to selective pressures.

In order to determine the role of phylogenetic constraints in shaping the ontogeny of sciaenids and its impact on niche separation, I accounted for a phylogenetic signal using phylogenetic comparative methods. Generally, pelagic sciaenids had larger bodies and eye diameter as well as longer premaxilla and lower jaw relative to benthic sciaenids regardless of the phylogeny used in the analysis. The relative size of eye diameter and lower jaw decreased as body size increased in benthic sciaenids but changed very little in pelagic sciaenids, which suggests that regardless of body size, pelagic sciaenids possess relatively long upper and lower jaw bones but shorter ascending processes relative to benthic sciaenids. Pagel's λ (an indication of phylogenetic signal) was low for most characters in pelagic sciaenids regardless of the topology used in the analysis, except for eye diameter, which suggests that the phylogenetic signal is low for ascending process, lower jaw, and premaxilla in pelagic sciaenids. Therefore, variations in the size of these structures are not predicted by the phylogenetic relationships of pelagic sciaenids but were perhaps shaped by selective pressures related to foraging and prey capture (Clifton and Motta, 1998; Hernandez et al., 2002). However when a molecular-based topology proposed by Lo et al. (*in review*) was used, a strong phylogenetic signal was detected for benthic sciaenids for the ascending process, lower jaw, and premaxilla, suggesting that phylogenetic relationships within Sciaenidae predict the similarity in these structures among benthic sciaenids (Hernández et al., 2013). Pagel's λ was intermediate ($\lambda = 0.58$) for the ascending process in benthic sciaenids, which suggests that relatedness does not account for all of the variation observed in ascending process length and that selection may influence the relative size and robustness of this structure in benthic sciaenids (Hernández et al., 2013). Therefore, the morphological patterns of the feeding apparatus are potentially due to selective forces related to foraging rather than phylogeny, especially for pelagic sciaenids. Although some phylogenetic constraints are present in the structure of the oral jaws in benthic sciaenids, especially for the premaxilla and lower jaw, natural selection is still acting on ascending process length, which can influence the relative protrusibility of the jaws (Hulsey et al., 2010). In general, the morphological trends identified in ELHS sciaenids from the Chesapeake Bay are not constrained by evolutionary history even though the examined sciaenids are hierarchically related to each other. Therefore, the shifts in feeding apparatus structure that correlate to diet represent ecomorphological patterns in ELHS sciaenids.

Nursery habitats are important for many early life history stage (ELHS) marine fishes because there is ample food supply and shelter from predators that can increase survival at such a vulnerable life history stage for fishes (Beck et al., 2001; Perez-Dominguez et al., 2006). However, in fishes with similar timing of ingress and settlement, niche partitioning can potentially reduce dietary overlap and interspecific competition in their nursery habitats (Zahorcsak et al., 2000). In adults, the ability to partition foraging niches is often associated with specializations to the feeding apparatus

(Chao and Musick, 1977; Hugueny and Pouilly, 1999; Albertson et al., 2008; Carlson and Wainwright, 2010). Shifts in habitat for ELHS fishes are attributed with changes to structural elements or sensory systems (Poling and Fuiman, 1998; Nunn et al., 2012).

Pelagic sciaenids foraged for prey in the water column regardless of ontogenetic stage although the variety of prey consumed expanded by 16.0 mm SL, especially for *C. nebulosus*. This corresponded to when shifts in sensory modality were observed. Since foraging habitat was not observed to shift during development, few morphological changes to their feeding apparatus would be expected (Clifton and Motta, 1998) because the elements are already suited to exploit pelagic prey by first feeding (Wittenrich and Turingan, 2011; Nunn et al., 2012). For pelagic sciaenids, elements of the feeding apparatus, especially premaxilla length, were not distinct from generalist sciaenids until the second divergence 30.4 mm SL but an increase in the toothed area of ceratobranchial 5 was associated with the expansion of their diet. *Leiostomus xanthurus* (benthic) was morphologically distinct in the structure of feeding apparatus elements from the other two guilds by the first split at 22.4 mm SL, which corresponds approximately to the size when dietary shifts occurred. Larger benthic sciaenids (>20 mm SL) fed on benthic worms, benthic crustaceans, pelagic shrimp, and pelagic fishes and this shift in diet was associated with significant increases in ascending process length and greater toothed areas of third pharyngeal toothplate and ceratobranchial 5 and significant decreases in lower jaw and premaxilla length ($p>0.05$). However, specializations to the secondary senses, particularly the olfactory and gustatory regions, were not observed until 47.0 mm SL. Even though late juvenile and adult benthic sciaenids forage exclusively along the benthos for food (Chao and Musick, 1977; Horodysky et al., 2008a), functional constraints of the sensory systems and feeding apparatus, as well as opportunistic foraging may result in benthic sciaenids foraging for prey found in the water column and along the bottom in the ELHS (Poling and Fuiman, 1998; Govoni, 1987). Dietary shifts for generalist sciaenids occur later during ontogeny (35.0 mm SL) relative to the other foraging guilds with larger individuals foraging on pelagic fishes, pelagic shrimp, benthic worms, and benthic crustaceans. This shift in diet was associated with significant changes to the toothed area of the third pharyngeal toothplate and ceratobranchial 5 as well as non-significant changes to lower jaw and premaxilla length. Generalist sciaenids experienced sensory specializations relatively early during ontogeny (14.1 mm SL) but are not morphologically distinct from pelagic sciaenids until 88.0 mm SL, suggesting that generalist sciaenids use a combination of secondary senses to locate prey but the types of prey consumed may be limited due to structural constraints on the feeding apparatus until the late juvenile stage.

Not much is known regarding the foraging ecology in many groups of marine fishes, although it is recognized that ontogenetic stage can influence the types of prey an ELHS fish can effectively locate, capture, and ultimately process (Anto et al. 2009; Anto and Turingan 2010; Nunn et al. 2012). In addition, the feeding apparatus is also under constant selective pressures, due to competition and foraging success, which has resulted in a wide range of specializations to the feeding apparatus that enable fishes to partition foraging habitats, reduce competition, and coexist within an ecosystem (Wainwright & Richard 1995; Hernandez et al. 2002). During ontogeny, the elements of the feeding apparatus undergo significant changes in shape and configuration that influence the functionality of the feeding apparatus, which can influence the ability of ELHS fishes to efficiently capture prey (Wainwright & Richard 1995; Hernandez et al. 2002; Anto and Turingan 2010). Therefore, interspecific variations in feeding apparatus development may enable ELHS fishes to partition their foraging habitats. However, interspecific patterns of feeding apparatus development, which may influence foraging success has not been assessed in estuarine-dependent ELHS fishes (Wittenrich & Turingan 2011). A caveat of this study is that without information regarding the age of each specimen, we cannot yet address intra-specific variation in ELHS sciaenids from the Chesapeake Bay. I have described the diet of ELHS sciaenids in their estuarine nursery habitats and put these data in an ontogenetic framework by examining changes to feeding apparatus structure and sensory modality during ontogeny to better understand the links that exist between ecology and morphology in ELHS fishes. In conclusion, ecomorphological patterns were identified and described in ELHS sciaenids that enable them to partition their foraging habits in nursery habitats.

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APPENDIX

VIMS Catalog Number	Genus	Species	Location of Capture	Collection Date	Latitude (Decimal Degrees)	Longitude (Decimal Degrees)
VIMS 22155	*Aplodinotus*	*grunniens*	Great Lakes, Michigan	6/17/2010	42.4	-82.7
VIMS 22156	*Aplodinotus*	*grunniens*	Great Lakes, Michigan	6/17/2010	42.4	-82.7
VIMS 22157	*Aplodinotus*	*grunniens*	Great Lakes, Michigan	6/17/2010	42.4	-82.7
VIMS 22158	*Aplodinotus*	*grunniens*	Great Lakes, Michigan	6/10/2010	42.4	-82.7
VIMS 22159	*Aplodinotus*	*grunniens*	Great Lakes, Michigan	6/24/2010	42.4	-82.7
VIMS 22160	*Aplodinotus*	*grunniens*	Great Lakes, Michigan	6/24/2010	42.4	-82.7
VIMS 22161	*Aplodinotus*	*grunniens*	Great Lakes, Michigan	6/17/2011	42.4	-82.7
VIMS 22162	*Aplodinotus*	*grunniens*	Great Lakes, Michigan	6/17/2011	42.4	-82.7
VIMS 22163	*Aplodinotus*	*grunniens*	Great Lakes, Michigan	6/17/2011	42.4	-82.7
VIMS 22164	*Aplodinotus*	*grunniens*	Minnesota	7/25/2006	44.9	-93.2
VIMS 22165	*Aplodinotus*	*grunniens*	Round Lake, Minnesota	7/28/2006	43.5	-95.4
VIMS 22166	*Aplodinotus*	*grunniens*	Round Lake, Minnesota	7/28/2006	43.5	-95.4
VIMS 22167	*Aplodinotus*	*grunniens*	Round Lake, Minnesota	7/28/2006	43.5	-95.4
VIMS 22168	*Aplodinotus*	*grunniens*	Round Lake, Minnesota	7/28/2006	43.5	-95.4
VIMS 22169	*Aplodinotus*	*grunniens*	Indian Lake, Minnesota	8/2/2006	43.5	-95.5
VIMS 22170	*Aplodinotus*	*grunniens*	Clear Lake, Minnesota	7/26/2006	45.4	-94.0
VIMS 22171	*Aplodinotus*	*grunniens*	Clear Lake, Minnesota	7/26/2006	45.4	-94.0
VIMS 22172	*Aplodinotus*	*grunniens*	Clear Lake, Minnesota	7/26/2006	45.4	-94.0
VIMS 22173	*Aplodinotus*	*grunniens*	Indian Lake, Minnesota	8/2/2006	43.5	-95.5
VIMS 22174	*Aplodinotus*	*grunniens*	Indian Lake, Minnesota	8/2/2006	43.5	-95.5
VIMS 22175	*Aplodinotus*	*grunniens*	Indian Lake, Minnesota	8/2/2006	43.5	-95.5
VIMS 22176	*Aplodinotus*	*grunniens*	Minnesota	No Data	44.9	-93.2
VIMS 22177	*Argyrosomus*	*inodorus*	Algoa Bay, South Africa	6/9/2011	-33.8	25.9
VIMS 22178	*Argyrosomus*	*inodorus*	Algoa Bay, South Africa	10/1/2011	-33.8	25.9
VIMS 22179	*Argyrosomus*	*inodorus*	Algoa Bay, South Africa	10/1/2011	-33.8	25.9
VIMS 22180	*Argyrosomus*	*inodorus*	Algoa Bay, South Africa	10/1/2011	-33.8	25.9
VIMS 22181	*Argyrosomus*	*inodorus*	Algoa Bay, South Africa	4/20/2011	-33.8	25.9
VIMS 22182	*Argyrosomus*	*inodorus*	Algoa Bay, South Africa	9/29/2010	-33.8	25.8
VIMS 22183	*Argyrosomus*	*japonicus*	Algoa Bay, South Africa	6/9/2011	-33.8	25.9
VIMS 22184	*Argyrosomus*	*japonicus*	Algoa Bay, South Africa	9/29/2010	-33.8	25.8
VIMS 22185	*Argyrosomus*	*japonicus*	Algoa Bay, South Africa	9/29/2010	-33.8	25.8
VIMS 22186	*Argyrosomus*	*japonicus*	Algoa Bay, South Africa	9/29/2010	-33.8	25.8
VIMS 22187	*Argyrosomus*	*japonicus*	Algoa Bay, South Africa	9/29/2010	-33.8	25.8
VIMS 22188	*Argyrosomus*	*japonicus*	Algoa Bay, South Africa	9/29/2010	-33.8	25.8
VIMS 22189	*Argyrosomus*	*japonicus*	Algoa Bay, South Africa	9/29/2010	-33.8	25.8
VIMS 22190	*Argyrosomus*	*japonicus*	Algoa Bay, South Africa	9/29/2010	-33.8	25.8
VIMS 22191	*Bairdiella*	*chrysoura*	Gloucester Point, Virginia	7/15/2011	37.6	-75.7
VIMS 22192	*Bairdiella*	*chrysoura*	Gloucester Point, Virginia	7/15/2011	37.6	-75.7
VIMS 22193	*Bairdiella*	*chrysoura*	Gloucester Point, Virginia	7/15/2011	37.6	-75.7

VIMS 22194	*Bairdiella*	*chrysoura*	Gloucester Point, Virginia	7/15/2011	37.6	-75.7
VIMS 22195	*Bairdiella*	*chrysoura*	Gloucester Point, Virginia	8/16/2011	37.6	-75.6
VIMS 22196	*Bairdiella*	*chrysoura*	Gloucester Point, Virginia	7/13/2011	37.6	-75.7
VIMS 22197	*Bairdiella*	*chrysoura*	Gloucester Point, Virginia	7/13/2011	37.6	-75.7
VIMS 22198	*Bairdiella*	*chrysoura*	Gloucester Point, Virginia	7/13/2011	37.6	-75.6
VIMS 22199	*Bairdiella*	*chrysoura*	Gloucester Point, Virginia	7/13/2011	37.6	-75.6
VIMS 22200	*Bairdiella*	*chrysoura*	Gloucester Point, Virginia	8/16/2011	37.6	-75.6
VIMS 22201	*Bairdiella*	*chrysoura*	Gloucester Point, Virginia	8/16/2011	37.6	-75.6
VIMS 22202	*Bairdiella*	*chrysoura*	Gloucester Point, Virginia	8/16/2011	37.6	-75.6
VIMS 22544	*Bairdiella*	*chrysoura*	Eastern Shore, Bayside, Virginia	10/23/1979	37.4	-76.0
VIMS 22545	*Bairdiella*	*chrysoura*	Eastern Shore, Bayside, Virginia	10/22/1979	37.4	-76.0
VIMS 22546	*Bairdiella*	*chrysoura*	Eastern Shore, Bayside, Virginia	10/22/1979	37.4	-76.0
VIMS 22203	*Bairdiella*	*chrysoura*	Pungue Island, Virginia	No Data	No Data	No Data
VIMS 22204	*Bairdiella*	*chrysoura*	Pungue Island, Virginia	No Data	No Data	No Data
VIMS 22205	*Bairdiella*	*chrysoura*	Pungue Island, Virginia	No Data	No Data	No Data
VIMS 22206	*Bairdiella*	*chrysoura*	Brown's Bay, Virginia	8/16/2010	37.3	-76.4
VIMS 22207	*Bairdiella*	*chrysoura*	Goodwin Islands, Virginia	7/23/2010	37.2	-76.4
VIMS 22208	*Bairdiella*	*chrysoura*	Goodwin Islands, Virginia	7/23/2010	37.2	-76.4
VIMS 22209	*Bairdiella*	*chrysoura*	Goodwin Islands, Virginia	7/23/2010	37.2	-76.4
VIMS 22210	*Bairdiella*	*chrysoura*	Goodwin Islands, Virginia	7/23/2010	37.2	-76.4
VIMS 22211	*Bairdiella*	*chrysoura*	Goodwin Islands, Virginia	7/23/2010	37.2	-76.4
VIMS 22212	*Bairdiella*	*chrysoura*	Goodwin Islands, Virginia	7/23/2010	37.2	-76.4
VIMS 22213	*Bairdiella*	*chrysoura*	Goodwin Islands, Virginia	7/23/2010	37.2	-76.4
VIMS 22214	*Bairdiella*	*chrysoura*	Goodwin Islands, Virginia	7/23/2010	37.2	-76.4
VIMS 22215	*Bairdiella*	*chrysoura*	Goodwin Islands, Virginia	7/23/2010	37.2	-76.4
VIMS 22216	*Bairdiella*	*chrysoura*	Brown's Bay, Virginia	8/16/2010	37.3	-76.4
VIMS 22217	*Bairdiella*	*chrysoura*	Brown's Bay, Virginia	8/16/2010	37.3	-76.4
VIMS 22218	*Bairdiella*	*chrysoura*	Brown's Bay, Virginia	8/16/2010	37.3	-76.4
VIMS 22219	*Bairdiella*	*chrysoura*	Brown's Bay, Virginia	8/16/2010	37.3	-76.4
VIMS 22220	*Bairdiella*	*chrysoura*	Brown's Bay, Virginia	8/16/2010	37.3	-76.4
VIMS 22221	*Bairdiella*	*chrysoura*	Brown's Bay, Virginia	8/16/2010	37.3	-76.4
VIMS 22222	*Bairdiella*	*chrysoura*	Mobjack Bay, Virginia	9/9/2010	37.4	-76.4
VIMS 22223	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	7/25/2012	37.2	-76.5
VIMS 22224	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	9/16/2010	37.2	-76.5
VIMS 22225	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	6/30/2010	37.2	-76.5
VIMS 22226	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	6/30/2010	37.2	-76.5
VIMS 22227	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	6/16/2010	37.2	-76.5
VIMS 22228	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	8/21/2009	37.2	-76.5
VIMS 22229	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	8/7/2009	37.2	-76.5
VIMS 22230	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	8/7/2009	37.2	-76.5
VIMS 22231	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	8/26/2008	37.2	-76.5
VIMS 22232	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	8/18/2008	37.2	-76.5
VIMS 22233	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	8/18/2008	37.2	-76.5
VIMS 22234	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	8/18/2008	37.2	-76.5

VIMS 22235	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	8/4/2008	37.2	-76.5
VIMS 22236	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22237	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22238	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22239	*Cynoscion*	*nebulosus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22240	*Cynoscion*	*nebulosus*	Gulf of Mexico, Texas	No Data	No Data	No Data
VIMS 22241	*Cynoscion*	*nebulosus*	Gulf of Mexico, Texas	No Data	No Data	No Data
VIMS 22242	*Cynoscion*	*nebulosus*	Gulf of Mexico, Texas	No Data	No Data	No Data
VIMS 22243	*Cynoscion*	*nebulosus*	Gulf of Mexico, Texas	No Data	No Data	No Data
VIMS 22244	*Cynoscion*	*nebulosus*	Gulf of Mexico, Texas	No Data	No Data	No Data
VIMS 22245	*Cynoscion*	*nebulosus*	Goodwin Islands, Virginia	7/23/2010	37.2	-76.4
VIMS 22246	*Cynoscion*	*nebulosus*	Goodwin Islands, Virginia	7/23/2010	37.2	-76.4
VIMS 22247	*Cynoscion*	*nebulosus*	Goodwin Islands, Virginia	7/23/2010	37.2	-76.4
VIMS 22248	*Cynoscion*	*nebulosus*	Goodwin Islands, Virginia	7/23/2010	37.2	-76.4
VIMS 22249	*Cynoscion*	*nebulosus*	Goodwin Islands, Virginia	7/23/2010	37.2	-76.4
VIMS 22250	*Cynoscion*	*nebulosus*	Oyster, Virginia	2012	37.3	-75.9
VIMS 22251	*Cynoscion*	*nebulosus*	Mobjack Bay, Virginia	7/31/2012	37.3	-76.4
VIMS 22252	*Cynoscion*	*nebulosus*	Mobjack Bay, Virginia	7/31/2012	37.3	-76.4
VIMS 22253	*Cynoscion*	*nebulosus*	Mattaponi River, Virginia	No Data	No Data	No Data
VIMS 22254	*Cynoscion*	*regalis*	Wachapreague, Virginia	7/14/2011	37.6	-75.6
VIMS 22255	*Cynoscion*	*regalis*	Wachapreague, Virginia	7/14/2011	37.6	-75.6
VIMS 22256	*Cynoscion*	*regalis*	Wachapreague, Virginia	6/19/2012	37.6	-75.7
VIMS 22257	*Cynoscion*	*regalis*	Wachapreague, Virginia	7/13/2011	37.6	-75.7
VIMS 22258	*Cynoscion*	*regalis*	Wachapreague, Virginia	7/13/2011	37.6	-75.7
VIMS 22259	*Cynoscion*	*regalis*	Wachapreague, Virginia	7/13/2011	37.6	-75.7
VIMS 22260	*Cynoscion*	*regalis*	Wachapreague, Virginia	7/13/2011	37.6	-75.6
VIMS 22261	*Cynoscion*	*regalis*	Wachapreague, Virginia	7/13/2011	37.6	-75.6
VIMS 22262	*Cynoscion*	*regalis*	Wachapreague, Virginia	7/13/2011	37.6	-75.6
VIMS 22263	*Cynoscion*	*regalis*	Wachapreague, Virginia	8/1/2012	37.6	-75.7
VIMS 22264	*Cynoscion*	*regalis*	Wachapreague, Virginia	8/1/2012	37.6	-75.7
VIMS 22265	*Cynoscion*	*regalis*	Wachapreague, Virginia	7/25/2012	37.6	-75.7
VIMS 22266	*Cynoscion*	*regalis*	Wachapreague, Virginia	7/25/2012	37.6	-75.6
VIMS 22267	*Cynoscion*	*regalis*	Wachapreague, Virginia	7/25/2012	37.6	-75.6
VIMS 22268	*Cynoscion*	*regalis*	Wachapreague, Virginia	7/25/2012	37.6	-75.6
VIMS 22269	*Cynoscion*	*regalis*	Nickawampus Creek, Virginia	7/29/2009	37.6	-75.7
VIMS 22270	*Cynoscion*	*regalis*	Nickawampus Creek, Virginia	7/29/2010	37.6	-75.7
VIMS 22271	*Cynoscion*	*regalis*	Gloucester Point, Virginia	7/25/2012	37.2	-76.5
VIMS 22272	*Cynoscion*	*regalis*	Gloucester Point, Virginia	8/25/2010	37.2	-76.5
VIMS 22273	*Cynoscion*	*regalis*	Gloucester Point, Virginia	8/25/2010	37.2	-76.5
VIMS 22274	*Cynoscion*	*regalis*	Gloucester Point, Virginia	8/25/2010	37.2	-76.5
VIMS 22275	*Cynoscion*	*regalis*	Gloucester Point, Virginia	6/21/2010	37.2	-76.5
VIMS 22276	*Cynoscion*	*regalis*	Gloucester Point, Virginia	6/16/2010	37.2	-76.5
VIMS 22277	*Cynoscion*	*regalis*	Gloucester Point, Virginia	9/9/2009	37.2	-76.5
VIMS 22278	*Cynoscion*	*regalis*	Gloucester Point, Virginia	9/9/2009	37.2	-76.5

VIMS 22279	*Cynoscion*	*regalis*	Gloucester Point, Virginia	9/4/2009	37.2	-76.5
VIMS 22280	*Cynoscion*	*regalis*	Gloucester Point, Virginia	8/27/2009	37.2	-76.5
VIMS 22281	*Cynoscion*	*regalis*	Gloucester Point, Virginia	6/17/2009	37.2	-76.5
VIMS 22282	*Cynoscion*	*regalis*	Gloucester Point, Virginia	8/26/2008	37.2	-76.5
VIMS 22283	*Cynoscion*	*regalis*	Gloucester Point, Virginia	8/26/2008	37.2	-76.5
VIMS 22284	*Cynoscion*	*regalis*	Gloucester Point, Virginia	8/18/2008	37.2	-76.5
VIMS 22285	*Cynoscion*	*regalis*	Gloucester Point, Virginia	8/4/2008	37.2	-76.5
VIMS 22286	*Cynoscion*	*regalis*	York River, Virginia	10/14/2009	37.2	-76.5
VIMS 22287	*Cynoscion*	*regalis*	York River, Virginia	9/7/2010	No Data	No Data
VIMS 22288	*Cynoscion*	*regalis*	York River, Virginia	9/7/2010	No Data	No Data
VIMS 22289	*Cynoscion*	*regalis*	York River, Virginia	6/7/2010	37.5	-76.8
VIMS 22290	*Cynoscion*	*regalis*	Mobjack Bay, Virginia	9/9/2010	37.4	-76.4
VIMS 22291	*Cynoscion*	*regalis*	Mobjack Bay, Virginia	9/9/2010	37.4	-76.4
VIMS 22292	*Cynoscion*	*regalis*	Chesapeake Bay, Lower, Virginia	10/6/2010	37.2	-76.4
VIMS 22293	*Cynoscion*	*regalis*	Chesapeake Bay, Lower, Virginia	9/1/2010	37.1	-76.0
VIMS 22294	*Cynoscion*	*regalis*	Chesapeake Bay, Lower, Virginia	9/1/2010	37.1	-76.0
VIMS 22295	*Cynoscion*	*nebulosus*	Goodwin Islands, Virginia	7/23/2010	37.2	-76.4
VIMS 22296	*Cynosion*	*regalis*	Wachapreague, Virginia	7/25/2012	37.6	-75.7
VIMS 22297	*Larimus*	*fasciatus*	Chesapeake Bay, Lower, Virginia	8/3/2011	37.4	-76.2
VIMS 22298	*Larimus*	*fasciatus*	Chesapeake Bay, Lower, Virginia	10/18/2011	37.4	-76.1
VIMS 22299	*Larimus*	*fasciatus*	Chesapeake Bay, Lower, Virginia	10/10/2011	37.0	-76.0
VIMS 22300	*Larimus*	*fasciatus*	Chesapeake Bay, Lower, Virginia	10/10/2011	37.1	-76.1
VIMS 22301	*Larimus*	*fasciatus*	Chesapeake Bay, Lower, Virginia	10/10/2011	37.1	-76.1
VIMS 22302	*Larimus*	*fasciatus*	Chesapeake Bay, Lower, Virginia	10/10/2011	37.1	-76.1
VIMS 22303	*Larimus*	*fasciatus*	Chesapeake Bay, Lower, Virginia	10/10/2011	37.1	-76.1
VIMS 22304	*Larimus*	*fasciatus*	Chesapeake Bay, Lower, Virginia	10/10/2011	37.1	-76.1
VIMS 22305	*Larimus*	*fasciatus*	Chesapeake Bay, Lower, Virginia	10/11/2010	37.1	-76.1
VIMS 22306	*Larimus*	*fasciatus*	Chesapeake Bay, Lower, Virginia	10/11/2010	37.1	-76.1
VIMS 22307	*Larimus*	*fasciatus*	Chesapeake Bay, Lower, Virginia	10/6/2010	37.4	-76.1
VIMS 22308	*Larimus*	*fasciatus*	Chesapeake Bay, Lower, Virginia	10/6/2010	37.4	-76.1
VIMS 22309	*Larimus*	*fasciatus*	Chesapeake Bay, Lower, Virginia	10/6/2010	37.3	-76.1
VIMS 22310	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	5/28/2009	37.2	-76.5
VIMS 22311	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	4/20/2010	37.2	-76.5
VIMS 22312	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	5/24/2010	37.2	-76.5
VIMS 22313	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	5/24/2010	37.2	-76.5
VIMS 22314	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	5/15/2010	37.2	-76.5
VIMS 22315	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	5/15/2010	37.2	-76.5
VIMS 22316	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	4/30/2010	37.2	-76.5
VIMS 22317	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	4/30/2020	37.2	-76.5
VIMS 22318	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	4/30/2010	37.2	-76.5

VIMS 22319	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	4/13/2009	37.2	-76.5
VIMS 22320	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	3/23/2009	37.2	-76.5
VIMS 22321	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	3/23/2009	37.2	-76.5
VIMS 22322	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	2/17/2009	37.2	-76.5
VIMS 22323	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	2/11/2009	37.2	-76.5
VIMS 22324	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	4/29/2008	37.2	-76.5
VIMS 22325	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	4/29/2008	37.2	-76.5
VIMS 22326	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	4/15/2008	37.2	-76.5
VIMS 22327	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	4/15/2008	37.2	-76.5
VIMS 22328	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	3/18/2008	37.2	-76.5
VIMS 22329	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	3/18/2008	37.2	-76.5
VIMS 22330	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	3/18/2008	37.2	-76.5
VIMS 22331	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	3/9/2008	37.2	-76.5
VIMS 22332	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	3/9/2008	37.2	-76.5
VIMS 22333	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	2/29/2008	37.2	-76.5
VIMS 22334	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	2/29/2008	37.2	-76.5
VIMS 22335	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	2/29/2008	37.2	-76.5
VIMS 22336	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	2/25/2008	37.2	-76.5
VIMS 22337	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	2/25/2008	37.2	-76.5
VIMS 22338	*Leiostomus*	*xanthurus*	Gloucester Point, Virginia	2/20/2008	37.2	-76.5
VIMS 22339	*Leiostomus*	*xanthurus*	Goodwin Islands, Virginia	6/2/2010	37.2	-76.4
VIMS 22340	*Leiostomus*	*xanthurus*	Goodwin Islands, Virginia	6/2/2010	37.2	-76.4
VIMS 22341	*Leiostomus*	*xanthurus*	Goodwin Islands, Virginia	6/2/2010	37.2	-76.4
VIMS 22342	*Leiostomus*	*xanthurus*	Goodwin Islands, Virginia	8/16/2010	37.3	-76.4
VIMS 22343	*Leiostomus*	*xanthurus*	Oyster, Virginia	3/17/2012	37.3	-75.9
VIMS 22344	*Leiostomus*	*xanthurus*	Oyster, Virginia	3/17/2012	37.3	-75.9
VIMS 22547	*Leiostomus*	*xanthurus*	Mattaponi River, Virginia	10/8/2008	37.5	-76.8
VIMS 22345	*Leiostomus*	*xanthurus*	York River, Virginia	6/3/2010	37.2	-76.4
VIMS 22346	*Leiostomus*	*xanthurus*	Mobjack Bay, Virginia	6/8/2010	37.3	-76.4
VIMS 22347	*Leiostomus*	*xanthurus*	James River, Virginia	5/21/2010	37.1	-76.6
VIMS 22348	*Leiostomus*	*xanthurus*	James River, Virginia	5/20/2010	37.0	-76.5
VIMS 22349	*Leiostomus*	*xanthurus*	James River, Virginia	5/20/2010	37.0	-76.4
VIMS 22350	*Leiostomus*	*xanthurus*	Chesapeake Bay, Lower, Virginia	6/10/2010	37.4	-76.0
VIMS 22351	*Leiostomus*	*xanthurus*	Chesapeake Bay, Lower, Virginia	6/10/2010	37.4	-76.0
VIMS 22352	*Leiostomus*	*xanthurus*	Chesapeake Bay, Lower, Virginia	6/4/2010	37.1	-76.0
VIMS 22353	*Leiostomus*	*xanthurus*	Chesapeake Bay, Lower, Virginia	6/2/2010	37.2	-76.0
VIMS 22354	*Leiostomus*	*xanthurus*	Chesapeake Bay, Lower, Virginia	6/2/2010	37.3	-76.3
VIMS 22355	*Leiostomus*	*xanthurus*	Chesapeake Bay, Lower, Virginia	6/2/2010	37.3	-76.3
VIMS 22356	*Leiostomus*	*xanthurus*	Chesapeake Bay, Lower, Virginia	6/2/2010	37.2	-76.2
VIMS 22357	*Leiostomus*	*xanthurus*	Chesapeake Bay, Lower, Virginia	6/2/2010	37.3	-76.3
VIMS 22358	*Leiostomus*	*xanthurus*	Chesapeake Bay, Lower, Virginia	6/2/2010	37.3	-76.3
VIMS 22359	*Leiostomus*	*xanthurus*	Chesapeake Bay, Lower, Virginia	5/19/2010	37.5	-76.0

VIMS 22360	*Leiostomus*	*xanthurus*	Chesapeake Bay, Lower, Virginia	5/19/2010	37.5	-76.0
VIMS 22361	*Leiostomus*	*xanthurus*	Chesapeake Bay, Lower, Virginia	5/19/2010	37.6	-76.3
VIMS 22362	*Leiostomus*	*xanthurus*	Chesapeake Bay, Lower, Virginia	5/19/2010	37.6	-76.2
VIMS 22363	*Leiostomus*	*xanthurus*	Chesapeake Bay, Lower, Virginia	5/19/2010	37.5	-76.0
VIMS 22364	*Leiostomus*	*xanthurus*	York River, Virginia	6/3/2010	37.1	-76.6
VIMS 22365	*Leiostomus*	*xanthurus*	Mattaponi River, Virginia	9/15/2009	37.7	-76.9
VIMS 22366	*Menticirrhus*	*sp.*	Wachapreague, Virginia	7/14/2011	37.6	-75.6
VIMS 22367	*Menticirrhus*	*sp.*	Wachapreague, Virginia	7/13/2011	37.6	-75.6
VIMS 22368	*Menticirrhus*	*sp.*	Wachapreague, Virginia	7/13/2011	37.6	-75.6
VIMS 22369	*Menticirrhus*	*sp.*	Wachapreague, Virginia	7/13/2011	37.6	-75.6
VIMS 22370	*Menticirrhus*	*sp.*	Wachapreague, Virginia	7/13/2011	37.6	-75.6
VIMS 22371	*Menticirrhus*	*sp.*	Wachapreague, Virginia	8/1/2012	37.6	-75.7
VIMS 22372	*Menticirrhus*	*sp.*	Wachapreague, Virginia	8/1/2012	37.6	-75.7
VIMS 22373	*Menticirrhus*	*sp.*	Wachapreague, Virginia	8/1/2012	37.6	-75.6
VIMS 22374	*Menticirrhus*	*sp.*	Wachapreague, Virginia	7/13/2011	37.6	-75.6
VIMS 22375	*Menticirrhus*	*sp.*	Pungue Island, Virginia	No Data	No Data	No Data
VIMS 22376	*Menticirrhus*	*sp.*	Cedar Island, Virginia	No Data	36.6	-75.9
VIMS 22377	*Menticirrhus*	*sp.*	Oyster, Virginia	2012	37.3	-75.9
VIMS 22378	*Menticirrhus*	*sp.*	York River, Virginia	12/2/2010	37.3	-76.5
VIMS 22379	*Menticirrhus*	*sp.*	York River, Virginia	9/7/2010	No Data	No Data
VIMS 22380	*Menticirrhus*	*sp.*	Chesapeake Bay, Lower, Virginia	9/21/2010	37.4	-76.1
VIMS 22381	*Menticirrhus*	*sp.*	Chesapeake Bay, Lower, Virginia	9/1/2010	37.1	-76.0
VIMS 22382	*Menticirrhus*	*sp.*	Chesapeake Bay, Lower, Virginia	9/1/2010	37.1	-76.0
VIMS 22383	*Menticirrhus*	*sp.*	Chesapeake Bay, Lower, Virginia	9/1/2010	37.1	-76.0
VIMS 22384	*Micropogonias*	*undulatus*	Wachapreague, Virginia	9/13/2012	37.6	-75.6
VIMS 22385	*Micropogonias*	*undulatus*	Wachapreague, Virginia	8/23/2012	37.6	-75.6
VIMS 22386	*Micropogonias*	*undulatus*	Wachapreague, Virginia	8/23/2012	37.6	-75.6
VIMS 22387	*Micropogonias*	*undulatus*	Wachapreague, Virginia	8/23/2012	37.6	-75.6
VIMS 22388	*Micropogonias*	*undulatus*	Wachapreague, Virginia	8/23/2012	37.6	-75.6
VIMS 22389	*Micropogonias*	*undulatus*	Wachapreague, Virginia	8/1/2012	37.6	-75.7
VIMS 22390	*Micropogonias*	*undulatus*	Wachapreague, Virginia	8/1/2012	37.6	-75.6
VIMS 22548	*Micropogonias*	*undulatus*	Wando River, South Carolina	3/1/1991	32.9	-79.8
VIMS 22549	*Micropogonias*	*undulatus*	Wando River, South Carolina	3/1/1991	32.9	-79.8
VIMS 22550	*Micropogonias*	*undulatus*	Wando River, South Carolina	3/1/1991	32.9	-79.8
VIMS 22391	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	3/8/2010	37.2	-76.5
VIMS 22392	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	2/23/2010	37.2	-76.5
VIMS 22393	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	2/13/2010	37.2	-76.5
VIMS 22394	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	2/13/2010	37.2	-76.5
VIMS 22395	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	2/13/2010	37.2	-76.5
VIMS 22396	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	1/19/2010	37.2	-76.5
VIMS 22397	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	1/19/2010	37.2	-76.5
VIMS 22398	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	1/5/2010	37.2	-76.5

VIMS 22399	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	1/5/2010	37.2	-76.5
VIMS 22400	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	1/5/2010	37.2	-76.5
VIMS 22401	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/29/2010	37.2	-76.5
VIMS 22402	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/29/2010	37.2	-76.5
VIMS 22403	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/29/2010	37.2	-76.5
VIMS 22404	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/20/2010	37.2	-76.5
VIMS 22405	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/20/2010	37.2	-76.5
VIMS 22406	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/6/2010	37.2	-76.5
VIMS 22407	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/6/2010	37.2	-76.5
VIMS 22408	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/21/2010	37.2	-76.5
VIMS 22409	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/10/2010	37.2	-76.5
VIMS 22410	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	10/11/2010	37.2	-76.5
VIMS 22411	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	10/11/2010	37.2	-76.5
VIMS 22412	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	10/11/2010	37.2	-76.5
VIMS 22413	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	10/6/2010	37.2	-76.5
VIMS 22414	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	9/27/2010	37.2	-76.5
VIMS 22415	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	9/27/2010	37.2	-76.5
VIMS 22416	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	9/13/2010	37.2	-76.5
VIMS 22417	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/21/2009	37.2	-76.5
VIMS 22418	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/21/2009	37.2	-76.5
VIMS 22419	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/3/2009	37.2	-76.5
VIMS 22420	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/3/2009	37.2	-76.5
VIMS 22421	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/16/2009	37.2	-76.5
VIMS 22422	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/16/2009	37.2	-76.5
VIMS 22423	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/4/2009	37.2	-76.5
VIMS 22424	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	10/20/2009	37.2	-76.5
VIMS 22425	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	10/1/2009	37.2	-76.5
VIMS 22426	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	10/1/2009	37.2	-76.5
VIMS 22427	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	9/16/2009	37.2	-76.5
VIMS 22428	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	9/16/2009	37.2	-76.5
VIMS 22429	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	2/2/2009	37.2	-76.5
VIMS 22430	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	2/2/2009	37.2	-76.5
VIMS 22431	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	1/22/2009	37.2	-76.5
VIMS 22432	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	1/22/2009	37.2	-76.5
VIMS 22433	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	1/22/2009	37.2	-76.5
VIMS 22434	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	1/6/2009	37.2	-76.5
VIMS 22435	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	1/6/2009	37.2	-76.5
VIMS 22436	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/29/2008	37.2	-76.5
VIMS 22437	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/29/2008	37.2	-76.5
VIMS 22438	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/15/2008	37.2	-76.5
VIMS 22439	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/25/2008	37.2	-76.5
VIMS 22440	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/25/2008	37.2	-76.5
VIMS 22441	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/3/2008	37.2	-76.5
VIMS 22442	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/3/2008	37.2	-76.5
VIMS 22443	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	10/27/2008	37.2	-76.5

VIMS 22444	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	10/27/2008	37.2	-76.5
VIMS 22445	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	9/29/2008	37.2	-76.5
VIMS 22446	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	9/29/2008	37.2	-76.5
VIMS 22447	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	9/16/2008	37.2	-76.5
VIMS 22448	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	9/16/2008	37.2	-76.5
VIMS 22449	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	2/20/2008	37.2	-76.5
VIMS 22450	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	2/5/2008	37.2	-76.5
VIMS 22451	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	2/5/2008	37.2	-76.5
VIMS 22452	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	1/7/2008	37.2	-76.5
VIMS 22453	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	1/7/2008	37.2	-76.5
VIMS 22454	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	1/7/2008	37.2	-76.5
VIMS 22455	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	1/4/2008	37.2	-76.5
VIMS 22456	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/27/2007	37.2	-76.5
VIMS 22457	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/27/2007	37.2	-76.5
VIMS 22458	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/7/2007	37.2	-76.5
VIMS 22459	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	12/7/2007	37.2	-76.5
VIMS 22460	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/15/2007	37.2	-76.5
VIMS 22461	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/15/2007	37.2	-76.5
VIMS 22462	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/15/2007	37.2	-76.5
VIMS 22463	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/15/2007	37.2	-76.5
VIMS 22464	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/11/2007	37.2	-76.5
VIMS 22465	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/11/2007	37.2	-76.5
VIMS 22466	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/11/2007	37.2	-76.5
VIMS 22467	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/8/2007	37.2	-76.5
VIMS 22468	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/4/2007	37.2	-76.5
VIMS 22469	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/4/2007	37.2	-76.5
VIMS 22470	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/4/2007	37.2	-76.5
VIMS 22471	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	10/15/2007	37.2	-76.5
VIMS 22472	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	10/15/2007	37.2	-76.5
VIMS 22473	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	10/15/2007	37.2	-76.5
VIMS 22474	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/27/2007	37.2	-76.5
VIMS 22475	*Micropogonias*	*undulatus*	Gloucester Point, Virginia	11/27/2007	37.2	-76.5
VIMS 22476	*Micropogonias*	*undulatus*	Goodwin Islands, Virginia	6/7/2010	37.2	-76.4
VIMS 22477	*Micropogonias*	*undulatus*	York River, Virginia	10/14/2009	37.2	-76.4
VIMS 22478	*Micropogonias*	*undulatus*	York River, Virginia	10/14/2009	37.2	-76.4
VIMS 22479	*Micropogonias*	*undulatus*	York River, Virginia	6/7/2010	37.5	-76.9
VIMS 22480	*Micropogonias*	*undulatus*	York River, Virginia	6/7/2010	37.5	-76.9
VIMS 22481	*Micropogonias*	*undulatus*	York River, Virginia	6/7/2010	37.5	-76.9
VIMS 22482	*Micropogonias*	*undulatus*	York River, Virginia	6/7/2010	37.5	-76.8
VIMS 22483	*Micropogonias*	*undulatus*	York River, Virginia	6/3/2010	37.2	-76.5
VIMS 22484	*Micropogonias*	*undulatus*	James River, Virginia	12/9/2010	37.1	-76.6
VIMS 22485	*Micropogonias*	*undulatus*	Chesapeake Bay, Virginia	7/7/2010		
VIMS 22486	*Micropogonias*	*undulatus*	Chesapeake Bay, Virginia	7/7/2010		
VIMS 22487	*Micropogonias*	*undulatus*	Chesapeake Bay, Virginia	7/7/2010		

VIMS 22488	*Micropogonias*	*undulatus*	Chesapeake Bay, Lower, Virginia	6/2/2010	37.4	-76.1
VIMS 22489	*Micropogonias*	*undulatus*	York River, Virginia	6/7/2010	37.5	-76.8
VIMS 22490	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	3/25/2008	30.2	-88.2
VIMS 22491	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	4/25/2007	30.2	-88.2
VIMS 22492	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	3/9/2007	30.2	-88.2
VIMS 22493	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	3/9/2007	30.2	-88.2
VIMS 22494	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	3/9/2007	30.2	-88.2
VIMS 22495	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	3/9/2007	30.2	-88.2
VIMS 22496	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	4/2/2010	30.2	-88.2
VIMS 22497	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	3/1/2010	30.2	-88.2
VIMS 22498	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	3/1/2010	30.2	-88.2
VIMS 22499	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	3/1/2010	30.2	-88.2
VIMS 22500	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	11/10/2008	30.2	-88.2
VIMS 22501	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	11/10/2008	30.2	-88.2
VIMS 22502	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	11/10/2008	30.2	-88.2
VIMS 22503	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	11/10/2008	30.2	-88.2
VIMS 22504	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	11/10/2008	30.2	-88.2
VIMS 22505	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	11/10/2008	30.2	-88.2
VIMS 22506	*Pogonias*	*cromis*	Gulf of Mexico, Alabama	10/29/2008	30.2	-88.2
VIMS 22551	*Sciaenops*	*ocellatus*	Wando River, South Carolina	3/1/1991	32.9	-79.8
VIMS 22552	*Sciaenops*	*ocellatus*	Wando River, South Carolina	3/1/1991	32.9	-79.8
VIMS 22553	*Sciaenops*	*ocellatus*	Wando River, South Carolina	3/1/1991	32.9	-79.8
VIMS 22554	*Sciaenops*	*ocellatus*	Wando River, South Carolina	3/1/1991	32.9	-79.8
VIMS 22555	*Sciaenops*	*ocellatus*	Wando River, South Carolina	3/1/1991	32.9	-79.8
VIMS 22507	*Sciaenops*	*ocellatus*	Gloucester Point, Virginia	9/9/2009	37.2	-76.5
VIMS 22508	*Sciaenops*	*ocellatus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22509	*Sciaenops*	*ocellatus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22510	*Sciaenops*	*ocellatus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22511	*Sciaenops*	*ocellatus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22512	*Sciaenops*	*ocellatus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22513	*Sciaenops*	*ocellatus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22514	*Sciaenops*	*ocellatus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22515	*Sciaenops*	*ocellatus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22516	*Sciaenops*	*ocellatus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22517	*Sciaenops*	*ocellatus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22518	*Sciaenops*	*ocellatus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22519	*Sciaenops*	*ocellatus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22520	*Sciaenops*	*ocellatus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22521	*Sciaenops*	*ocellatus*	Gloucester Point, Virginia	9/4/2007	37.2	-76.5
VIMS 22522	*Sciaenops*	*ocellatus*	Kitty Hawk Bay, North Carolina	10/25/1983	36.0	-75.7
VIMS 22523	*Sciaenops*	*ocellatus*	Kitty Hawk Bay, North Carolina	10/25/1983	36.0	-75.7
VIMS 22524	*Sciaenops*	*ocellatus*	Kitty Hawk Bay, North Carolina	10/25/1983	36.0	-75.7

VIMS 22525	*Sciaenops*	*ocellatus*	Gulf of Mexico, Texas	No Data	No Data	No Data
VIMS 22526	*Sciaenops*	*ocellatus*	Gulf of Mexico, Texas	No Data	No Data	No Data
VIMS 22527	*Sciaenops*	*ocellatus*	Mobjack Bay, Virginia	5/8/2012	37.3	-76.4
VIMS 22528	*Sciaenops*	*ocellatus*	Rappahanock River, Virginia	1/11/2012	37.6	-76.5
VIMS 22529	*Sciaenops*	*ocellatus*	Chesapeake Bay, Lower, Virginia	2/2/2012	37.2	-76.2
VIMS 22530	*Sciaenops*	*ocellatus*	Chesapeake Bay, Lower, Virginia	2/2/2012	37.2	-76.2
VIMS 22531	*Sciaenops*	*ocellatus*	Chesapeake Bay, Lower, Virginia	2/2/2012	37.2	-76.2
VIMS 22532	*Sciaenops*	*ocellatus*	Chesapeake Bay, Lower, Virginia	11/8/2011	37.7	-76.1
VIMS 22533	*Sciaenops*	*ocellatus*	Chesapeake Bay, Lower, Virginia	11/8/2011	37.6	-75.9
VIMS 22534	*Sciaenops*	*ocellatus*	Sandbridge, Virginia	9/21/2010	36.7	-75.9
VIMS 22535	*Stellifer*	*lanceolatus*	Wachapreague, Virginia	7/14/2011	37.6	-75.6
VIMS 22536	*Stellifer*	*lanceolatus*	Wachapreague, Virginia	7/14/2011	37.6	-75.6
VIMS 22537	*Stellifer*	*lanceolatus*	Wachapreague, Virginia	7/14/2011	37.6	-75.6
VIMS 22538	*Stellifer*	*lanceolatus*	Wachapreague, Virginia	7/14/2011	37.6	-75.6
VIMS 22539	*Stellifer*	*lanceolatus*	Wachapreague, Virginia	7/14/2011	37.6	-75.6
VIMS 22540	*Stellifer*	*lanceolatus*	Wachapreague, Virginia	7/13/2011	37.6	-75.7
VIMS 22541	*Stellifer*	*lanceolatus*	Wachapreague, Virginia	7/13/2011	37.6	-75.7
VIMS 22542	*Stellifer*	*lanceolatus*	Wachapreague, Virginia	7/13/2011	37.6	-75.7
VIMS 22543	*Stellifer*	*lanceolatus*	Wachapreague, Virginia	7/13/2011	37.6	-75.6

VITA

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Born in Landstuhl, Germany on November 29th, 1987. Graduated from Shenendehowa High School in Clifton Park, New York in 2005. Earned a B.S. in Marine Biology with a double-minor in Geology and Chemistry from the College of Charleston in 2009. Conducted a senior Honors thesis entitled "Influence of Central Pacific Oceanographic conditions on the vertical habitat of four tropical tuna species." Entered the doctoral program in College of William and Mary, School of Marine Science in 2009.