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ORIGINAL PAPER

Influence of feeding structures and early development on foraging guild assignment in four co-occurring fishes (Family Sciaenidae)

Alison L. Deary[1]

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Abstract

The use of a functional guild, which distills organisms into groups based on a shared role within an ecosystem, is a beneficial tool for fisheries management because it reduces data complexity, streamlines statistical analyses, and places species in an ecosystem context by defining their functional role within a community. However, few studies consider the ramification of ontogeny on guild assignments and assume species occupy a static foraging guild throughout their lives. The aim for this study was to examine the development of feeding structures and diet in four, closely related species of sciaenids (Family Sciaenidae) that forage in the water column throughout their life history (1) to determine if the structures needed to exploit microhabitat use of the water column are present at early ontogenetic stages and (2) to assess guild transitions using a hierarchical clustering approach. Significant differences were only detected in ascending process length and cb1 gill raker count among the examined sciaenids. *Larimus fasciatus* consumed zooplankton throughout ontogeny and possessed a shorter ascending process and a greater number of cb1 gill rakers. *Cynoscion nebulosus* transitioned from zooplanktivory in the larval period to piscivory as an early juvenile and possessed a longer ascending process and fewer cb1 gill rakers. *Bairdiella chrysoura* and *C. regalis* were both zooplanktivorous as early juveniles and consumed more epibenthic (benthic crustaceans and worms) prey and possessed more elongate gill rakers compared to *C. nebulosus*. Foraging studies that combine diet and morphological analyses are needed to place individuals into foraging guilds while capturing key life history transitions that influence foraging habits and guild assignment.

Introduction

Assigning fishes to functional groups, or guilds, through shared morphological and ecological characteristics is a useful approach to broadly monitor and manage marine communities (Reecht et al. 2013; Buchheister and Latour 2015). However, this approach does not incorporate the earliest life history stages (larvae and early juveniles), which influence the size of adult stocks through differential survival related to the quality of habitats and prey resources encountered during development (Nunn et al. 2012). Although foraging guilds have been shown to be extremely stable even under extreme fishing and environmental disturbance scenarios (Auster and Link 2009), this does not take into account the responses of members of these guilds in the earliest stages when individuals are most susceptible to environmental perturbations (Nunn et al. 2012). Additionally, diet is not static over the course of an individual's life (Nunn et al. 2012; Egan et al. 2018); therefore, assigning an individual to a foraging guild must take into account both taxonomy and ontogeny.

Morphology reflects many aspects of an organism's ecology because the ability to exploit a particular niche arises from a suite of characters that interact to enable a particular function (Arnold 1983; Wainwright 1996). Anatomical configuration can constrain the ability of individuals to exploit resources (Wainwright 1996), which is important in an ontogenetic context since the types of prey early stage fishes are able to capture changes through development (Anto et al. 2009; Nunn et al. 2012). For adult fishes that forage in open water, the body is streamlined to optimize the search and capture of widely distributed, evasive prey while minimizing energy expenditures (Svanbäck and Eklöv 2003). Pelagic

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✉ Alison L. Deary
alison.deary@noaa.gov

[1] Alaska Fisheries Science Center, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115, USA

foraging fishes possess longer elements of the oral jaws, smaller pharyngeal toothplates, larger eyes, and more gill rakers than benthic foraging fishes (Chao and Musick 1977; Bhagat et al. 2011; Deary and Hilton 2016, 2017). In addition, skeletal modifications during development coincide with dietary shifts and changes to guild assignment in early stage sciaenids (Deary et al. 2017).

In the Chesapeake Bay, sciaenids (Family Sciaenidae) exploit a broader range of foraging habitats than any other family of fishes. Despite their ability to exploit many different foraging niches, the foraging habitats of adult sciaenids can be categorized into three broad foraging guilds (pelagic, benthic, and generalist) based on similarity of sensory and feeding structure configurations that enable species within a guild to exploit similar prey resources (Chao and Musick 1977; Poling and Fuiman 1999; Horodysky et al. 2008a,b;). As benthic sciaenids settle to the benthos from a pelagic larval stage, elements of the jaws shorten and the ascending process elongates (Deary and Hilton 2016; Deary et al. 2017). These modifications enable benthic sciaenids, even in the early stages, to efficiently project the jaws down towards the benthos during foraging and exploit more benthic-oriented prey (Deary et al. 2017). Pelagic sciaenids, however, do not settle and continue exploiting resources primarily from the water column. Overall, the configuration of feeding structures changes relatively little during development and benthic prey are rarely observed in the diets of these fishes (Deary and Hilton 2016; Deary et al. 2017). Due to how little change is observed within the pelagic guild during development, it may be expected that phylogenetic constraints are restricting the configuration of the body and feeding elements in pelagic sciaenids. However, phylogenetic signal was low in these elements, suggesting that selective forces, likely related to capture of evasive prey, are driving adaptation in pelagic sciaenids (Deary and Hilton 2017). In addition, the highest species richness in the diet was observed in guilds where fishes primarily foraged in the water column (Buchheister and Latour 2015), supporting that selective forces are strong in the pelagic realm.

Pelagic foraging sciaenids generally follow the ecomorphological patterns observed in other groups of fishes. They possess elongate and streamlined bodies, large eyes, elongate jaws, a terminal mouth, and shorter ascending processes (Deary and Hilton 2017). Of the sciaenids that commonly utilize the Chesapeake Bay seasonally as foraging or nursery habitats, four species forage exclusively in the water column throughout ontogeny. Two of these species, *Bairdiella chrysoura* and *Larimus fasciatus* possess deep bodies as adults that is atypical of pelagic foraging sciaenids, although they possess other features that are typical (i.e., large eyes, long jaws, and a terminal, almost superior mouth) (Murdy and Musick 2013). Even in the larval stages, *B. chrysoura* and *L. fasciatus* possess relatively deep bodies (> 32% standard length, SL), although *L. fasciatus* larvae are deeper-bodied at ~ 44% SL (Powles 1980; Fahay 2007). The observed variation of morphometric data among the four pelagic foraging sciaenids suggests that pelagic sciaenids are likely exploiting resources from different aspects of the water column even in the early stages. The motivation for this study was to examine the development of feeding structures and diet in four, closely related sciaenids that forage in the water column (1) to determine if the structures needed to exploit microhabitats in the water column are present at early ontogenetic stages and (2) to assess guild transitions using a hierarchical clustering approach.

Methods

Specimen collection and processing

Between 2009 and 2014, larval samples were collected using a 1-m diameter ring plankton net equipped with 1-mm mesh during a weekly nighttime, shore-based ichthyoplankton sampling program in the York River estuary of the Chesapeake Bay (Ribeiro et al. 2015). Larval samples were also collected in the tidal inlets adjacent to the Virginia Institute of Marine Science (VIMS) Eastern Shore Lab in Wachapreague, VA, during ten nighttime sampling trips over two summers to target sciaenids found in coastal habitats using a 0.5-m diameter bongo net equipped with 1-mm and 370-µm mesh nets. Later stage sciaenids (Age-0 and Age-1) were collected from daytime surveys throughout the lower Chesapeake Bay and York River, including the VIMS Juvenile Fish and Blue Crab Trawl Survey (Tuckey and Fabrizio 2016), the VIMS Juvenile Striped Bass Seine Survey (Davis et al. 2016), and the Chesapeake Bay Multispecies Monitoring and Assessment Program (Latour et al. 2003). After sorting the plankton samples and identifying fishes (Richards 2006; Fahay 2007), standard length (SL) was measured for all specimens using digital calipers to the nearest 0.01 mm and fixed either in 10% buffered formalin (Eastern Shore samples) or 70% ethanol (all other specimens). To fill a size gap in the *L. fasciatus* developmental series, additional specimens of *L. fasciatus* ($n = 27$) from the Gulf Coast Research Lab's (University of Southern Mississippi) larval fish archive were included in the study.

Taxa were classified into one of three primary foraging guilds (benthic, generalist, or pelagic) based on where the adult sciaenids are known to forage (Murdy and Musick 2013; (Buchheister and Latour 2015; Deary et al. 2017). For this study, I focused only on the species that are categorized as pelagic foraging sciaenids, which are *Larimus fasciatus* ($n = 34$; 2.1–89.0 mm SL), *Cynoscion nebulosus* ($n = 37$; 3.7–118.0 mm SL), *Cynoscion regalis* ($n = 40$;

4.1–123.0 mm SL), and *Bairdiella chrysoura* ($n=22$; 4.3–43.7 mm SL) (Table 1).

Dietary analysis

Stomachs and elements of the feeding apparatus were analyzed from the same specimens ($n=133$). Stomach contents were identified to 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; Johnson and Allen 2005). These coarse prey categories were used to elucidate habitat-use patterns of the different early life history stage (ELHS) sciaenids found along the Western North Atlantic. The final prey categories were: pelagic crustaceans, benthic crustaceans, pelagic shrimps (mysids), benthic worms (e.g., polychaetes), pelagic fishes, pelagic eggs, and unicellular benthic phytoplankton. Specimens of each species were categorized into four length bins prior to calculating two diet indices, mean percent number and frequency of occurrence. Final length bins were hatch–10.0 mm, 10.1–20.0 mm, 20.1–30.0 mm, 30.1–50.0 mm. Since sample sizes were relatively low, the mean percent number of a given prey type was calculated to identify prey importance to reduce the bias associated with a few stomachs containing an anomalous number of prey items (Chipps and Garvey 2007). Mean percent number ($M\%N_{\mathrm{k}}$) of a given prey category (k) for each species was calculated as:

$$M\%N_k = \left(\Sigma P_{ik}/T_k\right)/S. \tag{1}$$

where P_{ik} is the number of prey items i in stomach k, T_k is the total number of prey in stomach k, and S is the total number of stomachs containing prey per species. Frequency of occurrence (FO) was also calculated to assess the common prey categories consumed for each species and length bin and was calculated as:

$$\mathrm{FO} = J_i/P, \tag{2}$$

where J_i is the number of fish with prey item i in their stomach and P is the number of fish with food in their stomachs (Chipps and Garvey 2007).

Feeding apparatus

Once stomachs were excised, specimens were cleared and double stained (so that cartilaginous structures appeared blue and calcified structures appeared red) following a protocol based on Taylor and Van Dyke (1985). For most specimens, oral and pharyngeal jaw elements of the feeding apparatus were measured following the protocols of Deary and Hilton (2016) using a Zeiss SteREO DiscoveryV20 microscope with AxioVision software. Additional *L. fasciatus* specimens were measured on a dissecting scope using the imaging software iSolutions Lite. Measurements included eye diameter, lengths of the ascending process, premaxilla, and lower jaw (anterior tip of dentary to the articulation of the anguloarticular and quadrate), toothed areas of the third and fourth pharyngobranchial toothplates and the fifth ceratobranchial, and gill raker counts along the cerato- and epibranchials of the first and second gill arches. Gill rakers occur as two rows along each gill arch but on the first gill arch, the exterior gill rakers, referred to here as the lateral gill rakers, are elongate and different in shape to the inner row of median gill rakers. On the first and second ceratobranchials, the mean length of three randomly selected gill rakers (median gill rakers on ceratobranchial 1) and gill filaments was used to obtain an average length for these elements. We calculated the average length of gill rakers and filaments to obtain a metric that was comparable across taxa and captured the variability of these elements along the ceratobranchial (Deary and Hilton 2016). Variation in the elements of the feeding apparatus was already observed among taxa of ELHS sciaenids occupying different foraging guilds, supporting the idea that these characters have functional implications for the types of prey that can effectively be consumed even in the early stages (Chao and Musick 1977; Wimberger 1991; Grubich 2003; Aguirre and Shervette 2005; Bhagat et al. 2011).

A principal component analysis (PCA) was used to identify morphometric characters that may be informative when considering guild assignment. A multivariate regression tree (MRT) analysis using the rpart package (Milborrow 2014) was run using the morphometric variables that explained the most variation on the PC1 and PC2 axes. Prior to conducting these analyses, the effect of body size on the condition of

Table 1 Number of specimens, Virginia Institute of Marine Science catalogue number, the length range in millimeter, and % of specimens with empty stomachs used in the study

Species	Count	VIMS catalogue number	Length range (mm)	% empty stomachs
Bairdiella chrysoura	22	22196–22197; 22200–22204; 22207–22221	4.3–43.7	4.5
Cynoscion nebulosus	37	22224–22235; 22240; 22245–22250; 22252–22253; 22295	3.7–118.0	35.1
Cynoscion regalis	40	22256–22258; 22260; 22263–22264; 22267–22268; 22270–22271; 22273–22274; 22276–22286; 22290–22291; 22296	4.1–123.0	37.5
Larimus fasciatus	34	22244; 22297–22302; 22500–22501; 42305–42331	2.1–89.0	2.9

these morphological variables was assessed using the method proposed by Elliott et al. (1995). All morphometric variables were standardized by the following formula:

$$M_{\mathrm{s}} = M_{\mathrm{o}}^{*}\left(L_{\mathrm{s}}/L_{\mathrm{o}}\right)^{\mathrm{b}}. \tag{3}$$

where M_s is the standardized measurement, M_o is the original variable measurement, L_s is the mean standard length of all fishes from all samples, and L_o is the standard length of the measured specimen. The term b was estimated using the allometric growth equation for each morphometric variable following:

$$b = \log M_{\mathrm{o}} / \log L_{\mathrm{o}}. \tag{4}$$

Of the nine feeding elements identified by the PCA, two characters were recovered as informative during the MRT analysis. To examine how these elements differed among the species, a standardized major axis approach was applied using the SMATR package due to the interest in assessing the slope of the best fit line for each species (Warton et al. 2012), which captures differences in the developmental trajectory of morphological variables. Prior to this analysis, the assumption for normality of the morphometric data was tested using a Shapiro–Wilk test and the ascending process length was log-transformed.

Data analysis

Data analysis was conducted in R version 3.5.2 using cluster, pvclust, rpart, partykit, lattice, indicspecies, and SMATR packages (R Development Core Team 2017). A cluster analysis on the diet data, both $M\%N$ and FO, was conducted to determine the presence of dietary shifts for ELHS pelagic sciaenids and to assess the statistical support for the identified clusters (Suzuki 2015). A dissimilarity matrix was calculated using Euclidean distances, the dendrogram was constructed using Ward's method, and multiscale bootstrapping was repeated 1000 times. An approximately unbiased (AU) p value of 95% was used to identify clusters that were strongly supported by the data (Suzuki and Shimodaira 2006). Dietary overlap among the species was examined using the niche overlap function in indicspecies and Pianka's niche overlap index (Pianka 1973; De Cáceres et al. 2014). Pianka's niche overlap index ranges from 0 to 1, with 1 denoting complete niche overlap and 0 denoting complete niche separation (Pianka 1973). All figures were assembled using Adobe Illustrator CS5.1.

Results

Feeding apparatus

We used a PCA to identify the morphometric characters most likely driving differentiation among the four pelagic sciaenid species examined in this study. PC1 explained 88% of the variance with premaxilla length, eye diameter, lower jaw length, pre-orbital length, ascending process length, and epibranchial (eb) 1 gill raker count contributing to more than 10% of the variance explained by this axis (Fig. 1). PC2 explains an additional 8% of the variance with pharyngobranchial 3 toothplate (pbtp3) area, ceratobranchial (cb) 1 gill raker count, cb5 area, and head length contributing more than 10% of the variance explained by this axis (Fig. 1). Although the PCA identified three clusters, pelagic sciaenids representing all four species were found in each group.

A multivariate regression tree was constructed using the morphometric characters identified in the PCA that explained more than 10% of the variation on PC axes 1 and 2. These characters were: premaxilla length, eye diameter, lower jaw length, pre-orbital length, ascending process length, and eb1 gill raker counts on PC1 and pbtp3 area, cb1 gill raker counts, cb5 area, and head length on PC2 (Fig. 1). The best fitting multivariate regression tree explained 74% of the variance and had three nodes (Fig. 2). Of the morphological factors inputted into the tree, only two of the variables (ascending process length and cb1 gill raker count) were considered to differentiate significantly among the species quantitatively (Fig. 2). *Larimus fasciatus* possessed a significantly shorter ascending process relative to the other three sciaenid species, which became evident by approximately 14.5 mm SL (Fig. 2). Some specimens of *C. regalis* also possessed a short ascending process relative to *C. nebulosus* and *B. chrysoura*, although this was more prevalent for *L. fasciatus* in the late larval/early juvenile stages. Generally, *L. fasciatus* had more gill rakers along cb1 relative to the other three species (more than 19) by 22.8 mm SL. *Bairdiella chrysoura* also had high number of gill rakers on cb1, although in the sizes examined the number of gill rakers did not exceed 20 on cb1, which was often surpassed in *L. fasciatus*. *Cynoscion nebulosus* and *C. regalis* tended to have less than 19 gill rakers along cb1 in the size ranges examined (Fig. 2).

To more closely examine the developmental trajectories of the elements identified by the multivariate regression among the four sciaenid species, a standardized major axis approach was used to test for significant differences among the slopes for the best fit line. *Larimus fasciatus* had a shorter ascending process relative to *Cynoscion*

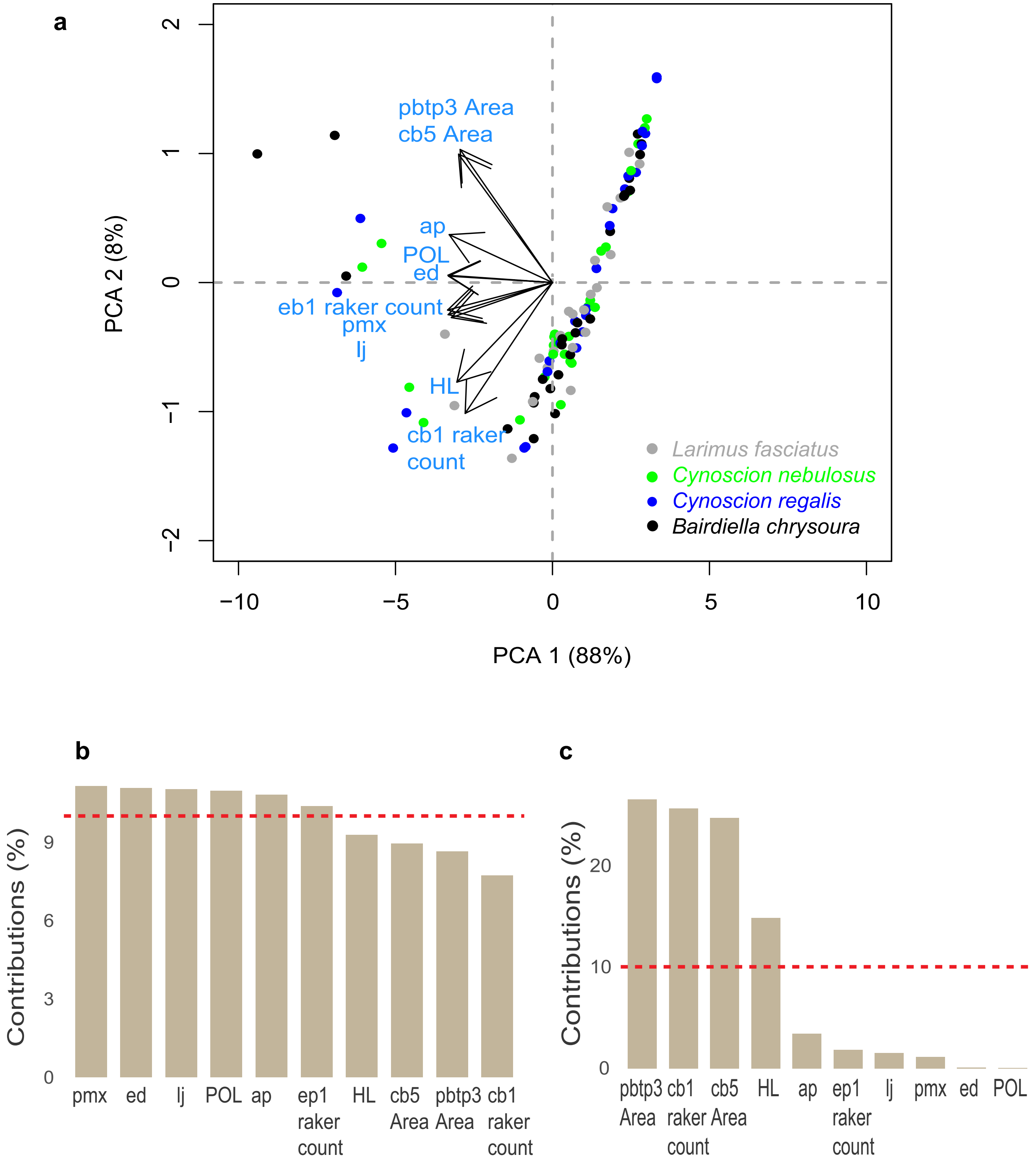


Fig. 1 Principal component (PC) analysis of the feeding apparatus elements of *Cynoscion regalis* (blue), *C. nebulosus* (green), *Larimus fasciatus* (gray), and *Bairdiella chrysoura* (black). Panel **b** shows the percent contribution of each element to PC1 and **c** shows the percent contribution of each element to PC2. The red line in panels **b** and **c** denotes the 10% contribution threshold. *ap* ascending process, *cb* ceratobranchial, *eb* epibranchial, *ed* eye diameter, *HL* head length, *lj* lower jaw length, *pbtp* pharyngobranchial toothplate, *POL* pre-orbital length, *pmx* premaxilla

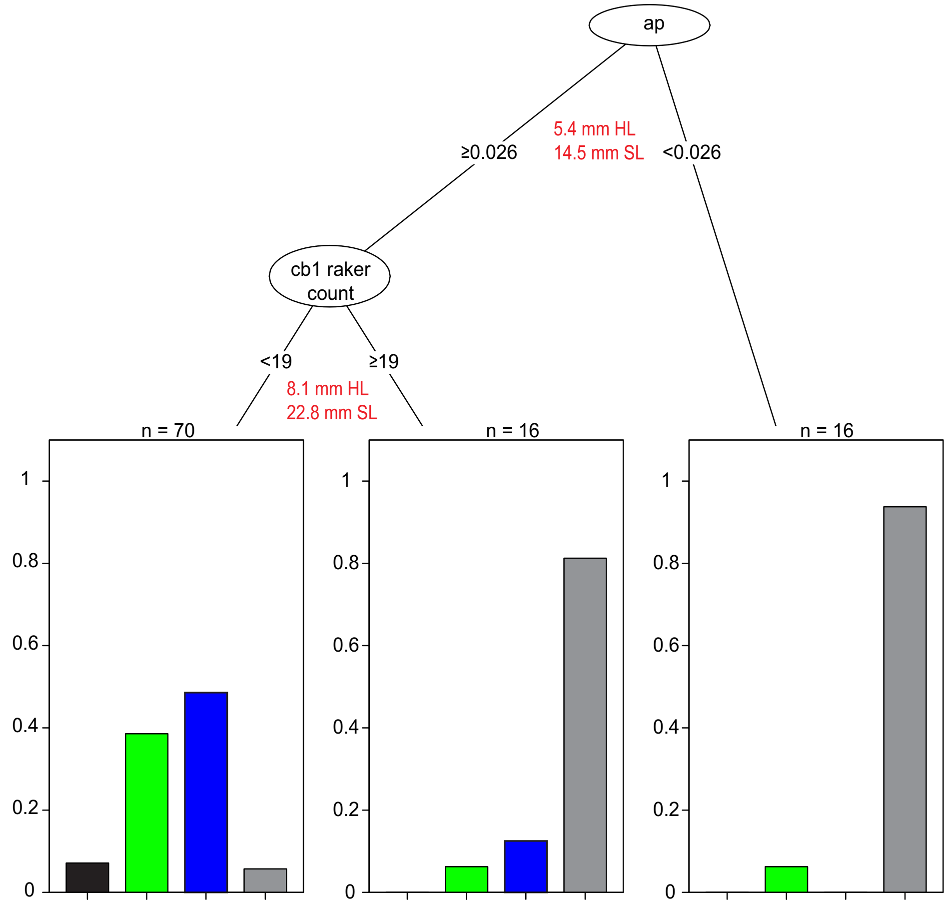


Fig. 2 Pruned multivariate regression tree of feeding apparatus elements. Black numbers denote the splitting criteria for the element highlighted in the circle; depending on the character the numbers are in mm (ap length) or a count (cb1 gill raker count). Red numbers denote the mean size in standard length (SL) and head length (HL) for that split. The bar plots at the terminal nodes depict the proportion of species with each character state. *Cynoscion regalis* (blue), *C. nebulosus* (green), *Larimus fasciatus* (gray), and *Bairdiella chrysoura* (black). *ap* ascending process, *cb* ceratobranchial

Table 2 Pairwise comparison for the standardized major axis analysis

ap length				
	C. nebulosus	*C. regalis*	*L. fasciatus*	*B. chrysoura*
C. nebulosus		*		
C. regalis	*		*	
L. fasciatus		*		
B. chrysoura				
cb1 gill raker count				
	C. nebulosus	*C. regalis*	*L. fasciatus*	*B. chrysoura*
C. nebulosus		**	***	
C. regalis	**			
L. fasciatus	***			***
B. chrysoura			***	

ap ascending process, *cb* ceratobranchial

The asterisks denote level of significance: * = 0.05, ** = 0.001, and *** = 0.001. No asterisks denote no significance

spp. and *B. chrysoura*, although it was only significantly shorter relative to *C.* regalis. *Cynoscion regalis* possessed the longest ascending process of the four examined sciaenid species, which was significantly longer in *L. fasciatus* and *C. nebulosus* (Table 2; Fig. 3). Cynoscion *nebulosus* possessed significantly fewer gill rakers on cb1 than *C. regalis* or *L. fasciatus* (Table 2). Early during ontogeny, all four sciaenid species had similar gill raker counts on cb1 but after ~ 12.0 mm SL, the number of cb1 gill rakers increased in *L. fasciatus* but plateaued in the other species (Fig. 3).

Overall, the oral jaw structure among the four sciaenid species was very similar and most of the variation was observed in tooth shape along the dentary and the premaxilla. Generally, the dentary and anglo-articular of the lower jaw were short and deep in juvenile *L. fasciatus* compared to *Cynoscion* spp. The teeth along the premaxilla and lower jaw were similar in early stage pelagic sciaenids but as juveniles, *L. fasciatus* possessed short, densely packed teeth, whereas the fang that is characteristic of adult *Cynoscion* spp. was prominent. In juvenile *C. regalis*, the teeth of the premaxilla were relatively short and densely packed posterior to the fang, whereas in *C. nebulosus* the teeth of the premaxilla were relatively long and recurved. Additionally, the lateral lines scales were robust in juvenile *L. fasciatus*.

Along cb1, gill rakers formed earliest in *L. fasciatus* at about 2.5 mm SL with the gill rakers first appearing at ~ 4.0 mm SL for the other three sciaenid species. Even in the early stages, the lateral gill rakers of *B. chrysoura* and *L.*

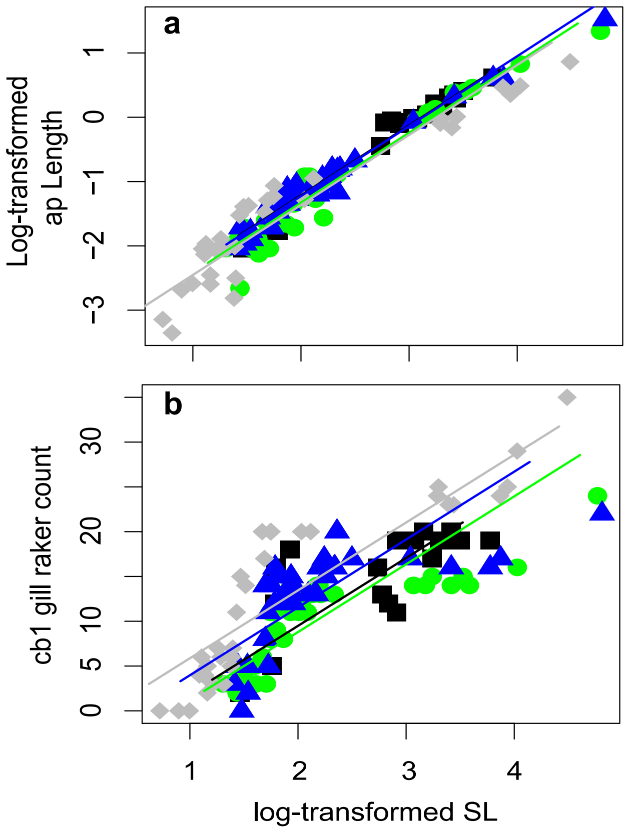


Fig. 3 Standardized major axis regression plots of **a** log-transformed ascending process (ap) length; **b** cb (ceratobranchial) 1 gill raker count relative to log-transformed standard length (SL). *Cynoscion regalis* (blue; triangles), *C. nebulosus* (green; circles), *Larimus fasciatus* (gray; diamonds), and *Bairdiella chrysoura* (black; squares)

fasciatus were more densely packed than in the *Cynoscion* species (Fig. 4). However, the lateral gill rakers of juvenile *L. fasciatus* were stouter and longer than those of juvenile *B. chrysoura*. Spicules formed on the lateral rakers by about 5.0 mm SL in *L. fasciatus*, 6.0 mm SL in *C. regalis*, and 8.0 mm SL in *C. nebulosus*. The lateral gill rakers of juvenile *B. chrysoura* were also covered with a dense layer of spicules. The spicules along the lateral gill rakers were sparse in juvenile *L. fasciatus* (Fig. 4). The lateral gill rakers were longer and more densely packed along the first gill arch in *C. regalis* than in *C. nebulosus*, although the number of spicules along each lateral gill raker was comparable between the two species (Fig. 4).

Even in the early larval stages, the shape of the gill rakers along cb2 were different among the species. In *Cynoscion* spp., the gill rakers were mound-like capped with a few elongate spicules whereas in *L. fasciatus*, they were taller, more peaked, and capped with about three stout spicules. In *B. chrysoura*, the gill rakers had round bases with pointed tops (Fig. 5). By the juvenile stage, the gill rakers along cb2 of *L. fasciatus* were cylindrical and capped with elongate spicules (Fig. 5). Spicules did not line the base of the gill rakers in *L. fasciatus*. The gill rakers of juvenile *B. chrysoura* were peaked, covered with short spicules and capped with a tuft of longer spicules. The gill rakers on cb2 of juvenile *C. nebulosus* were mound-like covered with short spicules and tightly packed (Fig. 5). The gill rakers were longer closer to the symphysis of cb2 and eb2. For juvenile *C. regalis*, the mound-like gill rakers were capped with elongate spicules and alternated between taller and shorter gill rakers along the gill arch (Fig. 5).

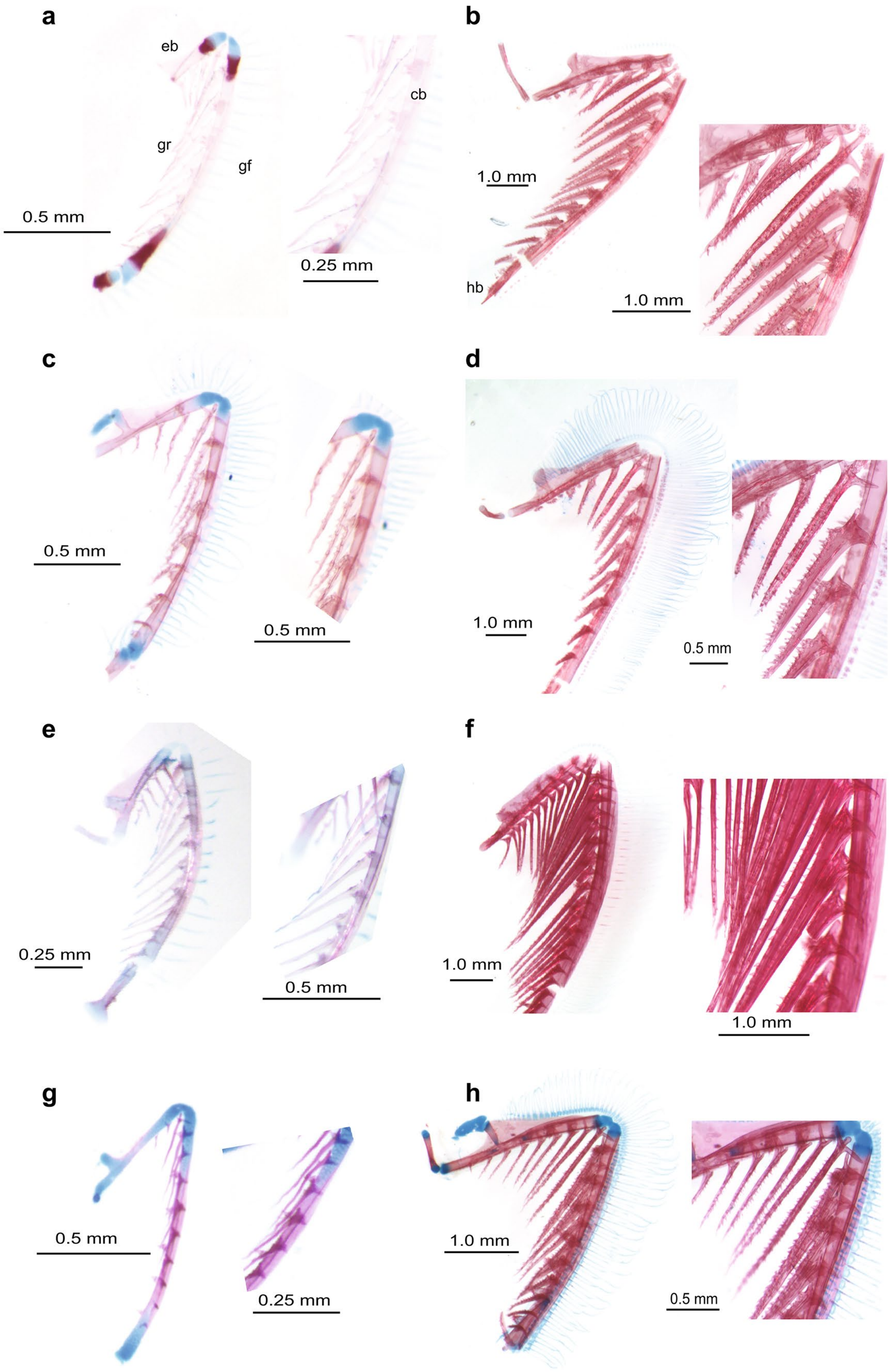
Diet

The agglomerative hierarchical clustering analysis recovered three clusters based on the diet data (Fig. 6). The analysis for the FO data is presented but a similar result was recovered using the M%N data.

Cluster 1 (AUP = 99%) was dominated by the smallest size bin for each species (hatch–10.0 mm SL). The dominant prey category for cluster one was pelagic crustaceans, primarily calanoid copepods (Table 3; Fig. 7), with some foraging on pelagic shrimp, primarily mysids, by *C. nebulosus* and *C. regalis*. Cluster 2 (AUP = 99%) was composed mainly of late larval *B. chrysoura* (10.1–20.0 mm SL) and juvenile *Cynoscion nebulosus* (20.1–30.0 mm SL) (Fig. 6). The dominant prey category for cluster two was pelagic crustaceans (calanoid copepods), pelagic shrimp (mysid shrimp), and benthic crustaceans (Table 3; Fig. 7). Cluster 3 (AUP = 99%) consisted of juvenile *L. fasciatus* (greater than 20.1 mm SL) that were foraging exclusively on pelagic prey, chiefly pelagic shrimp (mysids) and to a lesser degree, pelagic crustaceans (calanoid copepods) (Table 3; Figs. 6, 7).

Although not significant, two additional clusters were present. Cluster 4.ns (AUP = 72%) included juvenile specimens of *C. nebulosus* and *C. regalis* (30.1 and 50.0 mm SL) that consumed pelagic fishes and cluster 5.ns (AUP = 82%) that consisted of juvenile *B. chrysoura* (30.1–50.0 mm SL) that were foraging on a variety of prey categories such as pelagic crustaceans, pelagic shrimp, benthic crustaceans, and benthic worms (Table 3; Figs. 6, 7).

Niche overlap was highest in the smallest size bin for each species (hatch–10.0 mm SL) with complete niche overlap for *B. chrysoura* with *C. nebulosus* and *L. fasciatus* (Table 4). Overall, Pianka's niche overlap index was 0.95 or greater for each species comparison, indicating that the examined sciaenid species are exploiting similar prey resources in the larval stage (less than 10 mm SL). There were not enough individuals of each species to calculate niche overlap for the 10.1–20.0 mm SL size bin. However, by the early juvenile stage (20.1–30.0 mm SL), niche overlap was reduced for all of the species comparisons. Despite being closely related, *C. regalis* and *C. nebulosus* had the least niche overlap in


a
eb
cb
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0.5 mm
0.25 mm
b
1.0 mm
hb
1.0 mm
c
0.5 mm
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d
1.0 mm
0.5 mm
e
0.25 mm
0.5 mm
f
1.0 mm
1.0 mm
g
0.5 mm
0.25 mm
h
1.0 mm
0.5 mm

◀**Fig. 4** Development of lateral gill rakers along the first gill arch for: **a** *Cynoscion regalis* [10 mm standard length (SL)]; **b** *C. regalis* (48.2 mm SL); **c** *C. nebulosus* (14.3 mm SL); **d** *C. nebulosus* (56.1 mm SL); **e** *Larimus fasciatus* (7.6 mm SL); **f** *L. fasciatus* (56.1 mm SL); **g** *Bairdiella chrysoura* (6.0 mm SL); and **h** *B. chrysoura* (27.4 mm SL). To the right of each gill arch is a close-up view of the gill rakers along the ceratobranchial. The scale for each image is denoted by the black line. *cb* ceratobranchial; *eb* epibranchial, *gf* gill filament, *gr* gill raker, *hb* hypobranchial

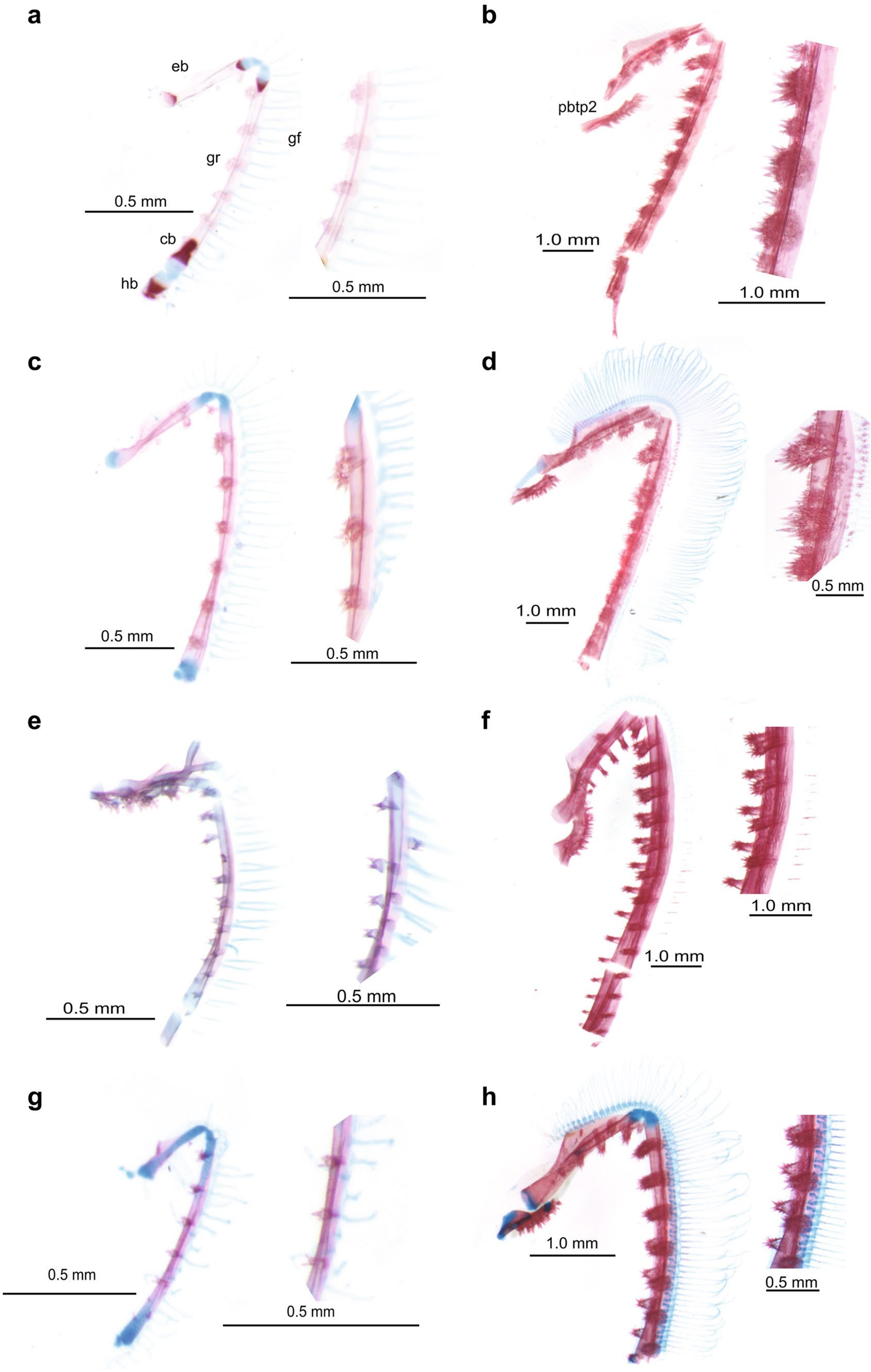
this size bin (Pianka's index of 0.55). As suggested by the diet cluster analysis, *C. regalis* and *B. chrysoura* had the highest niche overlap with a Pianka's index at 0.77 (Table 4). Individuals of *L. fasciatus* greater than 30.1 mm SL had very little niche overlap with *C. nebulosus* (Pianka's index of 0.17) and *B. chrysoura* (Pianka's index of 0.16) but moderate niche overlap with *C. regalis* (Pianka's index of 0.69) (Table 4).

Discussion

Trophic guilds are a useful tool to aggregate species that exploit food resources in a similar fashion (Buchheister and Latour 2015) but often foraging habits of early life history stage fishes are unknown (Nunn et al. 2012), making it difficult to assign individuals to a foraging guild. A compounding factor is that as an individual grows, it may change foraging guilds (Buchheister and Latour 2015), shifting how food resources are partitioned as well as inter- and intra-specific competition for prey. Anatomy, particularly of feeding structures, influences diet by constraining the range of prey sizes and the proficiency of capturing prey within that size range (Wainwright and Richard 1995). However, in the early stages, these factors are not yet established as they are in adult fishes due to allometric changes that modify the configuration of feeding structures (Kammerer et al. 2006; Anto et al. 2009). Although the morphological characteristics of the four examined pelagic sciaenids were similar throughout ontogeny, there were significant differences in ascending process length and cb1 gill raker count.

When comparing morphological characteristics of individuals from different trophic guilds, an examination of the elements involved in feeding (i.e., lower jaw length, premaxilla length, and pharyngeal toothplate areas) is often informative (Deary et al. 2017). Within the pelagic foraging sciaenid guild, this study found that lower jaw and premaxilla length were no longer informative because these oral jaw elements were already elongate and in a terminal position to maximize gape when foraging in the water column (Hunt von Herbing et al. 1996; Deary and Hilton 2016). However, the number of cb1 gill rakers did diverge among the species suggesting differences in prey preference. Although not recovered as significant features in the multivariate regression tree analysis, *Cynoscion regalis* and *C. nebulosus* had the longest heads but the smallest cb5 toothplates. *Cynoscion regalis* possessed the longest ascending process whereas *L. fasciatus* had the shortest ascending process. By the early juvenile stage (about 20.0 mm SL), the number of gill rakers along cb1 plateaued for both *Cynoscion* species and *L. fasciatus* possessed the most gill rakers on cb1. In the oral jaws, dentition along the premaxilla and dentary differed among the species with *L. fasciatus* possessing short, densely packed teeth compared to the elongate fangs of juvenile *Cynoscion* spp. *Cynoscion nebulosus* had relatively long and recurved teeth along the dentary and posterior to the premaxillary fangs, whereas *C. regalis* only possessed long, recurved teeth on the dentary. In this study, *B. chrysoura* was morphologically intermediate between *Cynoscion* spp. and *L. fasciatus* throughout development, which was also observed for juvenile sciaenids (Chao and Musick 1977).

In this study, one of the most ecologically informative morphological characters among the pelagic sciaenids was the number of gill rakers on cb1, although there are also structural differences among the gill rakers along the first two gill arches that support niche partitioning of larger juvenile sciaenids (Chao and Musick 1977; Aguirre and Shervette 2005). The primary function of the gill rakers is to retain food in the buccal cavity during foraging (Chao and Musick 1977; Hunt von Herbing et al. 1996) and therefore their shape and length are indicative of foraging habits (Aguirre and Shervette 2005; Bhagat et al. 2011). Fishes that possess relatively short and sparsely concentrated gill rakers tend to forage on larger prey (Aguirre and Shervette 2005), which I observed in the examined ELHS sciaenids. For example, *L. fasciatus,* which possessed numerous gill rakers on cb1 with long, densely packed lateral gill rakers that were not heavily spiculated, clustered with the other species and size bins that were dominated by pelagic zooplankton (i.e., copepods and mysid shrimp). By the juvenile stage, *L. fasciatus* had little niche overlap with *C. regalis* and *B. chrysoura*, which was related to these species foraging on a variety of benthic and pelagic prey. Juvenile *C. nebulosus* was piscivorous and possessed few lateral gill rakers that were robust, short, and covered with spicules. *Cynoscion regalis* and *B. chrysoura* had an intermediate morphology and number of gill rakers on cb1. These two species composed cluster 2 where a variety of prey, including both pelagic and benthic categories, was consumed. However, after having high niche overlap as early juveniles in cluster 2, *C. regalis* and *B. chrysoura* larger than 30.0 mm SL had no niche overlap due to *C. regalis* foraging on pelagic fishes and shrimp and *B. chrysoura* foraging mostly on benthic crustaceans, benthic worms, and pelagic crustaceans. In the earliest stages, larval sciaenids, like many other larval fishes, are gape-limited and have high niche overlap due to foraging exclusively on zooplankton, which is driven by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◂**Fig. 5** Development of gill rakers along the second gill arch for: **a** *Cynoscion regalis* [10 mm standard length (SL)]; **b** *C. regalis* (48.2 mm SL); **c** *C. nebulosus* (14.3 mm SL); **d** *C. nebulosus* (56.1 mm SL); **e** *Larimus fasciatus* (7.6 mm SL); **f** *L. fasciatus* (56.1 mm SL); **g** *Bairdiella chrysoura* (6.0 mm SL); and **h** *B. chrysoura* (27.4 mm SL). To the right of each gill arch is a close-up view of the gill rakers along the ceratobranchial. The scale for each image is denoted by the black line. *cb* ceratobranchial, *eb* epibranchial, *gf* gill filament, *gr* gill raker, *hb* hypobranchial, *pbtp* pharyngobranchial toothplate

morphological constraints of the oral jaws and lack of differentiation of other feeding elements (Krebs and Turingan 2003; Nunn et al. 2012), such as the gill rakers that were rudimentary and not well developed until after 7.0 mm SL.

Over 1/3 of the examined stomachs of *Cynoscion* spp. were empty compared to 4.5 and 2.9% empty for *B. chrysoura* and *L. fasciatus,* respectively. In *Cynoscion* spp., the individuals with empty stomachs were early larvae, less than 10.0 mm in length. Since larval collections were made at night, the predominance of empty stomachs in larval *Cynoscion* spp. suggests that early stage *Cynoscion* spp. individuals are not foraging at night. Diel foraging patterns in larval fishes are often species-specific, although they can be influenced by the presence of predators or favorable prey (Nunn et al. 2012). With the larval sampling design, I was not able to ascertain feeding phenology in the examined sciaenid species. Pelagic sciaenids are visual predators, especially in the early stages (Deary et al. 2016) so it is unlikely that *Cynoscion* spp. are less efficient at sensing zooplankton prey as the other two pelagic species. Many species of sciaenids have been documented to use selective tidal-stream transport to migrate further into estuaries to favorable settlement habitats (Rowe and Epifanio 1994; Rooker et al. 1998; Joyeux 1998; Holt and Holt 2000; Havel and Fuiman 2015). Therefore, foraging may be reduced in individuals of *Cynoscion* spp. that are actively moving between habitats in the earliest stages to reduce the risk of predation and maximize ingress distance.

Pelagic shrimp, particularly mysids, were consumed by individuals in all clusters suggesting this is an important prey to late larval and juvenile sciaenids, regardless of species or foraging guild (Deary et al. 2017). Ecologically, mysid shrimp act as a pathway linking benthic and pelagic food webs together because of diel vertical migrations (Buchheister and Latour 2015). Therefore, even though foraging was likely completed in the water column, the carbon likely originates from the benthic food web as mysids and other diel vertically migrating zooplankton migrate from depth during the night.

A caveat of this study is that most specimens of *L. fasciatus* ($n = 27$) were collected from the northern Gulf of Mexico, which may have a different prey field relative to the sciaenids collected in the Chesapeake Bay. Although species-specific prey communities are expected to differ between the Chesapeake Bay and the northern Gulf of Mexico, higher order taxonomic assemblages, such as those used to determine foraging guild assignments, are likely similar considering that a few taxa often dominate coastal communities (i.e., calanoid copepods, mysid shrimp) (Marques et al. 2006 and references therein; Carassou et al. 2014). Because I assessed the utility of functional group assignment in closely related, ecologically similar fishes, the use of broad prey categories aligns well with the goals of ecosystem-based fisheries management practices, which seek to reduce environmental complexity by grouping species into ecologically meaningful categories and is deemed appropriate to account for potential differences in the prey field (Auster and Link 2009).

Since broad prey categories were used in this study, future studies should further classify benthic crustaceans and benthic worms as infaunal, epibenthic, and structure-oriented.

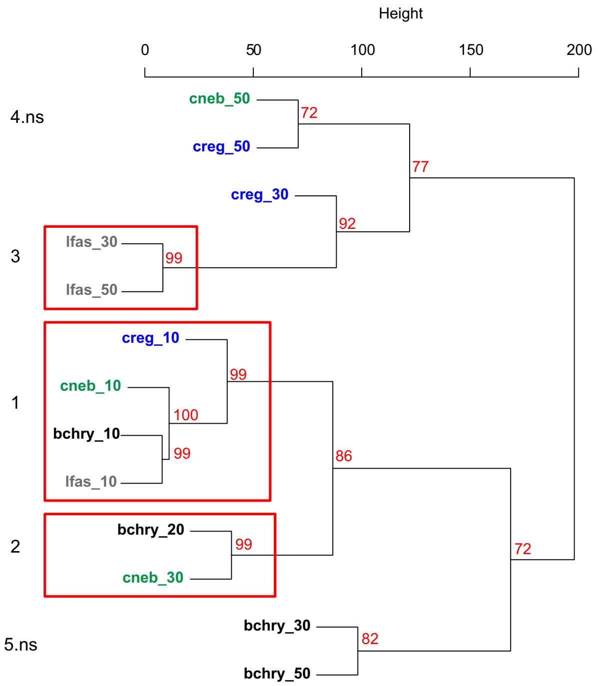

Fig. 6 Hierarchical cluster analysis of the diet by frequency of occurrence for *Cynoscion regalis* (creg; blue), *C. nebulosus* (cneb; green), *Larimus fasciatus* (lfas; gray), and *Bairdiella chrysoura* (bchry; black). The numbers behind each species abbreviations denotes the maximum standard length (SL) of the size bin. The size bins were: hatch–10.0 mm SL, 10.1–20.0 mm SL, 20.1–30.0 mm SL, and 30.1–50.0 mm SL. Red numbers indicate the approximately unbiased probability (AUP) values. Cluster identification is denoted by the black numbers to the left with clusters outlined in red having significant AUP values. Two additional, non-significant (ns) clusters are identified as 4.ns and 5.ns

Table 3 Mean percent number (*M%N*) and the frequency of occurrence (FO) for *Cynoscion regalis* (creg), *C. nebulosus* (cneb), *Larimus fasciatus* (lfas), and *Bairdiella chrysoura* (bchry)

M%N								FO						
Length bin	Pelagic crustacean	Pelagic shrimp	Pelagic fishes	Pelagic eggs	Benthic crustaceans	Benthic worms	Benthic phytoplankton	Pelagic crustacean	Pelagic shrimp	Pelagic fishes	Pelagic eggs	Benthic crustaceans	Benthic worms	Benthic phytoplankton
bchry_10	1.00							100						
bchty_20	0.67	0.50			0.28			83	33			50		
bchry_30	0.17	0.47			0.25	0.12		43	71			71	71	
bchry_50	0.27				0.44	0.29		100				100	50	
cneb_10	0.91	0.31		0.58				100	6		6			
cneb_30	0.28	0.47	0.13		0.13			75	50	25		25		
cneb_50	0.50		0.50					50		50				
creg_10	0.78	0.17					0.50	80	25					5
creg_30		0.50			0.50				50			50		
creg_50		0.50	0.50						50	50				
lfas_10	0.94				0.60			100				8		
lfas_30	0.29	0.71						33	100					
fas 50	0.10	0.90						25	100					

The numbers behind each species abbreviation denotes the maximum standard length (SL) of the size bin

The size bins were: hatch–10.0 mm SL, 10.1–20.0 mm SL, 20.1–30.0 mm SL, and 30.1–50.0 mm SL

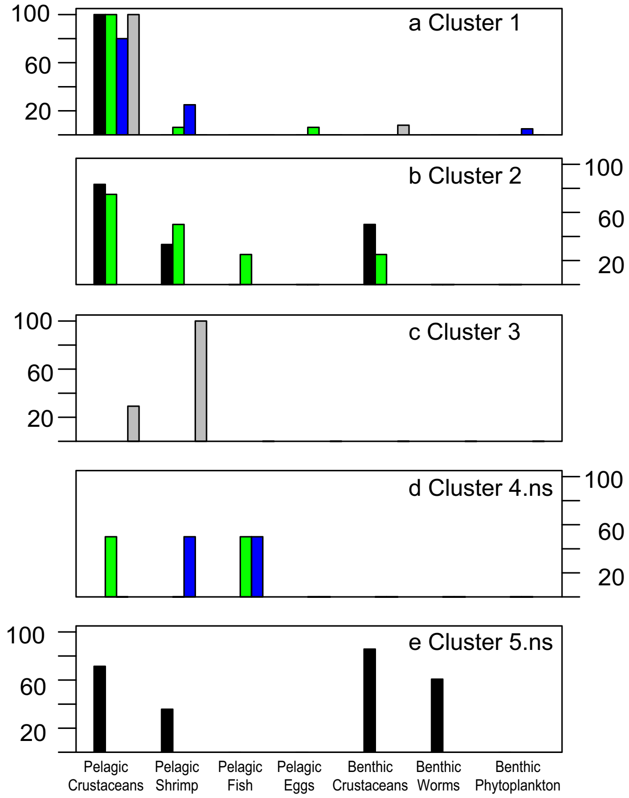

Fig. 7 Frequency of occurrence of each prey category by species for each cluster identified by the hierarchical cluster analysis. *Cynoscion regalis* (blue), *C. nebulosus* (green), *Larimus fasciatus* (gray), and *Bairdiella chrysoura* (black). Cluster 1 (**a**); cluster 2 (**b**); cluster 3 (**c**); cluster 4.ns (**d**); cluster 5.ns (**e**). The abbreviation ns denotes non-significant clusters

Table 4 Niche overlap values for pelagic sciaenids in the hatch–10.0 mm, 20.1–30.0 mm, and the 30.1–50.0 mm length bins

Hatch–10 mm				
	C. nebulosus	*C. regalis*	*L. fasciatus*	*B. chrysoura*
C. nebulosus		0.97	0.99	1.00
C. regalis	0.97		0.95	0.95
L. fasciatus	0.99	0.95		1.00
B. chrysoura	1.00	0.95	1.00	
20.1–30 mm				
	C. nebulosus	*C. regalis*	*L. fasciatus*	*B. chrysoura*
C. nebulosus		0.55	0.73	0.68
C. regalis	0.55		0.67	0.77
L. fasciatus	0.73	0.67		0.62
B. chrysoura	0.68	0.77	0.62	
30.1–50 mm				
	C. nebulosus	*C. regalis*	*L. fasciatus*	*B. chrysoura*
C. nebulosus		0.50	0.17	0.47
C. regalis	0.50		0.69	0.00
L. fasciatus	0.17	0.69		0.16
B. chrysoura	0.47	0.00	0.16	

For example, the benthic crustacean category defined in this study include gammarid amphipods and polychaete worms that, depending on genus, associate with seagrass (Johnson and Allen 2005), which are likely consumed by pelagic sciaenids off of the blades of seagrass (i.e., structure-oriented) and not picked of the benthos (epibenthic).

Conclusion

As a broad classification scheme, grouping individuals of *Cynoscion* spp., *B. chrysoura*, and *L. fasciatus* into a pelagic guild is appropriate, regardless of ontogenetic stage, due to each species foraging on pelagic prey almost exclusively. However, caution should be used when categorizing species into distinct foraging guilds, especially when ontogenetic stage is a factor, because of small scale differences in foraging that occur among species over development, which was highlighted in this study as a reduction in niche overlap among the species with increasing size. For example, adult *C. regalis* is piscivorous but through much of their early life history, this species is zooplanktivorous (Buchheister and Latour 2015; Deary et al. 2017). *Larimus fasciatus*, however, is zooplanktivorous throughout its entire life history, although the size class of zooplankton targeted does shift from small copepods to larger mysid shrimp. Guild-level perspectives are a practical method to employ as we shift from single species to ecosystem-level management approaches (Auster and Link 2009). High-resolution foraging studies must be conducted to appropriately place individuals into foraging guilds while also capturing key life history transitions that influence foraging habits and, ultimately, guild assignment.

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Data availability All physical specimens examined over the course of this study are deposited at the Virginia Institute of Marine Science, Nunnally Ichthyology Collection. Datasets and images generated and analyzed during the current study are available from the author upon reasonable request.

Compliance with ethical standards

Conflict of interest The author does not have a conflict of interest for the work that was conducted for the study.

Ethical approval All fish collection and handling procedures were approved by the College of William and Mary Institutional Animal Care and Use Committee (protocol number: IACUC-2014-05-12-9603-dtuck).

References

Aguirre WE, Shervette VR (2005) Morphological diversity of the *Cynoscion* group (Perciformes: Sciaenidae) in the Gulf of Guayaquil region, Ecuador: a comparative approach. Environ Biol Fishes 73:403–413. https://doi.org/10.1007/s10641-005-2227-3

Anto J, Majoris J, Turingan RG (2009) Prey selection and functional morphology through ontogeny of *Amphiprion clarkii* with a congeneric comparison. J Fish Biol 75:575–590. https://doi.org/10.1111/j.1095-8649.2009.02308.x

Arnold SJ (1983) Morphology, performance and fitness. Am Zool 23:347–361

Auster PJ, Link JS (2009) Compensation and recovery of feeding guilds in a northwest Atlantic shelf fish community. Mar Ecol Prog Ser 382:163–172. https://doi.org/10.3354/meps07962

Bhagat Y, Fox MG, Ferreira MT (2011) Trophic polymorphism in introduced pumpkinseed (*Lepomis gibbosus*) inhabiting Iberian reservoirs. Environ Biol Fishes 91:203–217. https://doi.org/10.1007/s10641-011-9773-7

Buchheister A, Latour RJ (2015) Diets and trophic-guild structure of a diverse fish assemblage in Chesapeake Bay, USA. J Fish Biol 86:967–992. https://doi.org/10.1111/jfb.12621

Carassou L, Hernandez FJ, Graham WM (2014) Change and recovery of coastal mesozooplankton community structure during the Deepwater Horizon oil spill. Environ Res Lett 9:124003

Chao LN, Musick JA (1977) Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River Estuary, Virginia. Fish Bull 75:657–702

Chipps S, Garvey JE (2007) 11 Assessment of food habits and feeding patterns. In: Guy C, Brown ML (eds) Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, pp 1–42

Davis CD, Fabrizio MC, Tuckey TD (2016) Estimation of juvenile striped bass relative abundance in the Virginia portion of Chesapeake Bay. Annual Report 2015. Virginia Institute of Marine Science, Gloucester Point, VA

De Cáceres M, Lapiedra O, Sol D (2014) An example of usage of the niche metric functions (former ' resniche ' package)

Deary AL, Hilton EJ (2016) Comparative ontogeny of the feeding apparatus of sympatric drums (Perciformes: Sciaenidae) in the Chesapeake Bay. J Morphol 277:183–195. https://doi.org/10.1002/jmor.20488

Deary AL, Hilton EJ (2017) Influence of cladogenesis on feeding structures in drums (Teleostei: Sciaenidae). Zoology 120:53–61. https://doi.org/10.1016/j.zool.2016.08.004

Deary AL, Metscher B, Brill RW, Hilton EJ (2016) Shifts of sensory modalities in early life history stage estuarine fishes (*Sciaenidae*) from the Chesapeake Bay using X-ray micro computed tomography. Environ Biol Fishes 99:361–375. https://doi.org/10.1007/s10641-016-0479-8

Deary AL, Latour RJ, Hilton EJ (2017) Niche partitioning in early life history stage, estuarine-dependent fishes (*Sciaenidae*). Estuar Coasts 40:1757–1770. https://doi.org/10.1007/s12237-017-0248-8

Egan JP, Gibbs S, Simons AM (2018) Trophic niches through ontogeny in 12 species of Indo-Pacific marine Clupeoidei (herrings, sardines, and anchovies). Mar Biol 165:153. https://doi.org/10.1007/s00227-018-3410-3

Elliott NG, Haskard K, Koslow JA (1995) Morphometric analysis of orange roughy (*Hoplostethus atlanticus*) off the continental slope of southern Australia. J Fish Biol 46:202–220

Fahay MP (2007) Early stages of fishes in the Western North Atlantic Ocean. Northwest Atlantic Fisheries Organization, Dartmouth

Grubich J (2003) Morphological convergence of pharyngeal jaw structure in durophagous perciform fish. Biol J Linn Soc 80:147–165. https://doi.org/10.1046/j.1095-8312.2003.00231.x

Havel LN, Fuiman LA (2015) Settlement-size larval red drum (*Sciaenops ocellatus*) respond to estuarine chemical cues. Estuar Coasts 39(2):560–570

Holt GJ, Holt SA (2000) Vertical distribution and the role of physical processes in the feeding dynamics of two larval sciaenids Sciaenops ocellatus and Cynoscion nebulosus. Mar Ecol Prog Ser 193:181–190

Horodysky AZ, Brill RW, FineMusick MLJa, Latour RJ (2008a) Acoustic pressure and particle motion thresholds in six sciaenid fishes. J Exp Biol 211:1504–1511. https://doi.org/10.1242/jeb.016196

Horodysky AZ, Brill RW, Warrant EJ, Musicka J, Latour RJ (2008b) Comparative visual function in five sciaenid fishes inhabiting Chesapeake Bay. J Exp Biol 211:3601–3612. https://doi.org/10.1242/jeb.023358

Hunt von Herbing I, Miyake T, Hall BK, Boutilier RG (1996) Ontogeny of feeding and respiration in larval Atlantic cod *Gadus morhua* (Teleostei, Gadiformes): 1. Morphol J Morphol 227:15–35

Joyeux J-C (1998) Spatial and temporal entry patterns of fish larvae into North Carolina estuaries: comparisons among one pelagic and two demersal species. Estuar Coast Shelf Sci 47:731–752. https://doi.org/10.1006/ecss.1998.0378

Johnson WS, Allen DM (2005) Zooplankton of the Atlantic and Gulf coasts. Johns Hopkins University Press, Baltimore

Kammerer CF, Grande L, Westneat MW (2006) Comparative and developmental functional morphology of the jaws of living and fossil gars (Actinopterygii: Lepisosteidae). J Morphol 267:1017–1031. https://doi.org/10.1002/jmor.10293

Krebs JM, Turingan RG (2003) Intraspecific variation in gape—prey size relationships and feeding success during early ontogeny in red drum, Sciaenops ocellatus. Environ Biol Fishes 66:75–84

Latour RJ, Brush MJ, Bonzek CF (2003) Toward ecosystem-based fisheries management: strategies for multispecies modeling and associated data requirements. Fisheries 28:10–22

Marques SC, Azeiteiro UM, Marques JC, Neto JM, Pardal MÂ (2006) Zooplankton and ichthyoplankton communities in a temperate estuary: Spatial and temporal patterns. J Plankton Res 28:297–312

Milborrow S (2014) Package "rpart.plot." 1–18

Murdy EO, Musick JA (2013) Fishes of Chesapeake Bay. Johns Hopkins University Press, Baltimore

Nunna D, Tewson LH, Cowx IG (2012) The foraging ecology of larval and juvenile fishes. Rev Fish Biol Fish 22:377–408. https://doi.org/10.1007/s11160-011-9240-8

Pianka ER (1973) The structure of lizard communities. Annu Rev Ecol Evol S 4(1):53–74

Poling KR, Fuiman LA (1999) Behavioral specialization in developing sciaenids and its relationship to morphology and habitat. Environ Biol Fishes 54:119–133

Powles H (1980) Descriptions of larval Silver Perch, *Bairdiella chrysoura*, Banded Drum, *Larimus fasciatus*, and Star Drum, *Stellifer Lanceolatus* (Sciaenidae). Fish Bull 78(1):119–136

R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing,Vienna, Austria. ISBN 3–900051–07-0. http://www.Rproject.org

Reecht Y, Rochet M-J, Trenkel VM, Jennings S, Pinnegar JK (2013) Use of morphological characteristics to define functional groups of predatory fishes in the Celtic Sea. J Fish Biol 83:355–377. https://doi.org/10.1111/jfb.12177

Ribeiro F, Hale E, Hilton EJ, Clardy TR, Deary AL, Targett TE, Olney JE (2015) Composition and temporal patterns of larval fish communities in Chesapeake and Delaware Bays, USA. Mar Ecol Prog Ser 527:167–180. https://doi.org/10.3354/meps11265

Richards WJ (2006) Early stages of Atlantic fishes: an identification guide for the western central North Atlantic. Taylor and Francis, New York

Rooker JR, Holt SA, Soto MA, Holt GJ (1998) Postsettlement patterns of habitat use by sciaenid fishes in subtropical seagrass meadows. Estuaries 21:318–327

Rowe PM, Epifanio CE (1994) Tidal stream transport of weakfish larvae in Delaware Bay, USA. Mar Ecol Prog Ser 110:105–114. https://doi.org/10.3354/meps110105

Suzuki R, Shimodaira H (2006) Pvclust: An R package for assessing the uncertainty in hierarchical clustering. Bioinformatics 22:1540–1542. https://doi.org/10.1093/bioinformatics/btl117

Suzuki R (2015) Hierarchical clustering with p-values via multiscale bootstrap. Package ’pvclust’

Svanbäck R, Eklöv P (2003) Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization ? Oikos 102:273–284. https://doi.org/10.1034/j.1600-0706.2003.12657.x

Taylor WR, Van Dyke GG (1985) Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilag estudy. Cybium 9:107–119

Tuckey TD, Fabrizio MC (2016) Estimating relative juvenile abundance of ecologically important finfish in the Virginia portion of Chesapeake Bay. Project No. F-104-R-20. Annual report to the Virginia Marine Resources Commission. Virginia Institute of Marine Science, Gloucester Point

Wainwright PC (1996) Ecological explanation through functional morphology: the feeding biology of sunfishes. Ecology 77:1336–1343

Wainwright PC, Richard BA (1995) Predicting patterns of prey use from morphology of fishes. Environ Biol Fishes 44:97–113

Warton DI, Duursma RA, Falster DS, Taskinen S (2012) Smatr 3- an R package for estimation and inference about allometric lines. Methods Ecol Evol 3:257–259. https://doi.org/10.1111/j.2041-210X.2011.00153.x

Wimberger PH (1991) Plasticity of jaw and skull morphology in the neotropical cichlids *Geophagus brasiliensis* and *G. steindachneri*. Evolution 45(7):1545–1563