# Larval fish assemblage dynamics in the York River estuary, Virginia, U.S.A.

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**Abstract—**The York River estuary (Chesapeake Bay) ichthyoplankton assemblage is described based on weekly sampling at a single site from 2007 to 2015. Larvae of 39 estuarine, marine, and diadromous taxa (24 families) were collected and patterns for 5 taxa (Atlantic menhaden [*Brevoortia tyrannus*], Atlantic croaker [*Micropogonias undulatus*], common anchovies [*Anchoa* spp.], American eel [*Anguilla rostrata*], and summer flounder [*Paralichthys dentatus*]) were analyzed. The most abundant taxa (collectively 92.6% of larvae encountered) were *Anchoa* spp., naked goby (*Gobiosoma bosc*), green goby (*Microgobius thalassinus*), Atlantic croaker, and Atlantic menhaden. Two distinct assemblages were present each year—a warm season assemblage (May to August) and a cool-season assemblage (September to April). Model-based predictions of mean species richness across the time series varied, with greatest richness from 2007 to 2009. Predicted mean seasonal species richness also varied, with stable richness from October to May and elevated richness from June to September. Analogous predictions of mean annual and seasonal Simpson's inverse diversity generally followed patterns of species richness. Predicted annual mean densities were relatively lower during the middle years of the time-series for Atlantic menhaden and summer flounder, consistently declined for *Anchoa* spp. and Atlantic croaker, and were generally constant for American eel. Seasonal patterns in predicted mean densities of those taxa reflected seasonality of spawning.

## Introduction

Temperate estuaries are complex and productive ecosystems where water temperatures can range widely and salinity gradients and vertical stratification vary seasonally, which results in diverse aquatic and intertidal habitats (Reay and Moore, 2009; Day et al., 2013). Estuaries support resident and transient fish species that use these habitats seasonally and at different stages of their life cycle (e.g., Whitfield, 1990; Franco et al., 2008; Able and Fahay, 2010; Murdy and Musick, 2013; Strydom, 2015). These dynamic environments provide refuge and nursery habitats for the early stages (inclusive of larval and small juvenile stages) of estuarine, marine, and diadromous fish species (Houde et al., 2022; Arevalo et al., 2023). Within estuaries globally, larval fish assemblages typically have a relatively low number of taxa with a few dominant species (e.g., Able, 2005; Bonecker et al., 2009; Ribeiro et al., 2015; Whitfield et al., 2022). The larval fish assemblage, defined as the spatiotemporal co-occurrences of early stages of multiple species, is shaped and maintained by the interaction of biological and environmental processes, including time and location of spawning (Miller, 2002), the timing of larval ingress to the estuary (Warlen and Burke, 1990), circulation patterns (e.g., Gray and Miskiewicz, 2000; Miller and Shanks, 2005), freshwater discharge (Taylor et al., 2010; Rodrigues et al., 2022; Wan et al., 2023), and larval behavior (Boehlert and Mundy, 1988; Teodósio et al., 2016). These factors can in conjunction act to disturb or maintain the larval fish assemblage according to the physical and climatic conditions that dominate each estuarine system (Zhang et al., 2022).

Inter-annual variability in abundance and high rates of mortality of early stages of fishes can define the strength of year-classes (Sissenwine, 1984; Taylor et al., 2009). Understanding the dynamics of the early stages of fishes is important because shifting physical processes may affect variability of juvenile abundance and therefore impact adult recruitment (Miller et al., 1988; Houde, 2008). For example, suboptimal environmental conditions may reduce larval growth and survival rates (Secor and Houde, 1995; Lankford and Targett, 2001; Able and Fahay, 2010). Long-term research can document temporal changes or stability of species abundances within the larval fish assemblage.

The Chesapeake Bay and its tributaries form a complex and productive ecosystem. It is also a dynamic environment in which surface water temperatures range from 0°C in winter to 30°C during summer and where salinity gradients (freshwater to polyhaline regimes) and vertical stratification vary seasonally depending on precipitation and freshwater discharge (Kemp et al., 2005; Reay and Moore, 2009). High productivity, combined with mixing of riverine fresh and oceanic salty waters, results in diverse aquatic and intertidal habitats (Reay and Moore, 2009). The Chesapeake Bay supports approximately 350 species of finfish: 32 year-round residents and more than 320 transient species (Murdy and Musick, 2013). Many of these species are of ecological and economic importance, including Atlantic menhaden (*Brevoortia tyrannus*), Atlantic croaker (*Micropogonias undulatus*), bay anchovy (*Anchoa mitchilli*), and summer flounder (*Paralichthys dentatus*) which are studied herein, as well as species such as striped bass (*Morone saxatilis*).

The phenology of the Chesapeake Bay's fish assemblage reflects the seasonal changes in environmental conditions. Physical processes and environmental variability (e.g., water temperature and freshwater discharge) influence the composition and abundance of estuarine larval fish assemblages (Miller, 2002; Able and Fahay, 2010). For example, juvenile and adult species diversity in tropical species is highest from late summer to early fall due to the ingress of recruiting juveniles. Before winter, tropical species either perish or emigrate from the Chesapeake Bay toward southern coastal and warmer waters (Able and Fahay, 2010; Murdy and Musick, 2013; Buchheister et al., 2013). Relatively little is known, however, about interannual changes in the Chesapeake Bay's larval fish assemblage and its temporal dynamics over long time periods.

With the exception of a long-standing time series in a single New Jersey estuary (Witting et al., 1999; Able and Fahay, 2010; Morson et al., 2019), research on larval fish assemblages in the Middle Atlantic Bight is limited (e.g., Cowan and Birdsong, 1985; Ribeiro et al., 2015). In the Chesapeake Bay, research has revealed the community structure of fishes at different spatial and temporal scales (e.g., Buchheister et al., 2013; Bonzek et al.[1]; Tuckey and Fabrizio[2]). Many of these efforts focus on the juvenile and adult fish assemblages (Jung and Houde, 2003), with fewer directed studies of the larval fish assemblage. Most studies of larval fishes in the Chesapeake Bay have emphasized the timing of larval fish ingress into the bay (e.g., Pearson, 1941; Olney, 1983; Ribeiro et al., 2015). The effect of environmental factors on the ingress of larval marine fishes into the Chesapeake Bay has been studied (e.g., Olney and Boehlert, 1988; Lozano and Houde, 2013), with most ingress research focusing on one or only a few species (e.g., Norcross, 1991; Hare et al., 2005; Schaffler et al., 2009). The temporal dynamics of the larval fish assemblage as a whole, however, remain relatively poorly known.

The primary goal of our research was to describe the annual and seasonal composition of the larval fish assemblage from the York River estuary, a subestuary of the Chesapeake Bay. In addition to describing patterns of the larval fish assemblage, density patterns for 5 target species were more closely examined (Atlantic menhaden, Atlantic croaker, common anchovies [*Anchoa* spp.], American eel [*Anguilla rostrata*], and summer flounder) because of their abundance and their ecological and economic importance in Chesapeake Bay and the York River estuary.

## Materials and methods

### Biological sampling

Samples of early-stage fishes were obtained once per week from 2007 through 2015 in the York River estuary at the public pier in Gloucester Point, Virginia (Fig. 1). At each sampling event, three 30-min passive tows were conducted in the top 2 m of the water column during night flood tides using a 1-m diameter conical plankton net (1-mm mesh size). A flowmeter was attached to the net to calculate filtered water volume. From July through August each year, sampling frequency and duration were reduced to 2 sampling events per month with 15-min tows to avoid net clogging due to elevated abundances of ctenophores and larvae and small juveniles of resident species such as bay anchovy (Ribeiro et al., 2015).

Samples were preserved in 70% ethanol and identified using primary reference identification guides for the larval fishes in the western North Atlantic Ocean (e.g., Richards, 2006; Fahay, 2007). Although we consistently use the term *larval*, other early stages of some taxa were collected, including small but transformed individuals (e.g., post-settlement summer flounder and glass-eel stage American eel). Specimens were deposited in the larval fish collection in the Nunnally Ichthyology Collection at the Virginia Institute of Marine Science.

### Annual and seasonal patterns in species composition

To explore annual and seasonal patterns in the larval fish assemblage we conducted a nonmetric multidimen-

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[1] Bonzek, C. F., J. Gartland, D. J. Gauthier, and R. J. Latour. 2022. Annual report—2021 data collection and analysis in support of single and multispecies stock assessments in Chesapeake Bay: the Chesapeake Bay Multispecies Monitoring and Assessment Program, 156 p. Va. Inst. Mar. Sci., Coll. William Mary, Gloucester Point, VA. [Available from https://doi.org/10.25773/k7xj-e205.]

[2] Tuckey, T. D., and M. C. Fabrizio. 2022. 2022 annual report—estimating relative juvenile abundance of ecologically important finfish in the Virginia portion of the Chesapeake Bay. Gloucester Point, Virginia. (1 July 2021–30 June 2022), 149 p. Va. Inst. Mar. Sci., Coll. William Mary, Gloucester Point, VA. [Available from https://scholarworks.wm.edu/reports/2826/.]

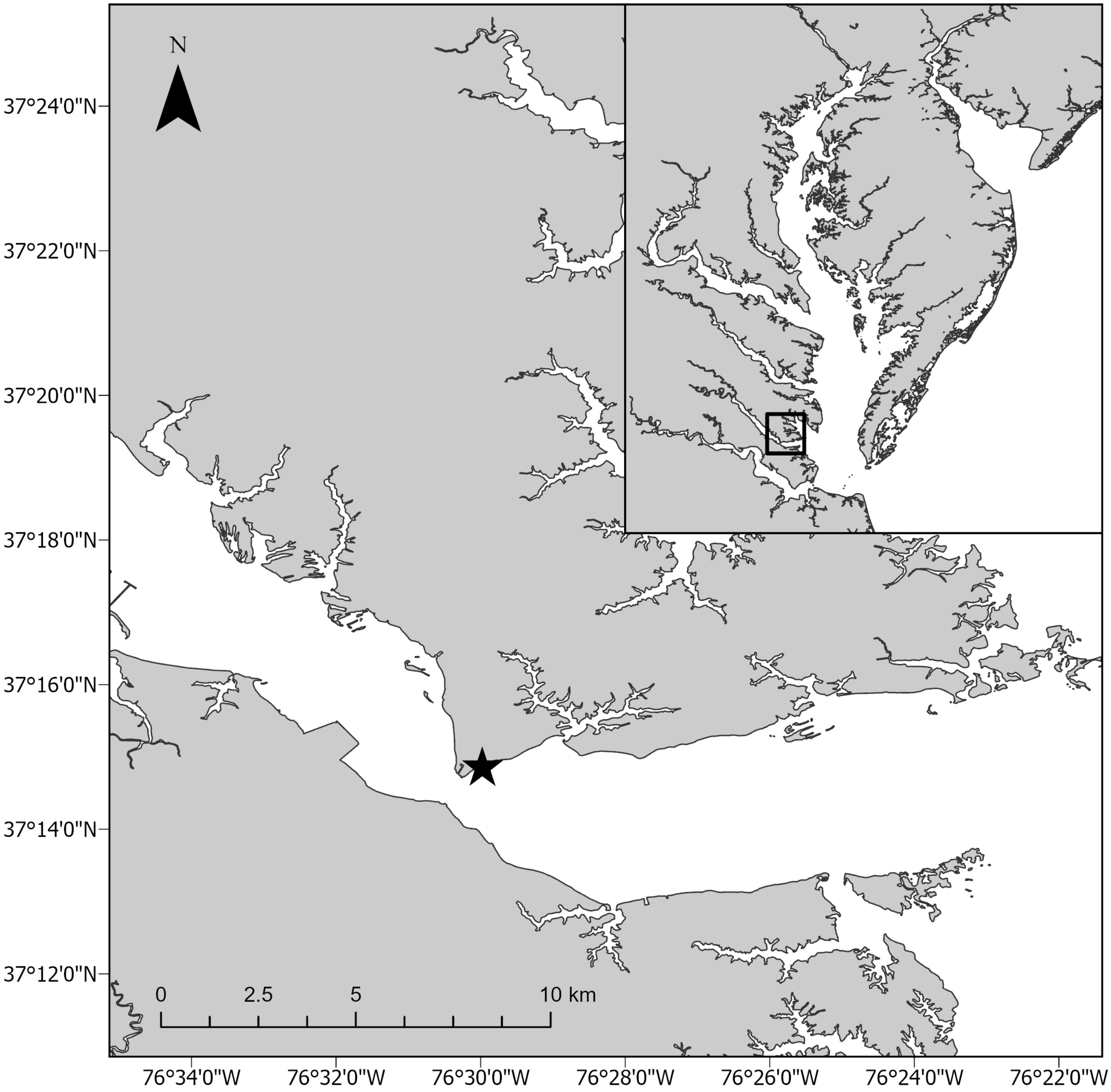

**Figure 1**

Map showing the location of the sampling station (star) in the York River estuary, in the southern portion of Chesapeake Bay, where early-stage fishes were collected from 2007 through 2015.

sional scaling (NMDS) analysis using the vegan library, vers. 2.5-7 (Oksanen et al., 2020) in R, vers. 4.3.0 (R Core Team, 2023). The NMDS plots were restricted to 2 dimensions based on a Bray–Curtis dissimilarity matrix. The goal of the NMDS analysis was to collapse the multidimensional larval fish assemblage abundance data into fewer (2) dimensions to aid species composition visualization and interpretation. Unlike other ordination approaches that rely on Euclidean distances or require a linearity assumption, NMDS is based on the rank order of the intersample dissimilarities and is thus an extremely flexible technique. We limited our analysis to the 15 most abundant taxa (with abundances ≥1 larvae/1000 $m^3$) which together comprised 99.4% of the total catch and thus provided a reasonable indication of the larval fish assemblage. Larval fish density data were square-root transformed to reduce the influence of outliers and reduce skewness. Although this transformation is widely used in ecological analyses (Anderson, 2001; Anderson et al., 2008), it can affect the dispersion of data within groups, which requires care when interpreting the data (Anderson et al., 2008). A permutational multivariate analysis of variance was conducted to identify samples that clustered together in the NMDS plots (Anderson et al., 2008); this analysis is typically applied to test for differences in mean abundance among samples using permutations. The permutational multivariate analysis of variance approach assumes only that samples are exchangeable under the null hypothesis. However, the permutation procedure implies independence and homogeneity of dispersions among samples. A betadisper test was conducted to assess homogeneity of multivariate dispersions among years. Statistically significant inferences were based on an alpha threshold of 0.05.

## Biodiversity indices

Two biodiversity indices were used to describe the York River estuary larval fish assemblage. The simple compositional measure of species richness (*S*) was tabulated as the number of species collected in each sample. Simpson's concentration was selected as the compound (structural) index combining richness and abundance. This index becomes Simpson's inverse (*D*) when expressed in terms of effective number of species (MacArthur, 1965; Jost, 2006):

$$D = \frac{1}{\sum_{i=1}^{S} p_i^2}, \tag{1}$$

where $p_i$=the proportion of individuals belonging to species *i*.

In the context of the mathematically unified family of biodiversity indices known as Hill numbers (Hill, 1973), *S* is biodiversity of order $q$=0, and *D* is biodiversity of order $q$=2. Because *S* is very sensitive to rare species (Roswell et al., 2021), the full larval fish data set was filtered to only include species present in at least 3% of the samples to mitigate the leverage of rare species (this led to exclusion of 18 species from the data). Since *D* combines richness and abundance, evaluation of this metric was based on the same filtered data set for consistency, although it is acknowledged that *D* provides higher leverage to common species (Roswell et al., 2021).

The biodiversity indices *S* and *D* were computed for each sample, although sampling events with zero catch (3 samples: weeks 18 and 48 in 2011 and week 44 in 2012) were excluded from the computation of *D*. The resulting data were analyzed with generalized linear models (GLMs; McCullagh and Nelder, 1989), which can be expressed generally as:

$$g\big(E(y)\big)=X\beta+\delta, \tag{2}$$

where E($y$) = the expected value of the response vector $y$;
$X$ = the fixed-effect design matrix;
$\beta$ = the vector of fixed-effect parameters;
$\delta$ = the offset vector; and
$g$ = the monotonic link function.

The covariates considered were *year* and *month* (both categorical) since the goal of the biodiversity analysis was to characterize annual and seasonal patterns in the larval fish community. A complete year was considered to extend from March of the first year to February of the second year to avoid truncating the year-class of winter-spawning species (years therefore ranged from 2007 to 2014). The response vector $y$ was defined as the biodiversity index (*S* or *D*) and the offset vector $\delta$ was defined to be the natural logarithm of the volume of water sampled.

The GLMs were implemented by applying the generalized additive models for location, scale, and shape regression framework (Stasinopoulos et al., 2017). A wide range of candidate probability distributions was considered for each biodiversity index (all available count distributions for *S* and positive real line distributions for *D*). Selection among competing probability distributions was achieved using Akaike's information criterion (Akaike, 1973; Burnham and Anderson, 2002) and through examination of quantile-quantile plots, worm plots (detrended quantile-quantile plots), analysis of residuals, and evaluation of overdispersion (count models for *S*). Predictions over the year and month domains were computed as marginal means (Searle et al., 1980) and associated estimates of precision were approximated using the delta-method (Seber, 1982). Biodiversity GLMs were implemented using the gamlss package (vers. 6.0-1; Rigby and Stasinopoulos, 2005).

## Target species

Annual and seasonal variation of larval fish densities (larvae/1000 m$^3$) was evaluated for 5 target taxa: Atlantic menhaden, *Anchoa* spp., Atlantic croaker, American eel, and summer flounder. For each taxon, the density data were summarized monthly and filtered to only include months when the target species appeared in at least 10% of the samples, in an effort to avoid including uninformative zero observations (i.e., periods of the year where larvae encounters would not be expected based on the timing of spawning and ingress to the bay). This led to the data sets including the following monthly time periods: Atlantic menhaden—October to May, *Anchoa* spp.—March to February, Atlantic croaker—September to March, American eel—December to May, and summer flounder—December to April (note that the data for the

**Figure 2**

Photographs of common early stages of fish species (anterior facing left) collected in the York River estuary from 2007 to 2015: (**A**) bay anchovy (*Anchoa mitchilli*), (**B**) naked goby (*Gobiosoma bosc*), (**C**) green goby (*Microgobius thalassinus*), (**D**) Atlantic croaker (*Micropogonias undulatus*), (**E**) Atlantic menhaden (*Brevoortia tyrannus*), (**F**) American eel (*Anguilla rostrata*), (**G**) summer flounder (*Paralichthys dentatus*), and (**H**) *Leiostomus xanthurus*. Photographs A–D are among the most abundant species recorded for the York River estuary. Scale bars equal 1 mm except for photograph F, which equals 5 mm.

defined monthly periods did include zero observations as these were deemed informative).

Following the biodiversity analyses, GLMs were again used to analyze the filtered density data for each target species (Equation 2 without the offset term). Model covariates were *year* and *month* (both categorical), and since each data set contained a mixture of zero and continuous non-zero observations, the Tweedie distribution (Jørgensen, 1987) was selected for density data associated with each target species (diagnostic quantile-quantile plots and analysis of residuals confirmed the appropriateness of the Tweedie distribution for all taxa). Predictions for the covariates *year* and *month* were computed as marginal means and the delta-method was used to estimate precision. The GLMs for the target species were implemented using the glmmTMB package, vers. 1.1.5 (Brooks et al., 2017) and model diagnostics were summarized using the DHARMa package, vers. 0.4.5 (Hartig, 2022).

## Results

From March 2007 to March 2015, 378 sampling events were conducted, and 146,334 fish larvae were collected, with representatives of 39 taxa from 24 families (Fig. 2, Table 1). Sciaenidae was the richest family with 8 species. Taxa in the collections reflected the diversity of estuarine (e.g., *Anchoa* spp. and silver perch [*Bairdiella chrysoura*]), marine (e.g., Atlantic menhaden), and diadromous (e.g., American eel) species that use the Chesapeake Bay and York River estuary.

Ranked by density (larvae/1000 m$^3$), the most abundant taxa were 3 residents (*Anchoa* spp., naked goby [*Gobiosoma bosc*], green goby [*Microgobius thalassinus*]) and 2 species that spawn offshore (Atlantic croaker and Atlantic menhaden); these 5 taxa accounted for 92.6% of larvae collected (Table 1). The dominant taxon was *Anchoa* spp., which accounted for 55.4% of the total catch. The proportion of each rare taxon varied annually, but the 5 most abundant taxa always dominated the assemblage. The complete taxonomic composition of the larval fish assemblage comprised mostly early stages of species that commonly inhabit the Chesapeake Bay. Some early-stage individuals from rarely recorded species in the Chesapeake Bay, such as the speckled worm eel (*Myrophis punctatus*), however, did occur in the York River catches.

## Multivariate analysis of the larval fish assemblage

The NMDS plots and permutational multivariate analysis of variance results revealed no annual differences in larval fish assemblages ($P$=0.36; Table 2). Within each year, a significant seasonal difference in larval assemblages showed 2 distinct assemblages ($P$=0.001; Table 2, Fig. 3), one from May to August (warm-season assemblage) and a second from September to April (cool-season assemblage). The cool-season assemblage was characterized by the presence of fewer species, primarily oceanic spawners, such as Atlantic menhaden, Atlantic croaker, summer flounder, and American eel, whereas the warm-season assemblage was formed by resident taxa such as *Anchoa* spp., naked goby, green goby, *Sygnathus* spp., and lined seahorse (*Hippocampus erectus*).

## Biodiversity indices

Data filtering designed to reduce the leverage of rare species on $S$ led to the exclusion of 18 taxa from the overall larval fish data set. For the remaining 21 species, model selection based on Akaike's information criterion and diagnostic plots of GLMs parameterized with competing distributions for $S$ supported selection of the Poisson-inverse Gaussian distribution. Model predictions revealed that annual mean $S$ ranged from 4.4 to 7.1 species, with the greatest richness occurring from 2007 to 2009; thereafter, mean annual $S$ remained constant (Fig. 4A). Precision of the mean annual $S$ estimates was generally good, as evidenced by narrow 95% confidence intervals. Predicted seasonal species richness ranged from 2.7 to 11.0 species, and showed a sharply contrasting pattern with stable mean monthly $S$ from October to May and highly elevated mean monthly $S$ from June to September (Fig. 4B). As with the annual mean $S$ results, the 95% confidence intervals of the mean monthly $S$ estimates were generally narrow and indicative of good precision.

Model selection procedures for the Simpson's inverse GLMs fitted with competing distributions for $D$ supported choosing the generalized inverse Gaussian distribution. Patterns in predicted mean annual and monthly $D$ generally followed those of mean $S$, respectively (Fig. 4C and D). Annually, mean $D$ peaked in 2008 and reached its lowest level in 2014, but was largely constant

**Table 1**

Taxonomic densities (number [no.] of larvae/1000 m$^3$) in the York River from March 2007 to March 2015. Mean density, total number of fish larvae, and frequency of occurrence (out of the 378 sampling events) from the entire time series are provided. *Anchoa* spp. includes bay anchovy (*Anchoa mitchilli*) and striped anchovy (*Anchoa hepsetus*). Blenniidae includes the co-occurring species striped blenny (*Chasmodes bosquianus*) and feather blenny (*Hypsoblennius hentz*).

| Rank | Taxa | Mean density (no. larvae 1000/m$^3$) | Total no. larvae | Frequency |
|---|---|---|---|---|
| 1 | *Anchoa* spp. | 356.73 | 80707 | 293 |
| 2 | *Gobiosoma bosc* | 111.54 | 21222 | 153 |
| 3 | *Microgobius thalassinus* | 59.67 | 14158 | 119 |
| 4 | *Micropogonias undulatus* | 43.63 | 10369 | 187 |
| 5 | *Brevoortia tyrannus* | 26.48 | 9008 | 200 |
| 6 | *Bairdiella chrysoura* | 9.67 | 1183 | 41 |
| 7 | *Anguilla rostrata* | 7.00 | 2244 | 156 |
| 8 | *Leiostomus xanthurus* | 6.04 | 2534 | 98 |
| 9 | *Syngnathus* sp. | 3.74 | 924 | 184 |
| 10 | *Symphurus plagiusa* | 3.10 | 833 | 77 |
| 11 | *Paralichthys* sp. | 2.54 | 846 | 107 |
| 12 | *Menidia* sp. | 2.29 | 679 | 97 |
| 13 | Blenniidae | 1.09 | 243 | 82 |
| 14 | *Cynoscion nebulosus* | 1.08 | 197 | 40 |
| 15 | *Sciaenops ocellatus* | 1.05 | 312 | 41 |
| 16 | *Cynoscion regalis* | 0.82 | 221 | 34 |
| 17 | *Gobiesox strumosus* | 0.72 | 148 | 43 |
| 18 | *Trinectes maculatus* | 0.50 | 109 | 28 |
| 19 | *Hippocampus erectus* | 0.46 | 109 | 45 |
| 20 | *Menticirrhus* sp. | 0.28 | 83 | 30 |
| 21 | *Stellifer lanceolatus* | 0.24 | 49 | 9 |
| 22 | *Peprilus* sp. | 0.19 | 34 | 11 |
| 23 | *Myrophis punctatus* | 0.13 | 36 | 14 |
| 24 | *Sphoeroides* sp. | 0.08 | 11 | 9 |
| 25 | *Clupea harengus* | 0.08 | 20 | 4 |
| 26 | *Alosa aestivalis* | 0.08 | 28 | 9 |
| 27 | *Conger oceanicus* | 0.03 | 5 | 4 |
| 28 | *Hyporhamphus meeki* | 0.02 | 5 | 2 |
| 29 | *Synodus foetens* | 0.01 | 4 | 3 |
| 30 | *Chaetodipterus faber* | 0.01 | 3 | 3 |
| 31 | *Lagodon rhomboides* | 0.01 | 3 | 3 |
| 32 | *Mugil cephalus* | 0.01 | 3 | 3 |
| 33 | *Chaetodon* sp. | 0.01 | 1 | 1 |
| 34 | *Ctenogobius boleosoma* | 0.01 | 1 | 1 |
| 35 | *Oligoplites saurus* | 0.00 | 1 | 1 |
| 36 | *Opisthonema oglinum* | 0.00 | 1 | 1 |
| 37 | *Urophycis regia* | 0.00 | 1 | 1 |
| 38 | *Prionotus* sp. | 0.00 | 1 | 1 |
| 39 | Sparidae | 0.00 | 1 | 1 |

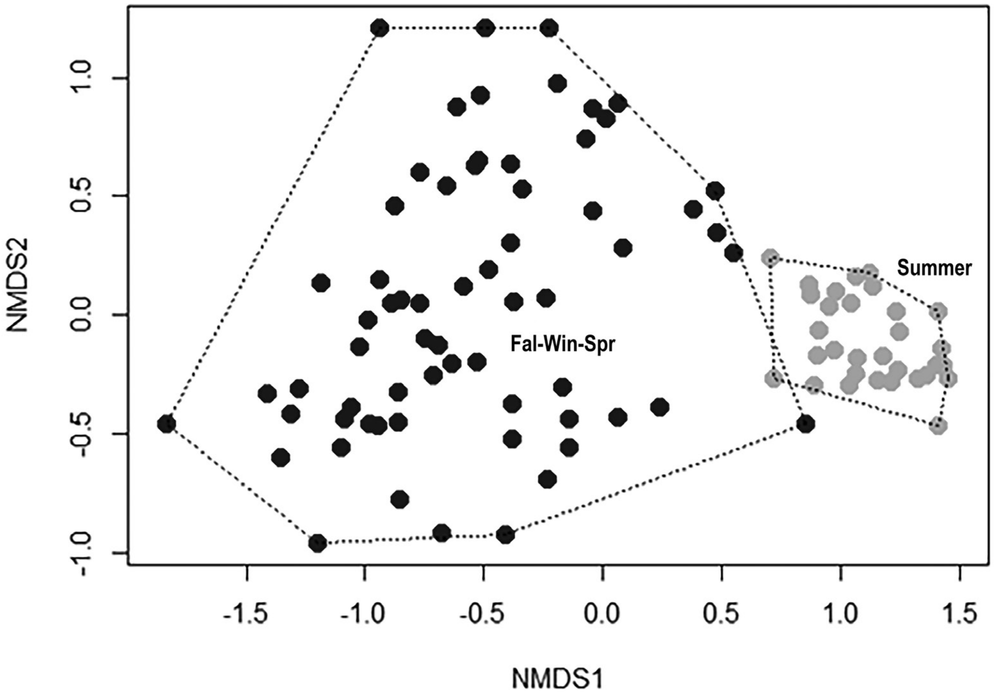

**Figure 3**

Two-dimensional nonmetric multidimensional scaling (NMDS) ordination plot of larval fish assemblage composition based on abundance data of larval fish species sampled from 2007 through 2014 in the York River estuary during cool (fall [Fal]-winter [Win]-spring [Spr]; September through April) and warm seasons (summer; May through August). The *y*- and *x*-axes represent the differences between samples based on Bray–Curtis distances. The stress level of this plot is 0.1324. Minimum polygons encompassing data points are included to emphasize the distinction between the Fal-Win-Spr and Summer assemblages.

**Table 2**

Permutational multivariate analysis of variance (PERMANOVA) results for the larval fish assemblage in the York River during 2007–2014. The PERMANOVA test is based on differences in the Bray–Curtis dissimilarity matrix. The model included *year* and *season*. The season factor had 2 levels as categorical variables: May through August (warm months) and September through April (cool months). An asterisk (*) indicates that a value is significant using a priori alpha level of 0.05. df=degrees of freedom; SS=sum of squares; MS=mean squares; F=pseudo-*F* test statistic; $R^2$=partial variance explained; P=*P*-value.

| | df | SS | MS | F | $R^2$ | P |
|---|---|---|---|---|---|---|
| Year | 7 | 1.29 | 0.18 | 1.10 | 0.05 | 0.36 |
| Season | 1 | 10.01 | 10.01 | 60.07 | 0.39 | 0.001* |
| Residuals | 87 | 14.50 | 0.17 | | 0.56 | |
| Total | 95 | 25.80 | | | 1.0 | |

over years. Seasonally, mean *D* was higher from June to August and stable at lower values for all other months. Generally narrow 95% confidence intervals for the estimated annual and monthly mean *D* estimates indicated good precision.

## Densities of target taxa

Patterns in annual and seasonal predicted densities of the 5 target taxa differed considerably, with the seasonal differences reflecting species-specific reproductive biology. Over the years of this study, predicted densities of Atlantic menhaden and summer flounder displayed *U*-shaped trends with lower values during the middle years (Fig. 5A and I). Predicted densities for both *Anchoa* spp. and Atlantic croaker showed consistently declining patterns (exception *Anchoa* spp. in 2012; Fig. 5C), while those for American eel were generally constant over time without a notable trend (Fig. 5G). The 95% confidence intervals of predicted annual densities showed fairly good precision across all taxa.

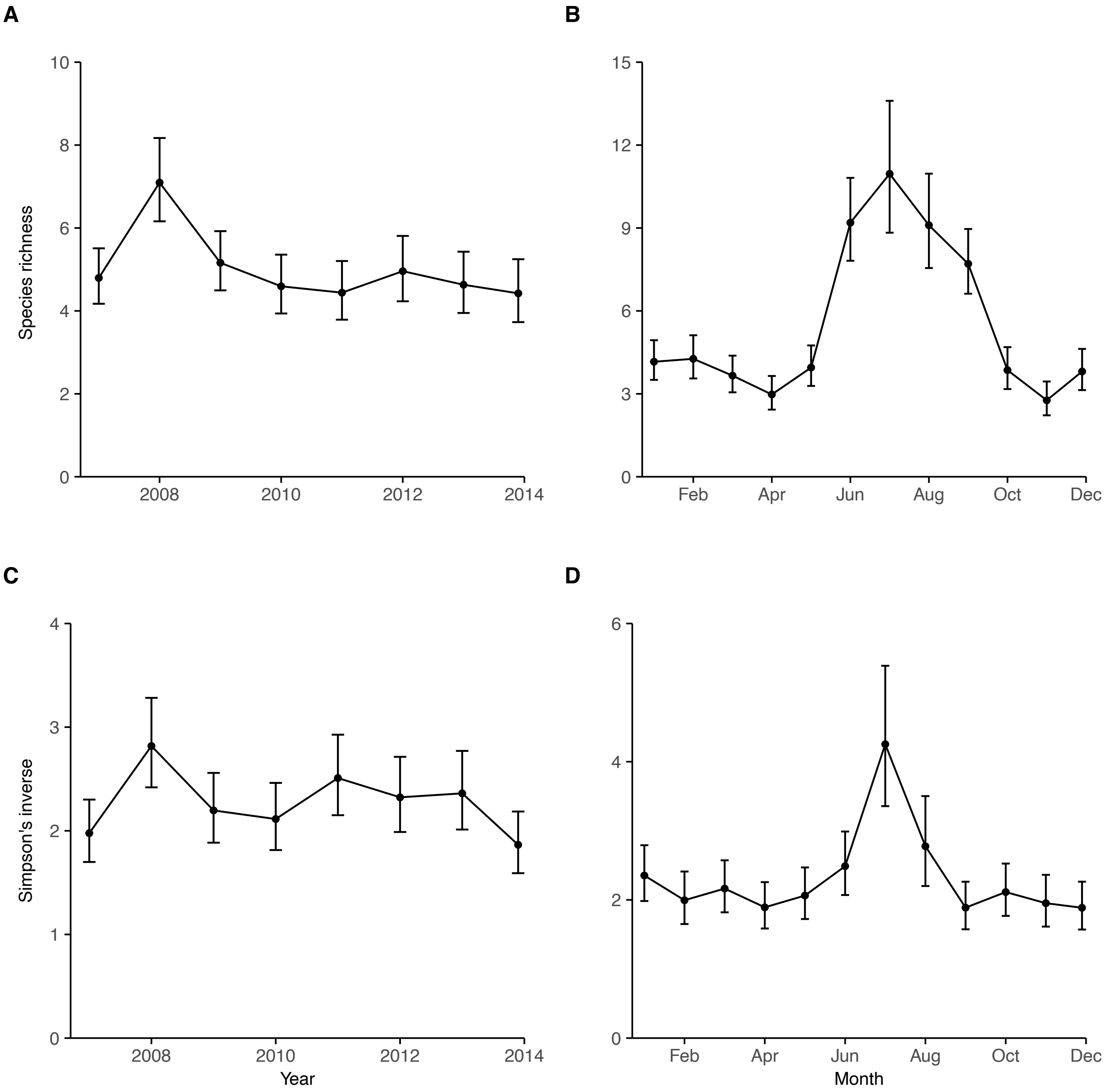

**Figure 4**

(**A**, **B**) Predicted species richness and (**C**, **D**) diversity of larval fish species in the York River from 2007 to 2014. Panels A and C show annual means, and panels B and D show monthly means. Error bars represent 95% confidence intervals. Feb=February; Apr=April; Jun=June; Aug=August; Oct=October; Dec=December.

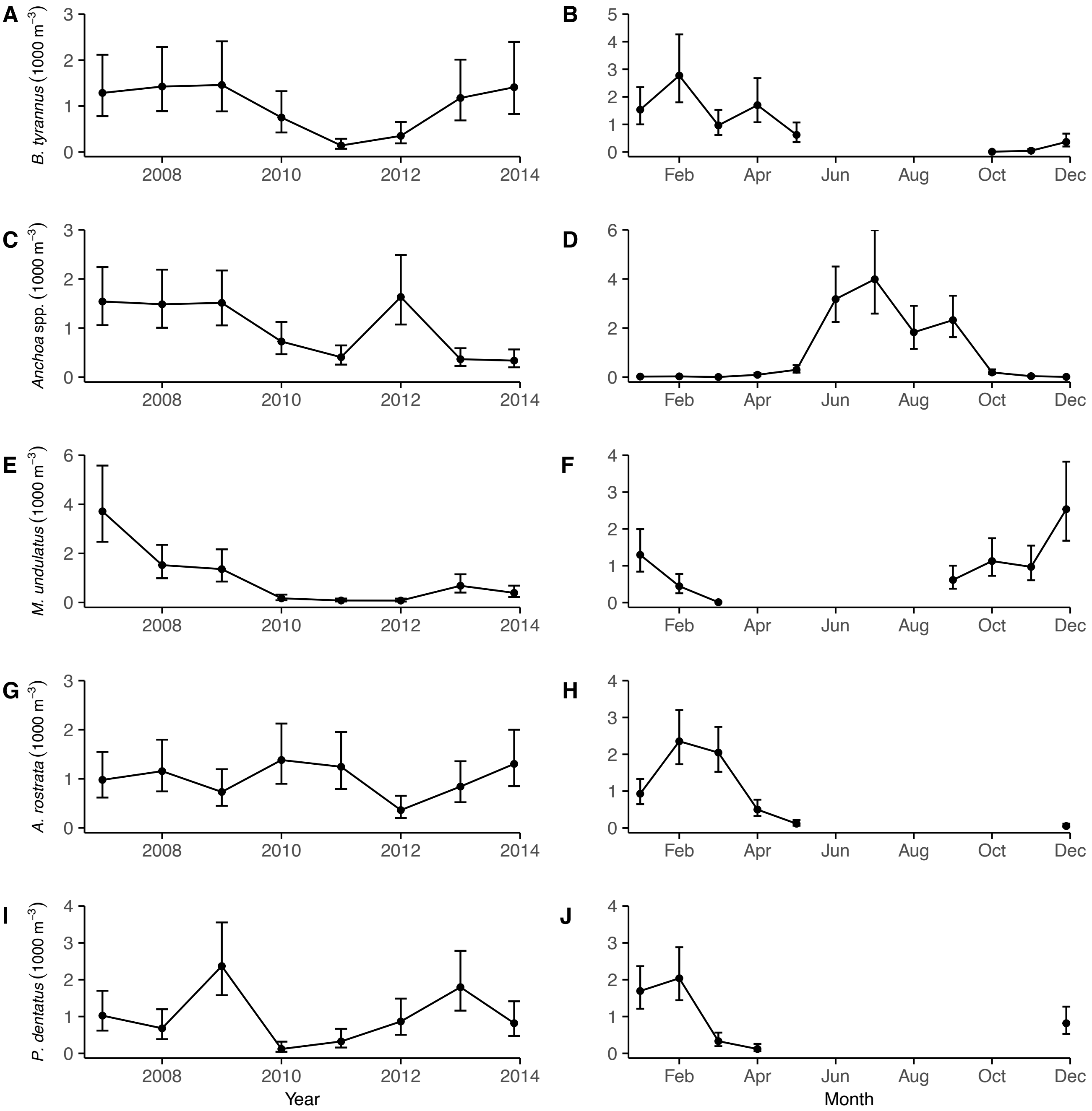

**Figure 5**

(Left panels) Annual and (right panels) monthly predicted abundances for (**A, B**) Atlantic menhaden (*Brevoortia tyrannus*), (**C, D**) *Anchoa* spp., (**E, F**) Atlantic croaker (*Micropogonias undulates*), (**G, H**) American eel (*Anguilla rostrata*), and (**I, J**) summer flounder (*Paralichthys dentatus*) sampled during 2007–2014 in the York River. To aid visualization, all predictions were scaled by dividing each time-series by its mean. Error bars represent 95% confidence intervals. Gaps in the monthly predicted abundances correspond to the months where the target taxon occurred in less than 10% of the samples. Feb=February; Apr=April; Jun=June; Aug=August; Oct=October; Dec=December.

Species-specific data filtering indicated that larvae from all taxa were consistently sampled over protracted time periods, ranging from 5 months for summer flounder to all months for *Anchoa* spp. Monthly predicted densities for all species showed dome-shaped patterns, with peaks occurring in February for species that ingress from offshore during the cooler months (Atlantic menhaden, American eel, and summer flounder; Fig. 5 B, H, and J), July for estuarine-spawning species during warmer months (*Anchoa* spp.; Fig. 5D), and December for offshore-spawning species during cooler fall months (Atlantic croaker; Fig. 5F). As with the annual predicted densities, 95% confidence intervals of the predicted monthly indices for all taxa were indicative of acceptable precision (Fig. 5).

## Discussion

### Larval fish assemblages

Estuaries are inherently dynamic environments, with fluctuating environmental conditions over a broad range of spatial and temporal scales (e.g., daily, annual, and longer time frames). Temperature, salinity, freshwater flow, and turbidity are widely considered to be key factors controlling ichthyoplankton assemblages in estuaries (e.g., Harris and Cyrus, 2000; Strydom, 2015; Rodrigues et al., 2022; Zhang et al., 2022; Wan et al., 2023). Furthermore, observed variability in ichthyoplankton assemblages may result from environmental factors that act differentially on particular taxa through indirect (e.g., growth) or direct (e.g., mortality) mechanisms (Arevalo et al., 2023).

The location of the York River estuary in the southern and seaward portion of the Chesapeake Bay supports a suite of marine and freshwater species (Hewitt et al., 2009), which is reflected in the larval fish assemblage. The assemblage, as described by the dominant species, was relatively stable across the time series in the York River estuary; the same taxa were consistently dominant in each year. *Anchoa* spp. were most abundant and, together with the naked goby and green goby, dominated density and rank order. Dominance of the larval assemblage by resident species has been reported in other studies of estuarine systems along the middle and southern Atlantic coasts of the United States, including the Great Bay-Little Egg Harbor (Able and Fahay, 2010), the southern portion of Chesapeake Bay (Ribeiro et al., 2015), and the North Inlet Estuary, South Carolina (Allen and Barker, 1990). Our study indicated stability of the larval fish assemblage in the York River estuary from 2007 to 2015, and results from statistical models also suggest a high degree of stability in taxonomic diversity and taxonomic richness at the seasonal and annual scales, despite some variability in the time of occurrence or peaks of abundance. Such annual stability of the assemblage structure was consistent with findings from studies on other North American east coast estuaries in 5 to 17-year timeframes (Allen and Barker, 1990; Witting et al., 1999; Able and Fahay, 2010). In contrast, studies of early-stage assemblages from other global regions have reported interannual variation in assemblage composition and taxon density. For example, in a 2-year time series, Ramos et al. (2006) reported the density of *Pomatoschistus* spp. (Gobiidae) in the Lima River estuary (Portugal) differed between years. Interannual variability in precipitation and river discharge was cited as a possible explanation. Wan et al. (2023) identified variability in temperature, salinity, and freshwater flow as the variables most related to changes in larval fish assemblages in the Yangtze River estuary. Variable and often unpredictable environmental conditions (e.g., high annual precipitation) that affect hydrologic conditions are a known source of variation in early-stage assemblages (Zhang et al., 2022).

Over longer time periods, variation in the structure of early-stage assemblages also have been noted. Zhang et al. (2022) reported shifts in the ichthyoplankton fauna of the Yangtze River estuary between the 1980s and mid-2010s, including reduced numbers of taxa included in the assemblage and a change in the dominant taxa. Although the reasons for such trends are unclear, Zhang et al. (2022) suggested that changing environmental factors due to natural and anthropomorphic factors and climate change influence the composition of early-stage assemblages. Based on a 26-year time series, Morson et al. (2019) found significant changes in the overall early stage assemblage in Little Egg Inlet (New Jersey) on the mid-Atlantic coast of North America. In that study, across the time series there was a significant increase in the density of southern-affiliated species and a significant decrease in northern-affiliated species, suggesting a northerly shift in spawning due to warming sea-surface temperatures. It may be that similar shifts in the ichthyoplankton assemblage are occurring in our Chesapeake Bay study area but the time series available to us was insufficient to detect such changes.

There was strong seasonal variability in the Chesapeake Bay larval fish assemblage with clear representation of warm-season and cool-season assemblages. This seasonality was also identified by Ribeiro et al. (2015) using both a cluster analysis and NMDS approach for an analysis of the larval assemblage near the mouth of the Chesapeake Bay based on a 3-year subset of the more extensive data in our analyses. A 2-group (warm-season and cool-season) assemblage pattern is also found in a South Carolina estuary (Allen and Barker, 1990), whereas 4 groups (summer, fall, winter, and spring) were identified for the more northern larval fish assemblage in the

Delaware Bay (Ribeiro et al., 2015). Peak taxonomic diversity also generally occurs in larval fish assemblages in the spring and summer in other temperate estuaries (e.g., Guadiana estuary, Portugal, Faria et al., 2006; Yangtze River estuary, China, Wang et al., 2017). Seasonal changes in the larval assemblage are in part related to the dynamics of the ichthyofauna and the reproductive patterns of many species that use the Chesapeake Bay and the York River estuary systems as spawning and nursery areas. For example, in the late summer fish diversity reaches a maximum and is coincident with warmer waters. Bay anchovy, the most abundant species in the Chesapeake Bay, exhibits a reproductive peak in mid-summer. In contrast, during the fall and winter, taxonomic diversity of fish larvae in the York River estuary decreases and coastal spawners, such as Atlantic menhaden and summer flounder, initiate their reproductive periods (Murdy and Musick, 2013; Nys et al., 2015). Some species that were collected during larval sampling, such as speckled worm eel, are rarely recorded by the Virginia Institute of Marine Science Juvenile Fish Trawl Survey (Tuckey and Fabrizio[2]), a probable bias attributable to the sampling gear used to survey juvenile fish.

Taxonomic diversity and taxonomic richness remained relatively constant among years, with minor variability. Some of the metrics in earlier years (2007–2009) indicated presence of a greater number of taxa and overall number of larval fishes, although this variation is not supported in Simpson's diversity index, which by definition incorporates number of species and density. Seasonal variability in factors such as current speeds, stratification, and primary production may affect the timing of migratory patterns and reproductive periods of the ichthyofauna in Chesapeake Bay (Jung and Houde, 2003; Able and Fahay, 2010; Buchheister et al., 2013). Annual variation in adult abundances and spawning output also may contribute to variability in larval densities.

## Temporal pattern of abundance for target taxa

Species-specific densities of larval *Anchoa* spp., American eel, Atlantic croaker, summer flounder, and Atlantic menhaden, the 5 target taxa in our analyses, differed among years. *Anchoa* spp., represented by the dominant bay anchovy and the less abundant striped anchovy (*Anchoa hepsetus*), was the most abundant taxon, which was an expected result because bay anchovy is the most abundant resident fish in the Chesapeake Bay, especially in the southern (seaward) portion of the Bay (Houde and Zastrow, 1991; Murdy et al., 1997; Jung and Houde, 2003; Auth et al., 2020). The dominance of *Anchoa* spp. in summer is coincident with higher temperatures that are associated with peak spawning during these months in the Chesapeake Bay and the York River (Luo and Musick, 1991; Rilling and Houde, 1999; Auth et al., 2020). In our study, mean density of larval *Anchoa* spp. increased notably during 2012, a peak that coincided with a peak in the relative abundance of trawled young-of-the-year bay anchovy in the lower Chesapeake Bay during that year (Tuckey and Fabrizio[2]). This result suggests a correspondence in the abundance patterns of larval *Anchoa* spp. at our York River site and young-of-the-year juvenile bay anchovy in a trawl survey conducted throughout the lower Chesapeake Bay (Tuckey and Fabrizio[2]).

The pattern of variability in mean annual abundance of *Anchoa* spp. larvae differed from that observed for coastal spawners such as Atlantic menhaden, Atlantic croaker, and summer flounder. For these species, higher densities were observed in the earliest years of the time series, followed by a decrease in 2010–2011 and an increase in 2013–2014. Environmental, physical, and biological factors (e.g., timing of spawning, hatching, and transport from the coast, prior to their ingress into the York River estuary) were not analyzed to evaluate potential relationships with larval densities. An analysis of such factors should be explored in the future since they may act to control larval supply and time of ingress of coastal spawners while local environmental factors could explain annual variability in densities of larvae produced by resident spawners.

Effects of monthly and annual changes in environmental conditions are species-specific and likely related to other aspects of life history, such as spawning location. It is important to note that the present study, while comprehensive, encompassed only 8 years of observations and was based on collections at a single fixed site in the lower portion of the York River estuary. Over the course of this survey, larvae of 39 taxa representing 30% of the finfish species known to occur in this portion of the York River estuary (approximately 130; Hewitt et al., 2009) were collected. Because a single fixed site was sampled, the analyses presented herein may not be fully representative of the larger estuarine assemblage in the York River system or the lower Chesapeake Bay.

## Conclusions

The ichthyoplankton assemblage in the York River estuary, a Chesapeake Bay subestuary, was described based on weekly samples from 2007 to 2015 and found to be represented by the larvae of 39 taxa (24 families), including estuarine, marine, and diadromous species. The assemblage was dominated by the resident taxa *Anchoa* spp., naked goby, green goby, and the seasonal migrants Atlantic croaker and Atlantic menhaden; collectively these taxa accounted for 92.6% of the total larvae encountered. Two distinct assemblages were present annually, a warm-season assemblage from May to August and a cool-season assemblage from September to April. The cool-season assemblage included fewer species that were primarily oceanic spawners, whereas the warm-season assemblage was formed by resident taxa. Model-based predictions of mean species richness across the time series showed that the greatest richness occurred from 2007 to 2009. Predicted mean seasonal species richness showed elevated richness from June to September, with lower, stable richness from October to May; predictions of mean annual and seasonal Simpson's inverse diversity generally followed the same patterns. Predicted annual mean densities for 5 target taxa (Atlantic menhaden, Atlantic croaker, *Anchoa* spp., American eel, and summer flounder) were relatively lower during the middle years of the time-series for Atlantic menhaden and summer flounder, consistently declined for *Anchoa* spp. and Atlantic croaker, and were generally constant across the time series for American eel. Seasonal patterns in predicted mean densities of those taxa reflected differences in seasonality of spawning.

Although not analyzed as part of this study, environmental, physical, and biological factors such as timing of spawning, hatching, and transport should be explored in the future to evaluate their influence on larval supply and timing of ingress of coastal spawners, and on the annual variability in densities of larvae produced by resident spawners. Our survey, however, provides baseline results from a relatively long time series of ichthyoplankton observations and, as such, serves as a good descriptor of the larval fish assemblage and scales of temporal variability and as a foundation upon which to gauge future changes in the ichthyofauna of the Chesapeake Bay system.

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