



Population Dynamics of Common Nearshore Forage Fishes in the Delaware Inland Bays, USA

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Abstract

In the Mid-Atlantic, four species of forage fish, *Menidia menidia* (Atlantic Silverside), *Fundulus heteroclitus* (Mummichog), *Fundulus majalis* (Striped Killifish), and *Cyprinodon variegatus* (Sheepshead Minnow), account for a large proportion of fish abundance in estuarine environments and are important food sources for state and federally managed predatory species. The population dynamics of these species are poorly understood, and factors affecting their populations are largely unclear or unknown. Seine samples were collected in the Delaware Inland Bays over 9 years (2011–2019), with indices and trends in abundance, as well as climatic and biotic drivers of population changes investigated at both combined estuary and individual bay scales. Average interannual decreases in abundance for all four species at the combined estuary scale ranged between 31.9 and 69.2%, while increases ranged between 65.9 and 178.6%, indicating the extreme variability these species show between years. Standardized models of abundance demonstrated long-term declines in abundance for Mummichog and Sheepshead Minnow at both the combined estuary and individual bay scales. Spring discharge affected Mummichog and Sheepshead Minnow abundance, and Sheepshead Minnow showed a strong negative correlation with Summer Flounder abundance. These data quantify the variability in abundance for an important portion of the forage base in Mid-Atlantic estuaries and should be considered as fisheries management shifts away from single-species approaches and recognizes the forage needs of managed species. Results indicate that even commonly encountered species can consistently vary through time and emphasize the need to examine other important but poorly studied forage species.

Keywords Forage fish · Mid-Atlantic · Mummichog · Striped Killifish · Sheepshead Minnow · Atlantic Silverside

Introduction

Forage fish species are typically small to medium-sized schooling fish that play an important role in trophic transfer from the base of the food chain to higher levels and are critical to the health and sustainability of economically and

ecologically valuable fish species (Ihde et al. 2015; MAFMC 2017). Globally, forage fish species annually contribute an estimated \$16.9 billion to fisheries' values, with an estimated \$11.3 billion resulting from the direct support forage fish provide to other fisheries (Pikitch et al. 2012). The value of forage fish also extends to seabirds and marine mammals, where they serve as an additional and important source of food (Garcia-Rodriguez and Auriol-Gamboa 2004; Cury et al. 2011; Smith et al. 2015). Due to their relatively short lifespans, forage fish populations are highly responsive to environmental conditions, with documented large annual fluctuations in response to changes in environmental suitability, which results in sizeable effects on other important fish species (Jung and Houde 2004; Reum et al. 2011; Engelhard et al. 2014). Furthermore, human harvesting of forage species can exacerbate natural fluctuations and result in collapse (Essington et al. 2015). When forage fish populations decline or collapse, the effects on piscivorous predators can be significant (Ball et al. 2007; Dickey-Collas et al. 2014; Kaplan et al. 2017).

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Given the importance of forage fish to numerous ecologically and economically important species, it is critical to understand their population dynamics, as well as the factors that influence these changes and the spatial and temporal scales over which they occur. These data become especially relevant as management agencies increasingly implement ecosystem-based management, which relies on an understanding of these very questions. In some instances, where population dynamics and food-web interactions are better understood, historic management decisions or current stock distribution can be evaluated, and management can be changed to account for the role forage fish play in community dynamics (Lindegren et al. 2009; Eero et al. 2012; Townsend et al. 2019). For example, within the Mid-Atlantic region of the USA, the fishing pressure imposed on Atlantic Menhaden (*Brevoortia tyrannus*) has been altered through management measures in an attempt to ensure enough biomass persists to support Striped Bass (*Morone saxatilis*) populations (SEDAR 2015; ASMFC 2020).

These types of management or stock evaluations rely on robust datasets for important forage taxa. While these types of data are available for Atlantic Menhaden, for many other Mid-Atlantic forage species not targeted by commercial fisheries, stock status, annual abundance changes, or spatial–temporal distributions are poorly known (Clay et al. 2014; Ihde et al. 2015; MAFMC 2016). This lack of information is particularly concerning when considering that recreational and commercial fishing in the region combined for an economic impact of over \$4 billion in 2015 (NOAA 2015). Any large changes in these species' abundance or distribution could have far reaching economic or ecological implications, and yet these changes may go unnoticed. This is particularly true for forage species that reside outside of areas typically captured by fisheries independent surveys, such as shallow-water, nearshore habitats that are inaccessible to commonly used survey gear like bottom trawls. Further, management agencies have identified the need to survey and document forage species in these areas (Ihde et al. 2015).

Within the Delaware Inland Bays (Rehoboth, Indian River, and Little Assawoman), a Mid-Atlantic coastal lagoon system located between Delaware Bay and Chesapeake Bay, three species of small nearshore estuarine resident fish, *Fundulus majalis* (Striped Killifish), *Fundulus heteroclitus* (Mummichog), and *Cyprinodon variegatus* (Sheepshead Minnow), and one transient nearshore fish, *Menidia menidia* (Atlantic Silverside), account for over 80% of fish abundance in the nearshore intertidal or shallow subtidal area (Boutin and Targett 2013; Balouskas and Targett 2016), similar to many other Mid-Atlantic estuarine systems (Roundtree and Able 1992; Wagner and Austin 1999; Myer et al. 2001). These small forage fish provide an important means of energy transfer from highly productive salt marshes or the

shallow nearshore environment to the greater estuary and offshore fisheries (Deegan et al. 2000; Stevens et al. 2006; Able et al. 2007a). Changes to populations of these forage fish species would likely have wide implications for commercially and recreationally important federally and state managed species such as Bluefish (*Pomatomus saltatrix*), Striped Bass (*Morone saxatilis*), and Summer Flounder (*Paralichthys dentatus*), as these nearshore fish species are a major component of these species' diets at some point in their life histories (Friedland et al. 1988; Roundtree and Able 1992; Tupper and Able 2000; Torre and Targett 2017).

Despite their importance to federal and state managed species, research on these forage fishes has been limited in scope and duration, often examining only a few variables over a short time period in small study areas (Weisberg and Lotrich 1986; Lockfield et al. 2013; Thompson 2015; Gobler et al. 2018). This lack of information is surprising given that each of these species constitutes the basis for bait for recreational fishers and thus is routinely harvested. Temporal changes in abundance for these species within a given year have been documented (Able and Fahay 2010). However, annual abundance changes, representing an average availability to predatory species for a given year, over decadal cycles have rarely been described, and it remains unclear what factors may be driving these changes. In light of these species' importance, it is critical to understand how their abundance can fluctuate annually and over longer time scales and investigate what variables may influence these changes and at multiple scales.

Numerous studies have examined the influence of local factors such as land use changes, food limitation, local marsh bank deterioration, and single marsh platform eutrophication on the short-term dynamics of nearshore forage species such as Mummichog (Weisberg and Lotrich 1986; Lockfield et al. 2013; Nelson et al. 2018; Kornis et al. 2017). However, much less attention has been given to the effects of ecosystem-wide climatic and biotic factors, for example, river discharge, the Atlantic Multidecadal Oscillation (AMO), winter severity, or predation pressure imposed by predatory fish species. Both climatic factors and predatory pressure have been reported as affecting other forage fish populations (e.g., Atlantic Menhaden), and so these same factors may play important roles in regulating nearshore forage fish populations (Overton et al. 2008; Reum et al. 2011; Buchheister et al. 2016). For instance, Mummichog are benthic feeders that consume detritus, algae, and a variety of small invertebrates such as copepods (Kneib 1986). They also derive a substantial portion of their diets from marsh macrophytes and have demonstrated changes in body size and growth rates to changes in primary production (Lockfield et al. 2013; Nelson et al. 2015). Both marsh productivity and common copepod prey species can be altered by changes in river discharge, which can be altered by variations in AMO, thus examining river discharge and

AMO may shed light on observed population changes in nearshore forage species such as Mummichog (Enfield et al. 2001; Kimmel and Roman 2004; Hu et al. 2011; Wieski and Pennings 2013). Similarly, especially harsh winters can affect the survival of Mummichog, Sheepshead Minnow, and Striped Killifish since all three species overwinter in the estuary by burying into sediments on the marsh surface or in nearby shallow creeks and could therefore be subjected to lethal freeze events (Bennett and Beitinger 1997; Able and Fahay 2010). Likewise, while Atlantic Silverside migrate out of the estuary and spend the winter offshore, winter mortality is still considerable (Conover and Ross 1982; Able and Fahay 2010). Lastly, while a few studies have examined the rates of predation certain nearshore species (most commonly Mummichog) can be subjected to, these studies do not link specific predatory fish species to nearshore fish population dynamics, nor study these dynamics over the long-term (Meredith and Lotrich 1979; Kneib 1982).

This study provides annual and long-term (9 years) population dynamics data from under sampled shallow water-habitats for three resident and one transient nearshore forage fish, filling a current void in the understanding of critical Mid-Atlantic forage fish species. The changes between years are compared with both climatic variables and juvenile indices of commercially and recreationally important predatory fish species' abundances to assess what influences the identified changes seen and the scale of changes that are occurring. This information is an important step in the process of transitioning from single species management to an ecosystem-based approach which accounts for the availability of nearshore forage species to the recreationally and commercially important species of Mid-Atlantic estuaries and how this availability changes over time in response to climatic and biotic changes.

Methods

Survey Methods

A total of 1,843 seine samples were collected between 2011 and 2019 by trained volunteers and staff members at 16 fixed sites in Indian River and Bay, Rehoboth Bay, and Little Assawoman Bay and tributaries (Fig. 1) from the end of April through October. Each year, one sampling event occurred during the second half of April, while two monthly sampling events occurred during the first and second halves of each month from May through October. Volunteers followed a US Environmental Protection Agency approved quality assurance plan and were trained in fish identification by staff and regional experts. Data was checked to ensure compliance with the quality assurance plan annually.

Study sites were selected that were within close proximity to a road or parking lot for ease of access by volunteers and staff in motor vehicles. Each site has an open shoreline area of at least 31 m in length, with a flat bottom and substrate firm enough to safely sample at all tidal stages. Twelve of the 16 sites were a mixture of sandy beach and fringing saltmarsh (*Spartina alterniflora* dominated) depending on the tide during sampling. Two of the other four sites were entirely sandy beach regardless of the tide cycle, but were within a few meters of salt marsh, and the last two sites were sandy at low tides but either a mixture of fringing *Spartina alterniflora* and large boulders or just large boulders from a breakwater structure during high tides.

At each site, a single haul was made using a 9.1 m long by 1.2 m high bag seine with 0.63-cm mesh. The bag is 1.2 m long, 1.2 m wide, and 1.2 m deep, located in the center of the net. One volunteer waded off the shoreline into deeper water, while another volunteer remained close to shore along the tide line, usually in 0.3 m or less of water. The net was drawn between them, fully extended, perpendicular to the shore, and was walked parallel to the shore for about 21 m, at which point the deeper water volunteer swung inshore and both volunteers walked the net onto shore, thereby seining 30.1 m of shoreline. The only exception to this procedure was at a single site where two 15-m hauls were made because a pier, too low to walk under, is located across the middle of the area. All fish were removed from the net, identified to species level, and counted. Each seine haul was designated as one unit of effort. The two approximately 15-m hauls at the site with the pier were combined and counted as one unit of effort.

Water temperature (measured to 0.1 degree Celsius, °C), dissolved oxygen (to 0.1 mg per liter, mg/l), and salinity (to 0.1 part per thousand, ppt) were measured with a YSI Pro 2030 m at the beginning of each survey. Tidal stage was not standardized throughout the study, but was recorded for each haul and categorized as low ebb or low flood if sampling began within 2 h of low tide, mid-flood or mid-ebb if sampling began within 2 to 4 h of low or high tide, and high ebb or high flood if sampling began within 2 h of high tide. Of the 1,843 seine samples taken, there were 14 instances where either low, mid, or high tide were missed at a site for a given year, and 43 instances where only one sample occurred, indicating that most sites in most years were well balanced with respect to tidal stage.

Indices of Abundance and Trend Analysis

Annual raw catch values for each species were divided by the total number of fish caught during that year to derive the proportion of total catch for each species for each survey year. Individual hauls were standardized using generalized additive models with a negative binomial error distribution

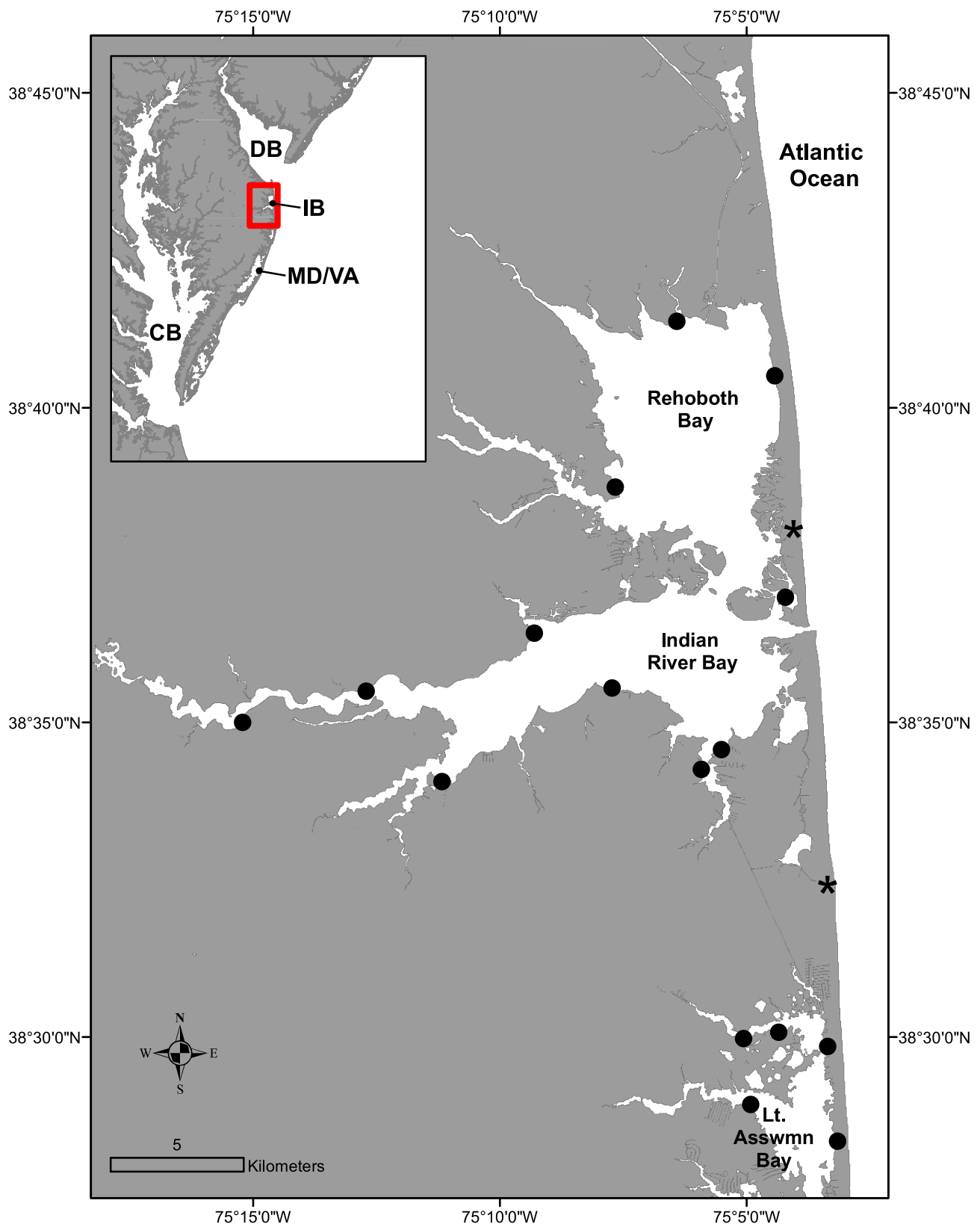


Fig. 1 The seining sites used for this study are indicated by the black circles. The weather stations used for winter temperatures are indicated by the black asterisks. The study area is highlighted by the red square in the inset map of the Delmarva Peninsula. CB, Chesapeake

Bay; MD/VA, Maryland and Virginia Coastal Bays; IB, Delaware Inland Bays; and DB, Delaware Bay. Image produced with ArcMap (ESRI, version 10.8)

(NBGAM) for each species and water body for each year of the study using the “gam” function in the “mgcv” package in R 3.5.2 (R 2008). Site, tide, and year were fitted as fixed effect factors, while dissolved oxygen (ppm), Julian date, temperature (°C), and salinity (ppt) were fitted as smooth terms with thin plate regression splines as the basis and k the dimension of the basis using the “gam” function in the “mgcv” package in R 3.5.2 (R 2008) for each species and water body combination (Drexler and Ainsworth 2013; Mathews et al. 2022). The estimation method applied was restricted maximum likelihood (REML). The parameters chosen for inclusion in the species-specific models were included in the models of abundance to standardize haul specific catches of these species according to variables that have the potential to affect species presence at an individual seine haul. The “predict” function in the “car” package of R 3.5.2 (R 2008) was used to generate estimates of annual mean catch using the tow-specific standardized models of catch to provide an annual mean index of abundance. Deviance explained and model dispersion were calculated to examine model performance. A likelihood ratio test was used to compare models with a null model (a model of annual mean catches with no dependent variables) for each index to determine if models were statistically significant. For all of the candidate GAMs, the best model was determined with an information-theoretic approach using the Akaike information criterion (AIC) score (Burnham and Anderson 2002; Bucheister et al. 2016). The annual mean standardized indices of abundance (NBGAM) for each species and bay were then fit with autoregressive integrated moving average (ARIMA) models using an iterative approach of 1,000 bootstrapped runs to estimate a median ARIMA fit for each index using the “surveyfit” and “surveyref” functions in the “fishmethods” package of R 3.5.2 (R 2008). The ARIMA models were used to estimate the probability that the terminal year (2019) was greater than the first quartile of the time series as well as the survey start year (2011) using a statistical level of confidence of $\beta=0.80$ with a Holm-adjusted probability of rejecting the null hypothesis regarding normality of model residuals (Box and Jenkins 1976; Helser and Hayes 1995; ASMFC 2017; Mathews et al. 2022). We used a Mann–Kendall trend test to analyze monotonic trends in the median ARIMA indices using the “mk.test” function in the “trend” package of R 3.5.2 (R 2008), after correcting for family-wise error rates in the statistical p values using the Holm method. The null hypothesis for this test was simply an extension of the Mann–Kendall trend test in that no monotonic trend existed in the time series and was verified by comparing initial p values vs. corrected p values allowing for an examination of statistically significant trends through time.

Percent Change Calculations

Annual percent changes for each species were calculated using the mean abundance values derived from the NBGAMs. The percent change between consecutive years was calculated for each species each year for each bay and for all bays combined. From this, the mean percent increase (average of years with percent increases) and the mean percent decrease (average of years with percent decreases) was calculated. Additionally, the maximum percent increase and decrease between consecutive years was noted for each species for each bay and for all bays combined.

Climatic and Biotic Variables

River Discharge

River discharge is taken at one location within the Delaware Inland Bays, the Millsboro Pond outfall. Data is taken every fifteen minutes, and daily data were downloaded beginning March 1st, 2011, through August 31st, 2020, from the US Geological Survey (https://waterdata.usgs.gov/de/nwis/uv/?site_no=01484525). Data were split into two time periods, spring discharge (March, April, May of each year), and summer discharge (June, July, August) of each year. Seasonal averages (average of all measurements taken during the three month period) were calculated for each year for spring and separately summer discharge. The decision was made to split discharge into spring and summer time periods because it was hypothesized that spring discharge would be substantially different than discharge typically observed during summer months and that grouping these two time periods together would mask potentially important time of year differences. An exploratory t test revealed that spring discharge was indeed different than summer discharge, with a mean spring discharge of 119.1 ± 41.56 ft³/s and a mean summer discharge of 64.8 ± 46.76 ft³/s ($t=3.0067$, $df=21.7$, $p=0.006$).

Atlantic Multidecadal Oscillation

The AMO represents the sea surface temperature anomaly from 0° to 60° N linearly detrended to account for anthropogenic climate change (Enfield et al. 2001; Nye et al. 2014). Monthly unsmoothed AMO index data were downloaded from the National Oceanic and Atmospheric Administration Physical Sciences Laboratory (<https://psl.noaa.gov/data/>

[timeseries/AMO/](#)). Yearly averages were calculated for 2011 through 2020.

Winter Temperatures

No widespread continuous water temperature monitoring data exist for the study area; therefore, air temperature data were used to approximate winter severity. Weather data from the Delaware Environmental Observation System were used to develop three indices of winter severity (DEOS, <http://www.deos.udel.edu/>). The weather station closest to the majority of sites in each bay was used for the entire bay. Indian River Life Saving Station data were used for both Rehoboth Bay and Indian River Bay, while the Bethany Beach Boardwalk Station data were used for Little Assawoman Bay. For comparisons at the combined estuary scale (all bays combined), data were used from Indian River Life Saving Station as they represented the largest number of sites.

Daily mean air temperatures were acquired from DEOS data for both stations. Reliable estimates of low temperature lethal limits for the four-target species were not found; therefore, we chose to use the air temperature at which, if water temperature matched, the water would freeze. An exploratory analysis revealed that the average salinity of all seine samples was 22.86 ppt ($n = 1,823$). Given this average salinity, the expected freezing point of the estuarine water at our sites would be on average -1.28 °C. The number of days when mean temperatures did not exceed -1.28 °C (single day freeze), the number of times when mean temperatures did not exceed -1.28 °C for at least 2 consecutive days (multiple day freeze), and the total number of days corresponding to multiple day freezes (cumulative number of multiple freeze days) were calculated for each bay, for each year. Data from November of the previous year through October of the survey year were used to tabulate the three, freeze metrics for each year.

Influence of Climatic Variables

Permutational multivariate analyses of variance (PERMANOVA; Anderson 2001) was used to investigate relationships between median ARIMA-fit species indices and spring and summer discharge, AMO, and winter severity indices to explore relationships among larger scale climatic phenomena. The PERMANOVA was carried out using the “adonis” function in the “vegan” package in R 3.5.2 (R 2008) with 9,999 permutations.

Predator Indices

Annually the Delaware Department of Natural Resources and Environmental Control (DNREC) operates a monthly

trawl survey from April through October at twelve sites in Indian River Bay and Rehoboth Bay for the purposes of determining juvenile indices of abundance for numerous state and federally managed fish species. The net used is a 4.9-m semi-balloon otter trawl with a 5.2-m headrope and a 6.4-m footrope, with a 3.8-cm stretch mesh number 9 thread body. A 1.3-cm knotless stretch mesh liner was inserted on the cod end. Six evenly spaced floats were located on the headrope and 0.3-cm chain was hung loop style on the footrope. Sampling consisted of a 10-min trawl tow typically made against the prevailing tide. In instances when gear failure or unexpected events prevented a 10-min tow, data was preserved if the tow was at least 5 min long. All catches were standardized to 10 min. All finfish were sorted, identified to species, and enumerated, and surface temperature (°C), salinity (ppt), dissolved oxygen (ppm), and tidal stage were recorded at the beginning of each tow. Annual catch indices for Bluefish, Summer Flounder, Striped Bass, and Weakfish (*Cynoscion regalis*) were evaluated using the same methods as previously described for the four nearshore forage species. Site, tide, and year were fitted as fixed effect factors, while dissolved oxygen (ppm), month (as samples were collected monthly in this survey), temperature (°C), and salinity (ppt) were fitted as smooth terms with thin plate regression splines as the basis and k the dimension of the basis using the “gam” function in the “mgcv” package in R 3.5.2 (R 2008) for each species. And similar to the forage fish indices, annual mean indices of abundance were predicted using the “predict” function in the “car” package of R 3.5.2 (R 2008) after being selected using an AIC approach. However, since several of the sites in the DNREC survey were located between both Indian River Bay and Rehoboth Bay, area-specific indices were not developed. Instead, an annual estimate of predator abundance for Indian River Bay and Rehoboth Bay combined was developed. Correlations using a Holm-adjusted probability were performed to assess the strength and direction of the linear association between annual estimates of predator abundance for Indian River Bay and Rehoboth Bay combined and the species and area-specific forage fish indices within Indian River Bay and Rehoboth Bay. An alpha value (α) of 0.05 was used for all statistical comparisons. Since size of the predatory specimen may influence the diet of that fish, size information (fork length (FL) \pm standard deviation, along with sample size) for the predator species used in this analysis are also reported.

Results

Raw Species Abundances and Proportion of Catch

Raw catch numbers for each target species for each survey year, along with the proportion of total catch from the entire

seine survey each species accounted for, are presented in Table 1. Atlantic Silverside, Mummichog, and Striped Killifish each individually accounted for at least 10% of the total survey catch for a given year. Atlantic Silverside were notably more abundant than the other four target species, accounting for over 50% of the total survey catch in 2 separate years, while Sheepshead Minnow were less prevalent than the other target species, never accounting for more than 7.73% of the total catch. Together, all four species combined accounted for over 74% of the total catch in 8 of the 9 survey years, highlighting these species' contribution to the nearshore fish biomass.

For predator species, insufficient numbers of Striped Bass were caught by the DNREC trawl survey, and therefore, this species was dropped from further analyses. There were 5,039 Weakfish caught by the DNREC trawl survey, and they were 92.49 mm FL ± 43.59. There were 216 Bluefish caught by the DNREC trawl survey, and they were 129.21 mm FL ± 51.53. Lastly, there were 586 Summer Flounder caught by the DNREC trawl survey, and they were 157.06 mm FL ± 91.95.

Model Fit

All species (target and predators) and survey combination NBGAMs were highly significant ($p < 0.001$) when compared to the corresponding raw data in the likelihood ratio tests. The deviance explained for the species and survey NBGAMs ranged from 25.0 to 74.7% depending on the model, with all dispersion values < 1.84 (Table 2) indicating good model fit across all standardized indices. For target nearshore forage species, site and year were selected as model parameters in all final model configurations, while tide was present in all but one model, Striped Killifish in

Little Assawoman Bay. Similarly, Julian date was selected for in all models as a covariate except for Striped Killifish in Indian River Bay. Other smoothed model parameters were not as consistently selected for in target species and waterbody-specific NBGAMs including dissolved oxygen (10 models), temperature (11 models), and salinity (5 models; Table 2). For predator species, site, year, month, and water temperature were selected for as model covariates in all three models, with salinity and dissolved oxygen also selected in one model each (Table 2).

Indices of Abundance and Trends

All four species showed high levels of interannual variability in the NBGAMs annual mean fits, with primary or secondary peaks in abundance towards the middle or end of the time series (Figs. 2–3). All four species also had large confidence intervals surrounding multiple survey years (Figs. 2–3).

No consistent trend in Atlantic Silverside abundance was present for any water body (all bays combined, Indian River Bay, Little Assawoman Bay, Rehoboth Bay) from 2011 to 2019 (Tables 3–4). There was a low probability of the ARIMA fit Atlantic Silverside abundance in 2019 being lower than the first quartile and less than the survey start year in all respective bay models, further indicating no negative trend in abundance over time (Table 3; Figs. 4, 5, 6, 7).

Mummichog were found to have detectable negative trends in abundance in all bays combined and in Little Assawoman Bay (Table 4). The terminal year value from the median fit ARIMA for Mummichog in all bays combined, as well as in Little Assawoman Bay had a high probability of being less than the survey start year value, and for all bays combined also had a high probability of being less than the first quartile further supporting the negative ARIMA

Table 1 Raw catch numbers for each target species, all target species combined, and all other species encountered during survey for each year. The proportion each species accounted for each year is listed in parenthesis below the raw catch number for that species

Species	2011	2012	2013	2014	2015	2016	2017	2018	2019
Atlantic Silverside	22,805 (45.10)	5,303 (11.54)	9,560 (35.71)	17,266 (41.25)	29,829 (50.35)	18,287 (33.63)	35,609 (59.40)	25,221 (46.19)	11,068 (34.30)
Mummichog	13,115 (25.94)	17,239 (37.51)	9,117 (34.05)	8,194 (19.58)	18,418 (31.09)	12,617 (23.20)	4,762 (7.94)	13,213 (24.20)	8,193 (25.39)
Sheepshead Minnow	747 (1.48)	2,306 (5.02)	596 (2.23)	3,234 (7.73)	1,018 (1.72)	808 (1.49)	1,452 (2.42)	2,257 (4.13)	76 (0.24)
Striped Killifish	9,588 (18.96)	9,193 (20.00)	2,540 (9.49)	5,469 (13.07)	6,554 (11.06)	10,778 (19.82)	7,444 (12.42)	6,489 (11.88)	1,927 (5.97)
All target species combined	46,255 (91.49)	34,041 (74.07)	21,813 (81.48)	34,163 (81.63)	55,819 (94.22)	42,490 (78.14)	49,267 (82.18)	47,180 (86.40)	21,264 (65.91)
All other fish species	4,305 (8.51)	11,915 (25.93)	4,959 (18.52)	7,690 (18.37)	3,422 (5.78)	11,887 (21.86)	10,685 (17.82)	7,425 (13.60)	11,000 (34.09)

Table 2 Standardized model (NBGAM) of abundance, deviance explained, total number of available tows (*n*), and dispersion for each survey and species. *IR* Indian River Bay, *LAB* Little Assawoman Bay, *RB* Rehoboth Bay

Model	Species	Water Body	Deviance explained (%)	<i>n</i>	Dispersion
Atlantic Silverside ~ factor(Site) + factor(Tide) + factor(Year) + s(D.O.) + s(jd) + s(Temp.)	Atlantic Silverside	All Bays	25	1742	1.31
Mummichog ~ factor(Site) + factor(Tide) + factor(Year) + + s(D.O.) + s(jd) + s(Temp.)	Mummichog	All Bays	47.4	1742	1.84
Sheepshead Minnow ~ factor(Site) + factor(Tide) + factor(Year) + s(D.O.) + s(jd)	Sheepshead Minnow	All Bays	62.7	1742	1.14
Striped Killifish ~ factor(Site) + factor(Tide) + factor(Year) + s(jd) + s(Temp.)	Striped Killifish	All Bays	42	1742	1.27
Atlantic Silverside ~ factor(Site) + factor(Tide) + factor(Year) + s(jd) + s(Temp.)	Atlantic Silverside	Little Assawoman Bay	39.8	530	1.46
Mummichog ~ factor(Site) + factor(Tide) + factor(Year) + s(D.O.) + s(jd) + s(Temp.)	Mummichog	Little Assawoman Bay	50.7	530	1.35
Sheepshead Minnow ~ factor(Site) + factor(Tide) + factor(Year) + s(jd)	Sheepshead Minnow	Little Assawoman Bay	66.2	530	0.84
Striped Killifish ~ factor(Site) + factor(Year) + s(jd) + s(Sal.)	Striped Killifish	Little Assawoman Bay	31.1	530	1.07
Atlantic Silverside ~ factor(Site) + factor(Tide) + factor(Year) + s(D.O.) + s(jd) + s(Sal.) + s(Temp.)	Atlantic Silverside	Indian River Bay	29.7	768	1.11
Mummichog ~ factor(Year) + factor(Site) + factor(Tide) + s(Temp.) + s(Sal.) + s(D.O.) + s(jd)	Mummichog	Indian River Bay	48.7	768	1.45
Sheepshead Minnow ~ factor(Site) + factor(Tide) + factor(Year) + s(D.O.) + s(jd) + s(Temp.)	Sheepshead Minnow	Indian River Bay	58.7	768	0.95
Striped Killifish ~ factor(Site) + factor(Tide) + factor(Year) + s(Temp.)	Striped Killifish	Indian River Bay	28.4	768	1.07
Atlantic Silverside ~ factor(Site) + factor(Tide) + factor(Year) + s(D.O.) + s(jd) + s(Temp)	Atlantic Silverside	Rehoboth Bay	25.1	444	1.07
Mummichog ~ factor(Site) + factor(Tide) + factor(Year) + + s(D.O.) + s(jd) + s(Temp.)	Mummichog	Rehoboth Bay	59.8	444	1.11
Sheepshead Minnow ~ factor(Site) + factor(Tide) + factor(Year) + s(jd)	Sheepshead Minnow	Rehoboth Bay	74.7	444	0.94
Striped Killifish ~ factor(Site) + factor(Tide) + factor(Year) + s(D.O.) + s(jd) + s(Temp.)	Striped Killifish	Rehoboth Bay	59.5	444	1.04
Bluefish ~ factor(Month) + factor(Site) + factor(Year) + s(TempC)	Bluefish	Rehoboth & Indian River Bays	47.9	661	0.39
Summer Flounder ~ factor(Month) + factor(Site) + factor(Year) + s(Salppt) + s(TempC)	Summer Flounder	Rehoboth & Indian River Bays	37.5	661	0.70
Weakfish ~ factor(Month) + factor(Site) + factor(Year) + s(DOppm) + s(TempC)	Weakfish	Rehoboth & Indian River Bays	69.0	661	0.92

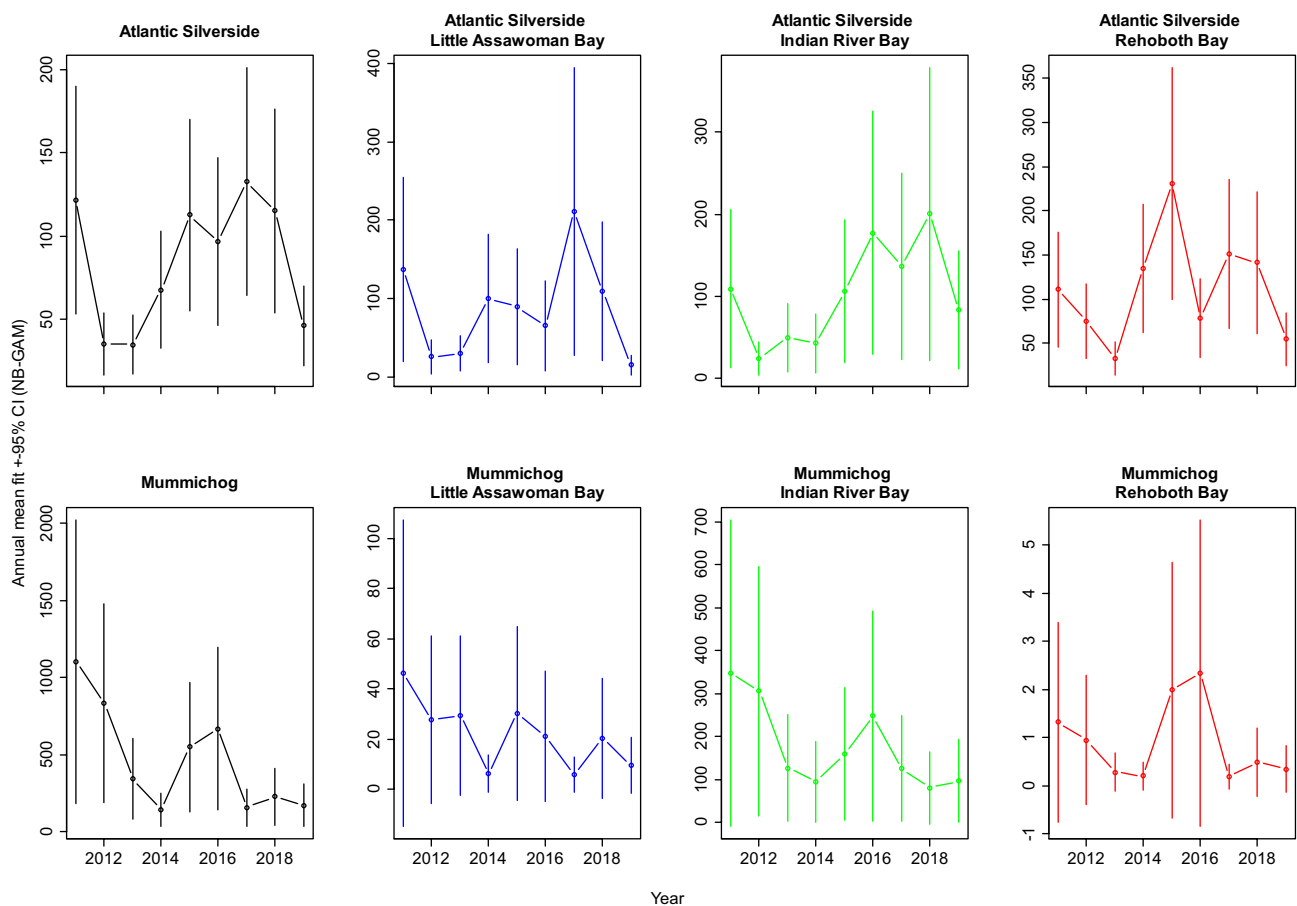


Fig. 2 Annual mean fit with a negative binomial, general additive model for each survey and waterbody for Atlantic Silverside and Mummichog combined with vertical bars representing the 95% confidence intervals for each year

trend (Table 3). Unfortunately, residuals were not normally distributed for the Indian River Bay Mummichog ARIMA indicating that the data representing the population is not normally distributed and results inferred from those analyses should be ignored or used with caution. While the trend does appear downward for Mummichog in Rehoboth Bay based on the plotted median ARIMA fit (Fig. 7), the scale of difference between the initial start year and the terminal year is minimal. Furthermore, the Mann–Kendall trend test did not indicate a trend in relative abundance occurred, and the corresponding probabilities that the terminal year was less than the first quartile or the survey start year were low, indicating no trend in abundance is present.

While the 2019 median fit ARIMA Striped Killifish index value for Indian River and for all bays combined had medium probabilities of being less than the first quartile and the survey start year, no significant trends in Striped Killifish abundance were found in any water body examined (Tables 3–4, Figs. 4–7). Unfortunately, residuals were not normally distributed for the Little Assawoman Bay median fit Striped Killifish ARIMA indicating that the data representing the population

is not normally distributed and results inferred from those analyses should be ignored or used with caution similar to the Mummichog ARIMA model in Indian River Bay.

Despite relatively low probabilities of the terminal ARIMA index year being less than the 25% or the survey start year, negative trends in Sheepshead Minnow abundance were detected for three of the four water bodies analyzed (Tables 3–4, Figs. 4–6). While the plotted ARIMA trend does visually appear downward for Sheepshead Minnow in Rehoboth Bay (Fig. 7), the scale of difference between the initial start year and the terminal year is half that of the other significant trends observed, and the Mann–Kendall trend test did not indicate a significant trend in relative abundance occurred.

For predatory species, combining both Indian River and Rehoboth Bays, no detectable trends in Bluefish abundance occurred, a significant increase in Summer Flounder was observed, and a significant decrease in Weakfish was observed (Table 5). Unfortunately, Striped Bass were caught too infrequently to generate meaningful models of abundance and were dropped from further analyses. The

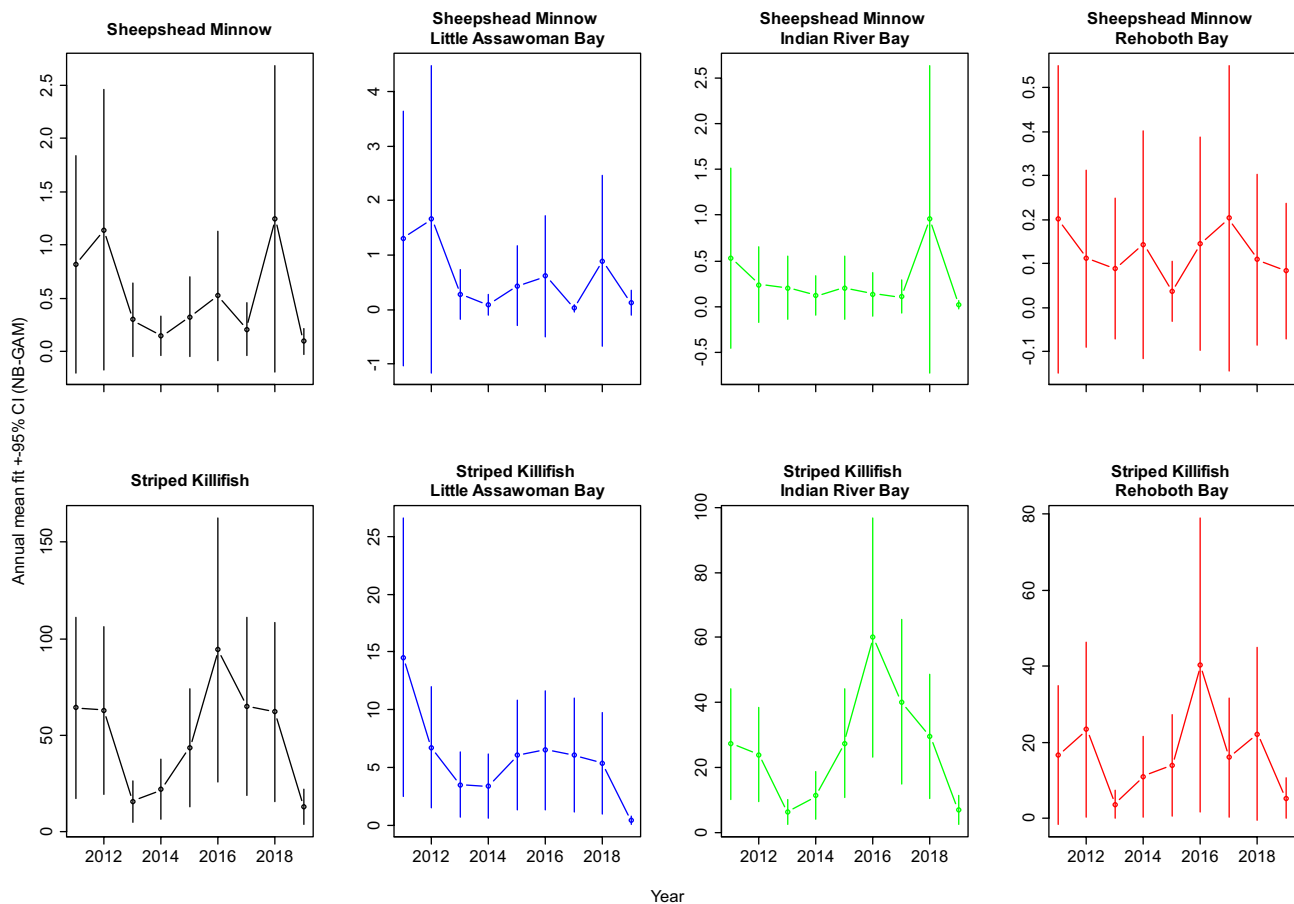


Fig. 3 Annual mean fit with a negative binomial, general additive model for each survey and waterbody for Sheepshead Minnow and Striped Killifish combined with vertical bars representing the 95% confidence intervals for each year

NBGAM for each species displayed large interannual variability (Fig. 8), but the ARIMA fits for Summer Flounder and Weakfish demonstrated significant changes in abundance have occurred for these species through time as evidenced by the Mann–Kendall trend tests (Table 5) and median fit ARIMA (Fig. 9).

Percent Change

All four target nearshore forage species showed dramatic interannual percent changes in NBGM abundance values (Table 6), and, in general, changes were greater at the individual bay scale vs. the combined estuary scale. At the combined estuary scale (all bays combined), mean interannual decreases of the four species ranged from 31.92 to 69.23%, while at the individual bay scale, the mean interannual decreases of the four species ranged from 35.98 to 83.04%. Mean interannual increases of the four species between consecutive years ranged from 65.90 to 178.61% at the combined estuary scale and 43.25 to 903.20% at the individual bay scale. Each species had a maximum decrease

between consecutive years over 50%, with most having maximum decreases of > 70%, while maximum increases between consecutive years were at least 67.05% but were frequently much > 100% between consecutive years. Of the four species, in general, Sheepshead Minnow displayed the most dramatic percent changes, though each species demonstrated considerable variability between years.

Influence of Climatic and Biotic Variables

The resulting values for each climatic variable are displayed in Table 7. Increased spring discharge negatively affected both Mummichog and Sheepshead Minnow abundance in multiple bays (Table 8). Mummichog abundance was negatively affected by increased spring discharge for Indian River ($F = 17.58$, $r^2 = 0.715$, $p = 0.004$), Little Assawoman Bay ($F = 8.6$, $r^2 = 0.551$, $p = 0.02$), and all bays combined ($F = 13.8$, $r^2 = 0.664$, $p = 0.008$). Sheepshead Minnow abundance was negatively affected by increased spring discharge in Indian River ($F = 8.15$, $r^2 = 0.538$, $p = 0.026$), Rehoboth Bay ($F = 6.79$, $r^2 = 0.499$,

Table 3 Summary statistics for median ARIMA results. *IR* Indian River Bay, *LAB* Little Assawoman Bay, *RB* Rehoboth Bay, *IR & RB* Indian River Bay and Rehoboth Bay combined. *W* Shapiro-Wilk statistic for normality; *p* Holm-adjusted probability of rejecting the null hypothesis regarding normality of model residuals; *N* number of years in time series; *r1*, *r2*, and *r3* the first three sample autocorrela-

tions for the first differenced logged series; θ moving average parameter; *SE* standard error of theta; σ^2c variance of index; *P* (*compyear < 25th pctl*) probability that the terminal index value was less than the first quartile for the time series; *P* (*2019 < start year*) probability that the terminal index value was less than the start year. *ARIMA fits with non-normally distributed residuals

Species	Waterbody	<i>W</i>	<i>p</i>	<i>n</i>	<i>r1</i>	<i>r2</i>	<i>r3</i>	θ	<i>SE</i>	σ^2c	<i>P</i> (comp year < 25th pctl)	<i>P</i> (2019 < start year)	Start year
Atlantic Silverside	All Bays	0.924	0.423	9	0.14	-0.29	-0.11	0.68	0.37	0.32	0.01	0.12	2011
Atlantic Silverside	LAB	0.948	0.667	9	0.03	-0.45	0.20	1.00	0.38	0.77	0.10	0.05	2011
Atlantic Silverside	IR	0.929	0.468	9	-0.28	0.21	-0.21	0.44	0.42	0.51	0.05	0.02	2011
Atlantic Silverside	RB	0.980	0.962	9	-0.23	-0.47	0.46	1.00	0.42	0.35	0.06	0.01	2011
Mummichog	All Bays	0.944	0.625	9	-0.22	-0.54	0.25	0.47	0.44	0.66	0.43	0.94	2011
Mummichog	LAB	0.917	0.370	9	-0.61	-0.05	0.40	0.70	0.30	0.65	0.25	0.89	2011
*Mummichog	IR	0.809	0.026	9	0.07	-0.69	-0.18	0.66	0.33	0.19	0.80	1.00	2011
Mummichog	RB	0.901	0.255	9	-0.20	-0.54	0.17	1.00	0.44	0.91	0.16	0.14	2011
Sheepshead Minnow	All Bays	0.962	0.815	9	-0.48	0.04	0.04	1.00	0.84	0.76	0.19	0.01	2011
Sheepshead Minnow	LAB	0.948	0.670	9	-0.58	-0.06	0.25	0.78	0.39	1.89	0.23	0.21	2011
Sheepshead Minnow	IR	0.881	0.162	9	-0.46	0.00	0.11	1.00	0.64	0.92	0.23	0.85	2011
Sheepshead Minnow	RB	0.973	0.916	9	-0.42	-0.15	0.24	1.00	0.37	0.22	0.19	0.83	2011
Striped Killifish	All Bays	0.884	0.173	9	0.01	-0.04	-0.42	0.03	0.44	0.72	0.54	0.64	2011
*Striped Killifish	LAB	0.768	0.009	9	0.09	-0.06	-0.16	1.00	1.03	0.67	0.14	0.32	2011
Striped Killifish	IR	0.914	0.348	9	0.15	-0.10	-0.46	0.20	0.36	0.72	0.37	0.41	2011
Striped Killifish	RB	0.903	0.273	9	-0.45	0.31	-0.48	1.00	0.37	0.54	0.11	0.00	2011
Bluefish	IR & RB	0.89134	0.2059	9	0.19	-0.25	-0.32	0.71	0.39	0.07	0.364	0.47	2011
Summer Flounder	IR & RB	0.95189	0.7109	9	-0.58	-0.14	0.46	0.64	0.28	0.28	0.01	0	2011
Weakfish	IR & RB	0.92217	0.4105	9	-0.1	-0.15	-0.13	0.69	0.47	0.29	0.222	0.584	2011

Table 4 Summary statistics for the Mann–Kendall trend tests of median fitted ARIMAs for each target nearshore forage species index. *IR* Indian River Bay, *LAB* Little Assawoman Bay, *RB* Rehoboth Bay. *Z* Mann Kendall Z score, *n* number of years in time series, *S* Ken-

dall score, σ^2 variance of Kendall score, τ Kendall’s tau statistic, *Rank* original *p* value rank, *Initial p* initial *p* value, *H-B p* the Holm-adjusted *p* value, *Trend* trend result (increase, decrease, or n.s.=not significant at the 0.05 alpha value) with significant trends bolded

Species	Waterbody	<i>Z</i>	<i>n</i>	<i>S</i>	σ^2	τ	Rank	Initial <i>p</i> value	H-B <i>p</i> value	H-B correction test	Trend
Atlantic Silverside	All Bays	0.313	9	4	92	0.11	13	0.755	0.009	Accept H_0	n.s
Atlantic Silverside	IR	2.398	9	24	92	0.67	6	0.016	0.005	Accept H_0	n.s
Atlantic Silverside	LAB	0.313	9	4	92	0.11	13	0.755	0.009	Accept H_0	n.s
Atlantic Silverside	RB	0.521	9	6	92	0.17	11	0.602	0.008	Accept H_0	n.s
Mummichog	All Bays	-3.232	9	-32	92	-0.89	3	0.001	0.004	Reject H_0	Decrease
Mummichog	IR	-1.981	9	-20	92	-0.56	9	0.048	0.006	Accept H_0	n.s
Mummichog	LAB	-3.649	9	-36	92	-1.00	1	0.000	0.003	Reject H_0	Decrease
Mummichog	RB	-1.981	9	-20	92	-0.56	9	0.048	0.006	Accept H_0	n.s
Striped Killifish	All Bays	-0.313	9	-4	92	-0.11	13	0.755	0.009	Accept H_0	n.s
Striped Killifish	IR	0.000	9	0	92	0.00	16	1.000	0.025	Accept H_0	n.s
Striped Killifish	LAB	-1.147	9	-12	92	-0.33	10	0.252	0.006	Accept H_0	n.s
Striped Killifish	RB	-0.104	9	-2	92	-0.06	15	0.917	0.017	Accept H_0	n.s
Sheepshead Minnow	All Bays	-3.024	9	-30	92	-0.83	5	0.002	0.004	Reject H_0	Decrease
Sheepshead Minnow	IR	-3.232	9	-32	92	-0.89	3	0.001	0.004	Reject H_0	Decrease
Sheepshead Minnow	LAB	-3.441	9	-34	92	-0.94	3	0.001	0.004	Reject H_0	Decrease
Sheepshead Minnow	RB	-2.189	9	-22	92	-0.61	7	0.029	0.005	Accept H_0	n.s

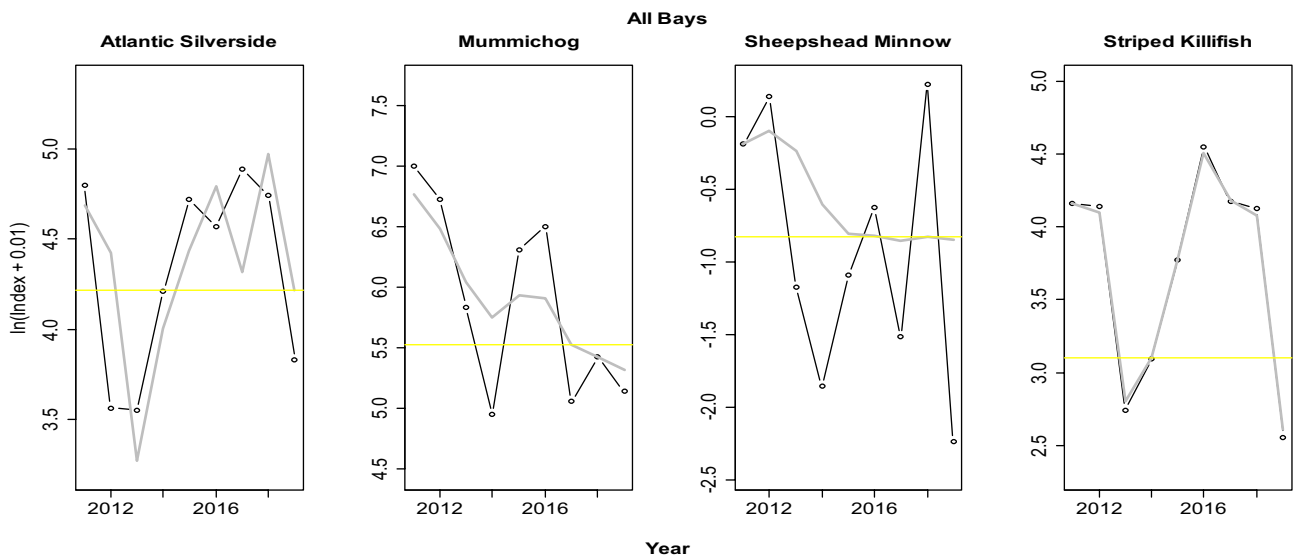


Fig. 4 ARIMA trends for each species for all bays combined (combined estuary scale). The black line is the NBGAM of relative abundance, while the gray line is the median fit ARIMA for each species, and the yellow line represents the first quartile for each survey

$p=0.035$), and Little Assawoman Bay ($F=8.76$, $r^2=0.556$, $p=0.026$). Mummichog abundance in Rehoboth Bay was also negatively affected by the number of multiple freeze days ($F=108$, $r^2=0.939$, $p=0.02$). No other significant

relationships existed between any climatic variable and species-bay combination.

There were five notable correlations between target nearshore forage species abundance and predator abundances

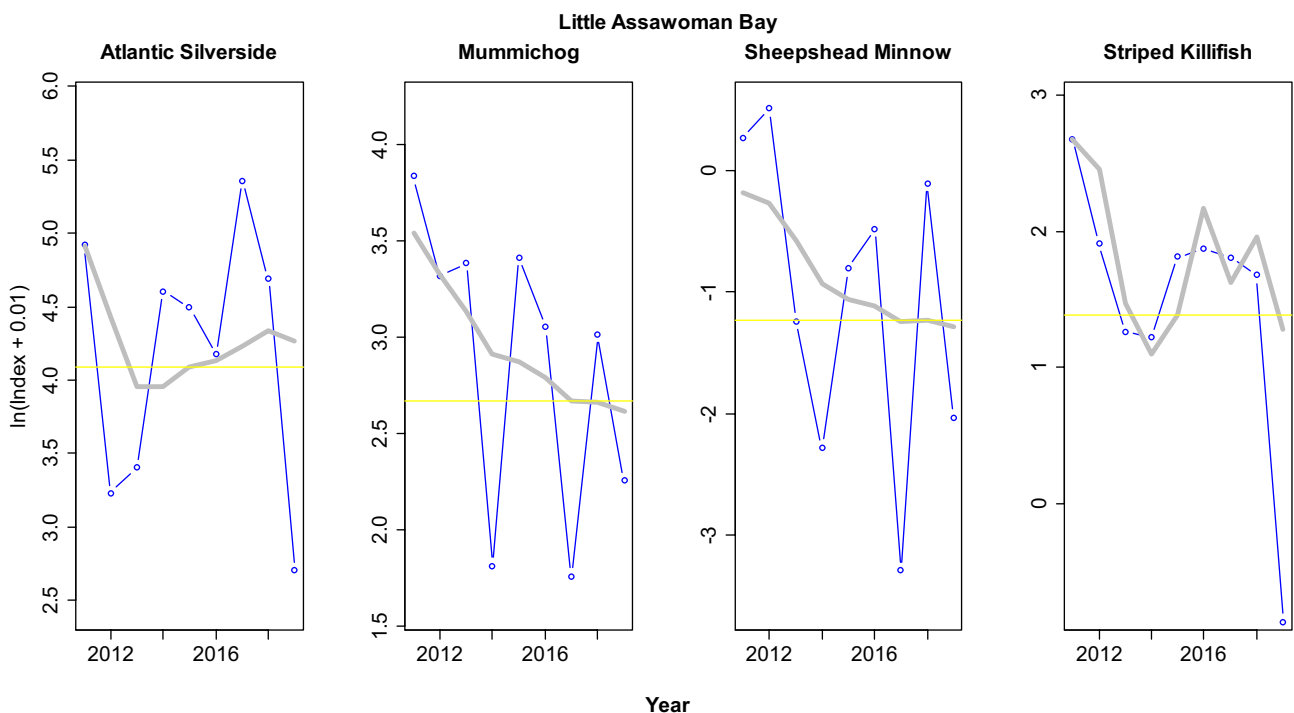


Fig. 5 ARIMA trends for each species for Little Assawoman Bay. The blue line is the NBGAM of relative abundance, while the gray line is the median fit ARIMA for each species, and the yellow line represents the first quartile for each survey

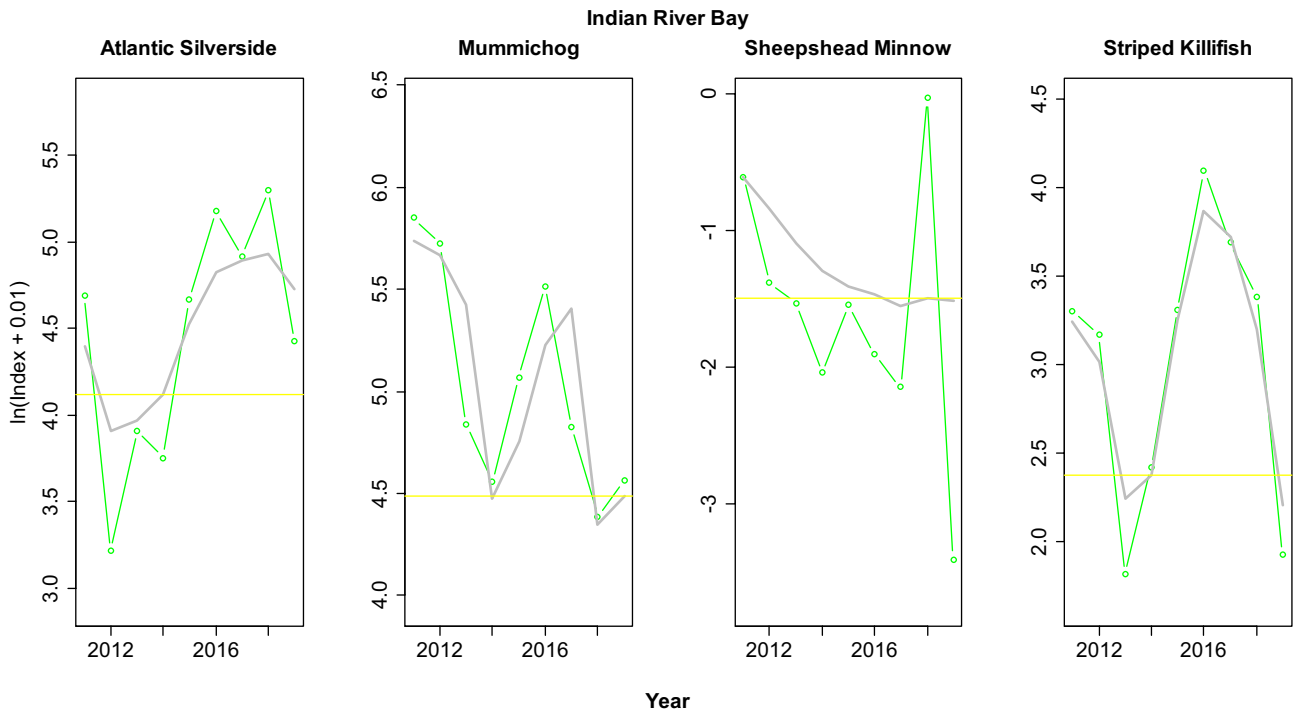


Fig. 6 ARIMA trends for each species for Indian River Bay. The green line is the NBGAM of relative abundance, while the gray line is the median fit ARIMA for each species, and the yellow line represents the first quartile for each survey

(Table 9). Atlantic Silverside abundance in Indian River Bay was negatively correlated with Weakfish abundance in Indian River and Rehoboth Bays combined ($\rho = -0.90$, $p = 0.05$). Sheepshead Minnow abundance in Indian River

and Rehoboth Bay was negatively correlated with Summer Flounder abundance in Indian River and Rehoboth Bays combined ($\rho = -0.96$, $p < 0.001$, $\rho = -0.91$, $p = 0.04$, respectively). Sheepshead Minnow abundance in Indian River Bay was also

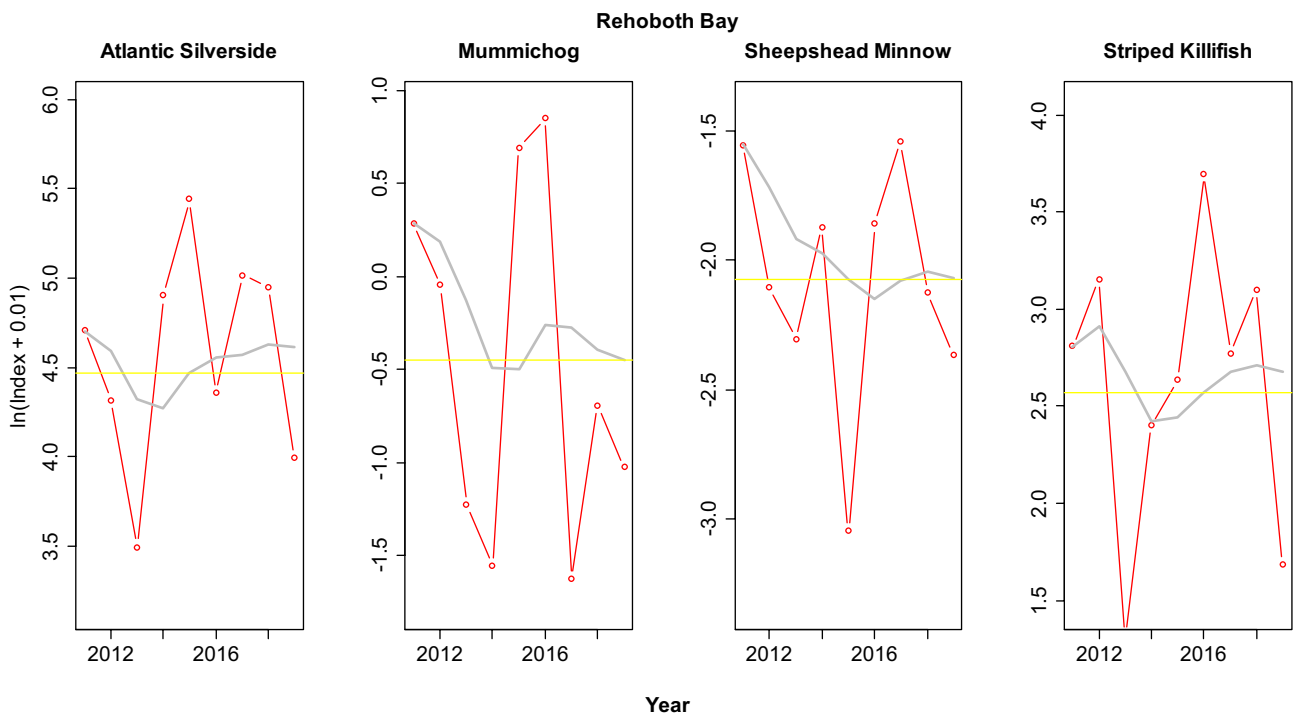


Fig. 7 ARIMA trends for each species for Rehoboth Bay. The red line is the NBGAM of relative abundance, while the gray line is the median fit ARIMA for each species, and the yellow line represents the first quartile for each survey

Table 5 Summary statistics for the Mann–Kendall trend tests of median fitted ARIMAs for each index of predator abundance derived from the DNREC survey. *Z* Mann Kendall Z score, *n* number of years in time series, *S* Kendall score, σ^2 variance of Kendall score,

τ Kendall's tau statistic, *Rank* original *p* value rank, *Initial p* initial *p* value, *H-B p* the Holm-adjusted *p* value, *Trend* trend result (increase, decrease, or n.s. = not significant at the 0.05 alpha value) with significant trends bolded

Species	Waterbody	<i>Z</i>	<i>n</i>	<i>S</i>	σ^2	τ	Rank	Initial <i>p</i> value	H-B <i>p</i> value	H-B correction test	Trend
Bluefish	IR & RB	−1.355	9	−14	92	−0.39	3	0.175	0.004	Accept H_0	n.s
Summer Flounder	IR & RB	3.649	9	36	92	1.00	1	0.000	0.003	Reject H_0	Increase
Weakfish	IR & RB	−2.815	9	−28	92	−0.78	2	0.005	0.003	Reject H_0	Decrease

positively correlated with Weakfish abundance in Indian River and Rehoboth Bays combined ($\rho = 0.91$, $p = 0.04$). Lastly, Summer Flounder abundance in Indian River and Rehoboth Bays combined was negatively correlated to Weakfish abundance in both bays ($\rho = -0.92$, $p = 0.03$).

Discussion

Raw Abundances, Proportion of Catch, and Percent Changes

Two important conclusions can be drawn from the raw abundance and proportion data. The first is that it is clear

that the majority of nearshore fish abundance is driven largely by the four-target species. While each species is not equal in its contribution, for instance, Atlantic Silver-sides accounted for a higher proportion than Sheepshead Minnow, each was still a major contributor to the overall catch of the survey and therefore of critical importance when assessing nearshore forage fish dynamics. The second conclusion is that although declines of our target species may be partially offset by increases in non-target species, non-target species never fully offset these declines. For example, from 2011 to 2012, our target species raw catch numbers declined by 12,214 fish (apparent in the ARIMA plots as well), while non-target species increased

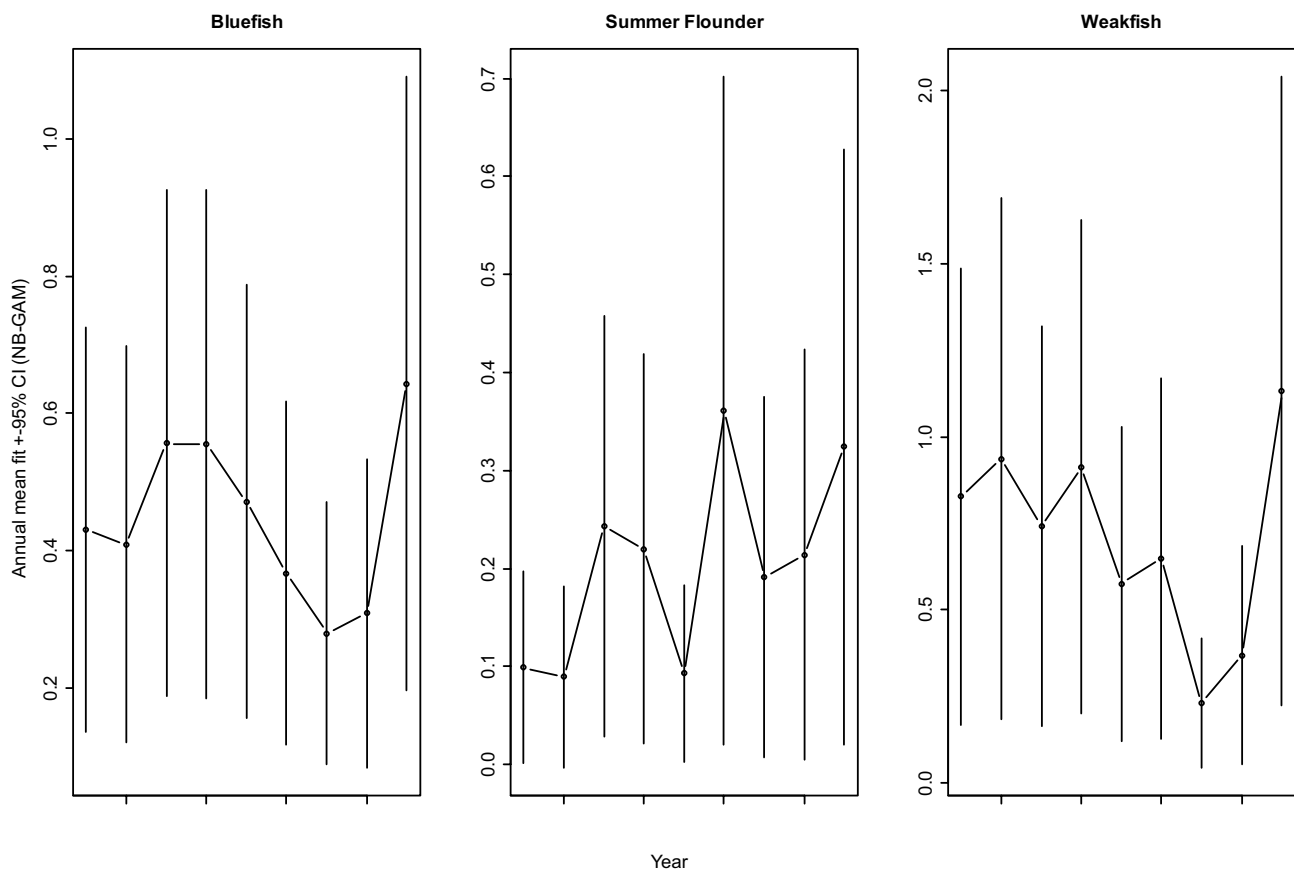


Fig. 8 Annual mean fit with a negative binomial, general additive model for three indices of abundance from the DNREC survey from Indian River and Rehoboth Bay combined with vertical bars representing the 95% confidence intervals for each year

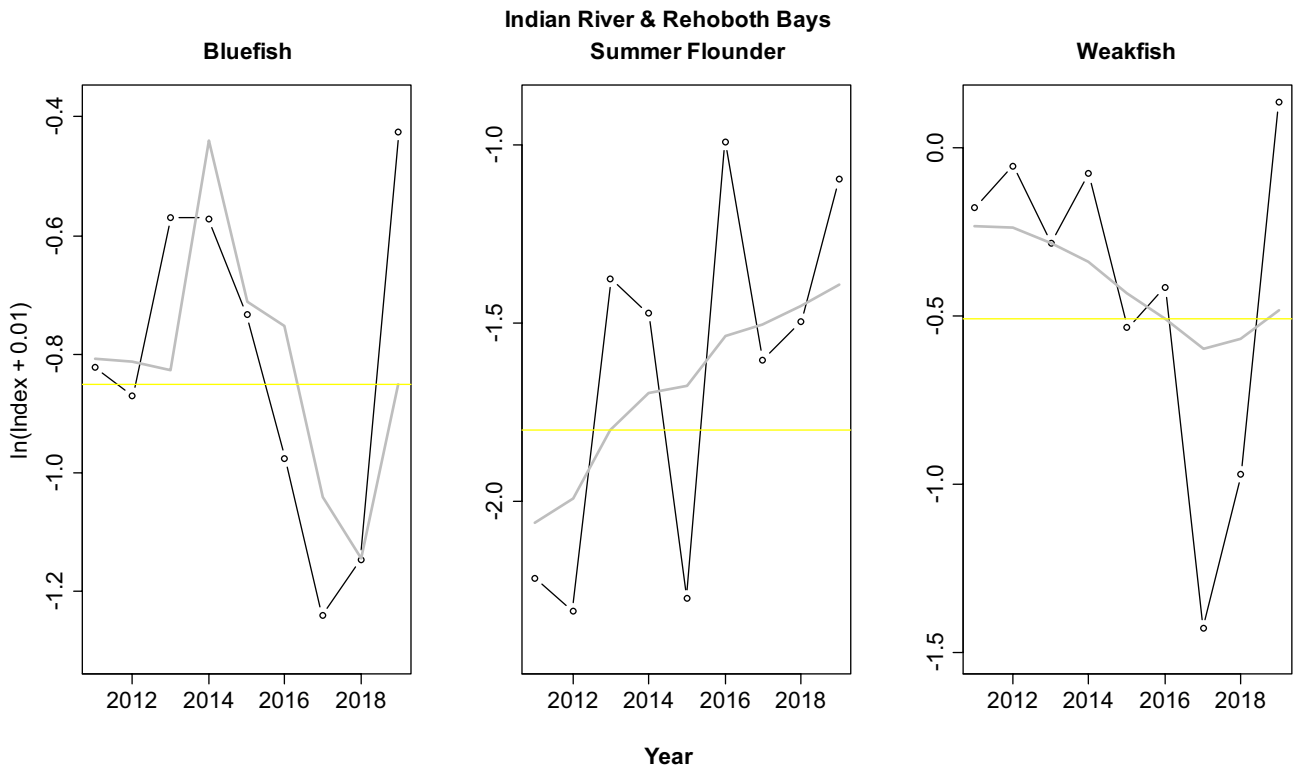


Fig. 9 ARIMA trends for each predatory species for Indian River and Rehoboth Bays combined. The black line is the NBGM of relative abundance, while the grey line is the median fit ARIMA for each spe-

cies, and the yellow line represents the first quartile for each species index of abundance

by 7,610 specimens, similar to 2018–2019 where target species declined by almost 26,000 specimens, whereas non-targets increased by only 3,575 specimens. These raw data illustrate that declines in the target species are unlikely to be offset by increases from other fish species within a single year and therefore likely represent a true loss of nearshore prey availability for predatory species.

The interannual fluctuations in individual species abundances between years at the combined estuary scale were large and even more pronounced at the individual bay scale. However, changes in abundance of these four species should also be examined together rather than separately. These species together typically account for > 80% of the nearshore fish abundance in the Inland Bays (Boutin and Targett

Table 6 Percent changes for each species for all bays combined (combined estuary scale) and for each bay. *IR* Indian River Bay, *LAB* Little Assawoman Bay, *RB* Rehoboth Bay

Species	Level	Mean decrease	Mean increase	Max % decrease	Max % increase
Atlantic Silverside	All Bays	31.92	65.90	70.98	93.82
Atlantic Silverside	IR	43.23	90.66	77.18	149.06
Atlantic Silverside	LAB	50.80	158.68	86.27	232.44
Atlantic Silverside	RB	44.46	157.52	66.07	308.56
Mummichog	All Bays	48.66	118.86	76.57	290.46
Mummichog	IR	36.13	47.56	58.69	67.05
Mummichog	LAB	55.16	218.14	79.29	395.49
Mummichog	RB	49.68	356.86	92.03	890.52
Sheepshead Minnow	All Bays	69.23	178.61	92.23	491.91
Sheepshead Minnow	IR	43.85	431.87	97.57	794.44
Sheepshead Minnow	LAB	83.04	903.20	95.55	3172.54
Sheepshead Minnow	RB	41.59	129.31	73.88	287.73
Striped Killifish	All Bays	38.46	85.38	79.23	116.35
Striped Killifish	IR	44.55	115.10	76.76	144.02
Striped Killifish	LAB	35.98	43.25	92.35	80.08
Striped Killifish	RB	73.40	98.21	84.03	195.45

Table 7 Yearly values with standard errors for the climatic variables. For the winter freeze data, values for the Indian River Life Saving Station are displayed as they represented the conditions at the largest number of seining locations

Year	Spring discharge (ft ³ /s)	Summer discharge (ft ³ /s)	AMO index	N single day freeze	N multiple day freeze	N cumulative multiple day freeze
2011	62.63 ± 1.92	19.66 ± 5.41	0.077 ± 0.022	20	7	19
2012	49.64 ± 2.13	21.43 ± 2.36	0.188 ± 0.05	4	1	2
2013	130.63 ± 7.43	188.16 ± 11.44	0.141 ± 0.024	9	2	8
2014	125.41 ± 4.28	56.23 ± 2.6	0.077 ± 0.046	27	6	20
2015	128.6 ± 5.36	45.48 ± 1.91	0.089 ± 0.042	24	4	16
2016	103.18 ± 2.3	53.21 ± 2.74	0.317 ± 0.032	12	2	9
2017	99.88 ± 4.3	82.65 ± 4.4	0.291 ± 0.02	7	2	5
2018	163.04 ± 15.8	113.22 ± 11.45	0.044 ± 0.026	18	1	13
2019	145.39 ± 6.53	55.11 ± 2.87	0.149 ± 0.03	7	2	6

2013; Balouskas and Targett 2016) and routinely > 74% in our study. Therefore, concurrent large-scale declines in a single year may represent a large loss of nearshore fish biomass, while conversely, strong increases in all four species in a single year may represent high prey availability to predator species. As an example, in 2012, all four species appear to have been abundant, while in 2019, three of the four species had notable declines in abundance compared to earlier years in the study. These types of fluctuations in target species abundance, especially with limited offsets from non-target species, may have large ramifications for energy transfer from the nearshore environment and warrant further investigation.

Species Trends

We observed significant declines in both Mummichog and Sheepshead Minnow abundance at both the combined estuary scale and the individual bay scale. Some of these declines were also supported by an increased probability that the terminal year of the survey would be less than the first quartile of the entire survey period and less than the survey start year. As described previously, interannual variability in the raw catch data, and even mean NBGAMS was considerable, with both showing primary or secondary peaks in abundance towards the middle or end of the time series. However, the use of a mean annual, generalized additive model controls for site-specific variability in each catch record or haul allowing for the inclusion of nonlinear relationships whereby site, tide, year, dissolved oxygen, day of year, and temperature is accounted for using a model of relative abundance (Hastie and Tibshirani 1986; Mateo and Hanselman 2014; Mathews et al. 2022). Further, the use of a median fit ARIMA model for each generalized additive model of relative abundance provides a quantitative method to control for variability in abundance, population level fluctuations, survey sampling variability, and variable

catchability (Pennington 1986; ASMFC 2017; Mathews et al. 2022), thereby providing a quantitative, mechanistic way to examine significant trends in relative abundance through time using a Mann–Kendall trend test (ASMFC 2017; Mathews et al. 2022). To our knowledge, our study represents the first documentation of this quantitative application to these species, as well as evidence of long-term trends in abundance at an estuary-wide scale. These results suggest that even ubiquitous and commonly encountered forage species can experience long-term declines in population abundance and further emphasize the need to begin examining other important but poorly studied forage taxa.

Both Mummichog and Sheepshead Minnow are considered salt marsh fish, and so these declines likely represent both a loss of two important nearshore prey species and also a potential loss of energy transfer from productive salt marsh habitats to the subtidal and offshore fisheries (Deegan et al. 2000; Able et al. 2007a). Saltmarsh fish convert marsh production and relatively low-quality food such as detritus into high quality biomass in a form that is readily useable by larger estuarine and offshore predators (Kneib 1986; Stevens et al. 2006). Because these species are important prey for predators that move between salt marshes, the greater estuary, and offshore areas, they represent an important pathway for energy transfer between these habitats (Able et al. 2007a). Therefore, long-term declines, of these species may have important ramifications for energy transfer across multiple habitats, particularly Mummichog which routinely accounted for almost a quarter of the nearshore fish abundance in this study.

While the declines observed in this study are reason for concern given these species potential energetic importance, the magnitude of the effect of their decline is unclear. Linkages between prey availability and Bluefish condition or Striped Bass recruitment (both major predators of Mummichog and Sheepshead Minnow) have been reported (Friedland et al. 1988; Martino and Houde 2010), which

Table 8 Summary statistics for the PERMANOVA tests for each species' ARIMA values and climatic factor for each bay and all bays combined. For the Waterbody column, *IR* Indian River Bay, *RB* Rehoboth Bay, *LAB* Little Assawoman Bay, *AB* all bays combined. *DF* degrees of freedom, *P* *p* value. *p* values less than 0.05 are in bold

Species	Atlantic Silverside				Mummichog				Striped Killifish				Sheepshead Minnow			
	IR	RB	LAB	AB	IR	RB	LAB	AB	IR	RB	LAB	AB	IR	RB	LAB	AB
Spring discharge	DF	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
	<i>F</i> statistic	1.44	0.794	3.2	0.188	17.58	-2.2	8.6	13.8	1.1	2.71	5.38	2.24	8.15	6.97	8.76
	<i>R</i> ²	0.17	0.102	0.314	0.02	0.715	-0.458	0.551	0.664	0.136	0.279	0.43	0.242	0.538	0.499	0.556
	<i>P</i>	0.262	0.412	0.114	0.693	0.004	0.73	0.02	0.008	0.328	0.144	0.053	0.172	0.026	0.035	0.026
Summer discharge	DF	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
	<i>F</i> statistic	0.034	1.85	2.58	4.77	0.077	1.44	0.365	0.895	1	0.031	0.843	1.38	0.473	0.663	0.237
	<i>R</i> ²	0.004	0.209	0.269	0.405	0.01	0.17	0.049	0.113	0.125	0.004	0.107	0.165	0.063	0.086	0.032
	<i>P</i>	0.885	0.211	0.153	0.089	0.817	0.283	0.595	0.368	0.366	0.873	0.409	0.284	0.525	0.433	0.668
AMO	DF	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
	<i>F</i> Statistic	0.451	0.124	0.182	0.012	1.84	-31.7	0.398	0.046	1.86	0.076	0.29	0.862	0.586	0.956	0.319
	<i>R</i> ²	0.06	0.017	0.025	0.001	0.208	1.28	0.053	0.006	0.21	0.01	0.039	0.105	0.077	0.12	0.043
	<i>P</i>	0.515	0.758	0.691	0.948	0.22	0.921	0.559	0.848	0.21	0.793	0.602	0.405	0.484	0.367	0.596
Single day freeze	DF	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
	<i>F</i> statistic	0.007	0.835	0.067	0.221	1.77	10.6	0.026	0.027	0.011	5.42	0.718	0.032	0.0009	0.0004	0.014
	<i>R</i> ²	0.001	0.106	0.009	0.03	0.202	0.604	0.003	0.003	0.001	0.436	0.093	0.004	0.0001	0.00006	0.002
	<i>P</i>	0.937	0.391	0.825	0.687	0.2219	0.136	0.881	0.876	0.956	0.055	0.418	0.877	0.984	0.989	0.907
Multiple day freeze	DF	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
	<i>F</i> statistic	0.325	0.218	0.171	0.005	0.018	108	1.29	1.58	0.053	0.919	0.377	0.018	1.65	1.72	0.645
	<i>R</i> ²	0.044	0.03	0.023	0.0008	0.002	0.939	0.155	0.184	0.007	0.116	0.051	0.002	0.191	0.198	0.084
	<i>P</i>	0.584	0.696	0.702	0.987	0.893	0.02	0.307	0.233	0.848	0.366	0.55	0.929	0.227	0.211	0.448
Cumulative multiple day Freezes	DF	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
	<i>F</i> statistic	0.006	0.434	0.01	0.146	0.83	-50.9	0.203	0.214	0.016	2.77	0.44	0.014	0.195	0.206	0.024
	<i>R</i> ²	0.0009	0.058	0.001	0.02	0.106	1.15	0.028	0.029	0.002	0.284	0.059	0.002	0.027	0.028	0.003
	<i>P</i>	0.948	0.517	0.942	0.763	0.379	0.96	0.669	0.656	0.933	0.139	0.521	0.933	0.663	0.66	0.876

Table 9 Summary statistics of the correlation tests for forage species abundance and predator abundance for each bay except Little Assawoman Bay. *AS* Atlantic Silverside, *MU* Mummichog, *SM* Sheepshead Minnow, *SK* Striped Killifish, *BF* Bluefish, *SF* Summer Flounder, *WF* Weakfish. *IR* Indian River Bay, *RB* Rehoboth Bay, *IR & RB*

Indian River Bay and Rehoboth Bay combined. The correlation tau value is presented for each species-bay combination, and the Holm corrected *p* value (alpha=0.05) is presented in the parenthesis next to the tau value, with significant correlations bolded

Species-Bay Combinations	BF IR&RB	SF IR&RB	WF IR&RB
AS IR	-0.56 (1)	0.76 (0.74)	-0.90 (0.05)
AS RB	-0.63 (1)	0.00 (1)	-0.20 (1)
MU IR	-0.07 (1)	-0.70 (1)	0.51 (1)
MU RB	-0.11 (1)	-0.82 (0.28)	0.67 (1)
SM IR	0.22 (1)	-0.96 (< 0.001)	0.91 (0.04)
SM RB	0.11 (1)	-0.91 (0.04)	0.83 (0.24)
SK IR	-0.35 (1)	0.06 (1)	-0.42 (1)
SK RB	-0.55 (1)	-0.42 (1)	0.31 (1)
BF IR&RB		-0.33 (1)	0.52 (1)
SF IR&RB			-0.92 (0.03)
WF IR&RB			

suggests that these predatory species are sensitive to declines in prey availability and may respond to declines in forage species like the ones reported in our study. However, these declines may not have been substantial enough to meaningfully alter predator condition or energy transfer between habitats. Many predatory species that feed on both Mummichog and Sheepshead Minnow also feed on numerous other prey items. While our raw data indicate that non-target fish species are unlikely to increase enough to offset target species declines between years, declines in Mummichog and Sheepshead Minnow abundance could in theory be offset by increases in invertebrate species such as mysid shrimp, or Blue Crab (*Callinectes sapidus*), which can be common prey items to predatory estuarine species (Tupper and Able 2000; Torre and Targett 2017). Further, despite a shift in number of prey items by species, there may exist a question in regard to the quality of other prey species for managed predators. Friedland et al. (1988) demonstrated that Bluefish condition was worse during years when invertebrates were the dominant prey item compared to years when fish species such as Striped Killifish and Atlantic Silverside were dominant. Thus, a better understanding of how changes in target species affect the condition of important predatory species is needed. This type of understanding would be especially relevant for inclusion of the target species into any ecosystem-based management approach that utilizes food-web interactions (for example, those referenced in Townsend et al. 2019), where managers would want to know how a decline in prey abundance affects predator condition and any subsequent body size or fecundity-based implications.

Influence of Climatic and Biotic Factors

The climatic factors we examined in our study were not frequently or strongly associated with changes in abundance for any of the target species. The exception to this observation was the apparent influence of spring discharge on Mummichog and Sheepshead Minnow abundance. Interestingly, spring discharge seemed to increase over the study period, while Mummichog and Sheepshead Minnow abundance decreased. Our results indicate that increased discharge may negatively affect these species, but it is not immediately apparent why this relationship would exist. Increases in freshwater input have been shown to decrease mesozooplankton diversity in the Maryland Coastal Bays, which reside just south of the Inland Bays (Oghenekaro and Chigbu 2019). Increased river discharge may therefore have altered an important food resource for our target species. However, Mummichog have previously shown flexibility in their diets in response to increases of freshwater input, with a switch to more phytoplankton-based diets (Nelson et al. 2015). Productivity of salt marshes may also be increased under increased riverine flow, which would presumably increase other food sources such as detritus and marsh macrophytes (Wieski and Pennings 2013).

Mummichog, Striped Killifish, and Sheepshead Minnow all overwinter within the estuary, typically by burying into marsh sediment or the shallow subtidal creek bottom (Bennett and Beitinger 1997; Able and Fahay 2010). High amounts of winter mortality in Atlantic Silverside have also been reported concomitant with lower water temperatures, which is a suggested mechanism affecting population

abundance (Conover and Ross 1982; Schultz et al. 1997). Winter mortality has also been reported to partially regulate the recruitment of other species that do not reside in the estuary year-round, similar to Atlantic Silverside (Hurst and Conover 1996). Therefore, it was expected for the three estuarine-resident species that harsher winters with more persistent freezing events may play a role in population control and affect abundance over time, with the possibility that this effect would also be seen in Atlantic Silverside. However, this theory was not supported as only one species and variable combination in one bay showed a meaningful relationship (Mummichog in Rehoboth Bay and the number of multiple day freeze events). The lack of relationships between harsh winters and abundance indicates that all four-target species are relatively resilient to mortality from frequently encountered winter temperatures or that the winter temperatures encountered over the last nine years were insufficient to cause mortality. Work by Raposa (2003) documented Mummichog moving upstream in the fall and some level of site selection preference for salt marsh pools with sediments that offered thermal refuge to avoid winter mortality, and so behavior may mediate the risk that winter temperatures play in relative abundance.

Interestingly, no relationships were evident between target species abundance and the AMO index in our study. However, Striped Killifish, Mummichog, and Atlantic Silverside have all recently been found to have positive relationships with the AMO at various spatial scales (Woodland et al. 2021) as have other estuarine juvenile fishes (e.g., Atlantic Croaker, Mathews et al. 2022). The study by Woodland et al. (2021) spanned two decades which allowed for a broader range of AMO index values, including negative index values. During our study period, the AMO index was entirely positive limiting our ability to compare relative abundance with the AMO. It is therefore possible that the range of AMO values over the 9 study years was not broad enough to elicit differences in target species abundance. However, since 1948 (the beginning of the data record), there have been 39 years when the index was positive (<https://psl.noaa.gov/data/timeseries/AMO/>), and within our study period, the tenth smallest positive index (2018) and the third largest positive index (2016) occurred. Thus, within the observed positive phase values, our study period experienced a wide range.

The influence of predators on the abundance of these four nearshore species cannot be overlooked. Kneib (1982) demonstrated that bird and Blue Crab predation can significantly affect Mummichog density. Likewise, Meredith and Lotrich (1979) estimated that predators may consume 50% of the adult Mummichog population annually. Research also suggests that at least in the case of Mummichog, cannibalism may be common (Able et al. 2007b). Given these high predation rates, it is likely that predator density plays a significant role in population dynamics over time. While

the sizes of the three predator species used in this study were relatively small, small fish still account for a large percentage of both age-0 Bluefish and age-0 Weakfish diets, which encompasses the mean sizes used in this analyses (Hartman and Brandt 1995; Scharf et al. 2004). Summer Flounder may feed more on invertebrates than fish at the mean size used in this analysis (Cernadas-Martin et al. 2021). But evidence of extensive piscivory at sizes less than the mean size used in this analysis (50–153 mm FL) and at slightly larger sizes (156–312 mm FL) that were also represented in our sample population have been documented (Roundtree and Able 1992; Taylor et al. 2019). Thus, the predators collected by the DRNEC trawl survey represent active predators to our target species.

Previous researchers have found significant relationships between other forage species including Atlantic Menhaden and the predators that similarly prey on these species like Bluefish and Striped Bass at varying levels of sensitivity among species (Friedland et al. 1988; Martino and Houde 2010; Buchheister et al. 2017). In our study, Sheepshead Minnow showed strong negative correlations with Summer Flounder predator abundance. Summer Flounder are active salt marsh predators, and within the mid-Atlantic, salt marsh fish species (such as Mummichog and Sheepshead Minnow) are regular components of their diet (Roundtree and Able 1992; Ziegler et al. 2019). Similarly, in our study, we found Summer Flounder abundance increased in Rehoboth and Indian River Bays combined, while Sheepshead Minnow abundance decreased in all three bays and in all bays combined. Correlations between Mummichog abundance in Indian River and Rehoboth Bays and Summer Flounder abundance were also strong ($\rho = -0.7, -0.82$, respectively). Unfortunately, no predator data from the DNREC trawl survey were available for Little Assawoman Bay where both Mummichog and Sheepshead Minnow abundance declined and so direct comparisons were not possible. Regardless, our data indicate clear relationships between an estuarine predator and two forage fish species. These relationships underscore the need for quantifying the effects of our observed target species declines on important managed species.

Two critical relationships between target species and predators were identified in our analyses. The first is the positive correlation seen between Sheepshead Minnow abundance and Weakfish abundance, which may be explained by the negative correlation between Summer Flounder abundance and Weakfish abundance. Summer Flounder, particularly adult specimens, are active predators of Weakfish (Buchheister and Latour 2011; Cernadas-Martin et al. 2021) and may have partially reduced Weakfish abundance or displaced Weakfish while concurrently, Sheepshead Minnow abundance fell. The second relationship we detected between forage and predator species was a strong negative correlation between Atlantic Silverside and Weakfish abundance.

Atlantic Silverside have not been previously found to account for a large proportion of Weakfish diet (Torre and Targett 2017; Boutin and Targett 2019). However, changes in dietary preferences between neighboring regions have been documented previously for Weakfish (Grecay 1990; Hartman and Brandt 1995). Our results indicate that Atlantic Silverside may contribute more to the diet of Weakfish than previously found suggesting a shift in the consumption of Atlantic Silverside may have occurred through time in these estuaries.

While this study chose to examine possible climatic and biotic variables, there are a few factors that were not investigated because of insufficient data that may also play a role in regulating the population dynamics of our target species. Nearshore land cover changes have been documented affecting several of our target species, where shoreline hardening negatively impacts species abundance (Kornis et al. 2017). The Inland Bays watershed has undergone a large amount of development over the past decade, and some of this development has inevitably resulted in shoreline hardening (Walch et al. 2016). Similarly, the Inland Bays watershed is highly eutrophied, and long-term eutrophication has negatively impacted Mummichog populations through decoupling creek and marsh habitats, limiting access to the marsh surface and reducing Mummichog populations (Walch et al. 2016; Nelson et al. 2018). It is possible that the effects of this long-term eutrophication are being observed via the declining trends in abundance of both Mummichog and Sheepshead Minnow. Salt marsh erosion may negatively impact species such as Mummichog through habitat loss and increased predation (McIvor and Odum 1988). While long-term datasets on marsh condition in the Inland Bays do not exist, widespread marsh drowning has been observed locally and has increased over time (Walch et al. 2016). These changes may negatively affect some of our target species as changes in flood frequency and hydroperiod have been shown to alter salt marsh fish behavior and predator–prey encounter rates (Hunter et al. 2009; Ziegler et al. 2019).

Management Conclusions

From a management perspective, this study has highlighted the need to begin examining trends in abundance of common forage species. The documented long-term estuary-wide declines in both Mummichog and Sheepshead Minnow are surprising given how frequently these species are encountered during seine samples. These declines demonstrate that unless these species are examined for changes in the relative magnitude of abundance, trends may go unnoticed in other Mid-Atlantic estuaries.

Understanding how understudied forage species change annually and through time is critical as fishery management begins to account for the forage needs of managed

species and transitions away from single-species management (Lindegren et al. 2009; Buchheister et al. 2017). Regionally, there have been calls for data documenting forage species dynamics and trends, with specific needs for data from shallow water areas (Ihde et al. 2015). The data from this study quantifies the variability both inter-annually and over 9 years for an important portion of the nearshore forage base in Mid-Atlantic estuaries and directly addresses those needs.

The work presented here also points to a natural follow-up study. The energetic effects on predatory species fitness from both the long-term declines and large interannual fluctuations of target species abundances documented by this study are unclear. However, given the target species' importance as prey items in the literature, their documented proportion to the overall nearshore fish assemblage in this study and others, and the observed relationships in abundance between target species and predators indicated in this study, effects on currently regulated state and federally managed predator species could be large particularly if changes are concurrent among target species. Previous work has documented how changes in prey fish size, quantity, and community structure can have important consequences for piscivorous predators (Ball et al. 2007). Thus, this study has documented a clear reason to explore quantifying these effects for our target species and their predators, aligning with a major recommendation of NOAA Fisheries to develop ecosystem modeling capacity and anticipate management needs (Townsend et al. 2019). Likewise, future studies should look to build on the results presented here and attempt to integrate how land use conversion and habitat changes may impact these species. With those questions partially or fully answered, the inclusion of these forage species into an eventual ecosystem-based management approach for regionally important predators such as Summer Flounder may become attainable.

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Declarations

Conflict of Interest The Delaware Center for the Inland Bays is a non-profit organization and a National Estuary Program. It was created to promote the wise use and enhancement of the Inland Bays watershed by conducting public outreach and education, developing and implementing restoration projects, encouraging scientific inquiry and sponsoring needed research, and establishing a long-term process for the

protection and preservation of the Inland Bays watershed. The authors declare that they have no conflict of interest.

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