


# Environmental Drivers of Forage Fishes and Benthic Invertebrates at Multiple Spatial Scales in a Large Temperate Estuary

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## Abstract

Vertebrate and invertebrate taxa that serve as forage for predators play a critical role in coastal ecosystems by linking lower trophic levels to ecologically and economically valuable predators in upper trophic levels. We analyzed long-term data from multiple monitoring surveys in Chesapeake Bay and its major tributaries to evaluate patterns and relative abundances of forage at two spatial scales and to identify drivers of forage availability. Time series of forage abundances showed positive spatial correlation, becoming increasingly similar with declining distance between tributaries and regions of Chesapeake Bay. Statistical models were fit to identify relationships among forage taxa and climatic, biological, and environmental variables. Annual abundance indices of many forage taxa were higher in years when spring water temperatures warmed slowly, as indicated by an annual 5 °C degree-day warming index that represented the rate of warming during late winter/early spring. Forage indices also were related (in taxon-specific ways) to winter–spring chlorophyll concentration and freshwater discharge, and to three summer water quality variables: dissolved oxygen, salinity, and water temperature, in addition to a broad-scale climate indicator (Atlantic Multidecadal Oscillation). Our findings broadly demonstrate that bottom–up climate forcing acts to control at least some taxa at lower trophic levels in Chesapeake Bay. Ongoing phenological changes in regional climate and evidence of spatial dependence in responses of forage to environmental conditions underscore the likelihood that spatiotemporal foraging conditions for predator species will change under projected climate conditions.

**Keywords** Food web · Bottom–up · Climate change · Forage · Spatial variability

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## Introduction

Small fishes and invertebrates comprise the diet of many predatory fishes in coastal ecosystems, including estuaries and nearshore shelf areas (Link and Garrison 2002; Pikitch et al. 2014; Buchheister and Latour 2015). The term forage fish is often used to describe small-to-medium-sized pelagic species, and while these small-bodied pelagic fishes can dominate the diet of predatory fishes in many ecosystems, the early-life stages of fish species that are large as adults can also be important prey for piscivorous predators (Sogard 1997; Köster and Möllmann 2000; Ihde et al. 2015). Among demersal species exploited in fisheries, biomass of benthic invertebrates, for example polychaetes, crustaceans, and bivalves, can contribute to diets in equal or greater proportions than finfish prey (Fuita et al. 1995; Garrison and Link 2000; Buchheister and Latour 2015). By serving as a trophic conduit between lower and higher trophic-level production, forage taxa are integral to food web dynamics in coastal regions that support economically valuable fisheries (Alder et al. 2008; Bigford 2014).

Bottom-up forcing is a key factor influencing local abundance and interannual variability of forage taxa that often display rapid maturity and short life spans (Palmer et al. 1996; Fréon et al. 2005; Alder et al. 2008; Szuwalski and Hilborn 2015). These life history traits allow forage populations to respond quickly to environmental changes and can result in large interannual variability in abundances and distributions. For example, in Chesapeake Bay, annual indices of forage fish abundance display wide fluctuations, as well as taxa-dependent synchrony or asynchrony in year-to-year patterns of relative abundance at decadal scales (Wood and Austin 2009; Buchheister and Houde 2016). At the ecosystem scale, interannual patterns in forage abundance in estuaries can be used to evaluate the role of large-scale environmental forcing variables such as climate and regional precipitation (Edgar and Barrett 2002; Buchheister et al. 2016). At smaller spatial and temporal scales, local factors such as water quality, and the availability of structured habitat are expected to influence forage distribution and abundance (Dauer et al. 2000; Maes et al. 2004).

Quantifying bottom-up relationships between environmental conditions and forage species can also provide insight into how coastal ecosystems and their associated food webs may respond to future conditions, both in terms of total productivity and compositional changes in the community (Frederiksen et al. 2006; Brown et al. 2010). Identifying the drivers of forage productivity and how assemblages of forage fish and invertebrate taxa are organized at multiple spatial and temporal scales is critical for predicting changes in availability of forage for predators (Hunsicker et al. 2011; Engelhard et al. 2013). Such knowledge informs our understanding of environmental controls on predator–prey dynamics and aids development of ecosystem-based models that can support holistic ecosystem-based fisheries management (Pikitch et al. 2004; Pikitch et al. 2012).

Here, our goal was to identify major environmental drivers of spatial and temporal forage abundance patterns to better understand factors that likely influence food web dynamics in the Chesapeake Bay. We analyzed long-term data for ten forage fish taxa and eight benthic invertebrate functional groups from multiple monitoring surveys in Chesapeake Bay and its major tributaries. Focal forage fishes included young-of-the-year (YOY) Atlantic croaker (*Micropogonias undulatus*), YOY white perch (*Morone americana*), and YOY spot (*Leiostomus xanthurus*), and mixed-age classes of alewife (*Alosa pseudoharengus*), bay anchovy (*Anchoa mitchilli*), blueback herring (*Alosa aestivalis*), mummichog (*Fundulus heteroclitus*), other killifish species (*Fundulus* spp.), Atlantic menhaden (*Brevoortia tyrannus*), and Atlantic silverside (*Menidia menidia*). Eight invertebrate functional groups, each composed of similar taxa, were analyzed: amphipods, isopods, gastropods, small crustaceans, small bivalves, large bivalves, polychaetes, and oligochaetes. To assess the role of spatial scale, analyses were conducted at the scales of individual tributaries and mainstem regions of Chesapeake Bay, and across the entire domain of system types (tributaries, mainstem) within Chesapeake Bay. This approach allowed us to analyze spatial patterns, covariation among forage species and functional groups, and biological–environmental relationships at two spatial scales.

## Methods

### Spatial Scope of Analyses

Chesapeake Bay is a large, partially stratified estuary located on the eastern coast of the USA with a surface area of 11,500 km<sup>2</sup> and a watershed of 164,200 km<sup>2</sup> (Kemp et al. 2005). It is relatively shallow (mean depth = 6 m) and highly productive, serving as a nursery and foraging area for a wide variety of economically important fish species (Jung and Houde 2003; Kemp et al. 2005; Woodland et al. 2012). Data from several ongoing monitoring programs and one historical survey of Chesapeake Bay were integrated to conduct this study (Table 1). Environmental and biological data were analyzed to provide annual estimates of predictor and response variables in five tributaries (Patuxent River, Potomac River, Rappahannock River, York River, and James River) and the mainstem of Chesapeake Bay that defined our study area (Fig. 1). These are the five largest tributaries located along the western shore of Chesapeake Bay, and each tributary was considered a distinct region for purposes of this study. The mainstem of the Bay was treated as (1) a single spatial unit and (2) delineated as three regions: the upper, middle, and lower. These three mainstem regions broadly correspond to oligohaline, mesohaline, and polyhaline salinity regimes, respectively, and are often used to delineate the hydrodynamic,

**Table 1** Summary of surveys used to derive forage indices for fish and benthic invertebrate prey groups and environmental indices

Data group	Data type	Variables	Regions	Years*	Months	Survey
Forage	Seine	CPUE (abundance)	Tributaries	1995–2015	Jul–Sep	MDDNR Juvenile Striped Bass Survey
		CPUE (abundance)	Tributaries	1995–2015	Jul–Sep	VIMS Juvenile Striped Bass Survey
	Trawl	CPUE (abundance)	Mainstem	1995–2007	Jan, Mar–Nov	Trophic Interactions in Estuarine Systems & Chesapeake Bay Fisheries Independent Monitoring Survey
	Grab	CPUE (biomass)	Main./Trib.	1995–2015	Jul–Sep	Chesapeake Bay Benthic Survey
Environment	WQ	Salinity	Main./Trib.	1995–2015	Jul–Sep	CBP Water Quality Monitoring Program
		Water temperature (°C)	Main./Trib.	1995–2015	Jul–Sep	CBP Water Quality Monitoring Program
		Chl- <i>a</i> (µg/l)	Main./Trib.	1995–2015	Feb–Jun	CBP Water Quality Monitoring Program
		Summer DO (mg/l)	Main./Trib.	1995–2015	Jul–Sep	CBP Water Quality Monitoring Program
	Discharge	Air & water temp. (°C)	Main./Trib.	1950–2015	Daily	National Data Buoy Center
		Discharge (m <sup>3</sup> /s)	Main./Trib.	1995–2015	Jan–Jun	USGS Hydrological Monitoring
Climate	AMO annual anomaly	Integrated	1995–2015	Annual	NASA	

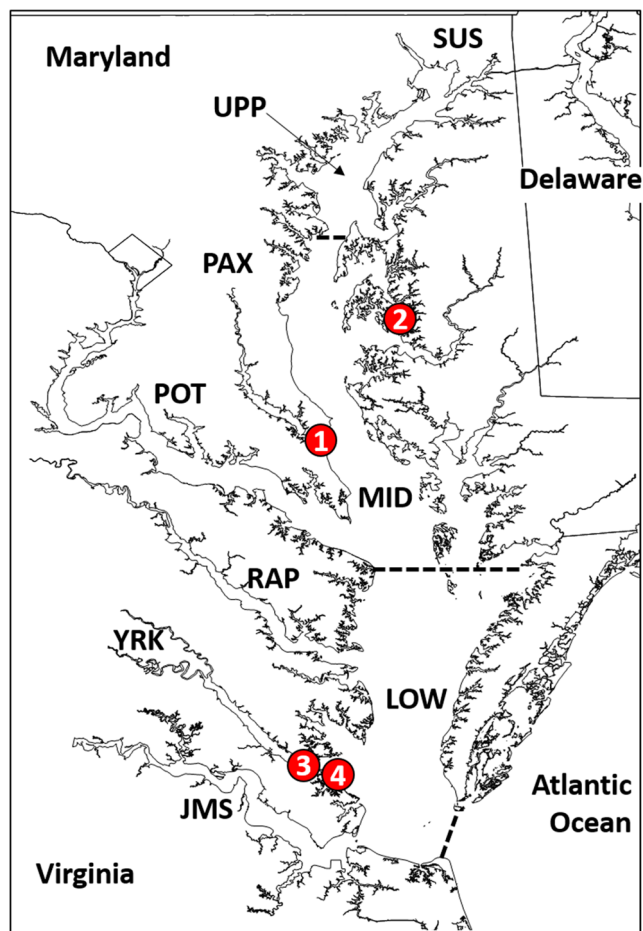
Indices were based on catch-per-unit-effort (CPUE) (fishes) or biomass (benthic invertebrates). Type of survey (Data type: seine—beach seine, trawl—midwater trawl, grab—benthic grab, WQ—water quality, discharge—river discharge, climate—large-scale climate indices), survey-derived variables, geographic regions of survey (Tributaries or Trib., Mainstem or Main., Integrated (coast-wide)), years of data availability (Years), months of data available or used, and survey identity provided. \*Data ranges shown are for the analyses used here; individual time series for some datasets are more extensive

physicochemical, and ecological gradients characterizing functional spatial subunits in the Chesapeake Bay (Boynton and Kemp 1985; Jung and Houde 2003; Kemp et al. 2005).

### Data Sources

Water quality data collected as part of the United States Environmental Protection Agency (USEPA) Chesapeake Bay Program (CBP) Water Quality Monitoring Survey were downloaded from the web (<http://datahub.chesapeakebay.net/>). Vertical water column profile measurements of water temperature (°C), salinity, dissolved oxygen concentration (mg/l) and chlorophyll-*a* concentration (µg/l) were collected one or more times per month at fixed stations distributed throughout Chesapeake Bay and its tidal tributaries. Measurements were taken at the surface, near the bottom, and at intervals of 1–3 m in the water column. Time series of mean monthly river discharge for each of the study tributaries as well as the Susquehanna River, which dominates freshwater input to the mainstem of Chesapeake Bay, were obtained from the United States Geological Survey flow gauge network (USGS; <http://waterdata.usgs.gov/nwis/sw>).

An annual index of large-scale regional climate (Atlantic Multidecadal Oscillation) was obtained from the Earth System Research Laboratory, National Oceanic and Atmospheric Administration (NOAA) Physical Sciences Division website (<http://esrl.noaa.gov/psd/data/timeseries/>). Daily water and air temperature data were sourced from four monitoring stations maintained by NOAA/National Ocean Service, NOAA/National Weather Service, Chesapeake Bay National Estuarine Research Reserve, and the Virginia Institute of Marine Science (Fig. 1; Online Resource 1). Two stations were located in the middle mainstem region, and two were located in the lower mainstem region. The strong and predictable relationship between air and water temperatures in Chesapeake Bay (Ding and Elmore 2015) allowed us to fill gaps in the daily water temperature time series record from each location, based on regional air temperature data (Online Resource 1). All regression equations used to convert air temperature to water temperature were significant ( $\text{adj-}R^2 \geq 0.96$ ,  $p < 0.05$ ) among stations and between the middle and lower regions. Eighteen percent of the water temperature time series was derived from the regressions. There were 3 days in which no water temperatures were available for



**Fig. 1** Map of Chesapeake Bay showing major regions of interest in this study, including mainstem sections following major salinity zones (dashed lines; Upper—UPP, Middle—MID, Lower—LOW) and tributaries (Patuxent River—PAX, Potomac River—POT, Rappahannock River—RAP, York River—YRK, James River—JMS). The mouth of the Susquehanna River (SUS) is provided for reference. Water and air temperature monitoring stations used to derive 5 °C degree-day phenology index shown as numbered, red circles (1—NOAA Station SLIM2 (8577330), 2—Royal Oak 2 SSW monitoring station, 3—Virginia Institute of Marine Science Ferry Pier monitoring station, 4—Chesapeake Bay National Estuarine Research Reserve Goodwin Islands monitoring station)

either the middle or lower region of the bay that were based completely on air temperature reconstructions. Daily water temperature data were averaged between stations in each region, then again between regions to derive a single, basin-wide index of mean daily water temperature from 1950 to 2015.

Annual indices of forage fishes (relative abundance) and invertebrate functional groups (biomass, analyzed as ash-free dry weight (AFDW)) were estimated from long-term seine surveys in the tributaries and Chesapeake Bay mainstem. Two seine surveys were selected to estimate forage fish relative abundances from Maryland (MD) and Virginia (VA) tributaries: (1) the Maryland Department of Natural Resources Juvenile Striped Bass Seine Survey (MJS, 1959–2015; data

provided by E. Durell personal communication), which samples the Potomac and Patuxent rivers, and (2) the Virginia Institute of Marine Science Juvenile Striped Bass Seine Survey (VJS, 1968–1973 & 1980–2015) that is conducted in the Rappahannock, York, and James rivers (Table 1). A comprehensive, long-term trawl survey that effectively samples smaller forage fishes throughout the mainstem of Chesapeake Bay does not exist; therefore, we combined two historical time series from the University of Maryland’s Center for Environmental Science’s Trophic Interactions in Estuarine Systems (TIES) and Chesapeake Bay Fishery-Independent Multispecies Survey (CHESFIMS) programs. Those programs were conducted from 1995 to 2007 using standardized midwater trawl gear and deployment methods in the mainstem of Chesapeake Bay (Jung and Houde 2003; Jung and Houde 2005). The TIES and CHESFIMS data were downloaded from the data portal (<http://hjort.cbl.umces.edu/chesfims.html>). Invertebrate forage indices were derived from the benthic survey data collected as part of the USEPA Chesapeake Bay Long-Term Benthic Monitoring and Assessment Program (1995–2015; <http://baybenthos.versar.com/default.htm>). Descriptions of gear and deployment methods for the forage fish surveys and benthic monitoring program are provided as supplementary information (Online Resource 2).

### Index Development: Predictors

Four environmental indices were derived from the USEPA CBP Water Quality Monitoring Survey. Monitoring stations used to calculate environmental indices for this study encompassed the spatial domain of forage fish and benthic surveys and were situated across the full salinity gradient in each mainstem region and each tributary. Indices of mean water temperature (TEMP), salinity (SAL), and chlorophyll-*a* concentration (CHL) were calculated based on integrated water column measurements (Smith and Kemp 1995). An index of mean dissolved oxygen concentration (DO) was calculated from sub-pycnocline or near-bottom (if a pycnocline was absent) measurements. Annual indices (1 per year per region) of temperature, salinity, and DO were calculated for the period June–September to coincide with the timing of forage sampling and to cover the primary period of poor water quality (e.g., low DO) in Chesapeake Bay (Murphy et al. 2011). The CHL index was calculated from observations obtained during late winter to spring (February–June) and was intended to represent the intensity of the winter–spring phytoplankton bloom in a given year (Testa et al. 2018).

Annual indicators of water quality were estimated from a general linear mixed-effects model in which region, year, and a region × year interaction term were considered fixed effects; depth was included as a continuous covariate, and station was treated as a repeated measurement. This resulted in a random

intercept model with a compound symmetry variance-covariance structure accounting for station level correlation through time (Zuur 2009). Model estimates were obtained by least squares means for each combination of region  $\times$  year at each spatial scale. Estimates of all model predictor variables from each tributary and mainstem region, including the four described above and all those described below, were expressed as standardized time series (i.e., mean = 0 and unit variance). In this study, all statistical models were fitted using SAS (v9.4), R (v3.3.3–3.6.1) or a combination of these two software packages.

Two water temperature degree-day (DD) indices were considered, a cumulative count of all DD in excess of 5 °C DD from 1 January to 30 June of each year and a phenological index calculated as the integer day of the year at which a cumulative threshold of 500 5 °C DD was achieved. Degree days were defined as the sum of mean daily water temperature residuals above a minimum threshold temperature. Days in which mean water temperatures were below the threshold were assigned a DD value = 0. The DD index was calculated from the basin-wide index of mean daily water temperature. We chose 5 °C as a functional DD temperature threshold because previous research has demonstrated biologically relevant DD threshold temperatures ranging from 5 to 14 °C for fish and invertebrate taxa (Hartman and Brandt 1995; Hurst and Conover 1998; Bunnell and Miller 2005; Humphrey et al. 2014). We selected the cumulative 500 5 °C DD threshold because it captures interannual variability in cumulative water temperature during the late winter/early spring seasons in the Chesapeake Bay region (January through April–May). Sensitivity tests of calculated annual cumulative DD values from January 1 to June 30 based on DD temperature thresholds of 5, 8, and 10 °C were strongly correlated ( $r_{\text{Pearson}} = 0.91\text{--}0.98$ ,  $p < 0.05$ ) and showed no difference in interannual patterns. Therefore, we elected to use 5 °C DD, the minimum temperature threshold selected in previous research, for calculation of an annual index.

We used mean monthly river discharge data from the USGS gauging stations located nearest to the tidal head of each river system to calculate a winter–spring freshwater discharge index (Table 1). The discharge (DISC) index was derived by averaging the mean monthly discharge values from 1 January through 30 June of each year. The upper York River splits into the Pamunkey and Mattaponi rivers below the head of tide; therefore, a grand mean for the York River was calculated from the average monthly discharge measured at gauging stations in both the Pamunkey and Mattaponi rivers (USGS gauge stations 01673000 and 1674500, respectively).

We evaluated the potential effects of a large-scale regional climate index, the Atlantic Multidecadal Oscillation (AMO) on forage species abundances or biomass. Large-scale climate patterns, such as the AMO, have been correlated with interannual patterns in the abundance of commercially harvested

species as well as assemblage-level changes in Chesapeake Bay's fish community (Wood and Austin 2009; Nye et al. 2014; Buchheister et al. 2016). The AMO index has oscillated between positive (warm) and negative (cool) phases over the period spanning 1950–2015 but was generally positive over the years of our study (1995–2015).

## Forage Indices

Forage functional groups and species were selected for analysis based on long-term stomach content data of a representative assemblage of predator fish species (striped bass *Morone saxatilis*, white perch, summer flounder *Paralichthys dentatus*, clearnose skate *Raja eglanteria*, Atlantic croaker; Buchheister and Latour 2015; Ihde et al. 2015). Eight functional groups composed of taxonomically similar invertebrates were selected (3 most important taxa by biomass provided for each group): amphipods (*Leptocheirus plumulosus*, *Apocorophium lacustre*, *Gammarus daiberi*), isopods (*Cyathura polita*, *Edotea triloba*, *Synidotea* spp.), gastropods (*Campeloma decisum*, *Goniobasis virginica*, *Acteocina canaliculata*), small crustaceans (Cumacea, Mysidacea, Tanaidacea), small bivalves (<5 cm max shell length; *Limecola balthica*, *Gemma gemma*, *Macoma mitchelli*), large bivalves (>5 cm max shell length; *Rangia cuneata*, *Corbicula fluminea*, *Mercenaria mercenaria*), polychaetes (*Neanthes succinea*, *Marenzelleria viridis*, *Heteromastus filiformis*) and oligochaetes (*Tubificoides* spp., *Branchiura sowerbyi*, *Limnodrilus hoffmeister*). Focal forage fishes included YOY of three species: Atlantic croaker, white perch, and spot; and all age classes of seven species: alewife, bay anchovy, blueback herring, mummichog, other killifishes, Atlantic menhaden, and Atlantic silverside.

A delta-generalized linear model (delta-GLM; Aitchison 1955; Maunder and Punt 2004) was used to estimate annual index values for benthic invertebrate functional groups. In the first stage of the delta-GLM, a binomial regression model was used to estimate the mean encounter probability of each functional group with three explanatory variables (class variables: region (tributary, 5 levels; mainstem, 3 levels) and year; continuous variable: station depth) and an interaction term (region  $\times$  year). In the second stage of the delta-GLM, a general linear model that included parameters identical to those in the binomial model component was fitted to log-transformed data to estimate the mean non-zero biomass of functional groups. Functional group biomasses (AFDW per m<sup>2</sup>) were calculated by summing the individual biomasses of all taxa within each functional group for each station. Mean encounter probability estimates were then multiplied by the bias-corrected, back-transformed estimates of mean biomass when present to yield the final index of mean biomass densities for all combinations of functional group, region, and year.

Forage fish index numerical estimates were derived from catch per unit effort (CPUE; hereafter, simply “abundance”) rather than biomass densities. Forage fish indices were modeled using delta-generalized linear mixed models (delta-GLMM) that coupled a mixed-effects binomial regression model with a general linear model applied to log-transformed data to account for repeated sampling at fixed stations in the forage fish surveys. The mixed-effects binomial regression component of the delta-GLMM was a random intercept model with a compound symmetry variance-covariance structure. Optimization methods for maximum likelihood estimation varied during development of the mixed-effects binomial model component because some species required particular optimization algorithms (e.g., Laplace, adaptive Gaussian–Hermite quadrature) to achieve model convergence. Similar to the benthic invertebrates, annual indices for each forage species were derived for each combination of region and year. All years of seine survey data were used to generate annual forage fish abundance estimates, but estimates from only 1995–2015 were used for further analysis to ensure temporal overlap with benthic invertebrate indices and the full suite of predictor variables.

### Spatial Patterns and Forage-Environment Models

We used correlation analysis, ANOVA, and ANCOVA to test for spatial patterns within and across forage functional groups. Pearson product-moment correlation was used to examine similarities or dissimilarities in interannual indices of relative abundance or biomass across forage groups and to explore spatial correlations across regions within forage groups. For correlation analysis, forage taxa were assigned to functional groups based on habitat. Forage fishes were classified as occupying either demersal, pelagic, or littoral habitats, and invertebrate forage were classified as either epibenthic or infaunal taxa. Forage taxa were assigned to functional groups as follows: demersal—YOY spot, YOY Atlantic croaker, and YOY white perch; pelagic—alewife, bay anchovy, blueback herring, and Atlantic menhaden; littoral—mummichog, other killifishes, and Atlantic silverside; epibenthic—amphipods, gastropods, isopods, and small crustaceans; infaunal—polychaetes, oligochaetes, and bivalves. Large bivalves were excluded for this analysis due to their large effect on the variability of infaunal functional group biomass estimates (grand mean ( $\pm$ SD) infaunal group biomass including large bivalves = 1.69 ( $\pm$  3.99) AFDW g/m<sup>2</sup>, excluding large bivalves = 0.28 ( $\pm$  0.15) AFDW g/m<sup>2</sup>).

Direct comparisons among forage taxa were limited to those taxa and regions that used the same survey methods. For example, tributary forage-fish indices were compared among tributaries, but were not compared with mainstem forage-fish indices because the sampling gears differed. Generalized linear models were used to analyze relationships

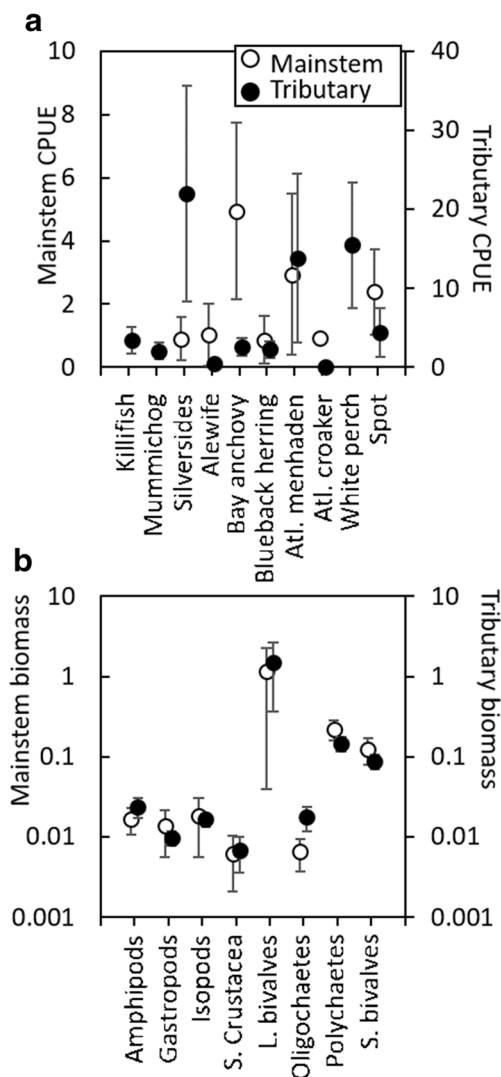
between annual indices of forage and environmental conditions (McCullagh and Nelder 1983; Guisan et al. 2002). Models were fitted for each tributary and mainstem region separately and then aggregated and fitted for all tributaries combined and all mainstem regions combined. Forage environment models were fitted assuming a gamma response distribution and log-link function. Correlation analysis of potential predictor variables indicated a strong, negative correlation between the two candidate degree-day environmental indices (Pearson correlation coefficient  $r_{\text{Pearson}} = -0.85$ ,  $p < 0.05$ ; see Online Resource 3). To avoid multi-collinearity, the cumulative degree-day index was removed from further analysis. The final list of uncorrelated environmental variables included as potential predictors in the models were DISC, CHL, DO, TEMP, SAL, DD (phenological degree-day index), and AMO. Model fit was assessed by comparing agreement between observed and predicted index values ( $r_{\text{Pearson}}$ ). Residuals were assessed to verify the parametric assumptions of the models (e.g., quantile–quantile plot diagnostics).

## Results

### Spatial Patterns in Forage Indices

Patterns of forage abundance indices differed spatially and taxonomically. Within the mainstem of Chesapeake Bay, forage fish abundance indices were highest for bay anchovy, Atlantic menhaden, and YOY spot and exhibited high spatial variability (Fig. 2). Across tributaries, Atlantic silverside, Atlantic menhaden, and YOY white perch were typically the most numerous forage fishes (Fig. 2). Following long-term declines in Chesapeake Bay and commensurate with low abundances reported previously (Limburg and Waldman 2009), alewife and blueback herring index values were relatively low in the mainstem and tributaries. Among benthic invertebrate indices, polychaete and large and small bivalve size classes had the highest mean index values in both mainstem and tributary habitats (Fig. 2).

Spatial patterns of abundance of forage taxa were evident among tributaries and mainstem regions (Fig. 3; see Online Resource 4). Only one forage taxon (bay anchovy) showed significant annual pairwise differences among regions in the mainstem trawl survey, with higher relative abundance (i.e., CPUE) observed in the upper Bay than the lower Bay (Fig. 3c). Whereas no other statistical comparisons were significant, a qualitative pattern of higher abundance in the upper Bay relative to the middle and lower Bay regions was observed in the seven remaining forage fish taxa for which sufficient data were available to obtain model estimates. Pairwise comparisons among tributaries from the seine surveys highlighted significantly lower abundance within taxa in the most northern tributaries (Patuxent and Potomac rivers)



**Fig. 2** Delta-general linear model estimates of indices (averaged across all years) for (a) forage fish relative abundance, and (b) benthic invertebrate group biomass, across regions within the mainstem of Chesapeake Bay (mainstem; trawl surveys 1995–2007) and across five Chesapeake Bay tributaries: Patuxent River, Potomac River, Rappahannock River, York River, James River (Tributary; seine surveys 1995–2015). Error bars are  $\pm$ SE (in some instances, error bars are obscured by data points)

compared with the more southern tributaries (Rappahannock, York, and James rivers; Fig. 3). There were significant pairwise differences between the Patuxent and Potomac rivers for mummichog, bay anchovy, other killifishes, blueback herring, and Atlantic silverside. With the exception of blueback herring (Fig. 3h), Patuxent River indices of abundance were higher than Potomac River values for these taxa. In the southern tributaries, patterns were more variable among taxa but indices of forage fish abundance were higher in the Rappahannock River compared with the York River for six taxa (YOY spot, YOY white perch, YOY Atlantic croaker, blueback herring, Atlantic menhaden, Atlantic silverside) and

higher than the James River for four taxa (YOY spot, blueback herring, Atlantic menhaden, Atlantic silverside).

Benthic forage did not show the same strong spatial similarities in rank order of biomass density that were observed for forage fishes (Fig. 4 see Online Resource 4). Relative abundance of amphipods, gastropods, polychaetes, oligochaetes, and small crustaceans were highest in the lower mainstem and one or more of the southern tributaries (Fig. 4a, b, c, e, h). In contrast, large bivalves, isopods, and small bivalves had higher biomass in the upper mainstem region and relatively high biomass in one or both of the northern tributaries (Fig. 4d, f, g). There were no consistent patterns in biomass between the northern and southern tributaries for the benthic forage taxa.

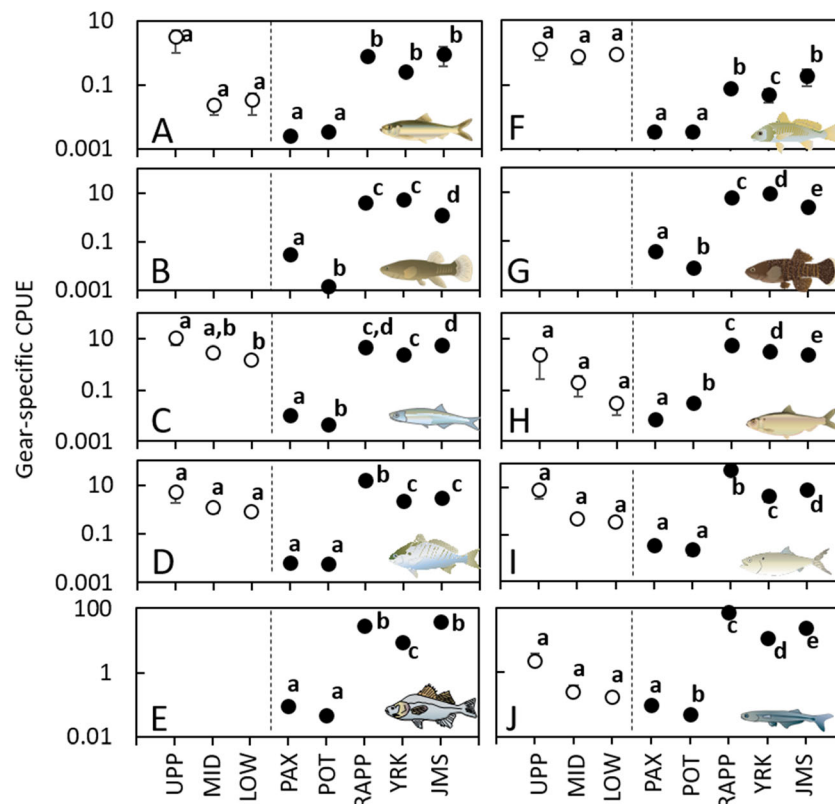
Spatial correlations of annual indices for individual functional groups were usually higher and positive in regions that were geographically close (Table 2, Fig. 5). This pattern of increased correlation with increasing spatial proximity was most pronounced across tributaries and less pronounced across mainstem regions (Table 2). Across tributaries and functional groups, declines in between-tributary correlations with increasing distance were significant (ANCOVA,  $n = 50$ , distance effect,  $F = 4.31$ ,  $p < 0.05$ ; Fig. 5a–b; (group  $\times$  distance interaction was not significant,  $F = 1.35$ ,  $p > 0.05$ )).

Correlations between functional groups (e.g., correlation between pelagic and littoral forage fish functional groups) were also present. Across mainstem regions, annual indices were positively correlated among functional groups of forage fishes ( $r_{\text{Pearson}} \geq 0.93$ ;  $p < 0.05$ ) and between invertebrate functional groups ( $r_{\text{Pearson}} = 0.80$ ;  $p < 0.05$ ; Table 3). Across tributaries, functional group correlations were more variable but only present for demersal and pelagic forage fishes, and for littoral and pelagic forage fishes (Table 3; Fig. 6a–d). Across both the mainstem and the tributaries, correlations between functional groups were never significant between a forage fish and invertebrate functional group (Table 3).

## Forage–Environment Relationships

Interannual patterns in relative abundances of particular forage groups were associated with different environmental variables, and these variables depended on the spatial scope of the data. Forage fish models typically performed better for the tributaries than for the mainstem as indicated by stronger correlations between predicted and observed abundance indices (likely due to larger sample sizes in the tributaries; Table 4).

Parameter estimates for mainstem forage models indicated each of the variables (AMO, CHL, DD, DO, DISC, SAL, TEMP) was significant for one or more of the forage taxa (Fig. 7a–g). The effect of AMO was positive for bay anchovy, Atlantic menhaden, alewife, blueback herring, YOY spot, and Atlantic silverside but negative for isopods, small crustaceans,



**Fig. 3** Delta-general linear model estimates of indices (averaged across all years) for forage fish from the upper (UPP), middle (MID), and lower (LOW) mainstem regions of Chesapeake Bay (trawl surveys 1995–2007) and five Chesapeake Bay tributaries (seine surveys 1995–2015): Patuxent River (PAX), Potomac River (POT), Rappahannock River (RAP), York River (YRK), James River (JMS). Forage fish are (a) alewife, (b) mummichog, (c) bay anchovy, (d) young-of-the-year (YOY) spot, (e) YOY white perch, (f) YOY Atlantic croaker, (g) other killifishes, (h) blueback

herring, (i) Atlantic menhaden, (j) Atlantic silverside. Vertical dashed line separates mainstem regions (open symbols) from tributaries (filled symbols). Error bars are  $\pm 1$  SE (positive error bars are often obscured due to log scale of y-axes). Symbols that do not share a lowercase letter are significantly different (Tukey post hoc HSD). Vector images are from the Integration and Application Network Image Library (<http://ian.umces.edu/imagelibrary>)

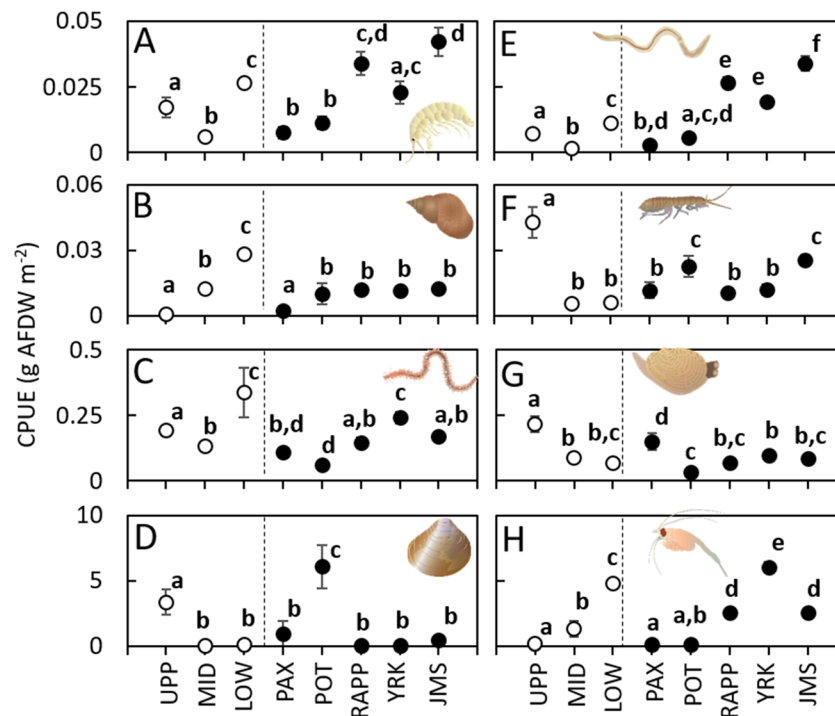
and polychaetes (Fig. 7a). CHL was negatively associated with blueback herring in the middle mainstem but positive for gastropods in the upper mainstem and for Atlantic silverside in the across-mainstem regions model (Fig. 7b).

The DD phenology index was positive for all mainstem models in which DD was significant, including mainstem models for forage fishes and invertebrates (Fig. 7c). DO was positive for all mainstem forage fish models and two invertebrate forage groups (amphipods, small crustaceans), but negatively related to isopods in the middle mainstem (Fig. 7d). Three pelagic forage fishes and three benthic invertebrates showed a positive relationship with DISC in the mainstem, but one benthic group (oligochaetes) was negatively related to DISC (Fig. 7e). Abundances of several forage fish and invertebrate groups were related to SAL in the mainstem, showing group-specific responses (positive or negative). Bay anchovy, Atlantic menhaden, and small bivalves showed region-specific responses in which SAL was positively related to abundance in one mainstem region but negatively related in another region (e.g., bay

anchovy: positive in the upper mainstem, negative in the middle mainstem; Fig. 7f). TEMP was positive for all mainstem models in which it was significant, including both forage fishes and invertebrates (Fig. 7g).

Among forage fishes in the tributaries, AMO was positively related to littoral and demersal functional groups, but negatively related to pelagic species (Fig. 7h). In the tributaries, AMO was negatively associated with most invertebrate groups (amphipods, polychaetes, gastropods, small crustaceans, small bivalves), but positively associated with large bivalves. CHL was significant (positive or negative) for several forage fishes and invertebrates (Fig. 7i). The sign of the relationships for alewife, blueback herring, and amphipods with CHL differed among tributaries and spatial scales (i.e., single tributaries or across tributaries). The effect of the DD index was positive in 17 of the 21 single-tributary models in which it was found to be significant, and positive in all seven across-tributary models in which it was significant (Fig. 7j). Model outcomes in which the DD variable was negative occurred in the Patuxent River (blueback herring, Atlantic menhaden) and the Rappahannock River (YOY Atlantic croaker,





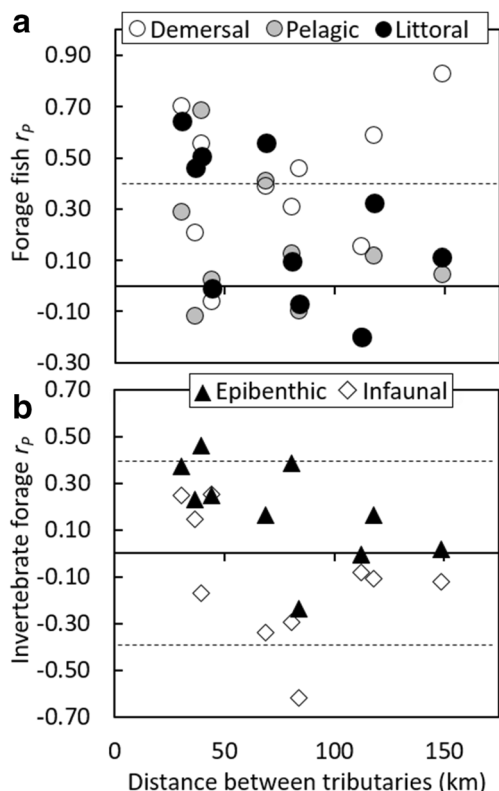
**Fig. 4** Delta-general linear model estimates of indices (averaged across all years) for benthic invertebrate forage group biomass from the upper (UPP), middle (MID), and lower (LOW) mainstem regions of Chesapeake Bay and five Chesapeake Bay tributaries: Patuxent River (PAX), Potomac River (POT), Rappahannock River (RAP), York River (YRK), James River (JMS). Benthic groups are (a) amphipods, (b) gastropods, (c) polychaetes, (d) large bivalves, (e) oligochaetes, (f) isopods,

(g) small bivalves, (h) small crustaceans. Vertical dashed line separates mainstream regions (open symbols) from tributaries (filled symbols). Error bars are  $\pm 1$  SE. Symbols that do not share a lowercase letter are significantly different (Tukey post hoc HSD). Images are from the Integration and Application Network Image Library (<http://ian.umces.edu/imagelibrary>) and the Inland Fisheries Ireland Image resources (isopod image only, <http://www.somethingfishy.ie>)

**Table 2** Pearson product moment correlation values ( $r_{\text{Pearson}}$ ) for functional forage groups between tributaries (PAX—Patuxent River, POT—Potomac River, RAP—Rappahannock River, YRK—York River, JMS—James River)

Forage groups		Tributary				Mainstem region	
		PAX	POT	RAP	YRK	LOW	MID
Forage fish	Demersal	POT	<i>0.21</i>				
		RAP	<i>0.31</i>	<i>-0.06</i>			
		YRK	<b>0.59</b>	<b>0.46</b>	<b>0.56</b>		
		JMS	<b>0.83</b>	<i>0.15</i>	<b>0.39</b>	<b>0.70</b>	
	Littoral	POT	<b>0.46</b>				
		RAP	<i>0.10</i>	<i>-0.01</i>			
		YRK	<i>0.32</i>	<i>-0.07</i>	<b>0.51</b>		
	Pelagic	JMS	<i>0.11</i>	<i>-0.20</i>	<b>0.56</b>	<b>0.65</b>	
		POT	<i>-0.12</i>				
Invertebrate forage	Epibenthic	RAP	<i>0.13</i>	<i>0.02</i>			
		YRK	<i>0.12</i>	<i>-0.10</i>	<b>0.69</b>		
		JMS	<i>0.05</i>	<i>-0.20</i>	<b>0.41</b>	<i>0.29</i>	
		POT	<i>0.23</i>				
	Infaunal	RAP	<i>0.39</i>	<i>0.25</i>			
		YRK	<i>0.16</i>	<i>-0.24</i>	<b>0.46</b>		
		JMS	<i>0.02</i>	<i>-0.01</i>	<i>0.16</i>	<i>0.37</i>	
		POT	<i>0.14</i>				
		RAP	<i>-0.29</i>	<i>0.25</i>			
	YRK	<i>-0.11</i>	<b>-0.62</b>	<i>-0.17</i>			
	JMS	<i>-0.12</i>	<i>-0.08</i>	<i>-0.34</i>	<i>0.25</i>		

Functional forage groups: Demersal—young-of-the-year (YOY) spot, YOY Atlantic croaker, YOY white perch; Littoral—mummichog, other killifishes, Atlantic silversides; Pelagic—alewife, bay anchovy, blueback herring, Atlantic menhaden; Epibenthic—amphipods, gastropods, isopods, small crustaceans; Infaunal—polychaetes, oligochaetes, bivalves (large bivalves excluded from these correlations). Models shown with  $r_p$  values corresponding with  $p$  values  $\leq 0.05$  (bold text) and  $p$  values  $> 0.05$  (italic text)



**Fig. 5** Pearson product-moment correlations ( $r_p$ ) of (a) fish and (b) invertebrate functional forage groups for five Chesapeake Bay tributaries plotted against the linear distance between tributaries (measured from the geographic mouth of each tributary). Functional forage groups: Demersal—young-of-the-year (YOY) spot, YOY Atlantic croaker, YOY white perch; Littoral—mummichog, other killifishes, Atlantic silversides; Pelagic—alewife, bay anchovy, blueback herring, Atlantic menhaden; Epibenthos—amphipods, gastropods, isopods, small crustaceans; Infauna—polychaetes, oligochaetes, bivalves (large bivalves excluded from these correlations). Dashed lines at  $|r_p| = 0.39$  indicate significance at  $\alpha = 0.05$

small bivalves). In the tributaries, DO was positively related to Atlantic silverside and alewife indices, negatively related to several forage fish and invertebrate group indices, and showed a tributary-specific response for YOY spot (Fig. 7k). The relationship between DISC and forage fishes and invertebrates was variable, with tributary-specific and across-tributary responses for several taxa, including Atlantic silverside, blueback herring, and large bivalves (Fig. 7l). In the tributaries, SAL was negatively associated with four forage fishes (mummichog, blueback herring, YOY Atlantic croaker, YOY white perch) and three invertebrate groups (amphipods, oligochaetes, small bivalves; Fig. 7m). In contrast, Atlantic silverside, gastropods, and small crustaceans showed a positive response to SAL in the tributaries. TEMP was typically positively associated with forage fishes and invertebrates in the tributaries, with exceptions being negative relationships between TEMP and mummichog (POT) and alewife (PAX), and three invertebrate taxa (amphipods, small crustaceans, large bivalves; Fig. 7n).

**Table 3** Pearson product moment correlation values ( $r_{\text{Pearson}}$ ) between functional forage groups across ecosystem types (System)

System	Forage-fish			Invertebrates
	Demersal	Littoral	Pelagic	Epifauna
Tributaries	Littoral	<i>0.37</i>		
	Pelagic	<b>0.51</b>	<b>0.49</b>	
	Epifauna	<i>-0.26</i>	<i>-0.40</i>	<i>-0.35</i>
	Infauna	<i>0.08</i>	<i>-0.29</i>	<i>-0.36</i>
Mainstem	Littoral	<b>0.93</b>		
	Pelagic	<b>0.94</b>	<b>0.97</b>	
	Epifauna	<i>-0.06</i>	<i>-0.01</i>	<i>0</i>
	Infauna	<i>0.05</i>	<i>0.10</i>	<i>0.08</i>

Functional forage groups: Demersal—young-of-the-year (YOY) spot, YOY Atlantic croaker, YOY white perch; Littoral—mummichog, other killifishes, Atlantic silversides; Pelagic—alewife, bay anchovy, blueback herring, Atlantic menhaden; Epibenthic—amphipods, gastropods, isopods, small crustaceans; Infaunal—polychaetes, oligochaetes, bivalves (large bivalves excluded from these correlations). Models shown with  $r_p$  values corresponding with  $p$  values  $\leq 0.05$  (bold text with \*) and  $p$ -values  $> 0.05$  (italic text)

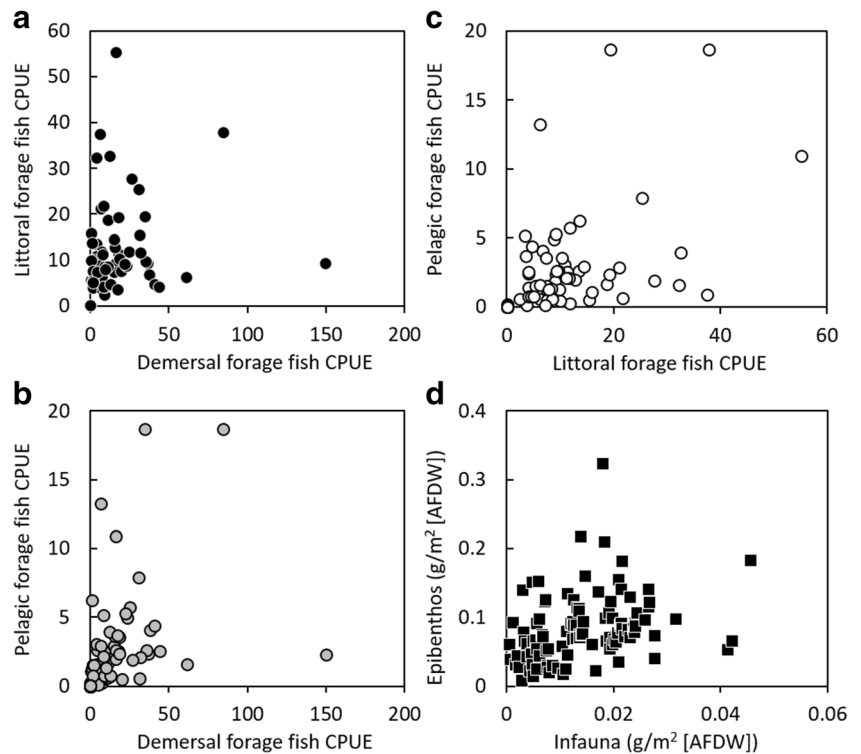
## Discussion

### Spatial Patterns of Forage Fishes and Invertebrates

We identified strong spatial patterns in composition and relative abundance of forage taxa for predatory fishes in Chesapeake Bay. Across taxa, spatial patterns in relative abundance of forage fishes were remarkably consistent. During the years 1995–2015, we observed higher relative abundances of forage fishes in the southern tributaries than in the northern tributaries. This was true early (1995–2007) and late in the time series (2008–2015; see Online Resource 4). Despite deployment of identical gear and catch-processing methods, comparisons of fish CPUE between northern and southern tributaries in Chesapeake Bay have been uncommon because the tributaries fall within different state jurisdictions (northern = Maryland, southern = Virginia) and are sampled by independent monitoring programs. With the exception of the bivalve functional groups and isopods in the Potomac River, we observed a similar, although less distinct, pattern in the benthic invertebrate forage groups. Conversely, in the Bay mainstem, there was a qualitative trend of higher relative abundances of forage fishes in the upper Bay relative to the middle and lower mainstem regions based on a reduced time series (1995–2007; see Online Resource 4).

Given similarities in sampling methodology, abundances (CPUE) of forage fishes should be comparable between Maryland and Virginia tributaries, and the higher CPUEs in the Virginia tributaries likely arise from environmental differences. For example, only the Maryland tributaries had a

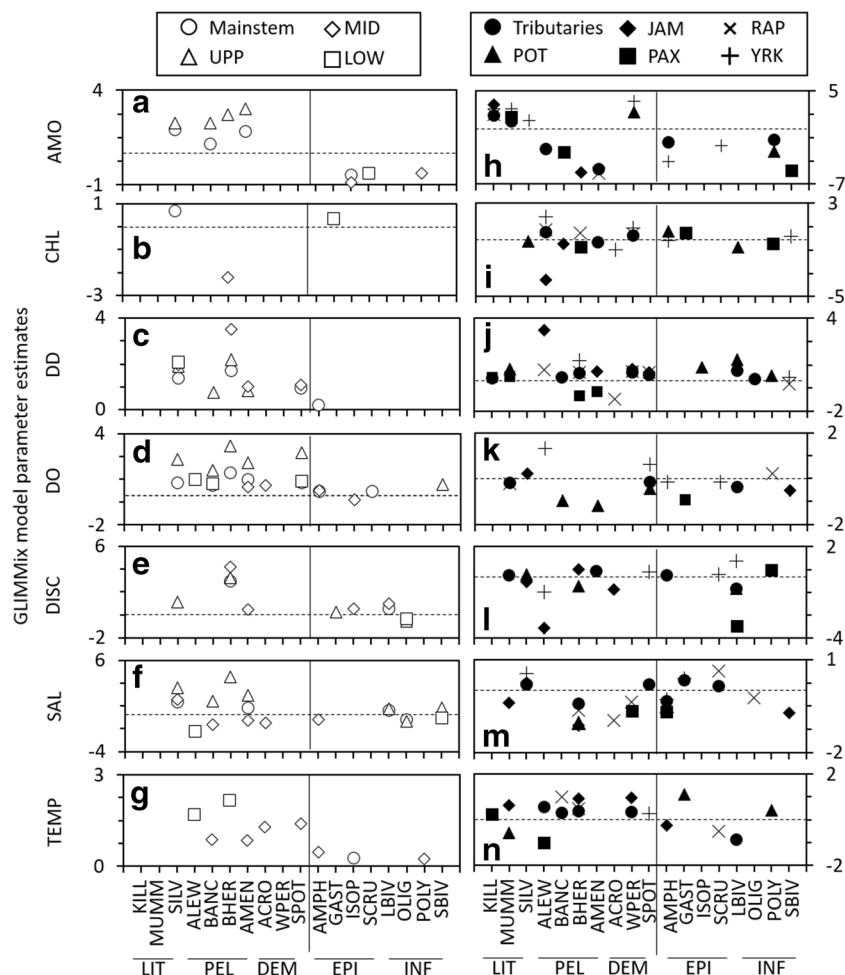
**Fig. 6** Annual mean catch-per-unit-effort (CPUE) for functional fish and biomass per unit area (ash-free dry weight (AFDW)) for invertebrate functional forage groups from five Chesapeake Bay tributaries plotted as (a) littoral vs demersal forage fish, (b) pelagic vs demersal forage fish, (c) pelagic vs littoral forage fish, and (d) epibenthic vs infaunal invertebrates. Functional forage groups: Demersal—young-of-the-year (YOY) spot, YOY Atlantic croaker, YOY white perch; Littoral—mummichog, other killifishes, Atlantic silversides; Pelagic—Alewife, bay anchovy, blueback herring, Atlantic menhaden; Epibenthos—amphipods, gastropods, isopods, small crustaceans; Infauna—polychaetes, oligochaetes, bivalves (large bivalves excluded from these correlations). Each datum is from a different tributary



**Table 4** Generalized linear mixed model performance for forage taxa in each geographic region (Upper (mainstem regions of Chesapeake) Bay—UPP, Middle Bay—MID, Lower Bay—LOW; Tributaries: PAX—Patuxent River, POT—Potomac River, RAP—Rappahannock River, YRK—York River, JMS—James River)

Type	Taxon	Tributaries					Mainstem sections			Regional	
		PAX	POT	RAP	YRK	JMS	UPP	MID	LOW	Tributaries	Mainstem
Finfish	Killifishes	<b>0.67</b>	<b>0.37</b>	<b>0.55</b>	<b>0.60</b>	<b>0.66</b>				<b>0.61</b>	
	Mummichog	<b>0.74</b>	<b>0.54</b>	<b>0.50</b>	<b>0.68</b>	<b>0.61</b>				<b>0.53</b>	
	Silversides	<b>0.42</b>	<b>0.58</b>	<b>0.45</b>	<b>0.82</b>	<b>0.56</b>	<b>0.58</b>	<b>0.84</b>	<b>0.74</b>	<b>0.40</b>	<b>0.52</b>
	Alewife	<b>0.67</b>	<b>0.50</b>	<b>0.43</b>	<i>0.53</i>	<b>0.85</b>	<i>0.54</i>	<i>0.39</i>	<b>0.81</b>	<b>0.37</b>	<b>0.46</b>
	Bay anchovy	<b>0.46</b>	<b>0.42</b>	<b>0.47</b>	<i>0.31</i>	<b>0.40</b>	<b>0.63</b>	<b>0.70</b>	<b>0.63</b>	<b>0.50</b>	<b>0.54</b>
	Blueback herring	<b>0.66</b>	<b>0.48</b>	<b>0.49</b>	<i>0.36</i>	<b>0.53</b>	<b>0.56</b>	<b>0.80</b>	<b>0.90</b>	<b>0.45</b>	<b>0.44</b>
	Atl. menhaden	<b>0.42</b>	<b>0.44</b>	<b>0.52</b>	<b>0.38</b>	<b>0.51</b>	<b>0.61</b>	<b>0.87</b>	<i>0.56</i>	<b>0.39</b>	<b>0.52</b>
	Atl. croaker	<b>0.67</b>	<b>0.87</b>	<b>0.71</b>	<i>0.35</i>	<b>0.61</b>	<i>0.37</i>	<b>0.73</b>	<b>0.63</b>	<b>0.33</b>	<b>0.42</b>
	White perch	<b>0.58</b>	<b>0.53</b>	<b>0.41</b>	<b>0.45</b>	<b>0.39</b>				<b>0.40</b>	
	Spot	<b>0.37</b>	<b>0.57</b>	<b>0.53</b>	<b>0.73</b>	<b>0.48</b>	<i>0.39</i>	<b>0.78</b>	<b>0.78</b>	<b>0.35</b>	<b>0.50</b>
Invertebrates	Amphipods	<b>0.74</b>	<b>0.47</b>	<b>0.79</b>	<b>0.88</b>	<b>0.81</b>	<b>0.47</b>	<b>0.75</b>	<b>0.45</b>	<b>0.68</b>	<b>0.66</b>
	Gastropods	<i>0.37</i>	<i>0.37</i>	<b>0.71</b>	<b>0.67</b>	<b>0.67</b>	<i>0.51</i>	<b>0.47</b>	<b>0.61</b>	<b>0.32</b>	<b>0.74</b>
	Isopods	<b>0.48</b>	<b>0.50</b>	<b>0.51</b>	<b>0.67</b>	<b>0.61</b>	<i>0.34</i>	<b>0.73</b>	<b>0.67</b>	<b>0.49</b>	<b>0.62</b>
	S. crustaceans	<i>-0.37</i>		<b>0.80</b>	<b>0.76</b>	<i>0.37</i>	<b>0.91</b>	<i>0.37</i>	<b>0.63</b>	<b>0.82</b>	<b>0.71</b>
	L. bivalves	<b>0.56</b>	<b>0.59</b>	<b>0.51</b>	<b>0.67</b>	<i>0.43</i>	<b>0.64</b>	<b>0.50</b>	<i>0.29</i>	<b>0.50</b>	<b>0.71</b>
	Oligochaetes	<b>0.66</b>	<b>0.54</b>	<b>0.62</b>	<b>0.57</b>	<b>0.61</b>	<b>0.66</b>	<b>0.55</b>	<b>0.64</b>	<b>0.84</b>	<b>0.66</b>
	Polychaetes	<b>0.63</b>	<b>0.58</b>	<b>0.62</b>	<b>0.67</b>	<b>0.48</b>	<i>0.35</i>	<b>0.74</b>	<b>0.55</b>	<b>0.51</b>	<b>0.46</b>
	S. bivalves	<b>0.74</b>	<i>0.35</i>	<b>0.74</b>	<b>0.74</b>	<b>0.69</b>	<b>0.60</b>	<b>0.45</b>	<b>0.56</b>	<b>0.49</b>	<b>0.65</b>

Presented as Pearson product-moment correlations ( $r_p$ ) between observed and predicted annual indices of abundance (Finfish) or biomass (Invertebrates) per unit area sampled ( $r_p$  values corresponding with  $p$  values  $\leq 0.05$  are bolded,  $p$  values  $> 0.05$  are italicized, insufficient data = ‘ ‘)



**Fig. 7** Parameter estimates associated with predictor variables (winter–spring discharge (DISC), spring water column chlorophyll-*a* concentration (CHL), summer water column salinity (SAL), summer water column temperature (TEMP), summer bottom water dissolved oxygen concentration (DO)) from significant generalized linear mixed models of forage fish and benthic invertebrate forage. Results are presented separately for the mainstem in panels **a–e**, including the upper (UPP), middle (MID), and lower (LOW) mainstem regions of Chesapeake Bay and an integrated mainstem model (Mainstem), and five Chesapeake Bay tributaries in **f–j**, Patuxent River (PAX), Potomac River (POT), Rappahannock River (RAP), York River (YRK), James River (JMS) and an integrated tributary model (Tributaries). Species abbreviations are as follows: other killifishes (KILL), mummichog (MUMM),

Atlantic silversides (SILV); alewife (ALEW), bay anchovy (BANC), blueback herring (BHER), Atlantic menhaden (AMEN), Atlantic croaker (ACRO), white perch (WPER), spot (SPOT), amphipods (AMPH), gastropods (GAST), isopods (ISOP), small crustaceans (SCRU), large bivalves (LBIV), oligochaetes (OLIG), polychaetes (POLY), small bivalves (SBIV). Dashed line = 0 on each y-axis, vertical line separates mainstream forage fish from invertebrates. Only significant parameters ( $p < 0.05$ ) from models with  $p$  value  $< 0.05$  of Pearson's product-moment correlation coefficient,  $r_p$ , between observed and predicted forage index values are shown. Solid lines below forage species indicate functional group membership of fishes: littoral (LIT), pelagic (PEL), demersal (DEM); and invertebrates: epifauna (EPI), infauna (INF)

combination of low summer means for both bottom water DO concentration and water column salinity (Table 5). These conditions are associated with more eutrophic conditions that are predisposed to poorer water quality (Deegan et al. 1997; Buchanan et al. 2005; Borja et al. 2011) and a salinity range (~5–10‰) typically associated with minima in estuarine faunal richness (Remane's artenminimum concept (1934); Deaton and Greenberg 1986; Wagner 1999; Schaffner et al. 2001; Vuorinen et al. 2015). The James River, although near the mouth of Chesapeake Bay, has a relatively low summer salinity value due to the location of the CBP water quality monitoring stations, but does not suffer from low DO

conditions in its bottom water (Table 5; Tuckey and Fabrizio 2016). Finally, water quality during the summer months (e.g., DO concentrations) in the lower mainstem region (the mainstem region adjacent to the southern tributaries) is typically higher than the middle mainstem region, a spatial pattern that has been linked to lower-than-expected macrobenthic biomass in the mid-Bay relative to the upper or lower mainstem regions (Table 5; Kemp et al. 2005). We also observed benthic biomass indices in the lower mainstem that were consistently higher or equivalent to the middle mainstem region (Fig. 4a–j). The relative quality of proximal mainstem habitats could

**Table 5** Regional annual mean ( $\pm$  SD) environmental variable values for winter–spring discharge (DISC), spring water column chlorophyll-*a* concentration (CHL), summer water column salinity (SAL), summer water column temperature (TEMP), summer bottom water dissolved oxygen concentration (DO)

Region	DISC (1000 ft <sup>3</sup> /s)	CHL ( $\mu$ g/l)	SAL	TEMP (°C)	DO (mg/l)
UPP	51.77 $\pm$ 13.50	8.71 $\pm$ 3.46	4.98 $\pm$ 1.73	25.65 $\pm$ 0.70	4.92 $\pm$ 0.47
MID	51.77 $\pm$ 13.50	11.78 $\pm$ 2.61	15.60 $\pm$ 1.57	25.29 $\pm$ 0.62	2.06 $\pm$ 0.30
LOW	51.77 $\pm$ 13.50	7.03 $\pm$ 2.60	23.26 $\pm$ 1.29	24.96 $\pm$ 0.74	5.21 $\pm$ 0.38
PAX	0.48 $\pm$ 0.17	14.59 $\pm$ 3.90	9.88 $\pm$ 1.56	26.19 $\pm$ 0.86	4.10 $\pm$ 0.55
POT	11.40 $\pm$ 4.19	9.86 $\pm$ 2.73	8.14 $\pm$ 2.10	26.05 $\pm$ 0.67	4.62 $\pm$ 0.57
RAP	2.20 $\pm$ 0.84	11.23 $\pm$ 2.81	14.97 $\pm$ 1.90	26.25 $\pm$ 0.64	4.25 $\pm$ 0.59
YRK	0.95 $\pm$ 0.47	7.84 $\pm$ 2.07	13.54 $\pm$ 2.47	26.36 $\pm$ 0.68	4.82 $\pm$ 0.33
JMS	9.43 $\pm$ 3.31	9.82 $\pm$ 3.78	8.62 $\pm$ 3.33	26.64 $\pm$ 1.16	6.38 $\pm$ 0.31

Regional (Upper (mainstem regions of Chesapeake Bay)—UPP, Middle Bay—MID, Lower Bay—LOW; Tributaries: PAX—Patuxent River, POT—Potomac River, RAP—Rappahannock River, YRK—York River, JMS—James River) annual mean ( $\pm$ SD) environmental variable values for winter–spring discharge (DISC), spring water column chlorophyll-*a* concentration (CHL), summer water column salinity (SAL), summer water column temperature (TEMP), summer bottom water dissolved oxygen concentration (DO). Data from 1995 to 2015; mainstem (UPP, MID, LOW) DISC values based on Susquehanna River data

be a factor influencing the among-tributary patterns we observed in forage abundance.

The increasingly positive correlation of relative abundances of most forage groups with decreasing distance between tributaries suggests regional conditions are an important determinant of year-to-year forage abundance. Similarities in regional weather patterns are likely to contribute to these spatial correlations, as are similarities in mainstem salinity regime at the mouths of proximal tributaries and landscape gradients in catchment land uses that can directly affect water quality and physicochemical conditions in the tributaries. For the demersal forage fish functional group, visual inspection of Fig. 5a shows that between-tributary correlations did not decline consistently with increased distance, unlike the other functional groups. While uncertain, the lack of a consistent spatial pattern in demersal forage fish abundances between tributaries could arise from the separation of egg/larval habitats from YOY habitats in the tributaries, particularly for shelf-spawning taxa such as spot and Atlantic croaker (Able and Fahay 1998). Opposing patterns in annual recruitment strength between these shelf-spawning demersal species and anadromous demersal species such as white perch are reported in Chesapeake Bay (i.e., Chesapeake Bay anadromous and shelf-spawning (CBASS) recruitment pattern; Wood and Austin 2009). The mechanism(s) responsible for the CBASS recruitment pattern may be linked to interannual variability in seasonal climate and functional group-specific consequences of bottom-up processes on annual recruitment (Wood and Austin 2009; Latour et al. 2017). Such life history differences among forage fish species within the demersal functional group could have contributed to the lack of a strong spatial correlation among tributaries.

### Forage–Environment Relationships

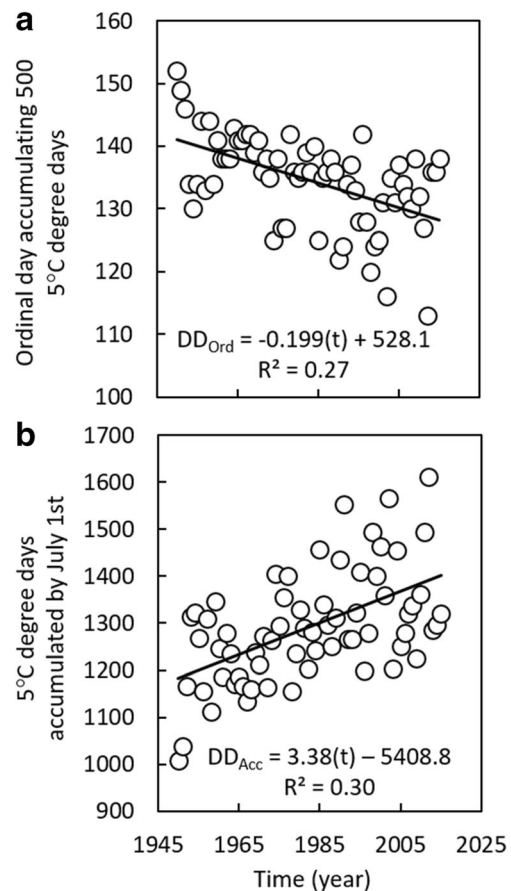
Our analysis documented a positive relationship between the 5 °C DD phenology variable and annual abundance of eight forage fishes and five invertebrate groups, indicating that years with a long warming trajectory in spring months tended to produce higher forage abundances. The inverse relationship between the annual summertime abundance of most forage taxa and the rate of water warming during spring, as indexed by the 5 °C DD phenology index, was remarkably consistent. Studies have often focused on the link between DD indices and size-at-age or size-at-day in fishes or invertebrates, many of which have documented a positive effect between growth rates and DD-based indices (Ward and Stanford 1982; Bunnell and Miller 2005; Neuheimer and Taggart 2007; Humphrey et al. 2014). Two forage groups (Atlantic menhaden, small bivalves) showed region-specific positive and negative relationships to the DD variable. Only one forage fish in a single tributary, YOY Atlantic croaker in the Rappahannock River, had a solely negative relationship to DD.

Potential mechanisms underlying the observed positive relationship between years with slow thermal accumulation (as indexed by the DD variable) and forage relative abundance in Chesapeake Bay include phenological processes that control the availability of suitable conditions for early-life stages of forage species (e.g., environmental conditions, prey match–mismatch), the timing of adult reproductive effort, and predation pressure. Changes in the environment during the late winter and early spring can directly affect survival of forage species during specific life stages, such as temperature effects on survival during larval and juvenile stages (Rumrill 1990; Pepin 1991; Gosselin and Qian 1997). For example, Secor and Houde (1995) showed that cohort-specific survival of larval striped bass in the Patuxent River was highest when water temperatures were intermediate (15–20 °C) during their first 25 days post-hatch.

It is also possible that the DD effect is an indirect ecological effect arising between forage taxa and their environment, such as match–mismatch scenarios in which the composition, duration, or timing of peak planktonic prey resources does not match the trophic demand of the forage taxa (Olson and Olson 1989; Cushing 1990; Rumrill 1990; Friedland et al. 2015). Previous research has demonstrated that phytoplankton–zooplankton bloom cycles and the timing of peak meroplankton abundance can occur earlier in years that warm sooner in marine and estuarine ecosystems (Edwards and Richardson 2004; Richardson 2008). For example, cold, wet winters delay the timing and increase the magnitude of peak spring concentrations of the copepod *Eurytemora carolleeae* in Chesapeake Bay and its tributaries such that up to 78% of annual recruitment variability of juvenile striped bass could be explained by a temperature-dependent development model and spring river discharge (Millette et al. 2019). Martino and Houde (2010) also reported a strong concordance between juvenile striped bass abundance and delayed, seasonal peak abundance of key zooplankton species (primarily *Eurytemora carolleeae* and *Bosmina longirostris*) in Chesapeake Bay. Nixon et al. (2009) documented weaker benthic–pelagic coupling and lower summertime epibenthic biomass in Narragansett Bay during years with earlier and weaker spring phytoplankton blooms. It is possible that changes in the timing and magnitude of the vernal phytoplankton bloom may have a similar effect on the productivity and summertime benthic biomass in Chesapeake Bay and its tributaries.

It was not possible to identify the specific mechanism associated with the inverse relationships between the phenology of warmer water and the relative abundance of forage taxa. Almost certainly, different species are responding to different physiological and ecological forces. Our finding is worth noting, however, given the clear trend in warming phenology observed in this study (Fig. 8) and expectation of long-term changes related to regional climate in the future (Najjar et al. 2010; Rice and Jastram 2015). For example, pervasive and regionally variable changes in warming phenology of sea surface temperatures across the northeastern North American continental shelf have been reported (Thomas et al. 2017). Also notable is the positive relationship detected between abundances of most forage fishes and invertebrates with summer water temperatures (Fig. 7g, n). The nuanced relationship between annual forage abundance and thermal conditions at different times of the year is an important consideration for predicting how food web dynamics in coastal ecosystems, such as Chesapeake Bay, are likely to respond to regional climate change.

Our model results indicate that forage responses to spring chlorophyll bloom intensities are complex and not easily captured with a single index over a fixed interval (i.e., CHL; Fig. 7b, i). A phenological approach that captures the timing of annual phytoplankton bloom conditions, for example our



**Fig. 8** Linear regression of annual time-series of 5 °C degree-day (a) phenology index (DD phenology) and (b) cumulative index (DD accumulated) against year (x-axis). Both models are significant at  $\alpha = 0.05$

DD approach, may yield better explanatory power for understanding the role of spring phytoplankton bloom dynamics on summer forage abundances (e.g., Malick et al. 2015). Changes in the phenology of seasonal plankton cycles have been proposed as a likely consequence of anthropogenic climate change in Chesapeake Bay (Najjar et al. 2010); such changes could induce shifts in production of forage taxa. To date, evidence for phenological and spatial shifts in winter–spring phytoplankton blooms has been identified in some regions of Chesapeake Bay, but not others (Testa et al. 2018).

The importance of climatological forcing is underscored by the significant covariation between several forage indices with annual spring river discharge and the AMO index. Unlike the DD phenology index, relationships of forage to these climate indicators were not unidirectional. For example, the positive relationship observed for resident and anadromous estuarine forage fish species with the AMO in the mainstem contrasts with the negative relationship for benthic invertebrates. In a synoptic study of Atlantic menhaden recruitment dynamics along the US Atlantic coast, Buchheister et al. (2016) reported the AMO to be negatively related to Atlantic menhaden recruitment in Chesapeake Bay, but positively related to

recruitment in other estuaries. Their findings of among-estuary differences and our findings of within estuary-differences in the relationship between AMO and regional Atlantic menhaden abundance underscores the importance of spatial scale when considering environmental consequences of climate forcing for forage populations. The reason (or reasons) for the negative relationship between AMO and invertebrate abundance is unclear, but the higher freshwater flows and warmer air temperatures present during the positive AMO phase (which was the case during the years of our study) could enhance stratification, increasing hypoxia in estuarine waters decoupling productive pelagic areas from benthic food webs, and negatively influencing the growth, productivity, or survival of benthic invertebrates (Nixon et al. 2009). Variability or weak relationships between climate indices and some forage groups could also reflect non-stationarity in the correlations of physical and ecological processes with climate indices over time, as has been demonstrated for some Pacific climate indices (Litzow et al. 2020).

Abundances of forage fishes and benthic invertebrates responded positively to winter–spring freshwater discharge in the upper and middle mainstem, but responses were more variable in the tributaries. The presence of an identifiable discharge response relationship in the upper Bay could be linked to the effect of discharge on the location of the salt front, thereby controlling the salinity structure and relative availability of osmotically suitable habitat for species residing at the boundary of the tidal fresh-oligohaline zone. River discharge can also influence the position, physical characteristics, and sediment resuspension dynamics of the estuarine turbidity maximum (ETM), a highly productive frontal region in the upper Chesapeake Bay that can be 10–30 km in extent (Boynton et al. 1997; Sanford et al. 2001). Low-discharge years have been linked to poor recruitment success for some fish species that use the ETM during their early-life stages, including white perch and striped bass (North and Houde 2003). There may be similar relationships between discharge, estuarine habitat structure, and benthic invertebrate forage taxa in Chesapeake Bay, as reported for invertebrates in other estuaries and coastal regions (Kimmerer 2002; Gillson 2011; González-Ortegón and Drake 2012; Palmer and Montagna 2015).

In our analysis, the absence of a consistent discharge abundance signal for more of the forage fishes in either the tributaries or mainstem was unexpected given the considerable evidence for effects of discharge on early-life survival, recruitment, and assemblage structure of estuarine species (e.g., Loneragan and Bunn 1999; North and Houde 2003; Wood and Austin 2009). It is possible that the shorter time series of forage fish data in the mainstem reduced our statistical power to identify a discharge relationship. However, that does not account for the absence of discharge responses in the tributaries. Alternatively, our definition of the winter–spring

interval (Jan–June) may be too broad to capture the specific temporal intervals during which discharge influences the abundance of forage fishes in Chesapeake Bay. By starting in January, we may have failed to account for earlier, fall–winter discharge conditions that could be an important determinant of forage biomass during the following year (Jung and Houde 2004; Wingate and Secor 2008). Winter–spring discharges are predicted to increase for Chesapeake Bay (Najjar et al. 2010). The consequences of changing freshet levels and covarying environmental conditions could substantially shift the seasonality of occurrence and the composition and productivity of forage communities in Chesapeake Bay.

### Limitations of this Study

Our research focused on investigating the relationship between forage relative abundance (fishes) or biomass (invertebrates) and environmental conditions at an annual time-step in Chesapeake Bay. While this provides a framework for assessing bottom–up forcing on forage abundance within the estuarine food web, there are several important limitations to the study. For example, we did not analyze individual taxa among the benthic invertebrates, emphasizing instead a functional group approach that presumes taxa within groups respond similarly to environmental conditions. Our approach increased sample size but reduced specificity. This was beneficial to calculate biomass indices for every combination of functional group, region, and year. Higher taxonomic resolution would have reduced the spatial and temporal scope of the analysis for many forage taxa, but it might have provided additional insight into the environmental response(s) of some forage taxa. Our bottom–up approach to investigate patterns in forage abundance did not consider top–down processes, for example effects of predator density on forage abundance or the role of fisheries exploitation on managed species indirectly affecting non-target, food web components at lower trophic levels.

There are numerous spatial and temporal gaps in the monitoring surveys of forage taxa in Chesapeake Bay that, if filled, could increase the power of future analyses to identify key forage–environment relationships. For example, a targeted forage fish survey does not exist in the mainstem of Chesapeake Bay. Zooplankton data were not included as a potential covariate of forage fish indices of abundance because zooplankton monitoring by the Chesapeake Bay Program ceased in 2002 (<http://www.chesapeakebay.net/what/data>). Zooplankton forms a direct trophic link between primary production and forage fishes, including larval, juvenile, and adult stages for some species. Because of their role as food for forage fishes, indices of zooplankton abundance, biomass, or productivity might contribute to explaining interannual variability in forage abundance.

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