Final Report

Environmental, Spatial and Temporal Patterns in Chesapeake Bay Forage Population Distributions and Predator Consumption

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Project summary

The research focused on evaluating: 1) evidence of spatial and temporal structuring of forage populations and predator consumption along environmental gradients and, 2) the effects of variability in abundance of multiple forage taxa on predator consumption patterns. The project built upon previous research (Buchheister 2016). We evaluated patterns patterns of relative abundance of important invertebrate forage taxa at a highly aggregated, functional group level. Invertebrate forage groups included *Macoma* spp. bivalves, non-*Macoma* (other) bivalves, polychaetes, and small crustaceans (including amphipods and isopods). Species-level analyses focused on forage fish previously identified as important or potentially important forage taxa in Chesapeake Bay (Ihde et al. 2015), including bay anchovy, young-of-the-year (YOY) Atlantic menhaden, YOY weakfish, YOY spot, YOY Atlantic croaker, Atlantic silversides, mummichog and killifishes. The river herrings, alewife and blueback herring, were included where possible due to strong interest in their recovery in Chesapeake Bay and their historically significant abundances in the ecosystem. Our results indicate that the relative interannual abundance of many of the forage group covaried with the timing of spring time warming of the water, winter-spring flow volume, and the Atlantic Multidecadal Oscillation (AMO). Annual mean per capita consumption by dominant predators – including several size-classes of striped bass, summer flounder, Atlantic croaker, weakfish, white perch and spot – did not covary with forage density in the mainstem but did show significant non-linear relationships with several key environmental variables. Multivariate diet analysis suggested the diet of several predators was influenced by environmental variables (particularly AMO) and that predator diets differed between Maryland and Virginia portions of the mainstem, however these spatial differences were subtle. Overall, we found that there is evidence to suggest that years in which winter water temperatures warm slowly are conducive to higher summertime forage abundances. We failed to find evidence that

per capita consumption was linked to relative abundance of individual forage taxa, but consumption did covary with environmental conditions in complex, generally non-linear ways.

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INTRODUCTION

Forage taxa are a critical component in ecosystem-based fisheries management because they link lower trophic levels of food webs to economically valuable predators (Bigford 2014). Recognizing this, the Sustainable Fisheries Goal Implementation Team of the Chesapeake Bay Program (CBP) committed to "*By 2016, develop a strategy for assessing the forage fish base available as food for predatory species in the Chesapeake Bay.*" The pivotal role of forage in ecosystem-based fisheries management (EBFM) was highlighted in a recent Forage Workshop sponsored by the CBP's Scientific and Technical Advisory Committee (Ihde et al. 2015) and summarized in the online Forage Fish Outcome Management Strategy (CBP 2015). The workshop produced research objectives aimed at evaluating the status and role of forage species in Chesapeake Bay. Pursuant to establishing these research objectives, recent research has documented: 1) diverse patterns in interannual abundance of forage taxa, including stochastic stability and low-frequency cycles; and 2) similar long-term trends in consumption of particular forage taxa by a suite of predators (Buchheister et al. 2016, Buchheister and Latour 2016). Those results suggest that the 'portfolio' of forage consumed by predators in Chesapeake Bay is largely controlled by relative availability of specific forage taxa. However, there remains knowledge gaps with respect to understanding how environmental conditions affect spatio-temporal distributions of forage and how fluctuations in forage availability affect consumption of forage groups (e.g., pelagic forage fishes) by predator fishes.

In this project, we addressed two objectives to investigate the knowledge gaps:

1. Objective 1 – *Identify environmental gradients associated with spatial and temporal patterns in relative abundance of forage taxa in Chesapeake Bay*
2. Objective 2 – *Explain how spatial and temporal gradients in environmental variables control consumption of forage taxa, and quantify the effect of forage abundance on consumer populations*

This final report provides a description of our efforts to address these objectives. Overall, we have accomplished our goals for this project although our findings suggest that a much larger effort will be required to fully understand predator-forage dynamics in Chesapeake Bay. Our findings highlight, a) intriguing relationships between forage groups and several key environmental variables linked to local (10's of km) and regional (1000's of km) climate conditions, b) a suggestion that predator consumption is related to environmental conditions but no evidence that *per capita* consumption covaries with indices of forage abundance, c) evidence of subtle spatial differences in predator diet in the mainstem across a management-relevant boundary (MD-VA state line), and d) that there is a shared, long-term trend toward reduced per capita consumption from 2002-2015 across the predator taxa considered here. These results are all indicative of a dynamic predator-forage condition in Chesapeake Bay that is responsive to environmental drivers. From a food web perspective, the predator assemblage appears typified by a long-term decline in the abundance of large predators that coincides with a long-term decline in per capita consumption.

METHODS

Data sources

Data from several sources were used in this study. We obtained time series of mean monthly river flow for those major river tributaries of Chesapeake Bay gauged by the United States Geological Survey (USGS; *n* = 9, http://waterdata.usgs.gov/nwis/sw). Two annual indices of large-scale regional climate were downloaded from the Earth System Research Laboratory, NOAA Physical Sciences Division website (http://www.esrl.noaa.gov/psd/data/timeseries/). Water quality data (chlorophyll-a, water temperature, dissolved oxygen concentration, salinity) at fixed stations throughout Chesapeake Bay were downloaded from the Chesapeake Bay Program (CBP) DataHub website (http://datahub.chesapeakebay.net/). Site water quality and depth data that were obtained simultaneously with sampled benthic invertebrates and forage fish were from two sources. For benthic invertebrates (Table 1), site-specific water quality and depth data were downloaded from the Versar Chesapeake Bay Benthic Monitoring Program website (http://www.baybenthos.versar.com/default.htm). For fishes, a combined 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 conducted from 1995-2007 was downloaded from the hjort.cbl.umces data portal (http://hjort.cbl.umces.edu/chesfims.html). Site-level survey data from the Virginia Institute of Marine Science (VIMS) Juvenile Striped Bass Survey (http://www.vims.edu/research/topics/fisheries), including forage fish catch-per-unit-effort (Table 1), water quality and depth data, were provided by collaborators M. Fabrizio and T. Tuckey. Data on predator stomach contents, catch-per-unit-effort and physical/environmental conditions were collected by the Chesapeake Bay Multispecies Monitoring and Assessment Program by PI Latour (ChesMMAP; http://www.vims.edu/research/topics/fisheries). Seine survey data on forage fish catch-per-unit-effort from Maryland tributaries (Table 1) were obtained from E. Durrell at Maryland Department of Natural Resources (MDDNR) for a previous Chesapeake Bay Trust-funded forage project (Buchheister et al 2016, CBL 2015-045CBT)[1].

Spatial scope of analyses – Time-series of environmental and biological data from the various surveys were analyzed to provide annual estimates of predictor and response variables in each of the major regions of interest in this study (Figure 1): Patuxent River, Potomac River, Rappahannock River, York River, James River, and the mainstem of Chesapeake Bay. The mainstem of the Bay was treated as a single spatial unit or delineated into sections corresponding to dominant salinity regimes. One treatment separated the mainstem into three sections (upper [oligohaline], middle [mesohaline], lower [polyhaline]) and the other treatment separated the mainstem into two sections (upper [oligo-mesohaline], lower [meso-polyhaline]). The inclusion of multiple section treatments was necessary to accommodate differences in the spatial availability of forage and predator data.

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[1] Maryland DNR data for 2014-2015 were not obtained in time to be included in the analyses presented in this report.

Water quality indicators – Environmental data from the CBP Water Quality Monitoring Survey at fixed stations were analyzed to provide annual estimates of several water quality variables. A comprehensive description of survey methods is available through the CBP DataHub portal. Briefly, vertically stratified data are collected at a frequency of ≤ 1 month at each station. Measurements are taken at 1–2-m intervals from the surface to near the bottom of the water column. Three environmental indices derived from the CBP Water Quality Monitoring Survey were estimated from below pycnocline measurements of salinity, temperature, and dissolved oxygen concentration, and one index was estimated based on the integrated mean value of measurements over the entire water column (chl-a). Indices of annual bottom-water salinity, temperature and dissolved oxygen concentrations were calculated for the summer season which corresponded to months of June – August. The chl-a index was calculated over the months from the late winter to late spring interval (February – April) and was intended to represent the intensity of the winter-spring phytoplankton bloom in a given year. For all water quality variables, annual estimates were derived using a repeated measures analysis of variance (ANOVA) in which region, month, season and all interaction terms were considered fixed effects, station depth was included as a continuous covariate and station was treated as a random effect to account for spatial autocorrelation. Models were run using the Proc Mixed procedure in SAS (v9.4) and estimates were the least-squares means for each combination of region × season × year at each spatial scale. Throughout this project, all statistical models were run using SAS, R or a combination of these two software packages.

This project focused on aspects of forage and consumption in the estuarine regions of the Bay; consequently, CBP monitoring stations were excluded if the mean salinity was < 1 over the full 1984–2015 interval. These tidal freshwater stations were excluded to avoid strong effects of freshwater conditions influencing estuarine water quality. The exceptions were those stations located in the upper mainstem region of the Bay (Stations: CB1.0, CB1.1, CB2.1, ET1.1), which were included in analyses to provide sufficient and representative measurements of water quality conditions in the upper Bay. Estimates of chl-a and salinity were strongly influenced by the inclusion of stations with salinity < 1 in the upper mainstem. Including the four indicated stations increased mean chl-a estimates and reduced salinity estimates. Excluding stations with salinity < 1 in other regions slightly reduced estimates of chl-a (-1.66 ± 1.03 µg/l), dissolved oxygen (-0.45 ± 0.10 mg/l) and water temperature (-0.05 ± 0.05 °C), and predictably increased salinity (+1.55 ± 0.73).

Thermal (Degree day [DD]) indicators – Degree day (DD) indices were included as potential predictor variables. We selected three central monitoring sites as integrative locations to describe baywide patterns for interannual differences in thermal conditions. Data were obtained for the Solomons, MD monitoring station (SLIM2; located along the mainstem of mid-Chesapeake Bay), the VIMS Ferry Pier monitoring location (Gloucester Point in the lower Bay, VA), and the Goodwin Islands monitoring station at the mouth of the York River (VA). Breaks in the Solomons time series were reconstructed from a relationship with regional air temperature records. There is a strong relationship between air and water temperatures in Chesapeake Bay (Ding and Elmore 2015) and a 4-year monthly time series of data at the SLIM2 station showed a positive, linear relationship between paired air- and water-temperature data (Figure 2). This linear model was used to convert air temperature to water temperature at the SLIM2 station. Air temperature data missing from the SLIM2 station time-series during the interval 1984-2001 were reconstructed from those at the Royal Oak, MD. Air temperature at these stations is highly correlated based on paired monthly average temperatures during the intervals 1950-1983 and 2002–2015 (Pearson Correlation coefficient, $r_{Pearson} > 0.99$, $p < 0.0001$). This process yielded a daily water temperature time series indicator from the Maryland portion of Chesapeake Bay spanning the years 1950 to 2015 (Figure 3a). Breaks in the VA station data also occurred (Figure 3b) and a regression of concurrent MD water temperatures against VA station water temperatures was used to reconstruct the complete 1950-2015 time series of mean daily water temperatures (Figure 3c). All regressions used to relate temperature data among stations or between regions were significant (Figure 4d-e).

We selected 5°C as a functional DD temperature threshold. Sensitivity tests of annual cumulative DD values from January 1 to June 30 based on DD temperatures = 5, 8 and 10°C were highly correlated ($r_{Pearson} = 0.91$–0.98, $p << 0.05$) and showed no difference in interannual patterns. We therefore selected to use only the 5°C DD threshold for calculation of two annual indices. The first DD index was a cumulative count of all DD in excess of the 5°C DD threshold from Jan 1 to June 30 of each year. The second index was a phenological index that was derived by calculating the integer day each year at which a cumulative threshold of 500 5°C DD was achieved. The phenological index provides information on interannual differences in the *timing* of accumulating warm water temperatures whereas the cumulative count index is a metric of *total* daily temperature anomalies > 5°C accumulated prior to July 1st.

Fluvial discharge – Mean monthly river discharge data were obtained from the USGS for those gauging stations that were located nearest to the tidal head in the Susquehanna, Patuxent, Potomac, Rappahannock, York and James Rivers. An index of annual fluvial discharge was derived by averaging the mean monthly discharge values from January 1st through June 30th of each year. For those tributaries with multiple gauge stations located near the tidal head, an average was taken of the monthly discharge measured across all gauges.

Hypoxic volume – Hypoxic volume estimates from 1985 to 2013 were generated using the Chesapeake Bay Program Interpolator (v4.6) and provided by Mike Lane (Old Dominion University) and Jeremy Testa (Chesapeake Biological Laboratory, *personal communication*). The interpolator is a cell-based model that uses a 3-D nearest-neighbor algorithm to estimate oxygen concentration each 1 × 1 km (horizontal) × 1 m (vertical) cell.

Climate variables – We considered two large-scale regional climate indices, the Atlantic Multidecadal Oscillation (AMO) and the North Atlantic Oscillation (NAO). Both of these indices 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. *in press*). Each index was downloaded as a standardized time-series (i.e., mean = 0 and unit variance). Initial testing showed the indices were negatively correlated ($r_{Pearson} = -0.43$, $p = 0.0004$); therefore, most analyses below used either AMO or NAO rather than both variables in the same model run to avoid collinearity in predictor variables.

Forage indices

Several statistical models were required to derive spatially-explicit indices of abundance for benthic invertebrate and fish forage taxa because of differences in survey methods that varied between invertebrates and fish surveys and between the states of Maryland and Virginia. Specific forage functional groups and species were selected for analysis based on long-term stomach contents data of selected predatory fish species (Ihde et al. 2015).

Benthic invertebrate forage indices – Invertebrate forage indices were estimated from the random station component of the CBP's Benthic Monitoring Survey. This survey includes a fixed station component that began in 1984 and a random station component that was initiated between 1994 and 1996. Both survey components continue to the present. Methods for both survey components are available at the CBP DataHub website; methods for the random station component are briefly described here. In this component, a total of 25 stations are selected annually in each of 10 different survey strata. A single deployment of a 440 cm^2 Young Grab from a research vessel is used to collect a sample of epibenthic and benthic fauna at each of the randomly chosen stations. The sampling is conducted in the interval extending from late July through September each year, but logistical and weather-related constraints lead to occasional sampling from early July to early October. On the vessel's deck, samples are sieved through a 500-um screen and organisms preserved in 10% formalin with Rose Bengal. All organisms are identified to the highest possible taxonomic resolution and then processed to obtain ash-free dry weight (AFDW) in a muffle furnace for 4 hrs at 500°C. Ash-free dry weights of taxa are scaled to a biomass estimate for a normalized area of 1 m^2 prior to analysis.

A delta-generalized linear model (Lynch et al. 2012) was used to estimate annual index values for several key groups of invertebrates previously identified as important forage for Chesapeake Bay predatory fish (Ihde et al. 2015; Table 1). Ash-free dry weight of each species within functional groups was summed for a particular sample. Estimates of presence-absence probabilities at each station were then analyzed using a logistic framework:

$$\text{logit}(\pi_i) \equiv \log\left(\frac{\pi_i}{1-\pi_i}\right) = \alpha + \beta' x + e$$

in which presence-absence of each functional group (i) was modeled as a binomial variable (π) that was dependent on three explanatory variables (class variables: region [tributary or mainstem section], year; continuous variable: station depth) and an interaction term (region x year).. Model intercept (α), slope parameters for each predictor or combination of predictors (β') and residual error term (e) are included. The resulting model provides least-squares means estimates that range from 0-1 and provide an estimate of the probability of observing each functional group in a given region in a given year.

The second stage of the delta-GLM involves removing all 0's from the dataset for each functional group, then using a generalized linear model to estimate the biomass of functional groups when present. Observed AFDW biomass for each forage functional group (F_i) was natural log-transformed and used as the response variable in the model:

$$\ln(F_i) = \alpha + \sum_1^l \beta_l (REG_j \times YR_k) + \beta_m Z + e$$

where parameter definitions are identical to those in the logistic component and least-squares means estimates of biomass when present were calculated. Probability estimates for each combination of region and year were then multiplied by the back-transformed estimates of biomass when present to yield final index estimates of annual biomass densities for each region for each functional group:

$$Index_{ijk} = \pi_{ijk} \times F_{ijk}.$$

Forage fish indices – Indices of relative forage fish abundance were developed for five ongoing and historical surveys in the Chesapeake Bay that used various gears and sampled multiple regions, seasons, and years. Focal forage fishes included: young-of-the-year (YOY) Atlantic croaker (*Micropogonias undulatus*), YOY weakfish (*Cynoscion regalis*), YOY white perch (*Morone americana*), and YOY spot (*Leiostomus xanthurus*), alewife (*Alosa pseudoharengus*), bay anchovy (*Anchoa mitchilli*), blueback herring (*Alosa aestivalis*), killifish (*Fundulus* spp.), Atlantic menhaden (*Brevoortia tyrannus*), mummichog (*Fundulus heteroclitus*), and Atlantic silverside (*Menidia menidia*). Unlike the previous CBT-supported forage project (Buchheister et al. 2016), we focused on individual survey datasets that were as comprehensive as possible within a given spatial region. We avoided integrated multiple surveys from different areas (e.g., the Conn method) due to concerns that spatial averaging during the estimation process could obscure regional trends arising from localized responses to environmental influences. Two seine-survey datasets were selected to estimate forage fish abundancnes from MD and VA tributaries--the MD DNR Juvenile Striped Bass Index seine survey (MJS, 1959-2013) which samples the Potomac and Patuxent Rivers and the VIMS Juvenile Striped Bass Seine Survey (VJS, 1968-1973 & 1980-2015) that is conducted in the Rappahannock, York and James Rivers. Trawl-survey data appropriate for estimating annual indices of abundance for forage fish species and YOY of managed fisheries species that also serve as forage were obtained from the VIMS Juvenile Fish and Blue Crab Trawl Survey (VJT; years 1988-2015; Mary Fabrizio and Troy Tuckey, *personal communication*). The VJT collects samples in the mainstem and tributaries of the Virginia portion of Chesapeake Bay. A similar long-term trawl survey is not available from the MD portion of Chesapeake Bay; 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 1995-2007 in the mainstem of Chesapeake Bay where samples were taken from near the bay mouth to the upper bay.

Index estimates were derived using the delta-GLM framework, but there were differences for each dataset due to unique characteristics of the fish surveys and the sparse catches of certain species (e.g., alosines in the TIES/CHESFIMS data set). For the TIES/CHESFIMS survey, we used an identical delta-GLM model structure to that described above for the benthic invertebrate forage. Model estimation methods varied because some species required particular approximation algorithms (e.g., Laplace, Gaussian-Hermite quadrature) to achieve model convergence due to high incidences of zero catches. Indices were derived for each region of the mainstem Bay and for the mainstem as an integrated whole.

In the MJS survey, two seine hauls are taken during each station visit. We discarded the data from the second seine haul and used only the first haul at each station to avoid issues with pseudo-replication. Additionally, data records for stations in which total catch of fishes was zero were not provided by MD DNR. While this missing data is a surmountable data gap, it could not be addressed or resolved in time for completion of this project. Therefore, an integrated index of abundance of forage fishes for MD tributaries as a whole was estimated for each forage species from the combined Patuxent and Potomac Rivers using the delta-GLM approach. For the VJS survey, indices of abundance of forage species were estimated for each VA tributary (VJS). For each of the MJS and VJS survey datasets, we applied a mixed-effects delta-GLM model to account for autocorrelation in catches arising from fixed stations. A compound-symmetry variance-covariance structure was assumed in these models and Laplace estimation was used because of the high prevalence of zero catches in the datasets. To provide a comparable index from VA tributaries that is comparable to the index from the MD tributaries, we calculated an integrated index for the VJS tributaries to provide a ‘state-level’ index, in addition to calculating tributary-specific indices for each species.

Predator consumption indices

Estimates of consumption relied on data collected by the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP) from 2002-2015, using the methods described by Buchheister et al. (2016). Details on the survey methodology and protocols are reported by Bonzek et al. (2014). Briefly, the survey relies on a random-stratified design, sampling in five latitudinal regions of the bay and in three depth strata (10-30 ft, 30-50 ft, and 50+ ft). A grid of 1.9 km^2 cells was superimposed over the mainstem, where each cell represented a potential sampling location. The number of stations sampled in each region and in each stratum was proportional to the surface area of water represented. ChesMMAP conducts five cruises per year (bimonthly from March to November) in the Bay’s mainstem, sampling approximately 80 stations per cruise. The survey uses a 45-foot balloon otter trawl with 6-inch stretch mesh on the body and 3-inch stretch mesh in the cod-end to collect late juvenile and adult fishes. The target tow speed for each sampling location was 3.0 kts but occasionally varied depending on wind and tidal conditions. Tows were 20 min duration, unless known obstructions or other logistical issues forced a tow to be shortened (if a tow duration was at least 10 minutes, it was considered valid). Upon tow retrieval, fish catches are sorted by species, divided into 3-4 size classes (if large size ranges occur for a species), and individuals are measured for length. Samples are selected for stomach removal and subsequent gut-content analysis in the laboratory. In the laboratory, stomach contents are identified to the lowest possible taxonomic resolution, enumerated, and weighed.

Data for six key predator fishes were utilized, including: striped bass (*Morone saxatilis*), summer flounder (*Paralichthys dentatus*), Atlantic croaker (*Micropogonias undulatus*), weakfish (*Cynoscion regalis*), white perch (*Morone americana*), and spot (*Leiostomus xanthurus*). Data for each predator species were divided into multiple size classes (designated as small, medium, and large) to account for ontogenetic shifts in diets (Buchheister and Latour 2015) and differences in presumed sampling-gear selectivity by size. Information on gear selectivity by size is not available for the survey; therefore, we defined the small size class cutoff as the mode of the length-frequency distribution (rounded to the nearest 5 cm) for each predator (Buchheister et al. 2016). Analogous to length-based catch-curve methods for estimating total mortality (Sparre and Venema 1998), we assumed that fish longer than the modal length (i.e. the medium size class) were fully recruited to the sampling gear. For striped bass and summer flounder that have the broadest length distributions, we also defined a large size class to account for observed dietary shifts (Buchheister and Latour, 2015), and a potential decrease in selectivity for striped bass since the trawl sampling gear is believed to have a dome-shaped selectivity for that species. The potential for this selectivity is acknowledged but sufficient data do not currently exist to account for this size-dependent selectivity in our consumption analyses. The cutoffs for the large size classes were selected to balance the number of available samples among the medium and large size classes and to approximate the sizes where dietary breaks are the strongest (Buchheister and Latour, 2015).

Mean weight of stomach contents – The mean mass (g) of stomach contents was calculated for each predator species/size class combination at each sampled station. The across-stations mean was then calculated by weighting each station and size-class combination by the number of fish caught in the station tow (e.g., cluster sampling estimation). Any stomachs determined to be empty were included in the calculation. If fewer than 30 stomachs were sampled in a year for a given size class of a predator, the mean stomach content weight across years was used to minimize error and excessive variability caused by low sample sizes. Of particular note, the global mean was used for spot from 2002-2007 due to inconsistent analysis of stomach samples during this time period resulting in very low sample sizes. This criterion of a minimum sample size represented a compromise between maintaining temporally-explicit stomach contents (for which most species and years had ample data) and generating biased estimates created by low sample sizes.

Diet compositions – Diet compositions were estimated using a cluster sampling estimator as described by Buchheister and Latour (2015). For each predator, the diet composition by weight (D) of prey group (*k*) was calculated as:

$$D_k = \left(\sum_{h=1}^{H} n_h q_{hk} \right) \left(\sum_{h=1}^{H} n_h \right)^{-1}$$

where H = the number of trawl tows that contained the predator of interest, n_h = the number of individuals of the predator collected at sampling location *h*, and $q_{hk} = m_{hk} m_h^{-1}$ such that m_h = the total mass of all prey groups encountered in the stomachs of the predator from sampling location *h*; and m_{hk} = the total mass of prey group *k* occurring in the predator stomachs from sampling location *h*. The cluster sampling estimator accounts for the lack of independence among sampled predators from the same station, and it thus provides a more reliable description of the diet at the population level (by weighting the catch by predator abundance). To investigate spatial changes in dietary composition (e.g., Maryland vs. Virginia), a non-metric multidimensional scaling

(NMDS) analysis was performed for each predator species/size class combination (see *Non-metric multidimensional scaling analysis* below: data are provided in Appendices 2 & 3).

Prey groups – Our analyses focused on prey groups that have been previously identified as important prey for predator fishes in Chesapeake Bay (Buchheister and Latour 2015, Ihde et al. 2015). Ten prey groups defined as important forage taxa are: bay anchovy, YOY Atlantic menhaden, mysids, bivalves, polychaetes, YOY spot, YOY Atlantic croaker, YOY weakfish, crustaceans (e.g. sand shrimp and mantis shrimp), and "other" prey. Identification of polychaetes and bivalves to the species or genus level was often not possible due to digestion and a lack of identifiable hard parts; consequently, differences in taxonomic resolution of prey groups was in part a logistical limitation of traditional diet analysis.

Consumption rates – Daily per capita consumption (*c*) was estimated using a gastric evacuation rate model (Eggers 1977, Elliott and Persson 1978). Daily per capita consumption (*c*) for each predator *i*, length group *l*, and six-month time period *t*, was defined as:

$$c_{i,l,t} = 24 \cdot S_{i,l}^{\gamma} \cdot E_{i,t}$$

Where the scalar 24 is the number of hours in a day, $S_{i,l}$ is the mean stomach contents (in grams) for predator i and length group l, γ is a shape parameter that was assumed to be 1 following other studies (Overholtz et al. 2000, Link and Sosebee 2008), and the evacuation rate $E_{i,t}$ is calculated as:

$$E_{i,t} = \alpha \cdot e^{\beta T_{i,t}}$$

Where α and β are fitted constants and $T_{i,t}$ is the average ambient water temperature (°C) for predator i in time period t. The α and β constants were set at 0.004 and 0.115, respectively, which are conservative values for teleost fishes (Durbin et al. 1983) and are commonly used in similar studies (Overholtz et al. 2000) because consumption results are not overly sensitive to these parameters (Overholtz et al. 2000, Link and Sosebee 2008). Mean water temperatures were calculated for each predator using *in situ* bottom temperature data from sites where the predator was captured. Seasonal water temperatures were calculated using data pooled across years because interannual differences were mostly non-significant and could be influenced by the exact timing of survey cruises (or by missing cruises).

Daily per capita consumption estimates were then scaled to six-month (i.e., "seasonal") periods and expanded using the estimates of abundance for each predator. Thus, the scaled population consumption $C_{i,l}$ (in mt/yr) was calculated as:

$$C_{i,l} = \sum_{l=1}^{3} \sum_{t=1}^{2} 182.5 \cdot c_{i,l,t} \cdot N_{i,l,t} \cdot 10^{-6}$$

Where 182.5 is the number of days in the half-year and $N_{i,l,t}$ is the minimum swept area estimate of abundance from the trawl survey and 10^{-6} is the conversion from grams to metric tons. Swept-area abundances were calculated using catch data for all survey strata to provide bay-wide abundance estimates. Abundance estimates are assumed to be conservative, minimum estimates of abundance because effects of size selectivity and variable catch efficiencies (e.g., due to gear avoidance) were not available for the examined predators.

For each predator species/size class combination, annual consumption was calculated as the sum of the consumption for two semi-year (i.e., six-month) periods. Use of a six-month period allowed us to capture the large changes in abundances and associated consumption witnessed for the migratory predators in Chesapeake Bay. The seasons for each predator were determined based on the six-month period in which predator abundances were highest (Appendix 1), as estimated from ChesMMAP data and historical ChesMMAP reporting (Bonzek et al. 2014).

Statistical modeling

Forage-environment analysis – Generalized linear models were selected to analyze relationships between annual indices of forage and environmental conditions. These flexible models include a response-predictor link function and are capable of accommodating non-normal residual distributions, making them well-suited for ecological analyses (Guisan et al. 2002). Correlation testing of potential predictor variables indicated significant correlations between several environmental indices (Pearson correlation coefficient, $p < 0.05$). To avoid multi-collinearity, one each of the correlated variables were removed until all remaining predictors were uncorrelated. The final list of environmental indices included as potential predictors in the models were: spring freshwater discharge (Flow), spring chlorophyll-*a* concentration (CHL), day of the year at which a threshold of n=500 5°C degree days is reached (DD; phenological DD variable), hypoxic volume (HYP) and the Atlantic Multidecadal Oscillation (AMO). An advantage of generalized linear models is the ability of the model to accommodate non-Gaussian data distributions, a common aspect of abundance indices and a condition present in this study. Several models of the underlying data distributions were tested (i.e., Normal, Lognormal, Negative binomial, Gamma) and the results compared using model convergence and an information theoretic criterion (Akaike's Information Criterion corrected for small sample size [AICc]; Wagenmakers and Farrell 2004). Stipulating a gamma distribution yielded optimal model performance, with all models successfully converging except for a single YOY weakfish model.

'Portfolio effect' of multiple suitable regions – This analysis quantified the degree to which interannual variability in forage indices of abundance was reduced when forage species were observed in multiple regions. This analysis is predicated on the expected reduction in variance due to averaging over multiple, non-correlated data-series, i.e., the portfolio effect (Doak et al. 1998, Tilman et al. 1998). From an ecological perspective, the availability of multiple suitable habitats should stabilize the year-to-year variability in forage abundance as long as the abundances in each habitat are not perfectly correlated (Doak et al. 1998). We used the approach of Kerr et al. (2009) in which the observed reduction in variability that occurs when integrating multiple time-series is compared to a null condition of perfect, positive correlation among time-series. For each forage group, we computed the coefficient of variation for each spatial region j over the time-series available (CV_j) and the CV of the time-series at the total or 'metapopulation' scale (CV_M). The time-series estimates were used to construct an index-weighted estimate of

metapopulation CV under the null condition of perfect, positive correlation (CV_{Null}) by summing the index-weighted CV_j values:

$$CV_{Null} = \sum_{j=1}^{j=n} \left(\frac{I_j}{I_T} CV_j \right)$$

where I_j is the proportion of the index (I) that spatial region j contributed to the total index value across regions (I_T). The portfolio effect (PE) is then calculated as the deviation from 1 of the ratio of CV_M to CV_{Null}:

$$PE = 1 - \left(\frac{CV_M}{CV_{Null}} \right).$$

Non-metric multidimensional scaling analysis – Non-metric multidimensional scaling (NMDS) was used to examine the patterns in dietary similarity for the different fish predators. NMDS is a non-parametric ordination technique that relies on the rank order of pairwise predator diet dissimilarities. One of its major benefits is that it does not make any underlying distributional assumptions of the data (Clarke and Warwick 2001). Predator diets were obtained from the ChesMMAP trawl survey, and diets were calculated for four predators (summer flounder, Atlantic croaker, weakfish, and striped bass[2]) by year, size class, and region (i.e., State). Predator size classes were defined following the same breaks as described above. We chose to examine diets using States (MD and VA) as the regional groups, to represent spatial differences in diet; data limitation prevented us from examining the diet at a finer spatial resolution. Diets were only evaluated using the 6-month index period when each of the predators occurs in greatest abundance in the Bay. Predator diets were summarized as the proportion by weight for each of 10 different functional prey groups: anchovies, Atlantic croaker, bivalves, Atlantic menhaden, mysids, other crustaceans, polychaete worms, spot, weakfish, and other prey. To minimize the effect of rare prey groups, the diets were square-root transformed. For each predator, similarities among year-size-State diets were assessed using a Bray-Curtis dissimilarity index. NMDS was chosen over other parametric ordination approaches because the diet data were skewed and not normally distributed. Predators were plotted in ordination space with each point representing a specific year-size-State estimate of a predator's diet. In the NMDS plot, distance among points is positively related to dietary dissimilarity (*i.e.*, points that plot more closely to one another are more similar). Prey group names on the NMDS plots indicate the loading of that prey on the ordination scale, and points will have a tendency to plot nearer to prey that are more important in the diet.

We used a permutation test to evaluate the strength and significance of the correlation of numerous environmental variables to the NMDS ordination. The explanatory variables included two factors (predator size and State) and 6 quantitative covariates (bottom water temperature, Flow, CHL, DD, NAO, and AMO). For the permutation test, the significance of each covariate or factor (at the P=0.05 level) was based on comparing the observed squared correlation

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[2] Diets for white perch and spot were not examined in the NMDS analysis due to limitations in the spatial or temporal range of the available data. See Appendix Tables 1 & 2.

coefficient (R^2) with the strength of the R^2 values obtained with randomly permuted data; explanatory variables will be non-significant if random permutations regularly result in comparable R^2 values. Significant factors and variables were added to NMDS plots. All multivariate analyses were conducted using the vegan package in R.

Predator consumption and condition analysis – Basin-scale analysis relating consumption to forage availability and environmental conditions was conducted using generalized additive models (GAMs; Hastie and Tibshirani 1990). GAMs are extensions of GLMs that replace the linear predictor by an additive predictor:

$$g(E(y)) = X\beta + \sum_{j=1}^{p} s_j(x_j)$$

where y is the vector of observations of the response variable, X is the fixed effects model matrix containing observations of the covariates, β is the vector of coefficients, g is the link function which is differentiable and monotonic, and s_j is a smoothing function such as a spline or a loess smoother that provides a partially non-parametric aspect to the model. For normally distributed data, the error covariance matrix of a GAM is given by $\varepsilon \sim N(0, \sigma^2 I)$, where I is the identity matrix.

GAMs provide a highly flexible means of investigating non-linear relationships among variables but require substantial information (i.e., degrees of freedom) to accomplish the fitting of non-linear smoothers. GAMs were used to model the relationship between individual predictor variables (environmental variables and mainstem forage indices) and consumption by each combination of predator and size-class. Therefore, GAMs were structured to include only one covariate for this analysis. The suitability of model fits to different variables were made by comparing diagnostic plots and model AICc values across single variable models. Basis dimension smoothers (i.e., 'wiggliness' of smoothers) was held low to control for overfitting models.

We analyzed common trends in consumption across all predators and size-classes over time using dynamic factor analysis (Zuur et al. 2003b). DFA is a multivariate dimension reduction technique designed for relatively short, non-stationary time-series data. The goal of DFA is to identify a set of common underlying trends that explain temporal variation in a collection of time-series through a linear combination of hidden random walks. The general form of a DFA model can be written as follows (Zuur et al. 2003a, Zuur et al. 2003b, Holmes et al. 2017):

$$k_t = \Gamma\alpha_t + \mathrm{D}x_t + \varepsilon_t \text{ where } \varepsilon_t \sim \mathrm{MVN}(0, \mathrm{R})$$

$$\alpha_t = \alpha_{t-1} + \eta_t \text{ where } \eta_t \sim \mathrm{MVN}(0, \mathrm{Q})$$

where k_t is the vector ($m \times 1$) of estimated condition values for all species/size-classes in year t, at is the vector ($r \times 1$) of common trends ($r < m$), Γ is the matrix (m × r) of species-specific loadings on the trends, x_t is the vector ($q \times 1$) of covariates, D is the matrix ($m \times q$) of covariate effects, and R and Q denote the variance-covariance matrices associated with the observation error vector ε_t ($m \times 1$) and process error vector η_t ($r \times 1$), respectively.

DFA allows simultaneous analysis of covariates, and in these cases allowed us to determine if any common trends in predator condition covaried with environmental conditions. Model variants were considered that included one or two common trends, with and without environmental covariates. A total of n = 42 DFA models were fitted using combinations of the following covariates DO, Salinity, CHL, Flow, NAO, AMO and model variants with no covariates. Model variants considered covariate interactions with one or two common trends and three different forms of the variance-covariance matrix. These included diagonal and equal (which is no covariance, equal variances for time-series); diagonal and unequal (which is no covariance, unique variances for time-series); and equal variance-covariance (which allows for covariance but all variances and covariances across time-series are the same). Model fit was assessed using AICc and visual examination of diagnostic plots.

RESULTS

Objective 1. Forage indices and forage-environment model results

Spatial patterns in forage indices – Time-series of forage abundance indices showed taxonomically- and regionally-dependent patterns. Among tributaries and different sections of the mainstem, invertebrate indices of abundance were all positively correlated (Pearson's product-moment correlation; $r_P \geq 0.16$, $p \leq 0.04$) with the exception of polychaetes and other (non-*Macoma*) bivalves (Figures 4–6). Among the tributaries, other bivalves were notably more abundant in the Potomac River than the other tributaries (Figures 4 & 5), whereas, relative abundances of other invertebrate functional groups were comparable across tributaries. In the mainstem, *Macoma* spp., other bivalves and small amphipod/isopod crustaceans were more abundant in the upper section of the Bay than the middle or lower sections (Figure 6). These high relative abundances were associated with relatively high interannual variability. Polychaete abundance patterns showed the opposite trend, with index values in the lower Bay typically exceeding those of the middle and upper Bay (Figure 6).

Forage fish indices also showed significant among-taxa correlations and spatially-explicit patterns in relative abundance. Within the tributaries, positive correlations ($\alpha = 0.05$) were observed between bay anchovy and Atlantic silversides ($r_P = 0.23$), and between mummichog and Atlantic silversides ($r_P = 0.26$). Atlantic menhaden was positively correlated with blueback herring ($r_P = 0.23$), Atlantic silversides ($r_P = 0.36$) and YOY spot ($r_P = 0.59$). Killifish abundance was correlated with abundances of two other estuarine residents, mummichog ($r_P = 0.70$) and Atlantic silversides ($r_P = 0.33$). All significant parametric correlations among species were positive. Several non-parametric negative correlations were significant (Spearman's rank-order correlation, r_S), including YOY Atlantic menhaden and killifish ($r_S = -0.33$), YOY Atlantic menhaden and mummichog ($r_S = -0.26$), and YOY spot and killifish ($r_S = -0.18$).

Across much of the 1980-2015 time-series, indices of relative abundance of alewife, Atlantic silversides, blueback herring, Atlantic menhaden and spot were higher in the Rappahannock River than in the other two VA tributaries (Figure 7). Conversely, mummichog and killifish indices of abundance were generally higher in the York River, particularly in the middle of the time-series. YOY white perch, YOY Atlantic croaker, and bay anchovy did not differ in relative abundance among the three VA tributaries. Within the mainstem, indices of relative abundance of all species, with the exception of YOY Atlantic croaker, were notably higher in the upper Bay near the end of the time-series (Figure 8). Throughout the time-series, indices of relative abundance of YOY Atlantic croaker, YOY weakfish and potentially bay anchovy and YOY spot were more similar among the upper, middle and lower sections of the mainstem than were the other species.

When aggregated by state, several forage fish indices of relative abundance were significantly correlated between MD and VA tributaries ($\alpha = 0.05$). Indices of abundance of blueback herring ($r_P = 0.32$), YOY spot ($r_P = 0.46$) and YOY white perch ($r_P = 0.52$) were all positively correlated between state tributaries. Non-parametric correlations suggested there were additional positive correlations for alewife ($r_S = 0.47$), bay anchovy ($r_S = 0.49$), and YOY Atlantic menhaden ($r_S = 0.77$). Differences in the scale and relative variability of relative abundance indices between states were apparent and remained following normalization (scaled to a range of 0-1; Figure 9). Despite these differences, the shared patterns indicated by correlation analyses were visually identifiable for most species. For others, temporal patterns in relative abundance appeared to follow dissimilar trends. Examples include the apparent reduction in abundances of several forage species in Maryland tributaries but not in Virginia tributaries, such as bay anchovy, killifish, mummichogs (Figure 9).

Forage-environment relationships – Mixed-effects GLMs indicated different environmental variables were associated with interannual patterns in forage relative abundance, depending on the taxa of forage and the spatial scope of the model. In the mainstem, model diagnostics indicated elevated dispersion of residuals (as indicated by χ^2/DF; 2) for forage fish relative to invertebrates, suggesting reduced model performance for forage fish. This is further indicated by the typically lower r_P between observed and model-predicted values. Parameter estimates for mainstem forage models indicated the AMO and DD variables were significant for several taxa of distinct forage groups, including fish and invertebrates (Table 3). The effect of AMO differed among taxa but was positive for all forage fishes and negative for invertebrates. The DD phenology variable was consistently positive for all models in which it was significant. Flow, CHL and Hypoxia were each indicated as significant in the models of one forage taxon.

Within the tributaries, performance indicators suggested forage fish models typically performed better than the mainstem models (likely due to higher sample sizes; Table 4). Among forage fishes, AMO was positively related to killifish, mummichog, and white perch indices but negatively related to YOY Atlantic menhaden and several invertebrate indices (Table 5). CHL was positively related to YOY white perch and Atlantic silversides indices and weakly associated with several other taxa. The effect of DD was again positive in all models in which it was found to be an important ($p < 0.05$) or potentially important ($p = 0.05–0.10$) variable, including both fish and invertebrate taxa. Flow was positively associated with YOY Atlantic menhaden, amphipods/isopods and *Macoma* spp., but negatively associated with bay anchovy.

In tributary models for forage fish aggregated by state, most MD models showed relatively poor model performance (e.g., higher residual dispersion, lower r_P values) compared to VA models for the same species (Table 6). This was particularly true for mummichog and killifish, for which the residual dispersion index exceeded 4.0. In the MD tributaries (Table 7), AMO and Flow, when significant, were consistently negatively associated with annual indices of forage fish abundance. CHL was positively (alewife, blueback herring) and negatively (bay anchovy, killifish, YOY spot) associated with some species in the MD tributaries. For the DD variable, the only significant negative relationship between this phenology variable and a forage fish index in any model run (across spatial scales and taxa) occurred for YOY Atlantic croaker in the MD tributaries. For some forage species, the significance of environmental variables differed between MD and VA tributary models, but the directionality (positive/negative) of effects were consistent when environmental variables were significant for a species in both regions, with one exception. The exception was the killifish index, which was positively related to CHL and AMO in the VA tributaries but negatively related to those variables in the MD tributaries.

'Portfolio effect' of multiple suitable regions – A reduction in *CV* was observed for each of the four invertebrate functional groups at the metapopulation scale relative to the null hypothesis of synchrony across tributaries and mainstem sections (Figure 11). These reductions lead to portfolio effect (PE) estimates of 26-52% for invertebrates. Differences in the sampling gear between tributaries and the mainstem and the unavailability of tributary-specific estimates in the MJS survey reduced the scope for analyzing the effect of multiple suitable regions on the *CV* of forage fish. Despite limiting the scope of the analysis to VA tributaries, there was still evidence that *CV*s declined at metapopulation scales for all of the forage fishes. PE values were low for some fish species, ranging from 9–13% for killifish, Atlantic silversides, spot, Atlantic croaker, white perch and Atlantic menhaden. For others, values were higher, ranging from 19–34% for alewife, blueback herring, mummichog, and bay anchovy.

Objective 2. Predator diet and consumption model results

NMDS diet results – Different explanatory variables were significantly related to the ordination of diets, but there was some consistency across the predatory species (Table 8). Predator size was significant for all predators analyzed, with higher correlations for summer flounder and striped bass. The differences attributable to size accentuate the importance of accounting for ontogenetic changes in feeding habits of fishes, as highlighted in other studies (Buchheister and Latour 2015 2016). State, acting as a regional factor, was significant for all predators except Atlantic croaker. For the quantitative covariates, AMO was significant for weakfish and striped bass, while NAO and CHL were significant for weakfish.

The NMDS plots for each predator highlight the dietary differences and the prey groups generally responsible for that variability. For summer flounder, diets seemed to shift gradually for small, medium, and large predators; smaller individuals had a greater focus on mysids, worms, and anchovies, while larger summer flounder included more fishes of typically larger body size in their diet (Figure 12). Summer flounder diet dissimilarities by state were less pronounced, but summer founder in MD had a slight tendency towards greater consumption of anchovies, YOY weakfish, and other prey. For Atlantic croaker, diets of small individuals were related to greater proportions of fishes and mysids, while medium individuals tended to eat more bivalves and crustaceans (Figure 13).

NMDS plots for weakfish and striped bass revealed a greater influence of additional environmental variables. For weakfish, five variables were identified as significant which complicated the interpretation (Table 8, Figure 14). Although differing significantly by size, weakfish diets overlapped substantially between sizes and between States. NAO, AMO, and CHL exhibited largely opposing effects on diet, hindering clear conclusions aside from acknowledging their significance. Striped bass exhibited a strong size patterns in diet (Figure 15), in part due to the larger range of sizes analyzed. Smaller individuals tended to consume anchovies, juvenile sciaenids, bivalves and mysids, whereas the largest individuals consumed more menhaden and spot. Again, State was significant, but there was substantial overlap, with MD diets having a tendency for more mysids, bivalves, worms, and spot in the diets. AMO was loaded in a similar direction for VA and MD, suggesting that predation of the same prey was greater for years with higher AMO values.

Predator-specific consumption patterns – A brief summary of major consumption patterns is provided here, primarily as an update to include most recent years not available for the Buchheister et al. (2016) report. For a more detailed description of major consumption patterns among predators, see **Appendix 4**.

Striped Bass – The yearly mean stomach contents of striped bass were relatively consistent over the 14-yr time series. Striped bass abundance did not indicate a trend over time. In general, the abundances of medium striped bass were greater than abundances of the large and small size classes throughout the time series, with the exception of the years 2002, 2012, and 2015 when small striped bass (primarily ages 1 and 2) were more abundant due to strong recruitment events. The total annual consumption by striped bass typically fluctuated around 500 mt, but reached a time-series maximum in 2006 of more than 1600 mt. Fish prey, primarily YOY menhaden and anchovies, were the dominant components of the striped bass diet and each accounted for about 40% of the total annual consumption. However, an increase in YOY menhaden and anchovy consumption has been observed since 2009, consistently accounting for >50% of the total annual consumption.

Summer Flounder – The stomach contents of summer flounder were also relatively consistent across the time series, although an anomalous peak in the large size class was observed in 2007. Summer flounder abundance was of similar magnitude across all size classes, with the medium size class being the most abundant from 2002–2007). Following 2007, all size classes declined in abundance until 2012 and remained relatively stable, albeit at low levels, thereafter. Consumption has declined drastically since 2007, a pattern noted previously by Buchheister et al. (2016). Total annual consumption by summer flounder size classes peaked in 2007 at roughly 600 mt and declined to a time-series low in 2014 at around 25 mt. The relative contribution of forage prey types was largely consistent and evenly distributed among those prey. The apparent increase in dietary importance of YOY spot since 2012 should be treated with caution due to low sample sizes for diet analyses.

Atlantic croaker – The mean weight of the stomach contents for Atlantic croaker showed a decrease across the time series for both small and medium size classes. This decrease was an order of magnitude more pronounced in the medium Atlantic croaker relative to the small size class. Abundance of medium sized individuals showed a pronounced decline after 2007 when 25 million fish were estimated, followed by a time series low in 2012 of approximately 1 million fish. Conversely, the small size class of Atlantic croaker has remained stable apart from the strong 2007 and 2013 year classes. Total annual consumption by Atlantic croaker reached a time-series maximum of nearly 10,000 mt in 2002. Following 2007, total annual consumption remained below 1,250 mt and reached a time-series low in 2012 of 127 mt. Polychaetes were the most dominant component of the annual consumption for Atlantic croaker, often comprising >50% of their diet throughout the time-series. Bivalves and other prey were periodically important to the annual consumptive profile. Mysids were at times the most dominant component of the profile, such as in 2005 where they accounted for roughly 40% of the annual consumption.

Weakfish – Similar to the pattern observed in Atlantic croaker, weakfish showed a decrease across the time-series in the mean weight of stomach contents for both small and medium size classes, where the decrease over time was more pronounced in the medium size class relative to the small size class. Abundance of medium weakfish reached a time-series maximum in 2004 of approximately 3.2 million individuals, but showed a large decline thereafter reaching a low in 2014 of less than 100,000 individuals. The abundance of small weakfish was relatively stable throughout the time-series, but has marginally declined in recent years. Total annual consumption by weakfish fluctuated between 2,200 mt and 500 mt from 2002 to 2005, but has declined and remained considerably lower (<100 mt) since 2011. Polychaetes and mysid shrimps were the two most dominant prey groups that contributed to the population level consumption in the early years of the time-series. An apparent increase in polychaete consumption, often in excess of 50% of the annual consumption, was observed following 2006. Due to the low sample size of weakfish during this timeframe, this trend should be interpreted with caution.

White Perch – Throughout the six-month index period, medium and small white perch had a stable, but low mean weight of stomach contents and daily per capita consumption (<0.9 g and <0.25 g, respectively). Abundance of small white perch was typically greater than the abundance of medium white perch and neither size class displayed trends or shifts in abundance throughout the time-series. However, abundance maxima were reached for both small and medium white perch in 2015. Population-level consumption during the six-month index period was similar between both size classes and relatively stable throughout the time-series. Despite high abundances, total annual white perch consumption was relatively small compared to the other species in this study, typically ranging from 300-700 mt with no apparent trend over time. Polychaetes and crustaceans (mainly gammarid amphipods) were the two most dominant prey groups consumed, accounting for 15–50% and 5–53%, respectively, of the total consumption, depending on the year.

Spot – Trends were relatively stable within the mean weight of the stomach contents as well as in the daily per capita consumption across the duration of the spot time-series. It should be noted that inconsistent analysis of stomach samples from 2002–2007 limited analyses of specific trends within that time period. Abundance of medium spot was relatively stable from 2002–2009, ranging from 4–10 million fish. Beyond 2009, abundance decreased to levels consistently below 4 million fish, reaching a time-series minimum in 2015 of <1 million individuals. After 2007, when stomach content analyses became more consistent for spot, polychaetes were often the dominant component (50%) of annual consumption. Bivalves and crustaceans (mainly amphipods) were also periodically important to the annual consumption profile of biological material. The “other” prey category, which at times exceeded 50% of the annual spot consumption, was typically detritus, apparently consumed while sifting through benthic matter to locate prey.

Patterns in total consumption across predators – Predator consumption values for each of the predators were aggregated to evaluate the consumptive pressure of predator groups within the Chesapeake Bay mainstem. Piscivorous fishes (i.e., striped bass, summer flounder, and weakfish) showed a nearly three-fold decline in total consumption across the duration of this study. The relative contributions of YOY Atlantic menhaden and bay anchovy to consumption by piscivorous fishes increased throughout the time-series. Conversely, the relative contribution of mysids decreased throughout the time-series. The benthivorous predators (i.e., Atlantic croaker, white perch, and spot) demonstrated a greater than ten-fold decline in total consumption; however, the relative contributions of specific forage prey varied minimally. The combined total annual consumption by all six predators declined by an order of magnitude from 13,000 mt in 2002 to 1,300 mt in 2015. Overall, benthivorous fishes had a higher total consumption than piscivorous fishes and this was noted in the relative contributions of forage prey by all six predators. However, the total amount of forage prey consumed by piscivores and benthivores was similar from 2008–2015. Among forage prey, polychaetes were the most important, although the relative contributions of YOY menhaden and bay anchovy increased over the time series due to consumption patterns of the piscivores. Periodic influxes of specific prey groups in the diets of the six predators highlighted the importance of annual pulses of prey in the Chesapeake Bay (e.g., mysids in 2002 and 2005, YOY spot in 2010).

Consumption-environment model results – For all predator species and size-class combinations, environmental covariates of per capita consumption tended to have a more important effect than did forage covariates. Optimal consumption-environmental covariates differed by predator species and size-class. Consumption by small size-class Atlantic croaker covaried with Flow, showing a modal pattern that peaked at intermediate Flow values (Figure 16). Medium size-class Atlantic croaker displayed a modal relationship to salinity, with high consumption occurring at low or high salinities but lower consumption at intermediate salinity. The small size class of spot also covaried most tightly with Flow, with a near monotonic increase in consumption as Flow increased that was most pronounced at the highest and lowest observed Flow values (Figure 17). Consumption by medium-sized spot covaried with NAO, showing a generally decreasing pattern of consumption with increasing NAO index values. Small weakfish consumption showed a curvilinear relationship with salinity with minimum consumption at intermediate salinities (Figure 18). Consumption by medium-sized weakfish covaried with CHL in a non-linear fashion suggestive of a negative modal response. The small size-class of summer flounder showed a generally negative relationship between consumption and CHL values (Figure 19). Consumption by the large size-class of summer flounder covaried positively with DO, although the observed pattern was likely influenced by a single datum of high estimated consumption during a year of relatively high average DO. The small size-class of white perch showed a generally negative relationship with NAO although the fitted curve was complex (Figure 20). The complexity of the small white perch consumption-NAO relationship is influenced strongly by a single datum at the lowest observed NAO index value. Among medium-sized white perch, there was a variable, negative relationship between consumption and DO. Consumption by the small striped bass size-class covaried with bottom-water DO in a highly non-linear fashion (Figure 21). With the exception of one datum (c. DO ~ 9.6 mg/l) that appears to heavily influence the relationship, consumption was generally higher during years in which mean DO was < 9.2 mg/l. Consumption by the medium size-class of striped bass showed a linear decline with increasing DO. Large striped bass consumption showed a positive curvilinear relationship with CHL, increasing at low CHL values and apparently reaching an asymptote at medium-to-high annual CHL values.

The Dynamic Factor Analysis of predator consumption indicated a long-term, negative trend in per capita predator consumption across species (Figure 22, a). Of the 42 models considered, AICc values consistently supported model variants with one common trend, no covariate, Comparison of AICc values among potential model variants supported an equal variance-covariance structure and did not support the presence of a secondary trend or the inclusion of any environmental covariates. Loadings of individual predators showed that the trend was most strongly influenced by Atlantic croaker, summer flounder, weakfish and white perch (Figure 22, b & c). Other predators showed no pattern or some evidence of increasing consumption (e.g., large striped bass).

DISCUSSION

Overall, we found that patterns in forage relative abundance and predator diet, consumption and condition covaried with spatial, temporal and environmental gradients. Forage fish and invertebrates in the mainstem and tributaries of Chesapeake Bay displayed significant, albeit different, responses to key environmental variables. After accounting for size and temporal factors, the diets of several predators differed between the upper and lower Bay and were significantly correlated with environmental covariates. Total per capita consumption by predators showed variable, sometimes complex relationships with environmental covariates. Time-series of predator condition indicated a basin-wide decline in weight-at-length that was shared among some predator species.

Linkages between forage and climate in Chesapeake Bay

The negative relationship between the rate of water warming during spring, as indexed by the 5° DD phenology variable, and annual summertime abundance of many forage taxa was remarkably consistent. Studies have often focused on the link between DD variables and size-at-age or size-at-day of fish or invertebrates, many of which have documented a positive-effect between growth rates and the DD variable (Ward and Stanford 1982, Neuheimer and Taggart 2007). For example, previous research has shown DD threshold temperatures of 5–6.9°C are necessary to maintain growth in weight of striped bass (Hartman and Brandt 1995, Hurst and Conover 1998) and 10°C to maintain growth in length (Hurst and Conover 1998). Bunnell and Miller (2005) used a DD threshold of 8.9°C to model intermittent growth and molt for Chesapeake Bay blue crabs (Smith 1997). Whereas these could be considered examples of 'positive' effects of increasing DD values, our analysis documented an inverse relationship between the 5° DD phenology variable and abundance of these forage taxa.

It is not known what drives the observed negative relationship although possibilities include changes in adult reproductive effort or early life survival rates of these forage taxa. Such changes could directly result from suboptimal thermal conditions during specific life-stages, particularly the vulnerable larval phases. 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. Also possible are indirect ecological effects arising between the forage species and their environment, such as match-mismatch scenarios in which the composition or timing of peak planktonic prey resource availability does not match trophic demand by forage taxa (Houde 1987, Cushing 1990) or the variable timing of predator occurrences controls forage taxa production. Previous studies have shown that components of phytoplankton-zooplankton bloom cycles can occur earlier in years with warmer late winter/spring water temperatures in marine and estuarine ecosystems (Edwards and Richardson 2004, Richardson 2008). In a marine system, Edwards and Richardson (2004) found that the timing of the peak abundance of pelagic larvae of benthic organisms (i.e., meroplankton) and dinoflagellates (but not diatoms) were among those components that shifted earlier during warmer years. Warming-induced earlier and less intense winter-spring phytoplankton blooms have been linked to weaker benthic-pelagic coupling and subsequently lower summertime epibenthic biomass in another Atlantic coast estuary (Narragansett Bay, Nixon et al. 2009). 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) and such changes could induce shifts in production of forage taxa.

Given the current level of our analysis, it is not possible to identify the specific mechanism causing the negative relationships between the phenology of water warming and the relative abundance of forage taxa. Almost certainly, different species are responding to different physiological and ecological forces. Our finding is worth noting, given the expectation of long-term changes to regional climate in the future. The importance of climatological forcing is underscored by the significant covariation between several forage indices, annual spring flow volume and the AMO index. Unlike the DD phenology index, relationships of forage to these other climate indicators were not all unidirectional. In the case of the AMO index, the positive relationship observed for resident and anadromous estuarine forage fish species but negative relationship for benthic invertebrates is notable. The apparent 60–70 yr cycle of the AMO is currently in a positive phase, following a recent nadir during the 1970s (Nye et al. 2014). Positive phases of the AMO are typically associated with warmer sea surface temperatures, low atmospheric pressure and positive northwesterly wind anomalies along the Mid-Atlantic Bight, as well as increased precipitation over the mid-Atlantic states (Nye et al. 2014). Positive AMO anomalies, or the climate conditions associated with positive AMO anomalies, are typically associated with higher year-class strength of anadromous species in estuaries along the US Atlantic coast (Wood and Austin 2009). For example, juvenile recruitment of striped bass are positively correlated with AMO in the Hudson River and Chesapeake Bay (Buchsbaum and Powell 2008, Nye et al. 2014). Similarly, in this study we found that YOY white perch abundance correlated positively with AMO. There was some evidence that these patterns did not hold in the more up-bay tributaries in MD. This discrepancy requires additional study to understand why the AMO relationship is not important in those tributaries. The mechanism underlying the negative relationship between AMO and invertebrates is unclear but higher freshwater flows and warmer air temperatures could enhance stratification and subsequent hypoxia of 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).

In this analysis, winter-spring flow volume was related to forage fish and invertebrates in the tributaries but not in the mainstem with the exception of the anadromous blueback herring. Interestingly, forage fish and invertebrate taxa showing a positive relationship with flow showed a negative relationship with AMO. This suggests that these species, which include Atlantic menhaden, amphipods/isopods, and *Macoma* spp., benefit during high flows years that are not associated with the other climatological aspects of AMO (e.g., warmer temperatures). Notably, this does not include any of the estuarine resident or anadromous species most often considered to benefit during years with warm, high-flow spring conditions. When integrating tributaries at the State-scale and analyzing State-level patterns, the relationships between certain forage taxa and winter-spring flow changed direction or disappears. Increased winter-spring flows are predicted in Chesapeake Bay (Najjar et al. 2010) and how these freshet conditions covary with water temperature is likely to have consequences for the composition and productivity of forage communities in Chesapeake Bay.

The absence of a strong flow-forage signal in the mainstem is unexpected given the considerable literature on the effects of flow 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 for forage fish in the mainstem reduced our statistical power to identify a flow relationship. For invertebrates, the lack of an apparent response to flow at the functional group-level is important from a top-down perspective (i.e., biomass of available prey does not correlate with flow) but the highly aggregated nature of the functional groups almost certainly obscures species-level relationships. If only one or several key forage species within a given functional group covaries strongly with flow, then our approach of aggregating taxonomically similar forage could fail to capture species-level forage-environment dynamics that may be important for certain predators. Finally, our definition of the winter-spring interval (Jan-June) may be too broad to capture the specific temporal intervals during which flow influences the abundance of forage in Chesapeake Bay. By starting in January, it is also possible that we failed to account for earlier, fall-winter flow conditions that could be important determinant of forage biomass during the following year (Wingate and Secor 2008).

Spatial patterns in predator diet

Initial attempts to parse the ChesMMAP predator diet dataset to allow spatially explicit analysis of annual consumption was unsuccessful because sample sizes were too small to support robust estimates of consumption after accounting for the known influence of temporal and size-based factors on predator diet as previously noted in Buchheister et al. (2016). Consequently, to analyze spatial patterns in predator-prey relationships in this project, we conducted a multivariate analysis of predator diet that related spatial, biological (size-class) and environmental factors to observed diets. However, this approach still required not including two predators (white perch, spot) from the analysis due to limited sample sizes.

Many of the observed patterns are consistent with previous analyses using the ChesMMAP dataset (Buchheister and Latour 2015, Buchheister and Latour 2016), underscoring the importance of body size in trophic structuring for all predators considered here. Previously, Buchheister and Latour (2016) highlighted latitudinal patterns in the consumption of mysids, anchovies, bivalves, and polychaetes, and one of the clearer regional patterns was a greater consumption of mysids in the lower bay for summer flounder and weakfish. In the present analysis we focused on the similarities in overall prey consumption that may identify other patterns not detected when focusing on individual prey as in the previous study. We detected spatial differences between upper and lower Chesapeake Bay for three of the four predator species although the differences were subtle. For example, the previously identified pattern of greater consumption by predator fishes in the lower Chesapeake Bay was born out in the present analysis for summer flounder, but not as clearly for weakfish. Spatial patterns for striped bass suggested increased foraging on mysids, bivalves, polychaetes and spot in the upper Bay, but not necessarily anchovies. One particularly unexpected result of the diet analysis was the suggestion that several types of forage fish were more important to the diet of small Atlantic croaker than the larger size-classes. This counter intuitive result (evidence of increased piscivory among smaller individuals) arises from anomalously high prevalence YOY Atlantic croaker (i.e., cannibalism) and menhaden in the stomachs of small Atlantic croaker in the upper region of the Bay during 2004 and 2008 (n = 7 in 2004, n = 29 in 2008). Given the sporadic nature of these observations and the likelihood that many of these instances of piscivory reflected consumption of larval fish rather than fully recruited juveniles, it appears that forage fish can be important diet components for small Atlantic croaker under certain circumstances, but our results do not support the conclusion that small Atlantic croaker are typically more piscivorous than larger size-classes. While many management decisions are made at regional rather than basinwide scales (e.g., State-level vs Chesapeake Bay level), it is important to recognize that natural processes respond to environmental gradients and that these gradients shift on an intra- and interannual basis. Accordingly, spatial differences between regions defined by State boundaries should be interpreted with caution and any extension of these findings beyond the domain of the analyzed data must consider the prevailing environmental gradients.

Identifying the specific effects of environmental covariates on diet composition is difficult in a complex multivariate data set; however, AMO and several other key variables were identified as significant for certain predators. We note that the AMO was not only significantly correlated with diet composition but that it also covaried with forage abundance. For example, YOY abundance of spot showed a weak positive correlation with AMO in the mainstem and, at the same time, the contribution of YOY spot to the diet of weakfish and striped bass was positively correlated with AMO. This is just one example of synchrony between an environmental variable and the abundance of a forage taxon in predator diets and the environment, but it reinforces the hypothesis that bottom-up mechanisms are ultimately a key factor influencing predator-prey dynamics, a finding supported previously for Chesapeake Bay (Buchheister et al. 2016).

Influence of forage and environment on predator consumption in Chesapeake Bay

Per capita consumption by small size-classes of Atl. croaker and weakfish covaried most strongly with environmental variables that strongly influence or quantify vertical or horizontal salinity structure in Chesapeake Bay, winter-spring flow, and local salinity (Officer et al. 1984). Consumption by the small size-class of spot covaried with the same environmental variables, however low sample size of small spot in the predator database reduce confidence in the reliability of these correlations. Salinity-associated variables did not covary significantly with per capita consumption by summer flounder, striped bass or white perch. Summer flounder is typically restricted to the higher salinities of the lower Bay (Buchheister and Latour 2011) where salinity structure is less variable than in mid- and upper-Bay regions and regional differences in consumption might have been expected. Conversely, given the broad physiological salinity tolerance of anadromous striped bass and white perch, the lack of an observable effect of salinity on consumption by these species might be expected.

The mechanism behind the observed pattern of high DO concentration associated with reduced per capita consumption for some size-classes of striped bass and white perch is unclear. If high daytime DO conditions are associated with hypoxic nighttime DO conditions due to diel photosynthesis-respiration cycles, then these patterns could be indicative of lost benthic foraging opportunities due to low conditions in bottom waters at night. High levels of primary productivity during daytime can be associated with high rates of plant-based respiration at night, leading to diel cycles in oxygen levels that have previously been linked to avoidance by some fish species (Bell and Eggleston 2005, Eby et al. 2005, Tyler and Targett 2007). The size-classes of striped bass and white perch (small to medium) that covaried negatively with water column DO often consume small epibenthic crustaceans, polychaetes and demersal fishes (Buchheister and Latour 2015, Buchheister et al. 2016, Buchheister and Latour 2016); forage taxa associated near-bottom habitats. Unlike the middle and upper regions of Chesapeake Bay, the lower region frequented by summer flounder is less prone to the formation of hypoxic zones (Kemp et al. 2005). The decoupling of the water column oxygenation-bottom water hypoxia relationship in the lower Bay could explain the positive correlation between per capita consumption by large summer flounder and in situ water-column DO concentrations.

Per capita consumption for several predator species and size-classes covaried with the NAO index and chlorophyll concentration. Like the AMO, the NAO is indicative of a suite of climatic conditions; however, the NAO oscillates on interannual to inter-seasonal scales in addition to longer-term, multi-decadal trends (Hurrell 1995). Positive phases of the NAO are associated with higher air temperatures, increased precipitation and increased storminess along the US Atlantic coasts (Hurrell 1995, Hurrell and Van Loon 1997). Small white perch and spot showed peaks consumption at intermediate NAO index values, except at the most negative NAO value observed during the time-series. As with the other environmental indices, these patterns suggest a complex relationship that is likely due to the interaction of numerous factors. Still, the fact that both the per capita consumption by small white perch and spot, and the relative annual abundances of YOY white perch and spot (as forage) covaried with large-scale climate indices emphasizes the potential for long-term shifts in both abundance and consumption between these species and their physical and biological environment. Uncertainties arising from such complexities are likely to become more prominent as climate change continues to influence regional and global climate patterns in unanticipated ways (Scavia et al. 2002, Wood et al. 2002, Najjar et al. 2010, Boesch et al. 2013).

Common trends in per capita consumption among predators – The decline in per capita predator consumption indicated by DFA was present across several of the predator species and size-classes (but not all). This pattern is suggestive of a long-term and ongoing shift in the consumption of forage by predators Chesapeake Bay. By using per capita consumption rather than total consumption, this analysis is independent of any temporal trend in the biomass of the predator population. This pattern appears robust, but we were unable to find significant environmental or biological (i.e., forage abundance) relationships with the pattern that could support broad conclusions regarding the mechanism(s) underlying the trend. For example, although the analysis provides insight that there is one common trend among several species there is no evidence that the environmental variables or the indices of forage abundance considered in our research function as overarching forcing variables. In addition, the individual fits to the time-series are poor for several predator size-classes (e.g., striped bass). With these caveats in mind, it is notable that this pattern of declining predator consumption is occurring over the same interval that abundance of many of these predators is also declining in Chesapeake Bay (Buchheister et al. 2016). While results from the current analysis on predator consumption are inconclusive regarding the role of the environment, future work should consider the potentially complementary information offered by the contemporaneous reductions in abundance and potentially condition of these predators in the Bay. Further exploration of these patterns may yield more insight and spawn additional important hypotheses regarding recent changes in the suitability of forage, feeding conditions and growth dynamics of predators in Chesapeake Bay.

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Table 1. Summary of surveys used for analyzing different forage indices for fish and benthic invertebrate prey groups. Indices were based on relative forage abundance (Fishes) or biomass-per-unit-area (Invertebrates). Sampling regions for each survey were in the Maryland (MD) and Virginia (VA) tributaries (trib) or along the mainstem of Chesapeake Bay. Gears used in the fish surveys were a beach seine (BS) or midwater trawl (MT). Four different types of benthic gear (BG) were used in the benthic invertebrate surveys: 1) hand operated box corer, 2) Wildco box corer, 3) Petite Ponar grab, and 4) Young grab. The shaded black boxes indicate prey species that were sufficiently present in the survey data to allow for estimates of relative abundance (fish) or biomass (invertebrates).

					Fishes											**Invertebrates**			
Survey	**Regions**	**Years**	**Months**	**Gear**	YOY Menhaden	Bay anchovy	YOY alewife	YOY blueback	Atl. silverside	YOY Atl. croaker	YOY weakfish	YOY spot	YOY white perch	Mummichog	Killifishes	*Macoma* spp.	Amphipod/isopods	Polychaetes	Other bivalves
MD DNR Seine (MJS)	MD trib	1959-2015	Jul-Sep	BS	■	■	■	■	■	■		■	■	■	■				
VIMS Seine (VJS)	VA trib	1968-73, 1980-2015	Jul-Sep	BS	■	■	■	■	■	■		■	■	■	■				
TIES/CHESF IMS (CFT)	Mainstem	1995-2007	Jan, Mar-Nov	MT	■	■	■	■	■	■	■	■							
CBP Benthic survey	Mainstem/ Tributaries	1984-2015	July-Sept	BG												■	■	■	■

Table 2. Model fit information from generalized linear mixed models relating indices of abundance of invertebrate and fish species and taxonomic groups to environmental parameters in the mainstem of Chesapeake Bay. Models integrate time-series of annual indices from upper, middle and lower mainstem sections of Chesapeake Bay. Number of data points (n), an indicator of residual dispersion (Pearson's chi-square [χ^2] / model degrees of freedom; χ^2/DF), and Pearson's correlation coefficient for the linear relationship between observed and predicted index values ($r_{Pearson}$, '*' indicates significance at $\alpha \leq 0.05$) are provided.

Estuary region	Forage type	Taxon	n	χ^2	χ^2/DF	$r_{Pearson}$	
Mainstem	Fish	Alewife	36	59.19	2.11	0.41	*
		Anchovy	36	31.50	1.13	0.47	*
		Blueback herring	36	102.3	3.65	0.26	
		Atl. croaker	36	53.16	1.90	0.46	*
		Atl. menhaden	36	42.42	1.52	0.43	*
		Silversides	36	47.71	1.70	0.39	*
		Spot	36	47.72	1.70	0.36	*
		Weakfish	36	38.79	1.39	0.33	*
	Invertebrate	Amphipods/Isopods	56	12.14	0.25	0.68	*
		Macoma clams	56	29.09	0.61	0.63	*
		Other bivalves	56	56.15	1.17	0.45	*
		Polychaetes	56	5.18	0.11	0.77	*

Table 3. Parameter estimates from generalized linear mixed models relating indices of abundance of invertebrate and fish species and taxonomic groups to environmental parameters in the mainstem of Chesapeake Bay. Models integrate time-series of annual indices from upper, middle and lower mainstem sections of Chesapeake Bay. Explanatory variables include the Atlantic Multi-decadal Oscillation (AMO), Spring chlorophyll-a intensity (CHL), 5° Degree Day phenology variable (DD), Jan-June flow intensity (Flow), and Hypoxic volume (HYP). See text for details on specific variables. Bolded parameter estimates are potentially informative at $\alpha \leq 0.10$-0.05, bolded estimates with an '*' indicates significance at $\alpha \leq 0.05$).

Estuary region	Forage type	Taxon	AMO	CHL	DD	Flow	HYP
Mainstem	Fish	Alewife	*0.96*	*-0.08*	*0.78*	*0.62*	*0.09*
		Anchovy	**0.94**	*-0.30*	**0.62***	*-0.32*	*-0.18*
		Blueback herring	*-0.63*	*0.90*	*1.41*	**2.18***	*-0.71*
		Atl. croaker	*0.56*	*-0.20*	*-0.0003*	*-0.68*	*0.37*
		Atl. menhaden	*1.14*	*-0.26*	*0.49*	*0.09*	*-0.21*
		Silverside	**1.85***	*0.90*	*0.29*	*0.04*	**-1.05***
		Spot	**1.86**	*-0.11*	*0.43*	*-0.61*	*-0.27*
		Weakfish	**1.12**	-0.41	**0.53**	*-0.63*	*-0.05*
	Invertebrate	Amphipods/Isopods	**-0.25***	*-0.03*	**0.26***	*0.05*	*0.03*
		Macoma clams	*-0.24*	*-0.06*	*0.19*	*0.15*	*-0.01*
		Other bivalves	*-0.12*	*-0.09*	*0.13*	*0.04*	*-0.08*
		Polychaetes	**-0.23***	**-0.13***	**0.11***	*-0.03*	*0.03*

Table 4. Model fit information from generalized linear mixed models relating indices of abundance of invertebrate and fish species and taxonomic groups to environmental parameters in the focal tributaries of Chesapeake Bay. Models integrate time-series of annual indices from the Patuxent River, Potomac River, Rappahannock River, York River, James River*. Number of data points (n), an indicator of residual dispersion (Pearson's chi-square [χ^2] / model degrees of freedom; χ^2/DF), and Pearson's correlation coefficient for the linear relationship between observed and predicted index values ($r_{Pearson}$, '*' indicates significance at $\alpha \leq 0.05$) are provided.

Estuary region	Forage type	Taxon	n	χ^2	χ^2/DF	$r_{Pearson}$	
Tributaries	Fish	Alewife	43	108.45	3.10	0.35	*
		Anchovy	82	67.49	0.91	0.37	*
		Blueback herring	73	79.66	1.23	0.53	*
		Atl. croaker	47	97.74	2.51	0.21	
		Killifish	82	32.41	0.44	0.68	*
		Atl. menhaden	82	218.18	2.95	0.4	*
		Mummichog	82	71.25	0.96	0.64	*
		White perch	82	108.54	1.47	0.41	*
		Silverside	82	49.42	0.67	0.45	*
		Spot	82	76.14	1.03	0.48	*
	Invertebrate	Amphipods/Isopods	89	44.86	0.57	0.48	*
		Macoma clams	89	35.80	0.45	0.61	*
		Other bivalves	88	102.11	1.31	0.51	*
		Polychaetes	89	24.78	0.31	0.62	*

*Forage fish models only include time-series of indices of abundance from the Rappahannock, York and James Rivers. Invertebrate forage models include time-series from all 5 tributaries.

Table 5. Parameter estimates from generalized linear mixed models relating indices of abundance of invertebrate and fish species and taxonomic groups to environmental parameters in the focal tributaries of Chesapeake Bay. Models integrate time-series of annual indices from the Patuxent River, Potomac River, Rappahannock River, York River, James River*. Explanatory variables include the Atlantic Multi-decadal Oscillation (AMO), Spring chlorophyll-a intensity (CHL), 5° Degree Day phenology variable (DD), Jan-June flow intensity (Flow), and Hypoxic volume (HYP). See text for details on specific variables. Bolded parameter estimates are potentially informative at $\alpha \leq 0.10$-0.05, bolded estimates with an '*' indicates significance at $\alpha \leq 0.05$).

Estuary region	Forage type	Taxon	AMO	CHL	DD	Flow	HYP
Tributaries	Fish	Alewife	*3.07*	*0.41*	**0.90***	*-0.32*	*0.33*
		Anchovy	*0.92*	*-0.12*	**0.37***	**-0.33***	*0.21*
		Blueback herring	*-0.31*	**0.28**	*0.23*	*0.18*	*0.15*
		Atl. croaker	*-2.00*	*-0.23*	*-0.09*	*-0.18*	**-0.64**
		Killifish	**3.08***	**0.13**	**0.17***	*-0.11*	*0.05*
		Atl. menhaden	**-4.22***	*-0.03*	*0.29*	**0.61***	*0.22*
		Mummichog	**2.35***	*0.02*	*0.04*	*-0.12*	*0.21*
		White perch	**1.90***	**0.48***	**0.53***	*0.07*	*0.11*
		Silverside	*-0.43*	**0.17***	**0.18***	**-0.35**	*-0.07*
		Spot	*0.77*	*0.01*	**0.35***	*-0.14*	*-0.04*
	Invertebrate	Amphipods/Isopods	**-2.73***	*0.02*	*0.10*	**0.20***	*-0.15*
		Macoma clams	**-1.56**	*0.06*	*-0.10*	**0.27***	*0.08*
		Other bivalves	*-0.48*	**-0.24**	**0.21**	*-0.14*	*0.20*
		Polychaetes	**-0.89**	*-0.02*	**0.10**	*-0.04*	*-0.04*

*Forage fish models only include time-series of indices of abundance from the Rappahannock, York and James Rivers. Invertebrate forage models include time-series from all 5 tributaries.

Table 6. Model fit information from generalized linear mixed models relating indices of abundance of invertebrate and fish species and taxonomic groups to environmental parameters in the focal tributaries of Chesapeake Bay as aggregated by state. Models integrate time-series of annual indices from the two Maryland tributaries: Patuxent River, Potomac River; and the three Virginia tributaries: Rappahannock River, York River, James River. Number of data points (n), an indicator of residual dispersion (Pearson's chi-square [χ^2] / model degrees of freedom; χ^2/DF), and Pearson's correlation coefficient for the linear relationship between observed and predicted index values ($r_{Pearson}$, '*' indicates significance at $\alpha \leq 0.05$) are provided.

Tributary state	Forage type	Taxon	n	χ^2	χ^2/DF	$r_{Pearson}$	
Maryland	Fish	Alewife	29	106	3.66	0.33	
		Anchovy	29	94.5	3.26	0.30	
		Blueback herring	29	151.74	5.23	0.48	*
		Atl. croaker	12	15.53	1.29	0.28	
		Killifish	29	129.15	4.45	0.26	
		Atl. menhaden	29	107.99	3.72	0.39	*
		Mummichog	29	173.71	5.99	0.43	*
		White perch	29	62.35	2.15	0.64	*
		Silverside	29	88.23	3.04	0.40	*
		Spot	29	114.12	3.94	0.24	
Virginia	Fish	Alewife	26	34.59	1.33	0.45	*
		Anchovy	29	9.9	0.34	0.46	*
		Blueback herring	29	14.2	0.49	0.60	*
		Atl. croaker	24	48.01	2	0.29	
		Killifish	29	6.14	0.21	0.62	*
		Atl. menhaden	29	34.5	1.19	0.34	
		Mummichog	29	9.49	0.33	0.55	*
		White perch	29	12.34	0.43	0.52	*
		Silverside	29	6.73	0.23	0.60	*
		Spot	29	16.61	0.57	0.33	

Table 7. Parameter estimates from generalized linear mixed models relating indices of abundance of invertebrate and fish species and taxonomic groups to environmental parameters in the focal tributaries of Chesapeake Bay. Models integrate time-series of annual indices from the two Maryland tributaries: Patuxent River, Potomac River; and the three Virginia tributaries: Rappahannock River, York River, James River. Explanatory variables include the Atlantic Multi-decadal Oscillation (AMO), Spring chlorophyll-a intensity (CHL), 5° Degree Day phenology variable (DD), Jan-June flow intensity (Flow), and Hypoxic volume (HYP). See text for details on specific variables. Bolded parameter estimates are potentially informative at $\alpha \leq 0.10$-0.05, bolded estimates with an '*' indicates significance at $\alpha \leq 0.05$).

Tributary state	Forage type	Taxon	AMO	CHL	DD	Flow	HYP
Maryland	Fish	Alewife	*4.77*	**2.78***	*1.42*	*0.71*	*1.23*
		Anchovy	**-13.21***	**-3.93***	*-0.81*	*-1.31*	*-1.70*
		Blueback herring	*2.20*	**3.69***	*1.11*	*-0.50*	**2.81***
		Atl. croaker	**-30.52**	**-13.97**	**-5.23***	*11.53*	**-12.88**
		Killifish	**-10.56***	**-3.25***	**2.37***	*-1.30*	*-1.78*
		Atl. menhaden	**-14.44***	**-1.77**	**1.15***	**-3.08***	*-0.38*
		Mummichog	*0.37*	*0.30*	**1.38**	*0.82*	*-0.66*
		White perch	**5.61**	*0.88*	*0.28*	*0.44*	*0.82*
		Silverside	**-4.97***	*-0.93*	*-0.36*	**-2.89***	*0.57*
		Spot	*-1.27*	**-2.28***	**3.01***	*-1.28*	**-1.76**
Virginia	Fish	Alewife	*0.33*	*0.53*	**1.19***	*0.33*	*-0.35*
		Anchovy	*0.57*	*0.07*	**0.32***	**-0.40**	*0.1*
		Blueback herring	*-1.15*	**0.82***	*0.21*	*0.21*	*-0.03*
		Atl. croaker	*-0.77*	*-0.3*	*-0.26*	*0.12*	*-1.11*
		Killifish	**2.19***	**0.35***	*0.15*	*-0.09*	*-0.09*
		Atl. menhaden	**-3.57***	*-0.14*	*0.18*	**0.55**	*-0.21*
		Mummichog	**2.08***	*0.13*	*-0.0005*	*-0.12*	*0.31*
		White perch	*1.52*	**0.71***	**0.46***	*0.01*	*0.24*
		Silverside	*-0.10*	*0.26*	**0.16**	**-0.38***	*0.13*
		Spot	*1.29*	*-0.25*	*0.28*	*-0.18*	*0.28*

Table 8. Results of the permutation test on diet ordinations. Values represent the correlation coefficients (*r*) for any variables that were significantly related to the diet NMDS ordination (at the $\alpha = 0.05$ level). Variables that do not have a value were not significant.

Predator	Size	State	AMO	NAO	CHL	Wtemp	Flow	DD
Summer flounder	0.64	0.24						
Atlantic croaker	0.28							
Weakfish	0.28	0.24	0.39	0.37	0.35			
Striped bass	0.62	0.26	0.28					

Figure 1.

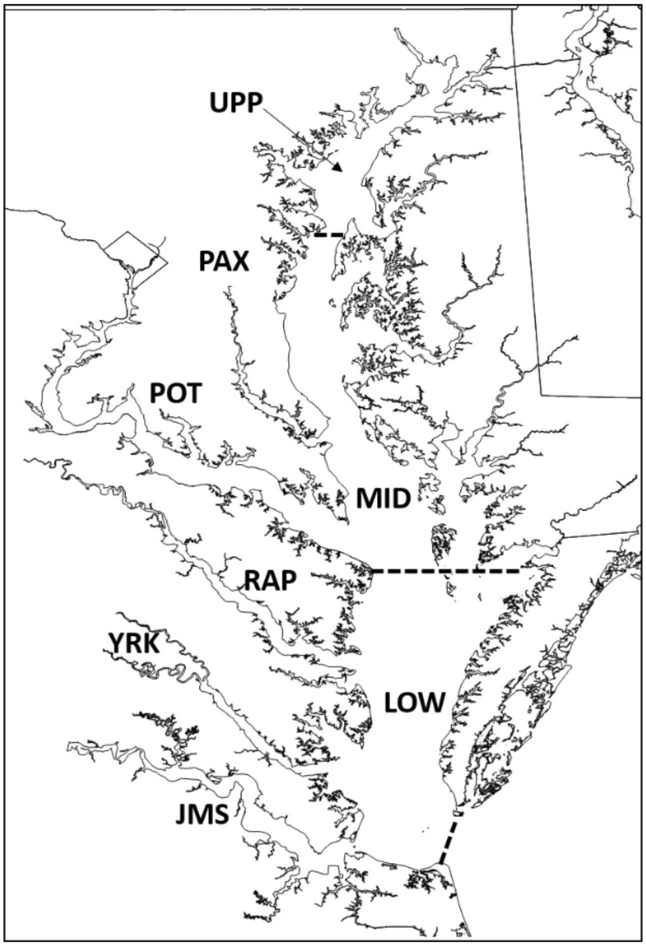


Figure 1. Map of Chesapeake Bay showing the major regions of interest for this study, including mainstem sections following major salinity zones (dashed lines; Upper – UPP, Middle – MID, Lower – LOW) and tributaries (Patuxent River – PAX, Potomac River – POT, Rappahannock River – RAP, York River – YRK, James River – JMS).

Figure 2.

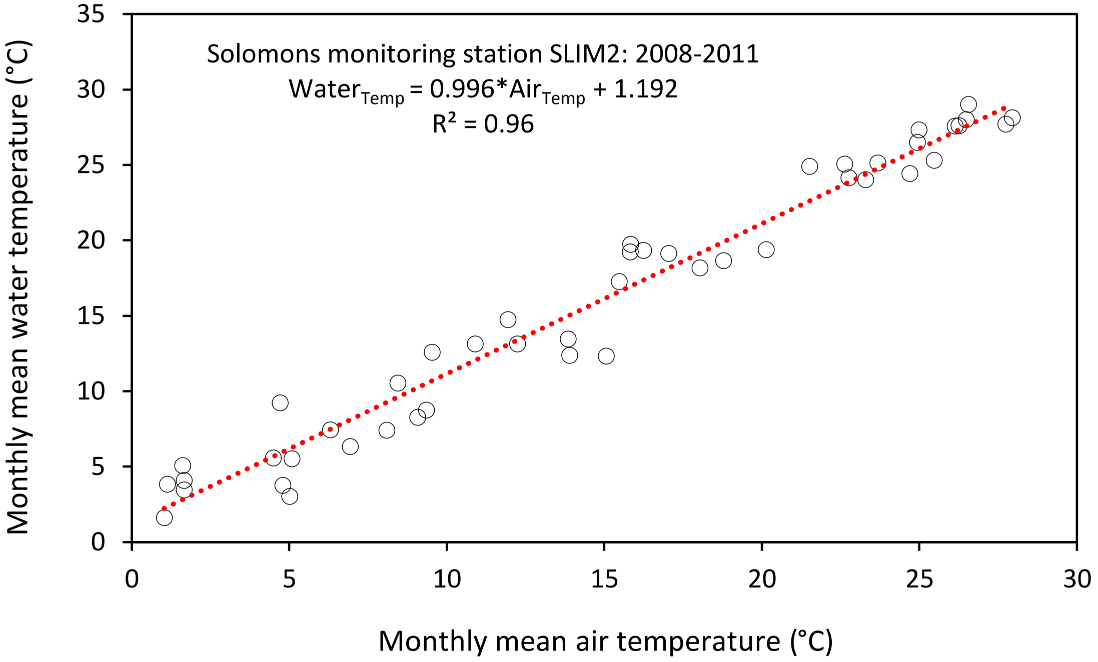


Figure 2. Relationship between water temperature and air temperature at the Solomons, MD, water quality monitoring station SLIM2. Red line: least-squares linear regression model fit to the data for Degree Day data reconstruction.

Figure 3.

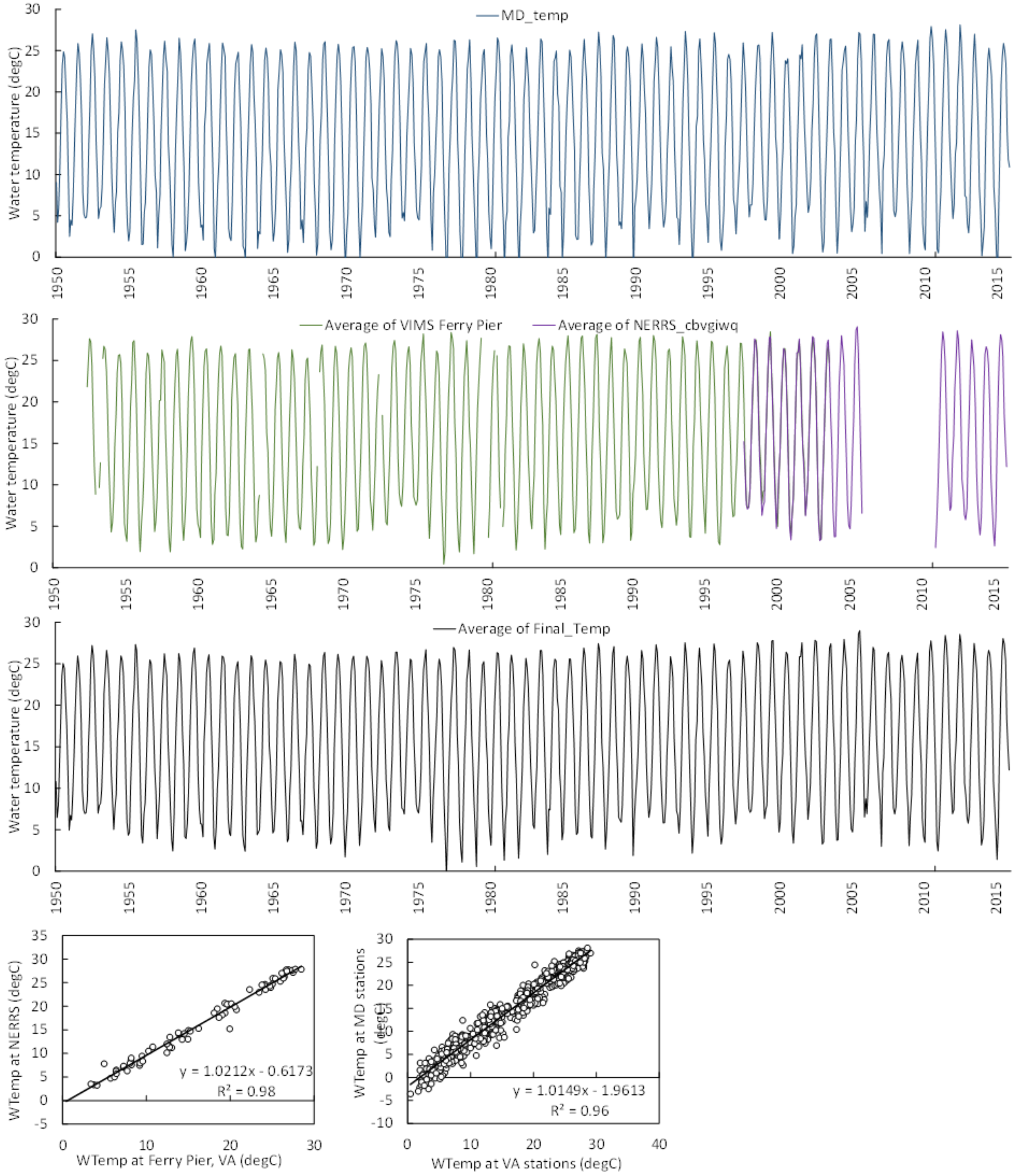


Figure 3. Time series of water temperature from the SLIM2 Solomons monitoring station (top), VIMS Ferry Pier and Goodwin Island NERRS stations (second panel), and final integrated time-series of daily values from 1950-2015 (third panel). Linear regressions (solid lines) fit to paired water temperatures and used in reconstructions of water temperatures at both locations (bottom panels) shown.

Figure 4

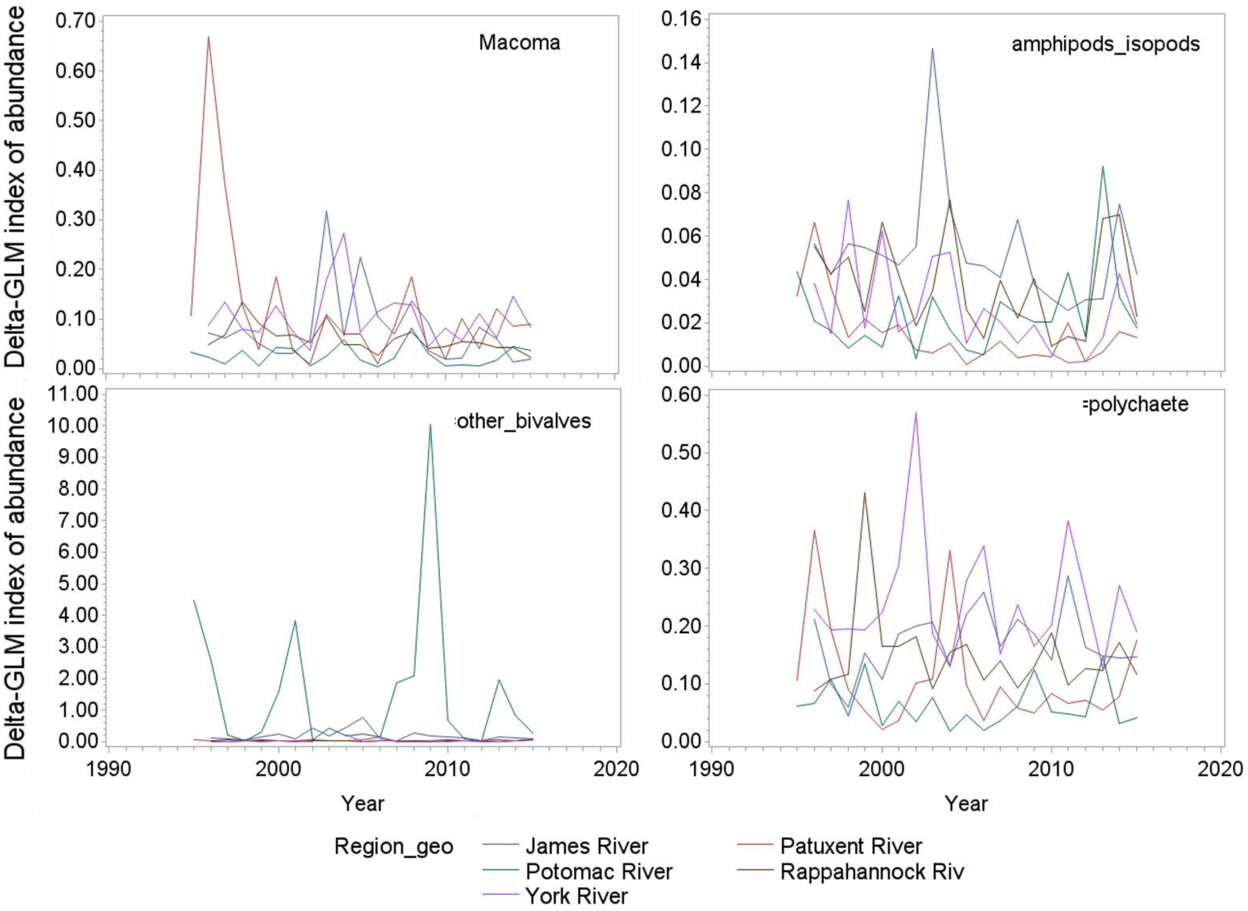


Figure 4. Delta-generalized linear model estimates of annual indices of benthic invertebrate forage abundance from five Chesapeake Bay tributaries: Patuxent River, Potomac River, Rappahannock River, York River, James River. Invertebrate groups include Macoma spp., non-Macoma bivalves, amphipods/isopods, and polychaetes.

Figure 5.

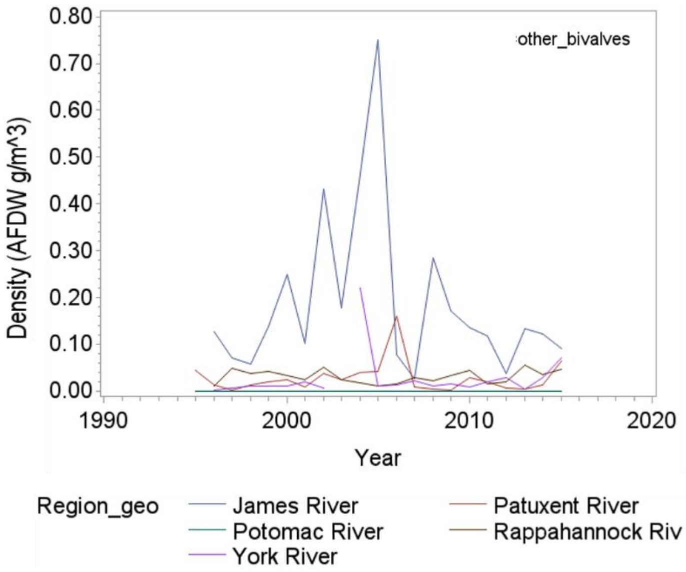


Figure 5. Replotted delta-generalized linear model estimates of annual indices of non-*Macoma* bivalve abundance from four Chesapeake Bay tributaries (Patuxent River, Rappahannock River, York River, James River) after removing the Potomac River data series (shown here as a flat line).

Figure 6.

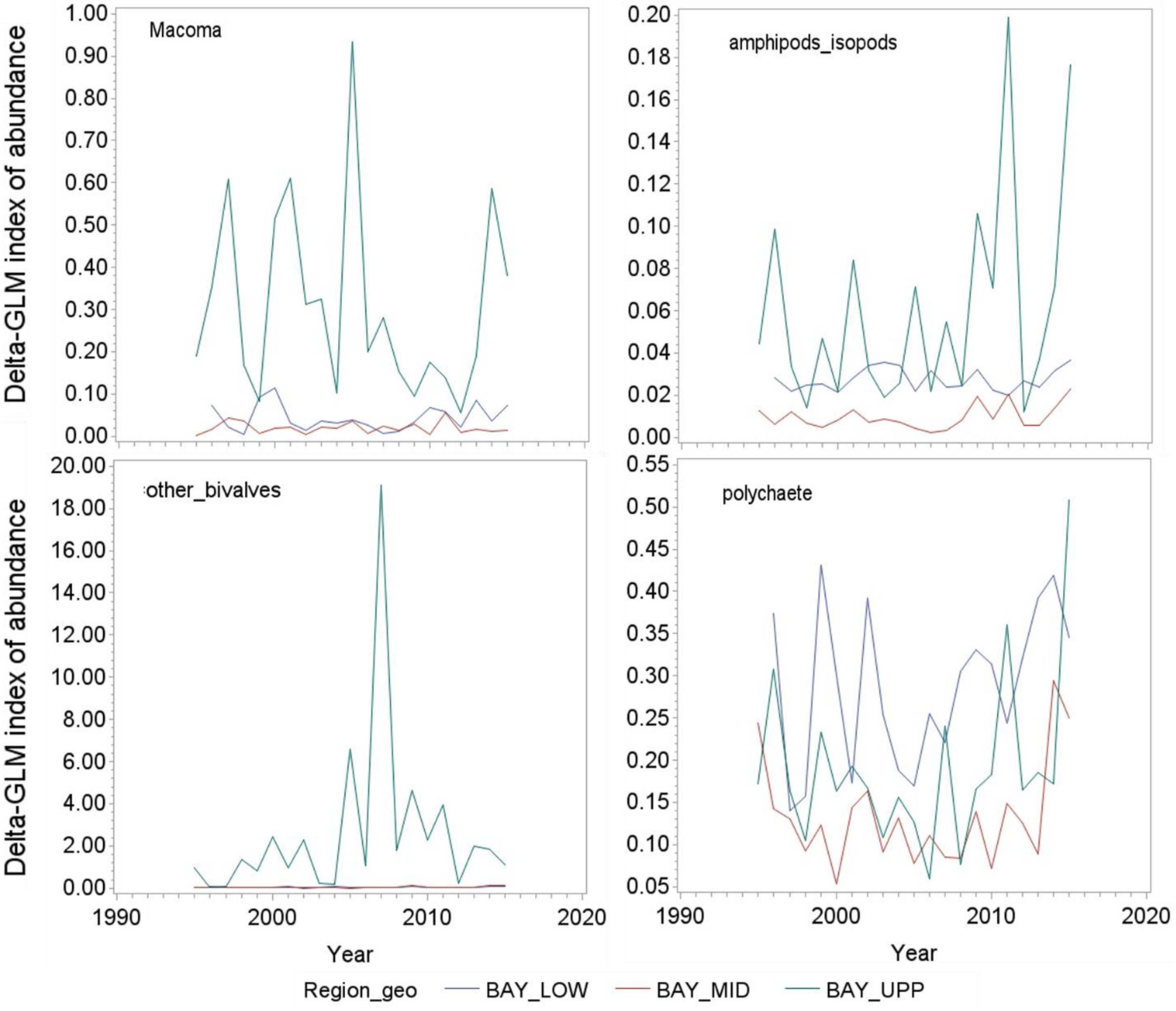
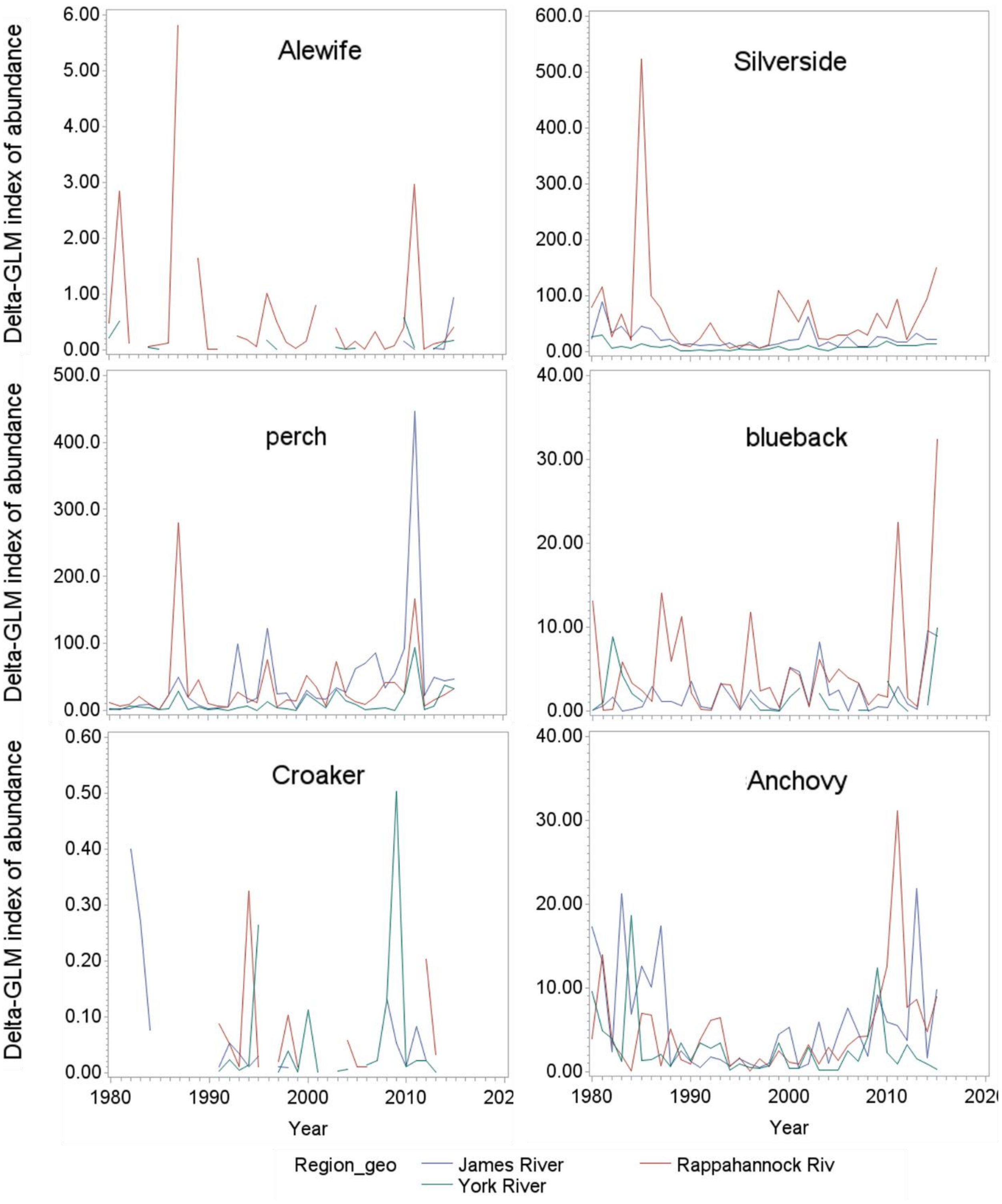


Figure 6. Delta-generalized linear model estimates of annual indices of benthic invertebrate forage abundance from the upper (BAY_UPP), middle (BAY_MID) and lower (BAY_LOW) sections of the Chesapeake Bay mainstem. Invertebrate groups include Macoma spp., non-Macoma bivalves, amphipods/isopods, and polychaetes.

Figure 7.



(**Figure 7.** *Continued on next page*)

(**Figure 7.** *Continued*)

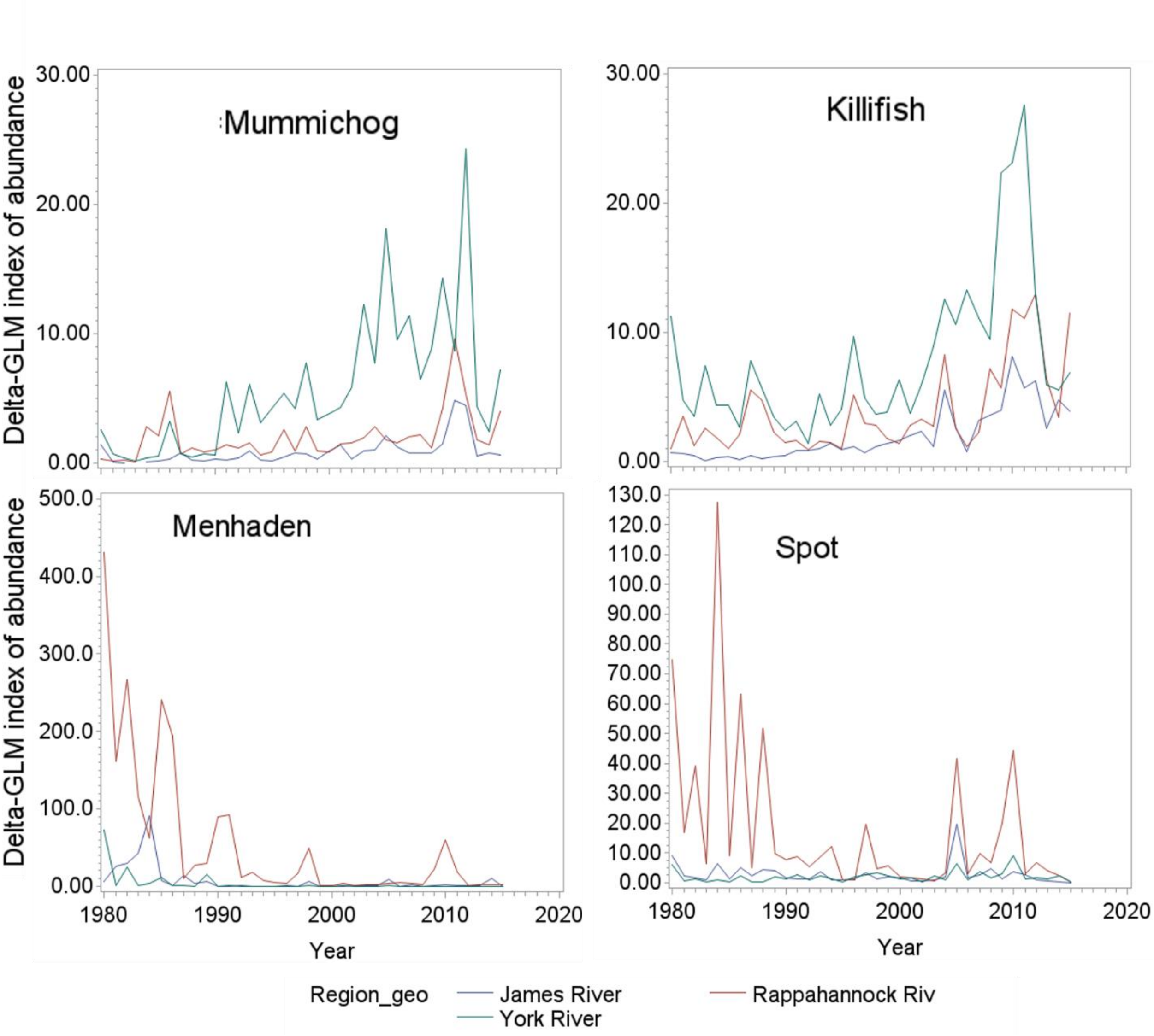


Figure 7. Delta-generalized linear model estimates of annual indices of forage fish abundance from three Chesapeake Bay tributaries: Rappahannock River, York River, and James River. Forage fish taxa include alewife, Atlantic silversides (Silverside), white perch (perch), blueback herring (blueback), Atlantic croaker (Croaker), bay anchovy (Anchovy), mummichog, killifish (Killifish), Atlantic menhaden (Menhaden), spot.

Figure 8

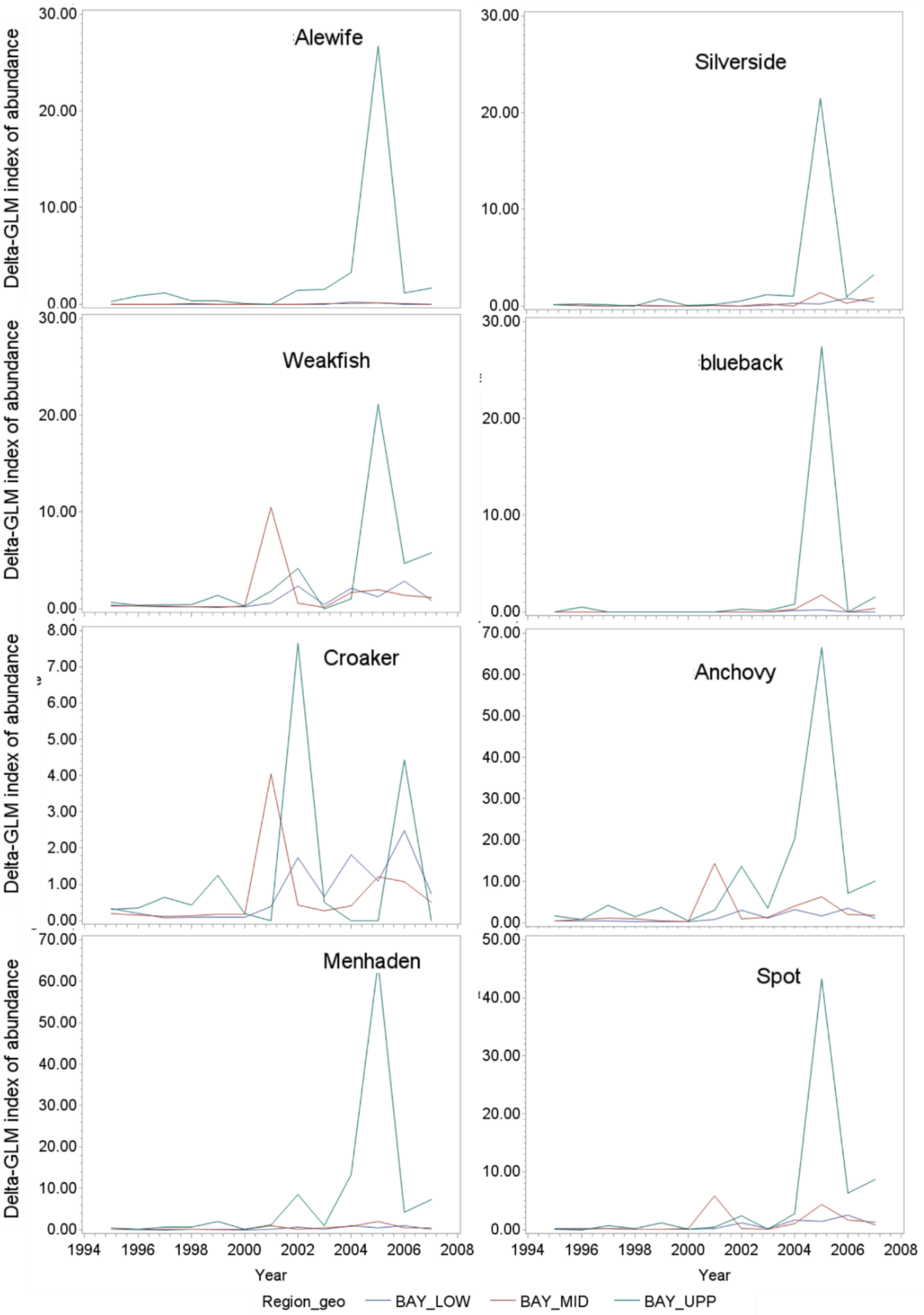
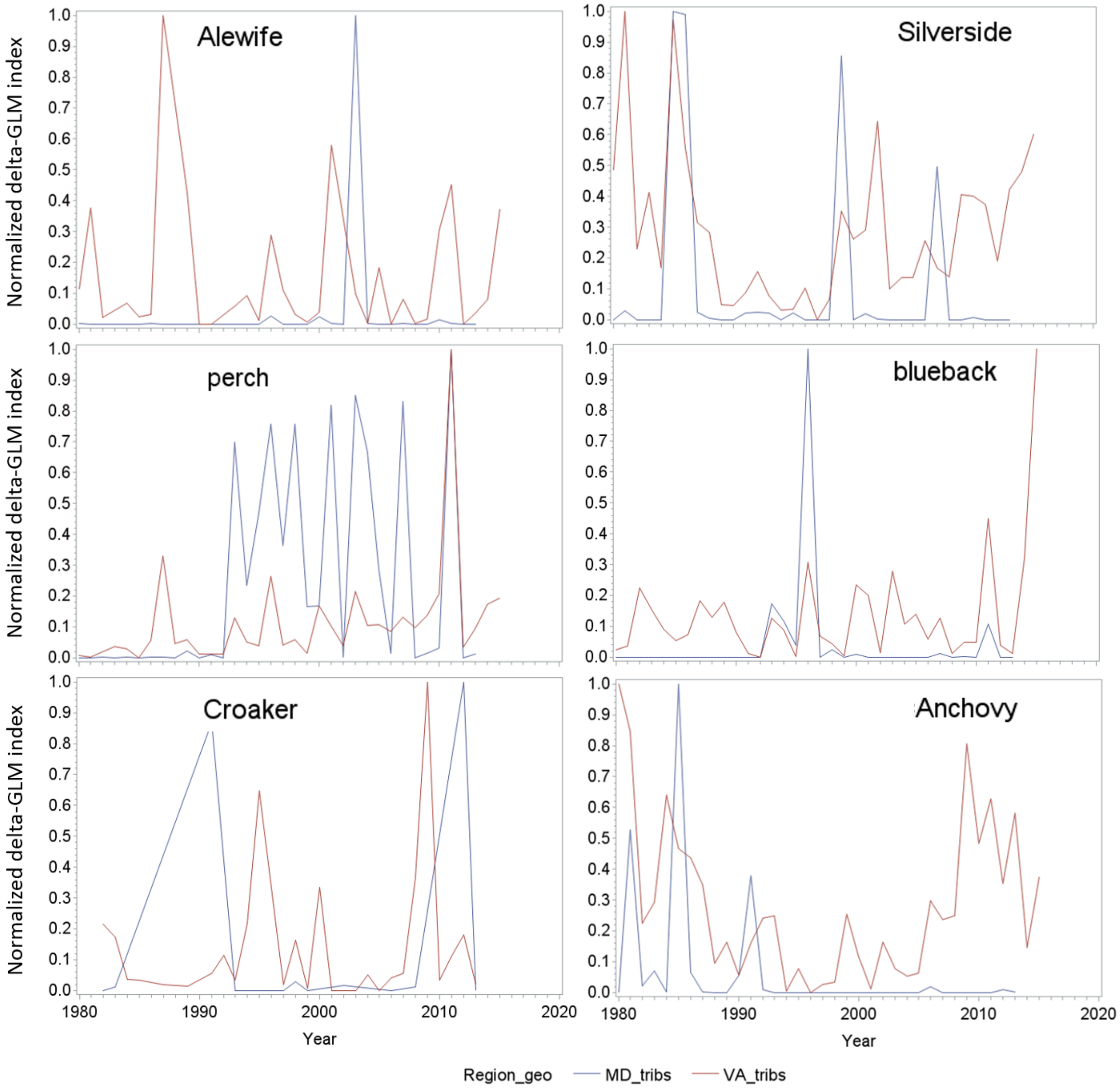


Figure 8. Delta-generalized linear model estimates of annual indices of forage fish abundance from the upper (BAY_UPP), middle (BAY_MID) and lower (BAY_LOW) sections of the Chesapeake Bay mainstem. Forage fish taxa include alewife, Atlantic silversides (Silverside), weakfish, blueback herring (blueback), Atlantic croaker (Croaker), bay anchovy (Anchovy), Atlantic menhaden (Menhaden), spot.

Figure 9.



(**Figure 9.** *Continued on next page*)

(**Figure 9.** *Continued*)

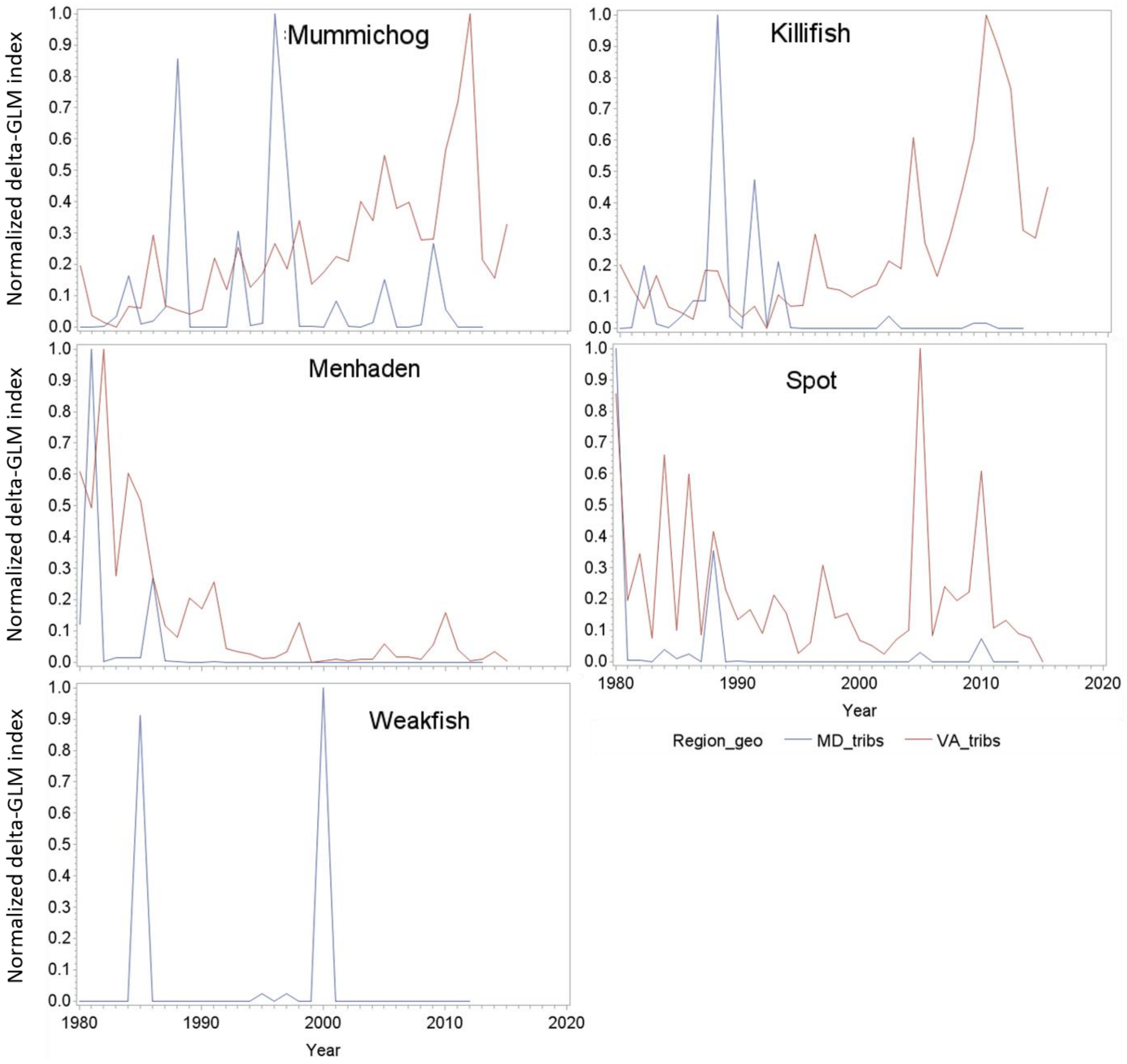


Figure 9. Delta-generalized linear model estimates of annual indices of forage fish abundance from state-aggregated (MD, VA) Chesapeake Bay tributaries. State-specific tributaries for MD: Patuxent and Potomac Rivers; for VA: Rappahannock River, York River, and James River. Forage fish taxa include alewife, Atlantic silversides (Silverside), white perch (perch), blueback herring (blueback), Atlantic croaker (Croaker), bay anchovy (Anchovy), mummichog, killifish (Killifish), Atlantic menhaden (Menhaden), spot, weakfish.

Figure 10.

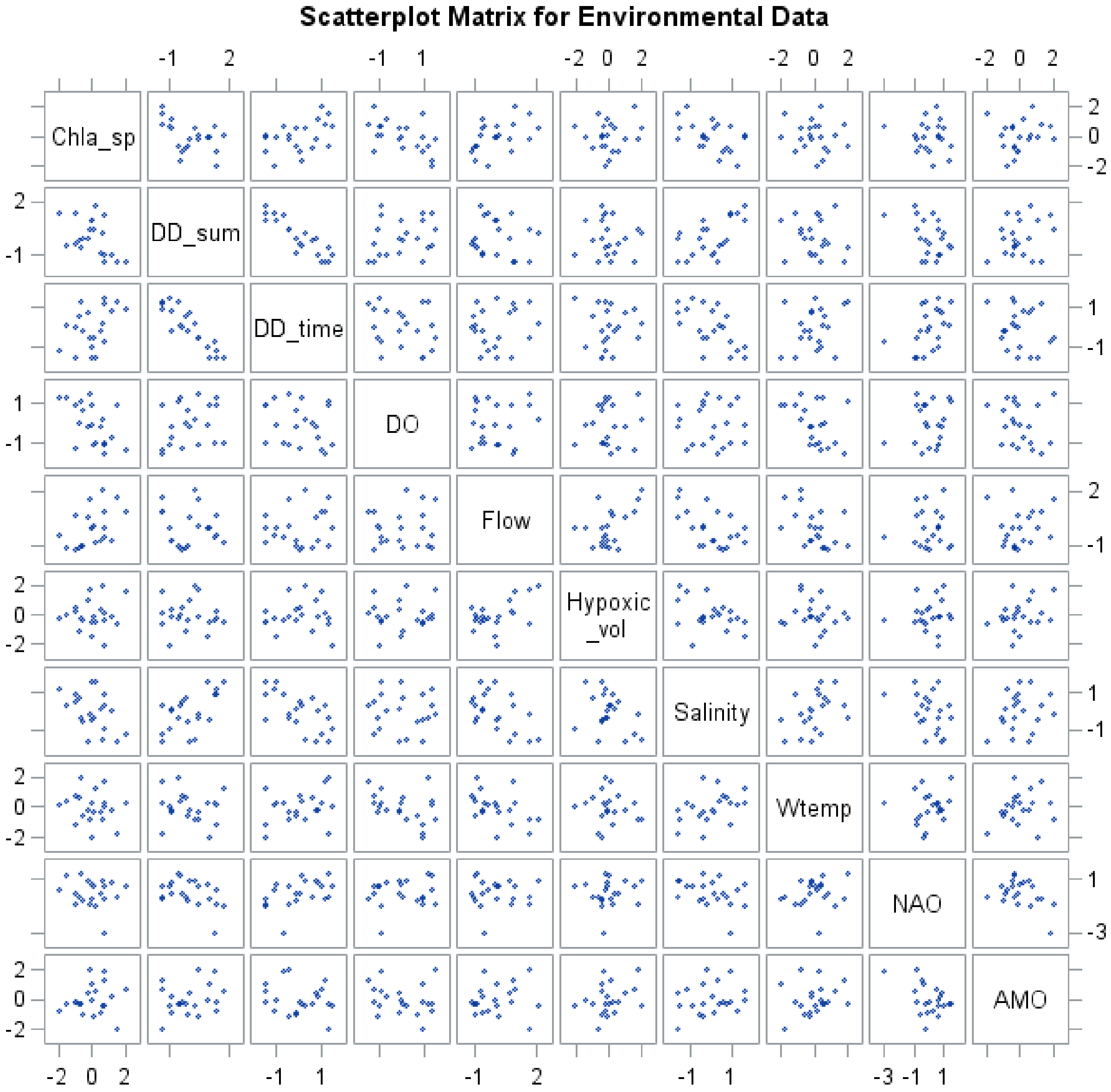


Figure 10. Scatter plot matrix of annual values of potential predictor variables from the mainstem of Chesapeake Bay (1995-2015). All predictors have been standardized. Abbreviations: Chla_sp – mean spring chlorophyll, Salinity – bottom water salinity, Wtemp – bottom water temperature, DO – bottom water dissolved oxygen concentration, flow – mean spring discharge, Hypoxic_vol – hypoxic bottom water volumes, DD_sum – cumulative 5°C degree days, DD_time – day of the year at which a threshold of n=500 5°C degree days is reached, NAO – North Atlantic Oscillation, AMO – Atlantic Multidecadal Oscillation.

Figure 11.

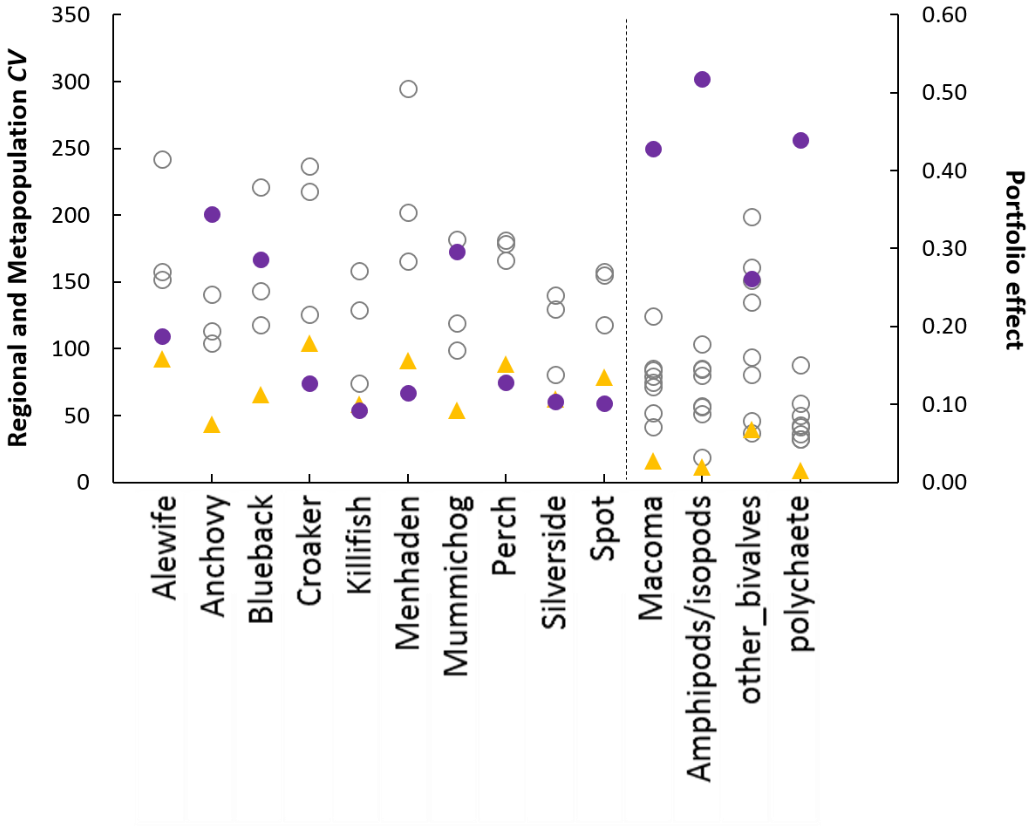


Figure 11. Spatially-explicit coefficient of variation (*CV*, open circle symbols) and metapopulation *CV*s (orange triangle symbols) for each forage fish and benthic invertebrate taxonomic group (primary y-axis). Portfolio effect associated with observed *CV*s for each forage group given on the secondary y-axis (filled purple cirles). Vertical dashed line separates forage fish (left) from invertebrate forage taxa.

Figure 12.

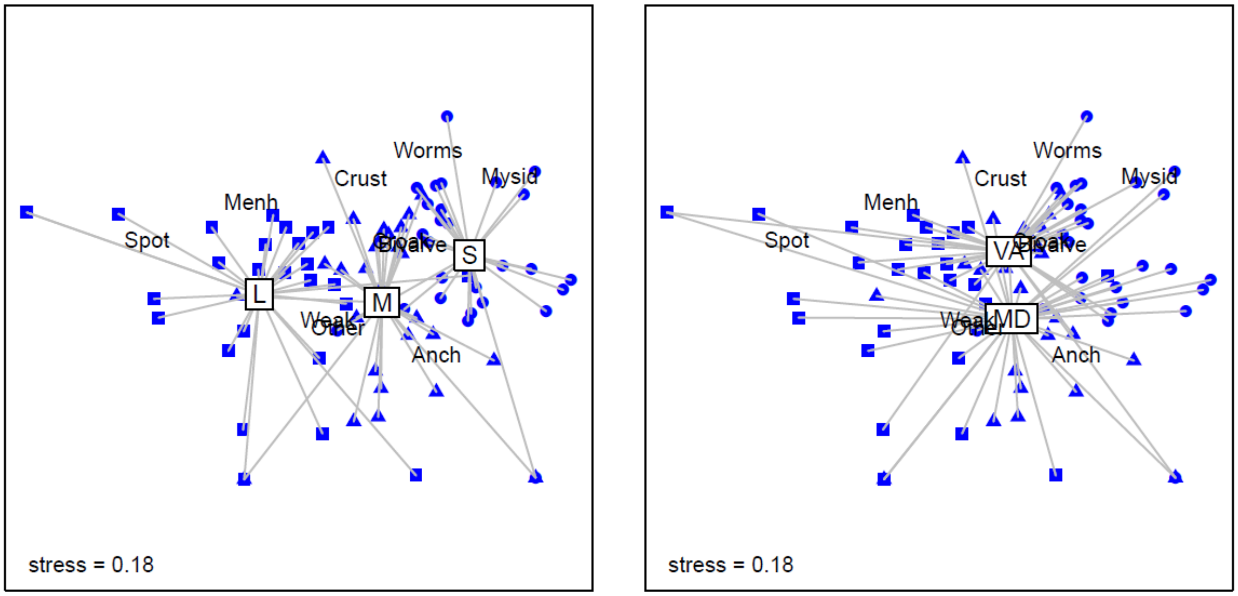


Figure 12. NMDS ordination plot of **summer flounder** diets. Points represent the available diet proportions for each predator by size class, state, and year in ordination space. Symbols represent predator size (circle – small [S], triangle – medium [M], square – large [L]). Predator diets that were more similar plot more closely to one another. Text represents the centroids for the prey (Anch – anchovy, Croak – Atlantic croaker, Bivalve – Bivalve, Menh – Atlantic menhaden, Mysid – Mysid, Other – Other prey, Crust – Other crustaceans, Worms – Polychaete worms, Spot – spot, Weak – weakfish). [Note that on the figure, Weak and Other overlap, as well as Bivalve and Croak.] Size and state (VA – Virginia, MD – Maryland) were significant factors in the permutation analysis (plotted on the separate panels for clarity), and points are joined by gray lines to the factor centroids which are located in the white boxes.

Figure 13.

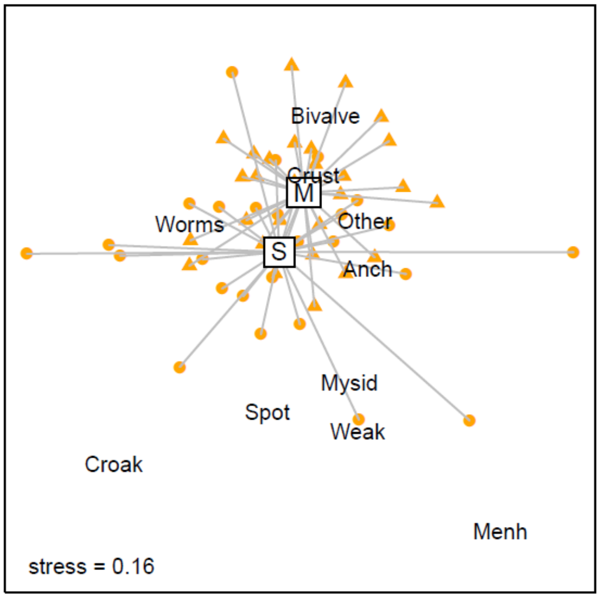


Figure 13. NMDS ordination plot of **Atlantic Croaker** diets. See Figure X for description of symbols, points, and prey. Size was a significant factor in the permutation analysis, and points are joined by gray lines to the factor centroids which are located in the white boxes.

Figure 14.

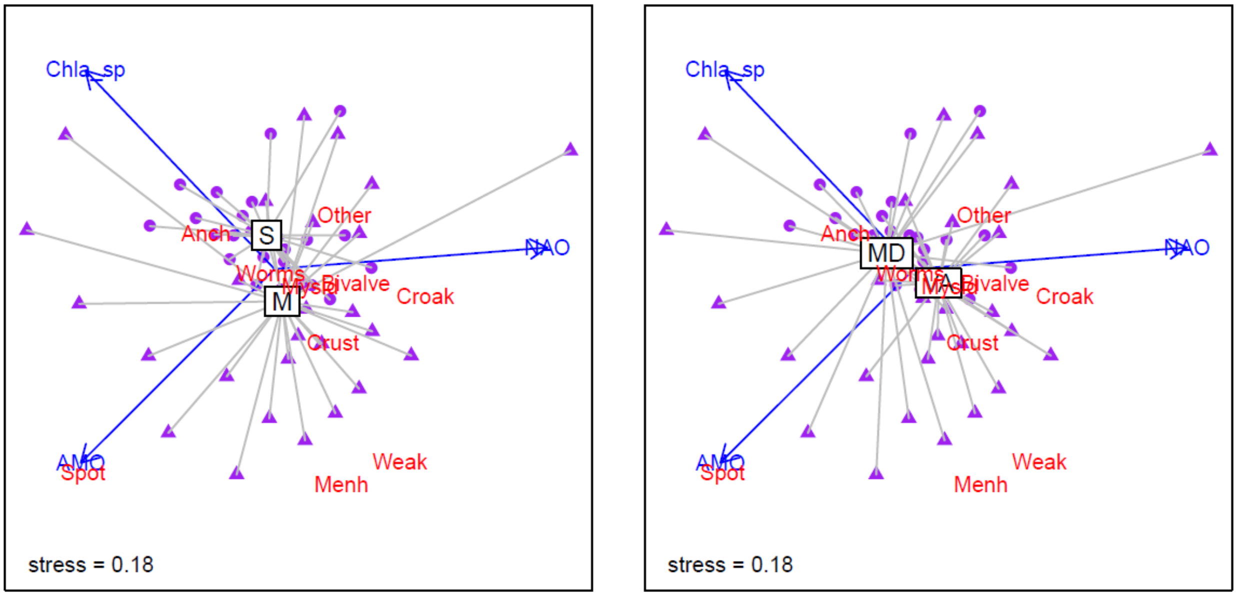


Figure 14. NMDS ordination plot of **weakfish** diets. See Figure X for description of symbols, points, and prey. Size and state (VA – Virginia, MD – Maryland) were significant factors in the permutation analysis (plotted on the separate panels for clarity), and points are joined by gray lines to the factor centroids which are located in the white boxes. Significant vectors are also plotted, including springtime Chlorophyll a (Chla_sp), AMO, and NAO.

Figure 15.

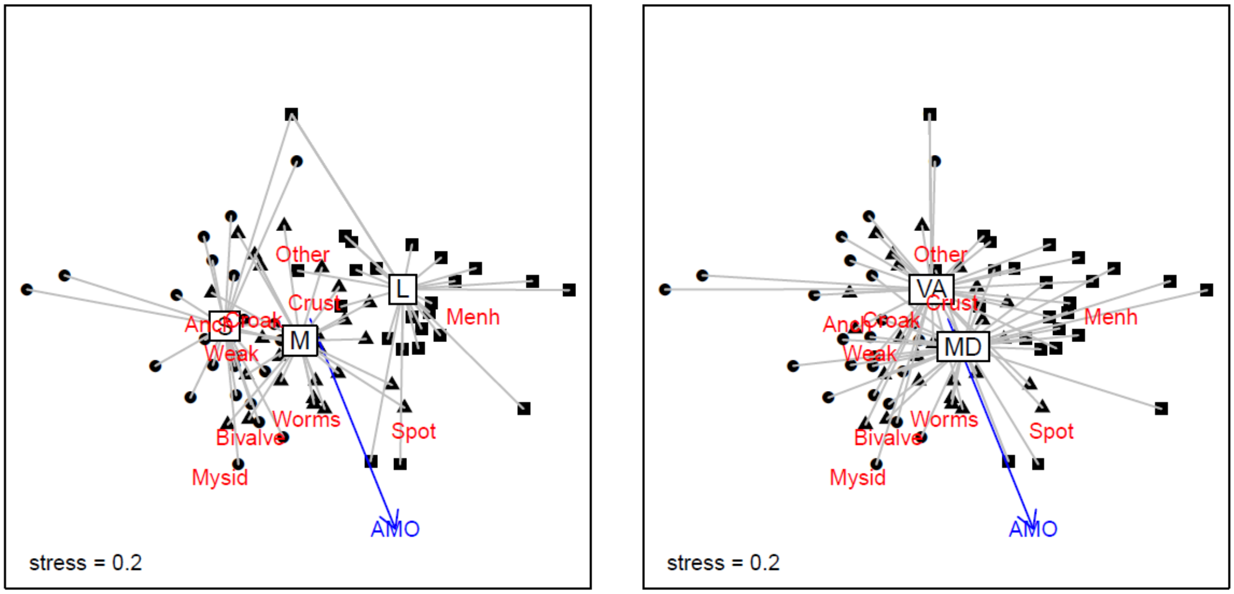


Figure 15. NMDS ordination plot of **striped bass** diets. See Figure X for description of symbols, points, and prey. Size and state (VA – Virginia, MD – Maryland) were significant factors in the permutation analysis (plotted on the separate panels for clarity), and points are joined by gray lines to the factor centroids which are located in the white boxes. AMO was also a significant vector.

Figure 16.

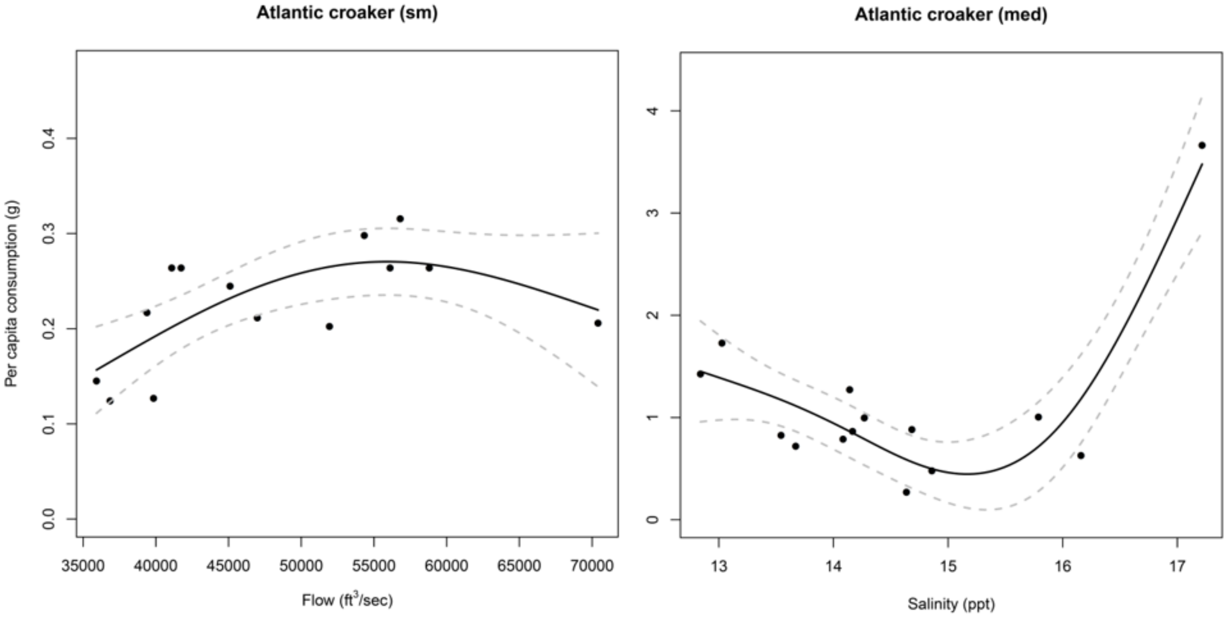


Figure 16. Predictions (solid black line) and 95% confidence intervals (dashed gray lines) from generalized additive models (GAMs) selected for inference based on AIC model selection and diagnostic plots for Atlantic croaker consumption-environment patterns in the mainstem of Chesapeake Bay. Species-specific size-classes (sm – small; med – medium) are defined in the text.

Figure 17.

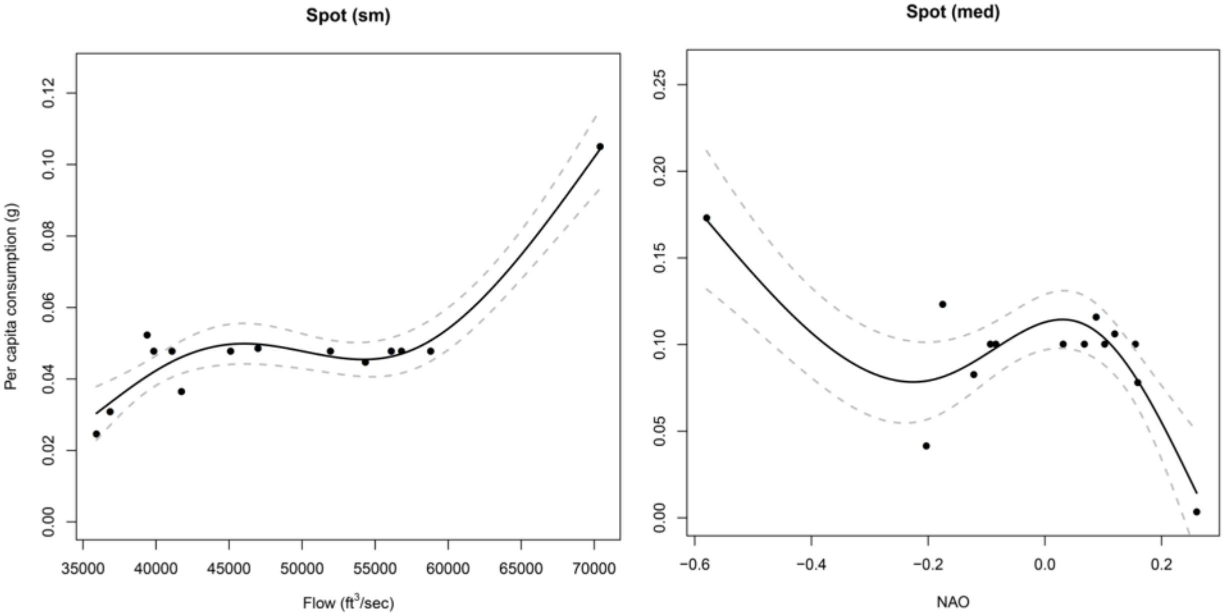


Figure 17. Predictions (solid black line) and 95% confidence intervals (dashed gray lines) from generalized additive models (GAMs) selected for inference based on AIC model selection and diagnostic plots for spot consumption-environment patterns in the mainstem of Chesapeake Bay. Species-specific size-classes (sm – small; med – medium) are defined in the text.

Figure 18.

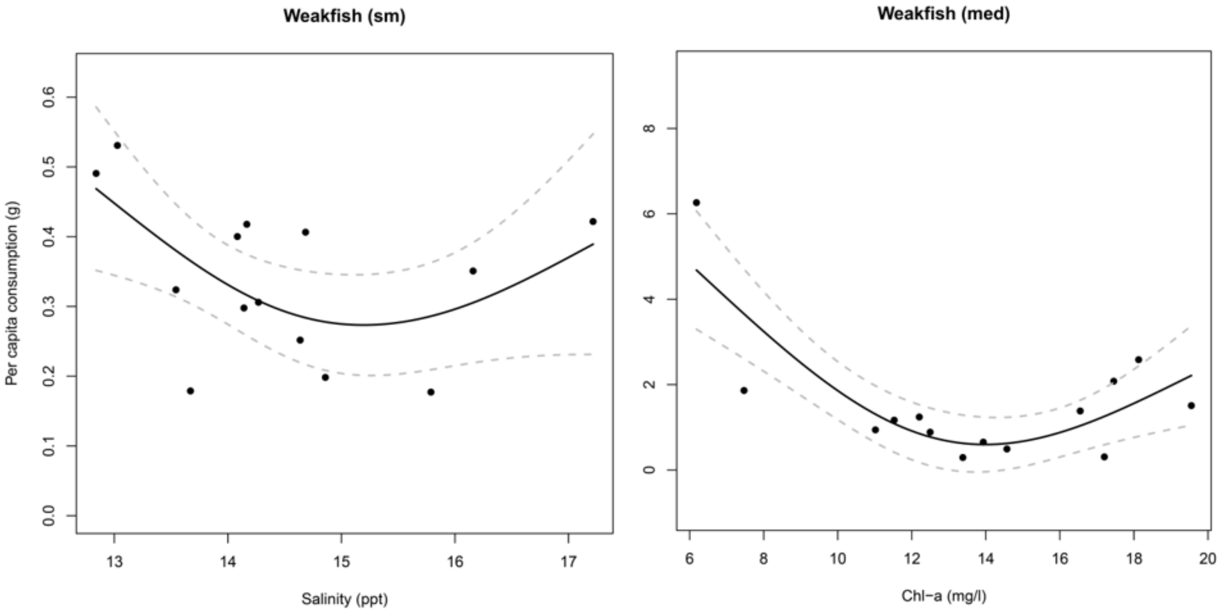


Figure 18. Predictions (solid black line) and 95% confidence intervals (dashed gray lines) from generalized additive models (GAMs) selected for inference based on AIC model selection and diagnostic plots for weakfish consumption-environment patterns in the mainstem of Chesapeake Bay. Species-specific size-classes (sm – small; med – medium) are defined in the text.

Figure 19.

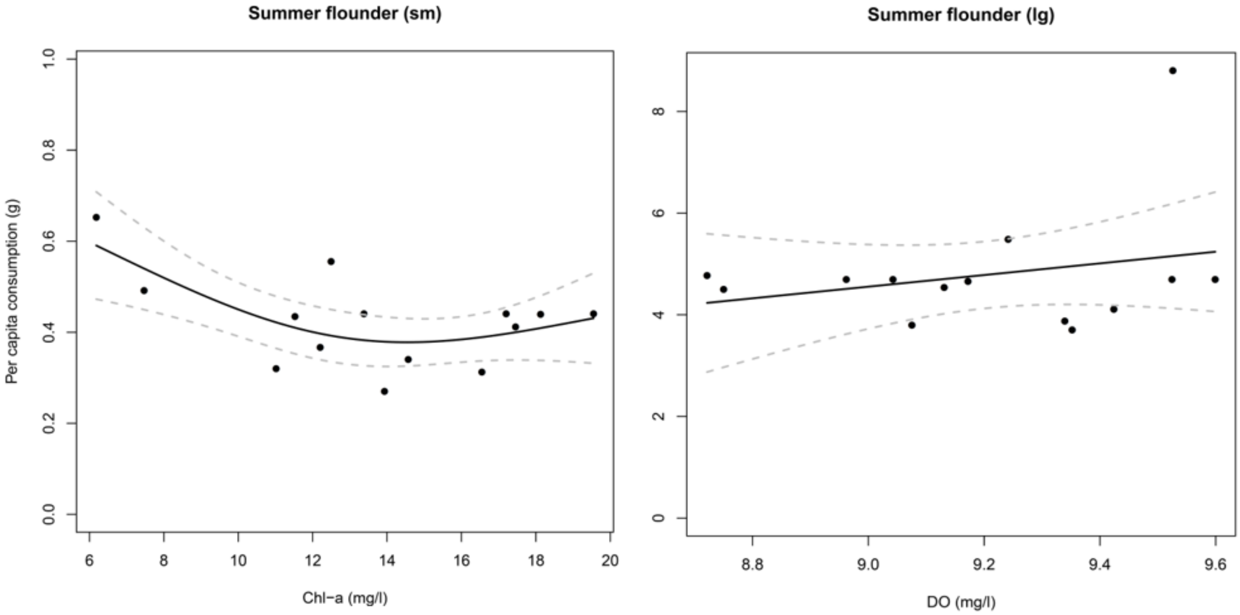


Figure 19. Predictions (solid black line) and 95% confidence intervals (dashed gray lines) from generalized additive models (GAMs) selected for inference based on AIC model selection and diagnostic plots for summer flounder consumption-environment patterns in the mainstem of Chesapeake Bay. Species-specific size-classes (sm – small; lg – large) are defined in the text.

Figure 20.

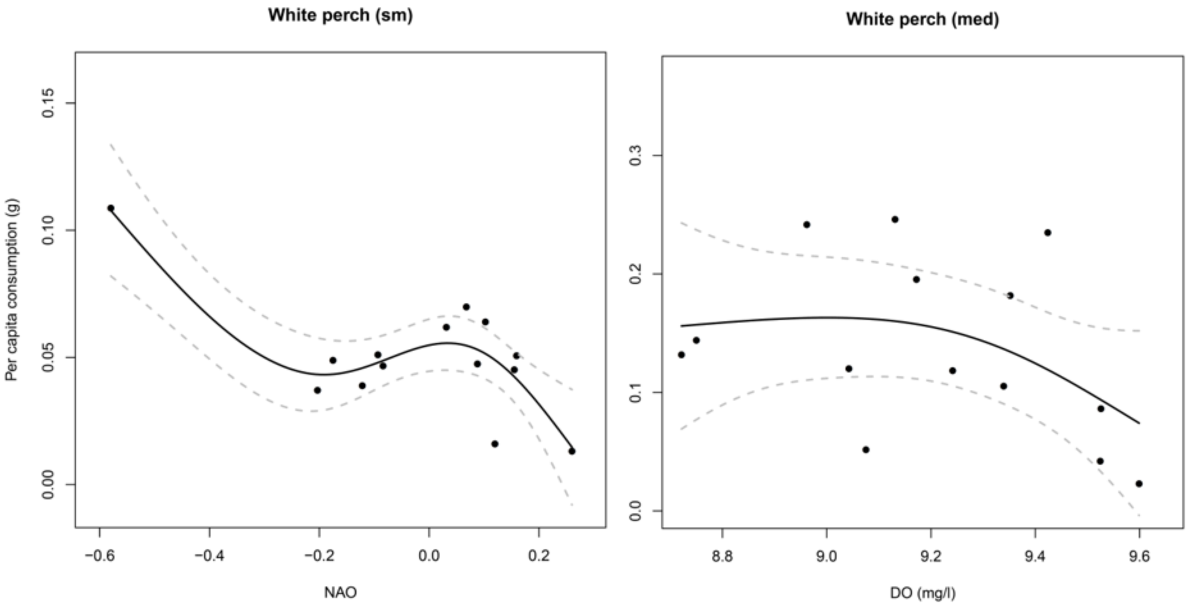


Figure 20. Predictions (solid black line) and 95% confidence intervals (dashed gray lines) from generalized additive models (GAMs) selected for inference based on AIC model selection and diagnostic plots for white perch consumption-environment patterns in the mainstem of Chesapeake Bay. Species-specific size-classes (sm – small; med – medium) are defined in the text.

Figure 21.

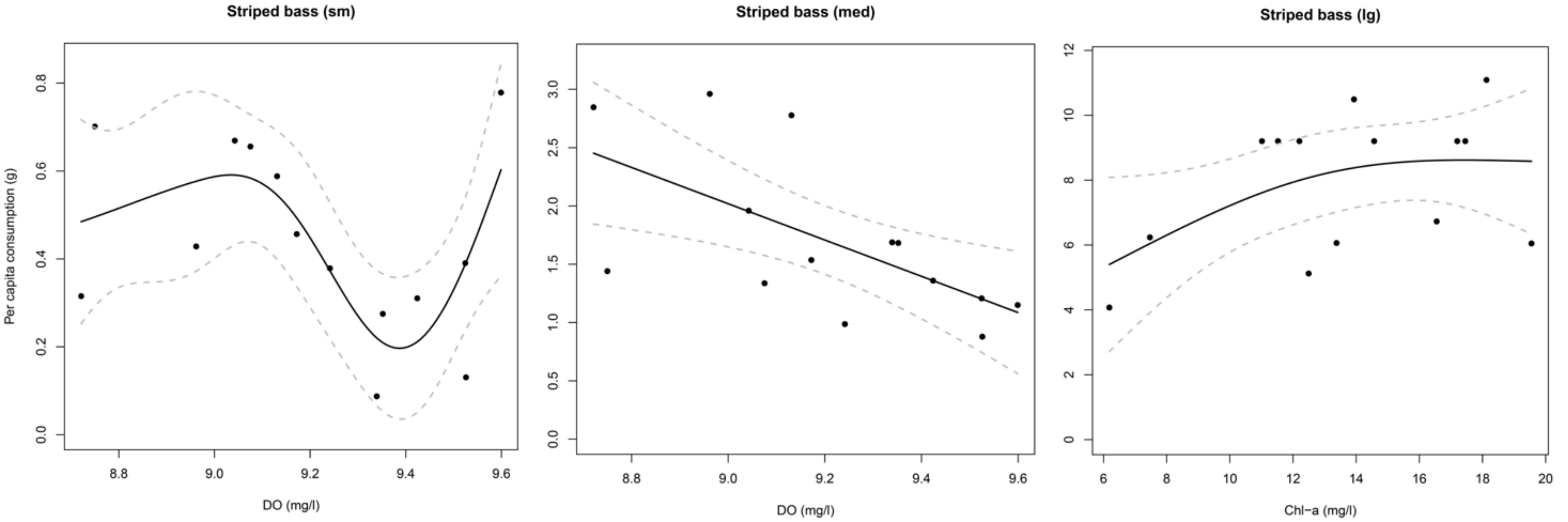


Figure 21. Predictions (solid black line) and 95% confidence intervals (dashed gray lines) from generalized additive models (GAMs) selected for inference based on AIC model selection and diagnostic plots for striped bass consumption-environment patterns in the mainstem of Chesapeake Bay. Species-specific size-classes (sm – small; med – medium, lg – large) are defined in the text.

Figure 22.

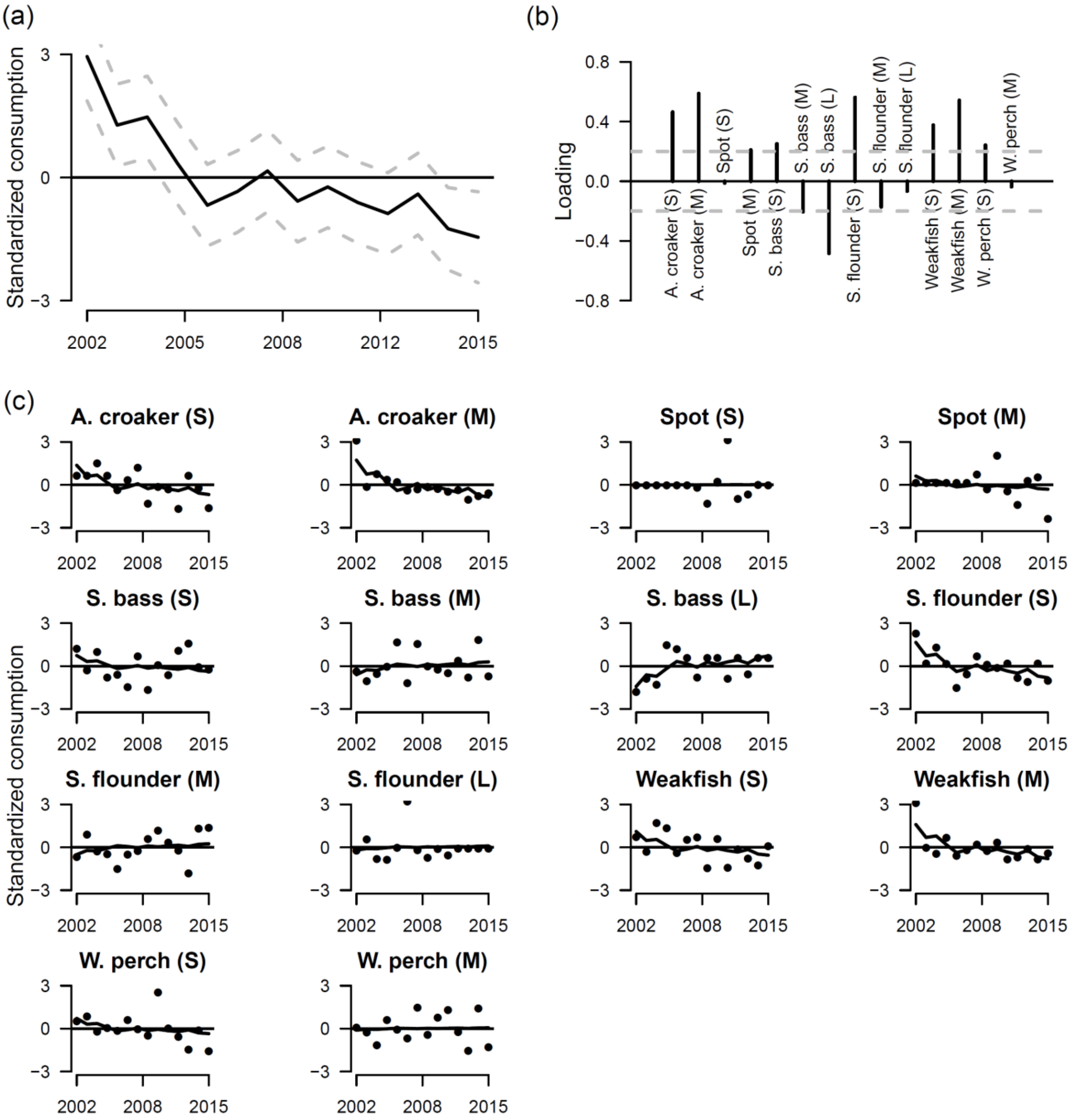
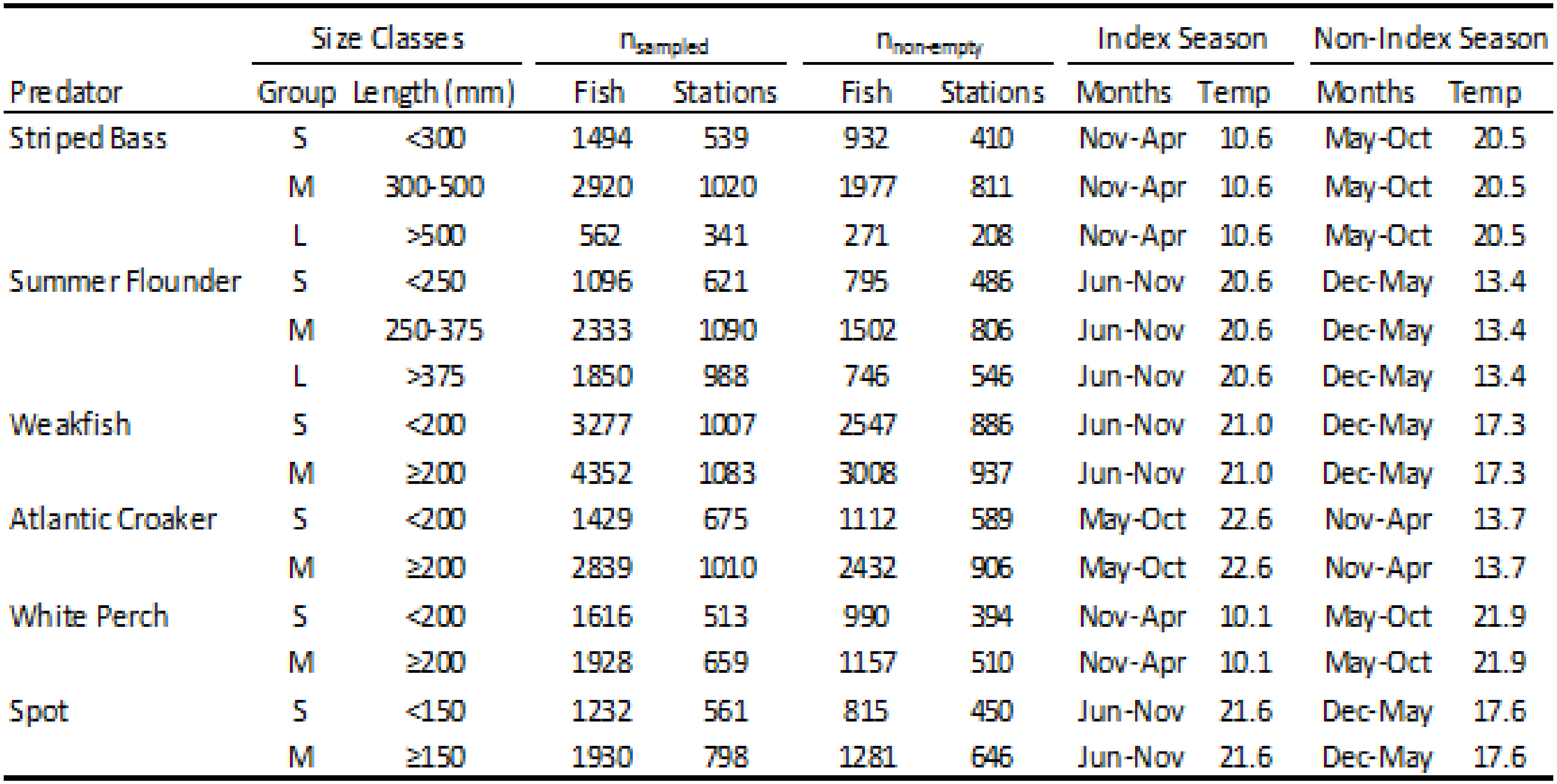


Figure 22. Dynamic factor analysis results showing the common trend of decreasing condition over time among predators (a) and the specific loadings (influence) each predator species contributed to the common trend (b). Species/size-class specific time-series are provided. Species codes: A. croaker = Atlantic croaker, S. bass = striped bass, S. flounder = summer flounder, W. perch = white perch; size-class definitions: S = small, M = medium, L = large; where appropriate).

Appendices 1–4.

Appendix 1. Sample and size-class information for the six predators used for consumption estimates. Size classes (S-small, M-medium, L-large) were based on fork lengths (mm). Sample sizes are reported for the numbers of fish and the numbers of stations that had any predator stomachs sampled (nsampled) and for non-empty samples (nnon-empty) that were used for diet analysis. Predators were divided into two six-month seasons based on when abundances were the highest ("Index Season") and when they were not ("Non-Index Season"). Average bottom water temperatures (°C) were calculated by pooling across years for stations where predators were sampled.



	Size Classes		$n_{sampled}$		$n_{non\text{-}empty}$		Index Season		Non-Index Season	
Predator	Group	Length (mm)	Fish	Stations	Fish	Stations	Months	Temp	Months	Temp
Striped Bass	S	<300	1494	539	932	410	Nov-Apr	10.6	May-Oct	20.5
	M	300-500	2920	1020	1977	811	Nov-Apr	10.6	May-Oct	20.5
	L	>500	562	341	271	208	Nov-Apr	10.6	May-Oct	20.5
Summer Flounder	S	<250	1096	621	795	486	Jun-Nov	20.6	Dec-May	13.4
	M	250-375	2333	1090	1502	806	Jun-Nov	20.6	Dec-May	13.4
	L	>375	1850	988	746	546	Jun-Nov	20.6	Dec-May	13.4
Weakfish	S	<200	3277	1007	2547	886	Jun-Nov	21.0	Dec-May	17.3
	M	≥200	4352	1083	3008	937	Jun-Nov	21.0	Dec-May	17.3
Atlantic Croaker	S	<200	1429	675	1112	589	May-Oct	22.6	Nov-Apr	13.7
	M	≥200	2839	1010	2432	906	May-Oct	22.6	Nov-Apr	13.7
White Perch	S	<200	1616	513	990	394	Nov-Apr	10.1	May-Oct	21.9
	M	≥200	1928	659	1157	510	Nov-Apr	10.1	May-Oct	21.9
Spot	S	<150	1232	561	815	450	Jun-Nov	21.6	Dec-May	17.6
	M	≥150	1930	798	1281	646	Jun-Nov	21.6	Dec-May	17.6

Appendix 2. Diet composition summary of forage prey taxa for six key predators (summer flounder, striped bass, Atlantic croaker, white perch, spot, and weakfish) in Maryland waters of the Chesapeake Bay from 2002–2015. Predatory fishes and sample size (n) were designated by size class (L – large, M – medium, S – small).

			Prey									
Predator	Size Class (n)	Year	Croaker	Weakfish	Spot	Menhaden	Anchovies	Bivalves	Other Crustaceans	Mysids	Polychaetes	Other
Summer flounder	L (22)	2002	0.0255	0.0317	0.0577	0	0.5314	0.0034	0.1108	0	0	0.2396
	M (58)	2002	0.0146	0.0880	0.0060	0	0.5088	0.0006	0.1423	0.0391	0.0097	0.1909
	S (14)	2002	0	0.0442	0.0390	0	0.6297	0	0.0332	0.1124	0	0.1415
Striped bass	L (9)	2002	0	0	0	0.1429	0.5238	0	0.0976	0	0	0.2357
	M (63)	2002	0	0.0159	0.0073	0.0838	0.3052	0.0216	0.0400	0.1123	0.0779	0.3359
	S (101)	2002	0.0001	0	0	0.0165	0.6575	0.0484	0.0103	0.1432	0.0472	0.0769
Atlantic croaker	M (13)	2002	0	0	0	0	0.0589	0.0026	0.0398	0.0302	0.3423	0.5263
	S (8)	2002	0	0	0	0	0.0264	0.0735	0	0.0046	0.5056	0.3899
White perch	M (226)	2002	0.0020	0	0	0	0.1108	0.0856	0.0001	0.0654	0.2697	0.4664
	S (124)	2002	0	0	0	0	0	0.0236	0.0562	0.0750	0.3556	0.4896
Spot	M (12)	2002	0	0	0	0	0	0.1341	0	0.0013	0.2906	0.5740
	S (0)	2002	0	0	0	0	0	0	0	0	0	0
Weakfish	M (124)	2002	0.0001	0.0387	0.0300	0.4547	0.2637	0.0008	0.0968	0.0146	0.0001	0.1004
	S (106)	2002	0.0006	0	0	0.0045	0.6528	0	0.0047	0.0569	0	0.2805
Summer flounder	L (4)	2003	0	0.7413	0	0	0.2500	0	0	0	0	0.0087
	M (24)	2003	0.0677	0.1342	0	0	0.3393	0	0	0.1485	0	0.3103
	S (0)	2003	0	0	0	0	0	0	0	0	0	0
Striped bass	L (8)	2003	0	0	0	0.3170	0	0.0292	0.0036	0.2339	0.3113	0.1049
	M (139)	2003	0.0085	0.0280	0	0.0024	0.1374	0.0379	0.0704	0.3625	0.1550	0.1979
	S (61)	2003	0	0	0	0	0.0732	0.0135	0.0042	0.2086	0.2749	0.4257
Atlantic croaker	M (2)	2003	0	0	0	0	0	0	0	0	0.6745	0.3255
	S (0)	2003	0	0	0	0	0	0	0	0	0	0
White perch	M (47)	2003	0	0	0	0	0.0236	0.0054	0	0	0.1775	0.7935

	S (44)	2003	0	0	0	0	0	0.0138	0	0.0967	0.3918	0.4977
Spot	M (1)	2003	0	0	0	0	0	0	0	0	0.1490	0.8510
	S (0)	2003	0	0	0	0	0	0	0	0	0	0
Weakfish	M (62)	2003	0.0037	0.0409	0.0353	0	0.3957	0	0.0691	0.1229	0	0.3324
	S (30)	2003	0	0	0	0	0.5408	0	0.0168	0.2009	0	0.2416
Summer flounder	L (5)	2004	0	0.6345	0.1667	0	0.0287	0.0014	0	0	0	0.1687
	M (39)	2004	0.4581	0.0718	0	0	0.3433	0	0	0.1004	0	0.0265
	S (19)	2004	0	0	0	0	0.1956	0.0274	0	0.3165	0.0278	0.4327
Striped bass	L (32)	2004	0	0	0	0.1053	0	0.0007	0.0551	0.0006	0.2136	0.6247
	M (176)	2004	0.0073	0.0009	0	0.0100	0.0276	0.0064	0.0305	0.0328	0.3397	0.5447
	S (140)	2004	0.1010	0	0	0	0.3344	0.0000	0.0004	0.0667	0.2175	0.2800
Atlantic croaker	M (27)	2004	0	0	0.0076	0	0	0.0608	0	0.0029	0.0851	0.8437
	S (7)	2004	0.1497	0	0.0152	0	0	0	0	0.1391	0.5807	0.1154
White perch	M (127)	2004	0.0006	0	0	0	0	0.0941	0.0011	0.0007	0.1205	0.7828
	S (83)	2004	0	0	0	0	0.0007	0.0285	0	0.0013	0.0534	0.9161
Spot	M (9)	2004	0	0	0	0	0	0	0	0	0.2265	0.7735
	S (1)	2004	0	0	0	0	0	0	0	0	0	1.0000
Weakfish	M (71)	2004	0.0774	0.2043	0	0.1680	0.2894	0	0	0.0456	0.0019	0.2134
	S (61)	2004	0.1316	0	0	0	0.2985	0	0.0021	0.4288	0.0038	0.1352
Summer flounder	L (6)	2005	0	0.4376	0.3000	0	0.0737	0	0	0	0	0.1887
	M (18)	2005	0	0	0.1196	0.0435	0.7301	0	0	0	0	0.1068
	S (94)	2005	0	0	0	0	0	0	0	0.8142	0.0000	0.1858
Striped bass	L (14)	2005	0	0	0	0.5113	0.0064	0	0	0	0.1686	0.3138
	M (164)	2005	0.0000	0.0378	0.0126	0.1851	0.1196	0.0205	0.0151	0.3071	0.0616	0.2405
	S (140)	2005	0	0	0.0028	0.0270	0.0470	0.0383	0	0.4761	0.0935	0.3152
Atlantic croaker	M (29)	2005	0.0176	0	0	0.0131	0.0617	0.1610	0.1829	0.0442	0.1602	0.3593
	S (1)	2005	0	0	0	0	0	0	0	0	0	1.0000
White perch	M (119)	2005	0	0	0	0	0.0269	0.1668	0	0.0584	0.1801	0.5677
	S (98)	2005	0	0	0	0	0.0180	0.0709	0	0.0715	0.0743	0.7654
Spot	M (1)	2005	0	0	0	0	0	0	0	0	0.2280	0.7720
	S (0)	2005	0	0	0	0	0	0	0	0	0	0

Weakfish	M (54)	2005	0	0.0638	0.0611	0.3950	0.3940	0	0	0.0001	0	0.0860
	S (53)	2005	0	0	0	0	0.7712	0	0	0.0248	0.0013	0.2027
Summer flounder	L (5)	2006	0	0	0	0	0.3750	0	0.0331	0.4132	0	0.1787
	M (34)	2006	0.0050	0.1026	0	0	0.6839	0	0.0383	0.0399	0	0.1303
	S (20)	2006	0	0	0	0	0.2674	0	0	0.6083	0	0.1243
Striped bass	L (18)	2006	0.0175	0	0.0207	0.6289	0.0063	0	0	0	0.0784	0.2482
	M (172)	2006	0.0001	0.0050	0.0057	0.1619	0.2133	0.0061	0.0006	0.0465	0.3332	0.2276
	S (63)	2006	0	0	0	0.0227	0.2721	0.0401	0.0256	0.0682	0.2832	0.2882
Atlantic croaker	M (53)	2006	0	0	0	0	0.0036	0.2037	0.0467	0.2023	0.4443	0.0994
	S (28)	2006	0	0	0	0	0	0.0211	0.0624	0.0802	0.1105	0.7258
White perch	M (112)	2006	0	0	0	0	0.0055	0.1707	0.0003	0.0576	0.3683	0.3977
	S (97)	2006	0	0	0	0	0	0.1768	0	0.0408	0.1897	0.5926
Spot	M (2)	2006	0	0	0	0	0	0.7326	0	0	0.2674	0
	S (1)	2006	0	0	0	0	0	0	0	0	0	0
Weakfish	M (35)	2006	0	0.0073	0.1853	0.0503	0.1264	0	0.0009	0.4699	0.0001	0.1596
	S (48)	2006	0	0	0	0	0.6720	0	0	0.2282	0.0000	0.0997
Summer flounder	L (7)	2007	0	0	0.3333	0	0.2222	0	0.2222	0.0002	0	0.2220
	M (39)	2007	0.1637	0.0295	0.1861	0	0.4085	0	0.0958	0.0214	0	0.0950
	S (4)	2007	0	0	0	0	0.0008	0	0	0.5972	0	0.4020
Striped bass	L (6)	2007	0	0	0.2500	0.6250	0	0	0	0	0.1183	0.0067
	M (91)	2007	0.0070	0	0	0.2285	0.1946	0.0054	0.0014	0.0386	0.1595	0.3649
	S (28)	2007	0	0	0	0.0175	0.4451	0.0090	0.0001	0.1736	0.0796	0.2751
Atlantic croaker	M (75)	2007	0	0	0	0	0.0111	0.3601	0.0150	0	0.5411	0.0726
	S (19)	2007	0	0	0	0	0.0300	0.2021	0	0.0499	0.2125	0.5055
White perch	M (94)	2007	0	0	0	0	0.1180	0.0732	0	0.0113	0.2220	0.5754
	S (120)	2007	0	0	0	0	0.0013	0.1427	0	0.0138	0.0878	0.7544
Spot	M (1)	2007	0	0	0	0	0	0	0	0	0	1.0000
	S (0)	2007	0	0	0	0	0	0	0	0	0	0
Weakfish	M (61)	2007	0.0212	0.0350	0.3723	0.0256	0.2272	0	0.2499	0.0047	0.0076	0.0565
	S (43)	2007	0	0	0	0	0.8754	0	0	0.0162	0	0.1084
Summer flounder	L (10)	2008	0	0	0.5996	0	0	0	0	0	0	0.4004

	M (35)	2008	0.0171	0.1046	0.2211	0.0399	0.3133	0.0233	0.0519	0.1629	0	0.0660
	S (12)	2008	0	0	0.0769	0	0.4705	0	0.0028	0.3728	0	0.0769
Striped bass	L (30)	2008	0	0	0.2172	0.3131	0.0935	0	0.0030	0	0.0261	0.3472
	M (142)	2008	0.0167	0	0.1081	0.1401	0.1508	0.0224	0.1247	0.0030	0.1932	0.2410
	S (39)	2008	0.0023	0	0	0.1339	0.2033	0	0.0164	0.0201	0.2858	0.3383
Atlantic croaker	M (32)	2008	0	0	0	0	0.0055	0.3737	0.0038	0.0036	0.4183	0.1951
	S (29)	2008	0	0	0	0.1337	0.2266	0.0205	0	0.3196	0.1068	0.1928
White perch	M (80)	2008	0.0042	0	0	0.0350	0.0385	0.2524	0.0001	0.0908	0.2440	0.3351
	S (97)	2008	0	0	0	0.0238	0.0364	0.2222	0.0001	0.0661	0.1579	0.4936
Spot	M (89)	2008	0	0	0	0	0	0.1415	0.0018	0.0065	0.2648	0.5854
	S (68)	2008	0	0	0	0	0	0.0302	0	0.0419	0.3157	0.6122
Weakfish	M (26)	2008	0	0	0.2816	0.1040	0.4601	0	0.0003	0.0002	0.0047	0.1491
	S (15)	2008	0.0282	0	0	0	0.5933	0	0	0.1568	0.0180	0.2037
Summer flounder	L (5)	2009	0	0.1667	0.1667	0	0.5	0	0	0	0	0.1667
	M (35)	2009	0.1114	0.2413	0	0	0.3619	0.0009	0.1335	0	0	0.1511
	S (6)	2009	0.1667	0	0	0	0.5349	0	0.0148	0.2836	0	0
Striped bass	L (8)	2009	0	0	0	0.4709	0.0291	0	0.2416	0	0.0084	0.2500
	M (75)	2009	0.0045	0	0	0.1729	0.2101	0.0368	0.0439	0.0363	0.0966	0.3988
	S (26)	2009	0	0	0.0142	0	0.0713	0	0.0251	0.0695	0.0992	0.7208
Atlantic croaker	M (20)	2009	0	0	0	0	0	0.6241	0	0	0.0908	0.2850
	S (7)	2009	0	0	0	0	0	0	0	0.5417	0	0.4583
White perch	M (48)	2009	0	0	0	0	0	0.4013	0	0	0.4263	0.1724
	S (56)	2009	0	0	0	0	0	0.1094	0.0027	0.0150	0.4744	0.3986
Spot	M (40)	2009	0	0	0	0	0	0.7169	0	0	0.0854	0.1977
	S (6)	2009	0	0	0	0	0	0	0	0	0.9134	0.0866
Weakfish	M (6)	2009	0	0	0	0.1301	0	0	0.0032	0	0	0.8667
	S (4)	2009	0	0	0	0	0.5000	0	0	0	0	0.5000
Summer flounder	L (6)	2010	0	0.0554	0.9209	0	0	0	0	0	0	0.0236
	M (17)	2010	0	0	0.6391	0.0151	0.1667	0	0.0199	0	0	0.1591
	S (4)	2010	0	0	0	0	0.4000	0	0	0.6000	0	0
Striped bass	L (12)	2010	0	0	0.0951	0.3649	0.0116	0.0009	0.0016	0	0.1591	0.3668

	M (84)	2010	0	0.0061	0.2230	0.0641	0.1180	0.0194	0.0016	0.0693	0.1878	0.3108
	S (18)	2010	0	0	0.0997	0	0.3196	0	0.0357	0.0922	0.0370	0.4158
Atlantic croaker	M (22)	2010	0	0	0	0	0.0022	0.0022	0	0.0276	0.8094	0.1586
	S (7)	2010	0	0	0	0	0	0	0	0.0064	0.9318	0.0618
White perch	M (80)	2010	0	0	0.3371	0	0.1393	0.0255	0.0003	0.1117	0.2252	0.1609
	S (53)	2010	0	0	0	0	0.3693	0.0293	0	0.0403	0.1437	0.4175
Spot	M (29)	2010	0	0	0	0	0.1023	0.0219	0	0	0.4227	0.4530
	S (55)	2010	0	0	0	0	0	0	0	0.0244	0.1111	0.8645
Weakfish	M (9)	2010	0	0	0.1304	0	0.8696	0	0	0	0	0
	S (18)	2010	0	0	0	0	0.7943	0	0	0.1325	0.0002	0.0730
Summer flounder	L (1)	2011	0	0	0	0	0.1263	0	0	0	0	0.8737
	M (9)	2011	0.3458	0	0	0	0.4806	0	0.0088	0.0016	0	0.1632
	S (3)	2011	0	0	0	0	0.4602	0	0	0.5395	0	0.0003
Striped bass	L (17)	2011	0	0	0	0.3378	0.2342	0.0056	0.0000	0	0.0271	0.3953
	M (60)	2011	0.0052	0.0533	0	0.0071	0.2359	0	0.0068	0.1456	0.2268	0.3193
	S (50)	2011	0.0786	0	0	0	0.2860	0.0003	0.0048	0.1894	0.0209	0.4201
Atlantic croaker	M (9)	2011	0	0	0	0	0	0.5003	0	0.0227	0.0547	0.4223
	S (15)	2011	0	0	0	0	0	0	0	0.0121	0.7038	0.2841
White perch	M (80)	2011	0.0316	0	0	0	0.0448	0.0852	0.0083	0.0609	0.2349	0.5344
	S (67)	2011	0.0237	0	0	0	0.0023	0.1181	0	0.0804	0.1412	0.6344
Spot	M (29)	2011	0	0	0	0	0	0.2813	0	0.0554	0.2304	0.4329
	S (0)	2011	0	0	0	0	0	0	0	0	0	0
Weakfish	M (5)	2011	0.0420	0	0	0	0.4000	0	0	0	0	0.5580
	S (10)	2011	0	0	0	0	0.5894	0	0	0.2478	0	0.1628
Summer flounder	L (1)	2012	0	0	1.0000	0	0	0	0	0	0	0
	M (2)	2012	0	0	0	0	0.3333	0	0	0	0	0.6667
	S (6)	2012	0	0	0	0	0.4170	0	0.1246	0.2430	0	0.2155
Striped bass	L (7)	2012	0	0	0	0.5826	0	0	0.0123	0	0.0862	0.3190
	M (52)	2012	0	0	0	0.1220	0.0208	0.0074	0.0172	0	0.2465	0.5861
	S (63)	2012	0	0.0238	0	0.0063	0.8040	0.0119	0	0.0009	0.0764	0.0767
Atlantic croaker	M (29)	2012	0	0	0	0	0.0544	0.0449	0.0273	0	0.5815	0.2919

	S (33)	2012	0	0	0	0	0	0.0758	0	0.0305	0.1472	0.7465
White perch	M (35)	2012	0	0	0	0	0	0.0979	0	0.0092	0.0920	0.8009
	S (44)	2012	0	0	0	0	0	0.1275	0	0	0.0803	0.7922
Spot	M (24)	2012	0	0	0	0	0	0.0083	0	0	0.7253	0.2663
	S (20)	2012	0	0	0	0	0	0.0223	0.0297	0.0004	0.1953	0.7523
Weakfish	M (7)	2012	0	0	0.4075	0	0.5398	0	0	0	0	0.0526
	S (7)	2012	0	0	0	0	0.2727	0	0	0	0	0.7273
Summer flounder	L (2)	2013	0	0.5000	0	0	0	0	0	0	0	0.5000
	M (1)	2013	0	0	0	0	0	0	0	0	0	1.0000
	S (3)	2013	0	0	0	0	0.3333	0	0	0.6289	0	0.0377
Striped bass	L (4)	2013	0	0	0	0.9241	0	0	0	0	0	0.0759
	M (35)	2013	0	0	0	0.3466	0.3122	0	0.0201	0	0	0.3211
	S (21)	2013	0.0094	0	0	0.0076	0.5163	0	0.1512	0	0.0045	0.3111
Atlantic croaker	M (27)	2013	0	0	0	0	0	0.3873	0.0009	0.0000	0.3109	0.3009
	S (21)	2013	0	0	0	0	0	0.2733	0	0	0.2956	0.4311
White perch	M (21)	2013	0	0	0	0	0	0.0103	0	0.0008	0.2597	0.7293
	S (27)	2013	0	0	0	0	0	0.1043	0	0.0827	0.1308	0.6822
Spot	M (36)	2013	0	0	0	0	0	0.0577	0	0	0.1933	0.7490
	S (12)	2013	0	0	0	0	0	0.0014	0	0	0.2203	0.7783
Weakfish	M (0)	2013	0	0	0	0	0	0	0	0	0	0
	S (0)	2013	0	0	0	0	0	0	0	0	0	0
Summer flounder	L (2)	2014	0	0	0	0	0	0	0	0	0	1.0000
	M (7)	2014	0.1418	0	0	0.1081	0.1419	0	0.3045	0	0.0367	0.2670
	S (1)	2014	0	0	0	0	1.0000	0	0	0	0	0
Striped bass	L (12)	2014	0	0	0	0.7324	0	0	0	0	0	0.2676
	M (97)	2014	0.0030	0.0142	0	0.2662	0.2589	0.0071	0.0124	0.0118	0.0821	0.3442
	S (32)	2014	0.0232	0	0	0.0650	0.3003	0.0355	0.0314	0.0199	0.1331	0.3916
Atlantic croaker	M (8)	2014	0	0	0	0	0	0.6903	0	0	0.2058	0.1039
	S (2)	2014	0	0	0	0	0	0	0	0	0.9331	0.0669
White perch	M (39)	2014	0	0	0	0	0.0039	0.0190	0	0.0035	0.2323	0.7413
	S (49)	2014	0	0	0	0	0	0.0406	0	0.0126	0.1603	0.7866

Spot	M (21)	2014	0	0	0	0	0	0	0	0	0.4032	0.5968
	S (0)	2014	0	0	0	0	0	0	0	0	0	0
Weakfish	M (1)	2014	0	0	0	0	1.0000	0	0	0	0	0
	S (0)	2014	0	0	0	0	0	0	0	0	0	0
Summer flounder	L (0)	2015	0	0	0	0	0	0	0	0	0	0
	M (12)	2015	0	0.1940	0	0	0.5968	0.0004	0	0	0	0.2087
	S (5)	2015	0	0.4454	0	0	0.2421	0.0059	0.1502	0	0	0.1564
Striped bass	L (6)	2015	0	0	0	0.9801	0	0	0	0	0	0.0199
	M (43)	2015	0	0	0	0.4386	0.0822	0.0063	0.0997	0.0004	0.1190	0.2538
	S (41)	2015	0.0013	0	0	0.0180	0.2490	0.0070	0.0332	0.0003	0.2289	0.4623
Atlantic croaker	M (14)	2015	0	0	0	0	0	0.32388	0	0	0.4746	0.2015
	S (2)	2015	0	0	0	0	0	0	0	0	1.0000	0
White perch	M (47)	2015	0	0	0	0	0.0670	0.0385	0.0002	0.0002	0.4912	0.4029
	S (32)	2015	0	0	0	0	0	0.0049	0	0	0.2947	0.7004
Spot	M (2)	2015	0	0	0	0	0.0069	0	0	0	0.2500	0.7431
	S (0)	2015	0	0	0	0	0	0	0	0	0	0
Weakfish	M (9)	2015	0	0	0	0	0.3127	0	0.0069	0	0	0.6805
	S (9)	2015	0	0	0	0	0.6129	0	0	0.2500	0.1289	0.0082

Appendix 3. Diet composition summary of forage prey taxa for six key predators (summer flounder, striped bass, Atlantic croaker, white perch, spot, and weakfish) in Virginia waters of the Chesapeake Bay from 2002–2015. Predatory fishes and sample size (n) were designated by size class (L – large, M – medium, S – small).

			Prey									
Predator	Size Class (n)	Year	Croaker	Weakfish	Spot	Menhaden	Anchovies	Bivalves	Other Crustaceans	Mysids	Polychaetes	Other
Summer flounder	L (89)	2002	0.0086	0.2102	0.0279	0	0.0906	0	0.4188	0.0025	0	0.2415
	M (146)	2002	0.0950	0.0871	0.0047	0	0.1204	0	0.1899	0.2261	0	0.2769
	S (58)	2002	0.0210	0.0592	0.0059	0	0.1355	0	0.0385	0.5170	0.0001	0.2229
Striped bass	L (7)	2002	0.0959	0	0	0.1640	0.0617	0	0.1918	0	0	0.4867
	M (24)	2002	0	0.0323	0	0.0253	0.3343	0	0.0253	0	0	0.5828
	S (1)	2002	0	0	0	0	1.0000	0	0	0	0	0
Atlantic croaker	M (60)	2002	0	0	0	0	0.0045	0.0030	0.0174	0.0097	0.2330	0.7323
	S (2)	2002	0	0	0	0	0	0	0	0.0803	0.6368	0.2829
White perch	M (0)	2002	0	0	0	0	0	0	0	0	0	0
	S (0)	2002	0	0	0	0	0	0	0	0	0	0
Spot	M (6)	2002	0	0	0	0	0	0.0051	0	0.0762	0.0073	0.9114
	S (1)	2002	0	0	0	0	0	0.0180	0	0	0.1724	0.8097
Weakfish	M (221)	2002	0.0016	0.0250	0.0221	0.0276	0.3440	0.0002	0.2631	0.2084	0.0094	0.0986
	S (92)	2002	0	0	0	0	0.5641	0	0.0199	0.1744	0.0168	0.2248
Summer flounder	L (70)	2003	0.1380	0.1492	0.0834	0	0.0532	0	0.1743	0.0640	0	0.3379
	M (181)	2003	0.0472	0.0355	0.0000	0	0.0930	0.0000	0.2365	0.4918	0	0.0959
	S (13)	2003	0.0406	0.0771	0	0	0	0	0.2133	0.6594	0	0.0096
Striped bass	L (18)	2003	0.0177	0	0	0.2473	0.0223	0.0002	0.3161	0.0318	0.0002	0.3643
	M (64)	2003	0.0786	0.0222	0	0	0.1557	0.0000	0.2265	0.0882	0.0336	0.3951
	S (6)	2003	0	0	0	0	0	0	0	0	0.1667	0.8333
Atlantic croaker	M (58)	2003	0	0	0	0	0	0.0905	0.0211	0.1498	0.3521	0.3865
	S (2)	2003	0	0	0	0	0	0.0663	0.5660	0	0.2264	0.1413
White perch	M (0)	2003	0	0	0	0	0	0	0	0	0	0
	S (0)	2003	0	0	0	0	0	0	0	0	0	0

Spot	M (2)	2003	0	0	0	0	0	0	0	0	0	1
	S (0)	2003	0	0	0	0	0	0	0	0	0	0
Weakfish	M (334)	2003	0.0145	0.1422	0.0188	0.0137	0.1336	0	0.0727	0.4820	0.0024	0.1202
	S (158)	2003	0.0052	0.0099	0.0012	0	0.2915	0	0.0464	0.4823	0	0.1635
Summer flounder	L (77)	2004	0	0.1677	0.0264	0.0092	0.2047	0.0092	0.1734	0.0178	0.0017	0.3901
	M (100)	2004	0.0184	0.0172	0.0047	0	0.1585	0.0257	0.2578	0.2766	0	0.2412
	S (99)	2004	0.0025	0.0251	0.0025	0	0.1271	0	0.0928	0.6016	0.0263	0.1220
Striped bass	L (6)	2004	0	0.0658	0	0.1665	0.1677	0	0.4543	0	0.0019	0.1439
	M (67)	2004	0.0074	0.0101	0	0.0308	0.2247	0.0001	0.0537	0.1246	0.0586	0.4900
	S (10)	2004	0.0012	0.0893	0	0	0	0	0.0849	0.4361	0.0556	0.3329
Atlantic croaker	M (177)	2004	0.0001	0	0	0.0007	0.0028	0.1313	0.1953	0.0104	0.2588	0.4007
	S (25)	2004	0	0	0	0	0	0.0077	0.0033	0.1751	0.5902	0.2237
White perch	M (0)	2004	0	0	0	0	0	0	0	0	0	0
	S (0)	2004	0	0	0	0	0	0	0	0	0	0
Spot	M (6)	2004	0	0	0	0	0	0	0	0	0.0232	0.9768
	S (2)	2004	0	0	0	0	0	0	0	0	0.0769	0.9231
Weakfish	M (483)	2004	0.0035	0.0292	0	0.0119	0.1803	0.0008	0.0946	0.3500	0.0115	0.3181
	S (217)	2004	0	0	0	0	0.3515	0	0.0664	0.4501	0.0196	0.1125
Summer flounder	L (94)	2005	0	0.0707	0.4473	0	0.0471	0.0106	0.1641	0.0331	0	0.2273
	M (179)	2005	0.0091	0.1478	0.0152	0.0029	0.1446	0.0075	0.1082	0.4687	0	0.0959
	S (80)	2005	0.0035	0.0885	0	0	0.0568	0	0.1614	0.6155	0.0001	0.0742
Striped bass	L (20)	2005	0	0.0051	0.0804	0.5476	0.0709	0	0.0804	0	0.0014	0.2142
	M (92)	2005	0.0010	0.0078	0.0751	0.5781	0.0405	0.0001	0.0196	0.0483	0.0820	0.1477
	S (18)	2005	0	0	0	0	0.0222	0	0.0602	0.3235	0.2065	0.3876
Atlantic croaker	M (188)	2005	0	0.0089	0	0.0002	0.0040	0.0933	0.0360	0.3660	0.2925	0.1991
	S (21)	2005	0	0	0	0	0	0.0101	0.0000	0.3646	0.3215	0.3038
White perch	M (0)	2005	0	0	0	0	0	0	0	0	0	0
	S (0)	2005	0	0	0	0	0	0	0	0	0	0
Spot	M (2)	2005	0	0	0	0	0	0	0.0769	0	0	0.9231
	S (0)	2005	0	0	0	0	0	0	0	0	0	0
Weakfish	M (506)	2005	0	0.2465	0.0655	0.1879	0.1759	0.0008	0.0440	0.1326	0.0072	0.1396

	S (250)	2005	0	0.0020	0	0.0135	0.5212	0	0.0093	0.3340	0.0070	0.1129
Summer flounder	L (99)	2006	0.0243	0.2516	0.1438	0.0039	0.2266	0	0.1565	0.0000	0	0.1934
	M (138)	2006	0.0159	0.0803	0.0065	0	0.2504	0.0011	0.2612	0.2316	0	0.1530
	S (91)	2006	0.0877	0.0653	0	0	0.0571	0	0.1753	0.4883	0.0057	0.1207
Striped bass	L (14)	2006	0.0307	0	0	0.7296	0.0072	0	0.0476	0	0	0.1848
	M (89)	2006	0.0004	0.0344	0.2419	0.0013	0.2983	0.0011	0.0785	0.1478	0.0694	0.1270
	S (17)	2006	0	0	0	0	0.1925	0.0018	0.2895	0.1040	0.2267	0.1856
Atlantic croaker	M (504)	2006	0	0	0	0.0016	0.0279	0.0259	0.0394	0.0208	0.5727	0.3117
	S (84)	2006	0	0	0	0	0	0.0062	0.0659	0.3244	0.4524	0.1511
White perch	M (0)	2006	0	0	0	0	0	0	0	0	0	0
	S (0)	2006	0	0	0	0	0	0	0	0	0	0
Spot	M (1)	2006	0	0	0	0	0	0	0	0	0	1
	S (2)	2006	0	0	0	0	0	0	0	0	0.0952	0.9048
Weakfish	M (220)	2006	0	0.1634	0.0183	0	0.2932	0	0.1078	0.2605	0.0022	0.1547
	S (193)	2006	0	0.0308	0	0	0.4703	0	0.0288	0.3249	0.0164	0.1289
Summer flounder	L (50)	2007	0.0457	0.2381	0.2652	0	0.0964	0	0.1838	0.0086	0	0.1622
	M (127)	2007	0.0019	0.0212	0	0	0.2024	0.0026	0.2815	0.1724	0.0001	0.3180
	S (56)	2007	0	0.0119	0.0140	0	0.2601	0.0030	0.1481	0.4267	0.0005	0.1357
Striped bass	L (7)	2007	0	0	0	0.4085	0	0	0.0715	0	0	0.5200
	M (66)	2007	0.0132	0.0009	0	0.1728	0.5074	0.0026	0.0301	0.0307	0.0541	0.1881
	S (7)	2007	0	0	0	0	0.6316	0	0	0.0604	0	0.3079
Atlantic croaker	M (303)	2007	0	0	0	0	0.0046	0.2601	0.0024	0.0034	0.5316	0.1979
	S (49)	2007	0	0	0	0	0	0.1297	0	0.2365	0.4462	0.1877
White perch	M (2)	2007	0	0	0	0	0	0	0	0	0.0119	0.9881
	S (1)	2007	0	0	0	0	0	0	0	0	0.9907	0.0093
Spot	M (0)	2007	0	0	0	0	0	0	0	0	0	0
	S (1)	2007	0	0	0	0	0	0	0	0	0	1.0000
Weakfish	M (153)	2007	0	0.0484	0.0197	0.0320	0.3687	0.0246	0.0472	0.2590	0.0143	0.1862
	S (136)	2007	0	0	0	0	0.4590	0.0014	0.0369	0.2728	0.0311	0.1988
Summer flounder	L (60)	2008	0.0645	0.0282	0.3069	0.0270	0.0586	0	0.0990	0	0	0.4159
	M (68)	2008	0.0651	0.0191	0.0210	0	0.2093	0.0004	0.2100	0.1237	0.0163	0.3350

	S (112)	2008	0.0939	0.0025	0.0266	0	0.1622	0.0009	0.1242	0.5130	0.0009	0.0758
Striped bass	L (5)	2008	0	0	0.2000	0.4000	0.1713	0	0	0	0	0.2287
	M (49)	2008	0	0.0067	0.1064	0.0869	0.1379	0.0031	0.1083	0.0493	0.3438	0.1576
	S (11)	2008	0.0120	0	0	0	0.2121	0	0.0318	0.2292	0.1133	0.4015
Atlantic croaker	M (171)	2008	0	0	0	0	0.0067	0.4580	0.0200	0.0288	0.2426	0.2438
	S (129)	2008	0	0	0	0	0.0007	0.1215	0.0916	0.0295	0.2631	0.4937
White perch	M (0)	2008	0	0	0	0	0	0	0	0	0	0
	S (0)	2008	0	0	0	0	0	0	0	0	0	0
Spot	M (222)	2008	0	0	0	0	0.0082	0.2284	0.0010	0.0179	0.3014	0.4430
	S (166)	2008	0	0	0	0	0	0.0632	0.0127	0.0201	0.2509	0.6530
Weakfish	M (142)	2008	0.0020	0	0.0603	0	0.5789	0	0.0268	0.1501	0.0023	0.1796
	S (105)	2008	0	0	0	0	0.3425	0.0046	0.0784	0.4332	0.0098	0.1315
Summer flounder	L (45)	2009	0.0585	0.1976	0.1325	0	0.1212	0	0.1494	0.0021	0	0.3387
	M (73)	2009	0.0494	0.1527	0.0163	0	0.1728	0	0.2014	0.2528	0.0011	0.1535
	S (53)	2009	0.0252	0.0173	0	0	0.1706	0.0358	0.0966	0.5280	0.0022	0.1242
Striped bass	L (1)	2009	0	0	0	0	0	0	0	0	0	1.0000
	M (10)	2009	0.1667	0	0	0	0.2774	0.0569	0.0817	0	0.0254	0.3920
	S (0)	2009	0	0	0	0	0	0	0	0	0	0
Atlantic croaker	M (153)	2009	0	0	0	0	0.0401	0.0434	0.0044	0.0032	0.3857	0.5232
	S (127)	2009	0	0	0	0	0.0073	0.2239	0.0010	0.0097	0.3925	0.3655
White perch	M (0)	2009	0	0	0	0	0	0	0	0	0	0
	S (0)	2009	0	0	0	0	0	0	0	0	0	0
Spot	M (198)	2009	0	0	0	0	0	0.0497	0.0000	0.1184	0.3782	0.4537
	S (98)	2009	0	0	0	0	0	0.0716	0	0.0333	0.1074	0.7876
Weakfish	M (87)	2009	0	0.0225	0	0.0276	0.4818	0	0.0685	0.1663	0.0246	0.2086
	S (235)	2009	0	0	0	0	0.4874	0	0.0067	0.2388	0.0091	0.2580
Summer flounder	L (46)	2010	0	0.1343	0.3333	0.0429	0.0637	0.0009	0.0779	0	0	0.3470
	M (66)	2010	0.0134	0.0287	0.0881	0	0.3521	0.0000	0.2002	0.0796	0	0.2377
	S (52)	2010	0	0.0067	0.0081	0	0.1179	0	0.3137	0.5055	0	0.0481
Striped bass	L (1)	2010	0	0	0	0	0	0	0	0	0	1.0000
	M (8)	2010	0	0	0.5109	0.0790	0.1250	0	0.1194	0	0	0.1657

	S (0)	2010	0	0	0	0	0	0	0	0	0	0
Atlantic croaker	M (134)	2010	0	0	0	0	0.0047	0.1057	0.0369	0.0232	0.5084	0.3211
	S (96)	2010	0	0	0	0	0	0.1060	0.0151	0.0043	0.5870	0.2876
White perch	M (0)	2010	0	0	0	0	0	0	0	0	0	0
	S (0)	2010	0	0	0	0	0	0	0	0	0	0
Spot	M (134)	2010	0	0	0	0	0.0250	0.0680	0	0.0061	0.4901	0.4109
	S (204)	2010	0	0	0	0	0	0.0572	0	0.0279	0.3348	0.5802
Weakfish	M (135)	2010	0	0.0102	0.4435	0.0133	0.3053	0.0003	0.0323	0.0425	0.0030	0.1496
	S (298)	2010	0	0	0.0006	0	0.7208	0.0040	0.0524	0.1183	0.0009	0.1031
Summer flounder	L (33)	2011	0.0476	0.0476	0.0908	0.1211	0.0322	0	0.1827	0	0	0.4780
	M (42)	2011	0.0883	0.0652	0.0005	0	0.2366	0.0027	0.3372	0.0771	0.0028	0.1895
	S (10)	2011	0	0	0	0	0.0862	0	0.0918	0.7900	0	0.0320
Striped bass	L (2)	2011	0	0	0	0.5	0	0	0	0	0.1021	0.3979
	M (10)	2011	0.0000	0	0	0.0714	0.1105	0	0.4689	0	0.0239	0.3253
	S (2)	2011	0	0	0	0	0.5000	0	0	0	0	0.5000
Atlantic croaker	M (125)	2011	0	0	0	0	0.0011	0.2802	0.0034	0.0006	0.2940	0.4208
	S (91)	2011	0	0	0	0	0	0.2744	0.0837	0.0012	0.4061	0.2345
White perch	M (0)	2011	0	0	0	0	0	0	0	0	0	0
	S (0)	2011	0	0	0	0	0	0	0	0	0	0
Spot	M (163)	2011	0	0	0	0	0	0.0161	0	0.0076	0.3960	0.5803
	S (47)	2011	0	0	0	0	0	0.3475	0	0	0.1034	0.5490
Weakfish	M (76)	2011	0.0096	0.0112	0	0	0.4379	0	0.0186	0.0657	0.0132	0.4438
	S (185)	2011	0	0.0155	0	0	0.2883	0.0325	0.0223	0.1234	0.0284	0.4896
Summer flounder	L (4)	2012	0	0	0.2500	0	0	0	0.2493	0	0	0.5007
	M (2)	2012	0	0	0	0	1.0000	0	0	0	0	0
	S (17)	2012	0	0	0	0	0.3395	0.0379	0	0.2499	0	0.3727
Striped bass	L (9)	2012	0	0	0	0.4866	0.0007	0	0.2650	0	0	0.2477
	M (23)	2012	0	0.0610	0.0284	0	0.2116	0	0.0498	0	0	0.6491
	S (26)	2012	0	0	0	0	0.2292	0.0018	0.0005	0	0	0.7685
Atlantic croaker	M (49)	2012	0	0	0	0	0.0022	0.2106	0.0279	0	0.5805	0.1787
	S (130)	2012	0	0	0	0	0.0023	0.0263	0.0383	0.0144	0.4556	0.4631

White perch	M (0)	2012	0	0	0	0	0	0	0	0	0	0
	S (0)	2012	0	0	0	0	0	0	0	0	0	0
Spot	M (69)	2012	0	0	0	0	0	0.0126	0.0007	0	0.3495	0.6372
	S (61)	2012	0	0	0	0	0.0067	0.0319	0	0.0067	0.2825	0.6722
Weakfish	M (83)	2012	0	0	0	0.0031	0.6231	0.0061	0.0121	0.0270	0.0316	0.2971
	S (132)	2012	0	0	0	0	0.6119	0	0.1541	0.0131	0.0164	0.2045
Summer flounder	L (1)	2013	0	0	1	0	0	0	0	0	0	0
	M (10)	2013	0.0060	0.0100	0	0	0.2981	0	0	0.1319	0	0.5540
	S (26)	2013	0	0.0407	0	0	0.0861	0	0.0714	0.5599	0.0032	0.2387
Striped bass	L (1)	2013	0	0	0	0	0	0	0	0	0	1.0000
	M (41)	2013	0	0.0446	0.0089	0.0418	0.4473	0	0.1380	0	0	0.3194
	S (9)	2013	0	0	0	0	0.5698	0	0.0674	0	0	0.3628
Atlantic croaker	M (25)	2013	0	0	0	0	0.0026	0.3094	0	0.0420	0.3641	0.2819
	S (119)	2013	0	0	0	0	0	0.0441	0.0148	0.0403	0.3206	0.5802
White perch	M (0)	2013	0	0	0	0	0	0	0	0	0	0
	S (0)	2013	0	0	0	0	0	0	0	0	0	0
Spot	M (130)	2013	0	0	0	0	0	0.0408	0	0.0135	0.3146	0.6311
	S (55)	2013	0	0	0	0	0	0.0132	0	0.0009	0.1738	0.8121
Weakfish	M (64)	2013	0	0	0.0078	0	0.2030	0.0012	0.0241	0.2744	0	0.4895
	S (53)	2013	0.0130	0	0	0	0.4175	0	0.0527	0.1350	0.0188	0.3629
Summer flounder	L (2)	2014	0	0.3333	0	0	0	0	0	0	0	0.6667
	M (13)	2014	0	0.1176	0	0	0.4677	0	0.0029	0.0009	0	0.4108
	S (12)	2014	0	0	0	0	0.4118	0	0	0.2873	0	0.3009
Striped bass	L (0)	2014	0	0	0	0	0	0	0	0	0	0
	M (21)	2014	0.0043	0	0.1558	0.2706	0.1410	0	0.0089	0	0.0009	0.4185
	S (1)	2014	0	0	0	0	0	0	0	0	0	1.0000
Atlantic croaker	M (31)	2014	0	0	0	0	0.0018	0.2430	0.0002	0	0.0927	0.6623
	S (27)	2014	0	0	0	0	0	0.0602	0.0001	0.0000	0.8029	0.1368
White perch	M (0)	2014	0	0	0	0	0	0	0	0	0	0
	S (0)	2014	0	0	0	0	0	0	0	0	0	0
Spot	M (45)	2014	0	0	0	0	0	0.0673	0	0.0145	0.2400	0.6783

	S (16)	2014	0	0	0	0	0	0	0	0	0.3320	0.6680
Weakfish	M (13)	2014	0	0	0	0	0.1444	0	0.0049	0.1431	0	0.7077
	S (51)	2014	0	0	0	0	0.5927	0.0048	0.0722	0.1389	0.0129	0.1785
Summer flounder	L (7)	2015	0	0	0.1429	0	0.0047	0	0.1437	0	0	0.7088
	M (27)	2015	0.1341	0.0524	0.0811	0	0.2297	0	0.2045	0	0	0.2982
	S (13)	2015	0	0	0	0	0.1771	0	0.0348	0.2038	0	0.5844
Striped bass	L (2)	2015	0	0	0	0.3685	0.3682	0	0	0	0.2633	0
	M (21)	2015	0	0.0547	0	0.0669	0.1798	0	0	0	0	0.6986
	S (8)	2015	0	0	0	0	0.9886	0	0	0	0	0.0114
Atlantic croaker	M (49)	2015	0	0	0	0	0.0811	0.1391	0.0079	0	0.2754	0.4965
	S (39)	2015	0	0	0	0	0.0004	0.0580	0.0099	0.0000	0.7305	0.2011
White perch	M (0)	2015	0	0	0	0	0	0	0	0	0	0
	S (0)	2015	0	0	0	0	0	0	0	0	0	0
Spot	M (7)	2015	0	0	0	0	0	0	0	0	0.3703	0.6297
	S (1)	2015	0	0	0	0	0	0	0	0	0	1
Weakfish	M (42)	2015	0	0.2216	0.0092	0	0.2940	0.0040	0.1248	0.0320	0.0335	0.2809
	S (75)	2015	0	0	0	0	0.5148	0.0070	0.1035	0.1063	0.0169	0.2515

Appendix 4. Summary of predator-specific consumption patterns (*updated* from Buchheister et al. 2016). All figure references refer to Appendix figures below this sections (renumbered to start at A1 for ease of reference). Size-class designations used in this report and update follow those of Buchheister et al. (Figure 1; 2016).

Striped Bass

The yearly mean stomach contents of striped bass were relatively consistent over the 14 year time series. Mean contents were typically 10–20 and 20–30 grams higher in large individuals compared to the medium and small individuals, respectively (Figure A2). Trends in daily per capita consumption during the 6-month index season were similar to the trends observed in the mean stomach contents; however, the overall magnitude is lower due to the slower digestion rates that are taken into account in the evacuation rate model during the cold index months (Figure A3). Conversely, higher daily per capita consumption trends were observed during the 6-month non-index season as temperatures were significantly warmer, thus elevating gastric evacuation rates. Striped bass abundance did not indicate a trend over time (Figure A4). In general, the abundances of medium striped bass were greater than abundances of the large and small size classes throughout the time series, with the exception of the years 2002, 2012, and 2015 when small striped bass (primarily ages 1 and 2) were more abundant due to strong recruitment events (Figure A4). Population-level consumption for the six-month index period tended to be driven by consumption of the medium size class, primarily due to higher abundances (Figure A5). However, the observed peaks in consumption 2006, 2008, and 2014 in the medium striped bass were mostly driven by a greater amount of stomach contents. Population-level consumption of small striped bass was generally of the lowest magnitude relative to the other size classes, except during the strong recruitment years. Large striped bass had population-level consumption that were intermediate between the large and small size classes, reaching a peak in 2006 and a time-series low in 2015.

The total annual consumption by striped bass typically fluctuated around 500 mt, but reached a time-series maximum in 2006 of more than 1600 mt (Figure A6 top panel), primarily due to an increase in consumption of medium and large individuals. Fish prey, primarily YOY menhaden and anchovies, were the dominant components of the striped bass diet and each accounted for about 40% of the total annual consumption. However, an increase in YOY menhaden and anchovies consumption has been observed since 2009, consistently accounting for >50% of the total annual consumption (Figure A6 bottom panel).

Summer Flounder

The stomach contents of summer flounder were also relatively consistent across the time series, although an anomalous peak in the large size class was observed in 2007. On average, stomachs of small, medium, and large fish contained approximately 0.4, 1.2, and 4.5 g of prey, respectively (Figure A7). Daily per capita consumption patterns and magnitudes during the 6-month index period were nearly identical to mean stomach content weights because gastric evacuation occurs more rapidly at warmer temperatures in the summer and fall (as compared to colder temperatures in the striped bass index period in the winter and spring) (Figure A8). Summer flounder abundance was of similar magnitude across all size classes, with the medium size class being the most abundant from 2002–2007 (Figure A9). Following 2007, all size classes declined in abundance until 2012 and remained relatively stable, albeit at low levels, thereafter. Population level consumption during the six-month index period illustrated the greatest magnitude of consumption within the large size class of summer flounder relative to the other size classes, but a drastic decline in consumption was observed since 2007 (Figure A10).

Total annual consumption, when both index and non-index periods are considered, by all summer flounder size classes peaked in 2007 at roughly 600 mt and declined to a time-series low in 2014 at around 25 mt (Figure A11 top panel). The relative contribution of forage prey types was largely consistent and evenly distributed among those prey (Figure A11 bottom panel). The apparent increase in dietary importance of YOY spot since 2012 should be treated with caution due to low sample sizes for diet analyses.

Atlantic croaker

The mean weight of the stomach contents for Atlantic croaker showed a decrease across the time series for both small and medium size classes (Figure A12). However, the decrease over time was an order of magnitude more pronounced in the medium Atlantic croaker relative to the small size class. Daily per capita consumption of both size classes of Atlantic croaker followed patterns observed in the mean weight of the stomach contents, with the index season having a higher relative per capita consumption than the non-index season due to seasonal differences in temperature (Figure A13). Abundance of medium sized individuals showed a pronounced decline after 2007 when 25 million fish were estimated, followed by a time series low in 2012 of approximately 1 million fish (Figure A14). Conversely, the small size class of Atlantic croaker has remained stable apart from the strong 2007 and 2013 year classes. The six-month index period scaled population-level consumption highlights the large consumptive decline in the medium Atlantic croaker, where at times the magnitude of consumption fell below that of the small size class (Figure A15).

Total annual consumption by Atlantic croaker reached a time-series maximum of nearly 10,000 mt in 2002 and fluctuated between 2,500 mt and 8,000 mt from 2003-2007 (Figure A16 top panel). Following 2007, total annual consumption remained below 1,250 mt and reached a time-series low in 2012 of 127 mt. Polychaetes were the most dominant component of the annual consumption for Atlantic croaker, often comprising >50% of their diet throughout the time-series (Figure A16 bottom panel). Bivalves and other prey were periodically important to the annual consumptive profile. Highlighting the opportunistic nature of Atlantic croaker consumption, mysids were at times the most dominant component of the profile, such as in 2005 where they accounted for roughly 40% of the annual consumption.

Weakfish

Similar to the pattern observed in Atlantic croaker, weakfish showed a decrease across the time-series in the mean weight of stomach contents for both small and medium size classes, where the decrease over time was more pronounced in the medium size class relative to the small size class (Figure A17). Daily per capita consumption by weakfish followed identical patterns as the mean weight of stomach contents during the six-month index period for both size classes of weakfish (Figure A18). During the non-index period, daily per capita consumption was lower relative to the index period due to the effect of lower temperatures in the gastric evacuation model. Abundance of medium weakfish reached a time-series maximum in 2004 of approximately 3.2 million individuals, but showed a large decline thereafter reaching a low in 2014 of less than 100,000 individuals (Figure A19). The abundance of small weakfish was relatively stable throughout the time-series, but has marginally declined in recent years. The six-month scaled population consumption highlighted the large decline since 2005 in medium weakfish and that population level consumption has remained below 300 mt since. Small weakfish showed peaks in consumption in 2005, 2007, and 2010, which correspond to years of strong recruitment (Figure A20). However, consumption in recent years (2011 to present) has remained below 30 mt for small weakfish.

Total annual consumption by weakfish fluctuated between 2,200 mt and 500 mt from 2002 to 2005, and has since declined below 500 mt (Figure A21 top panel). Population level consumption has remained considerably lower (<100 mt) since 2011. Polychaetes and mysid shrimps were the two most dominant prey groups that contributed to the population level consumption in the early years of the time-series. An apparent increase in polychaete consumption, often in excess of 50% of the annual consumption, was observed following 2006 (Figure A21 bottom panel). Due to the low sample size of weakfish during this timeframe, this trend should be interpreted with caution.

White Perch

Throughout the six-month index period, medium and small white perch had a stable, but low mean weight of stomach contents and daily per capita consumption (<0.9 g and <0.25 g, respectively) (Figures 22 & 23). Daily per capita consumption during the non-index period was elevated relative to the six-month index period due to an increase in temperature and its effect on gastric evacuation rates and therefore consumption. Abundance of small white perch was typically greater than the abundance of medium white perch and neither size class displayed trends or shifts in abundance throughout the time-series (Figure A24). However, abundance maximums were reached for both small and medium white perch in 2015. Population-level consumption during the six-month index period was similar between both size classes and relatively stable throughout the time-series (Figure A25).

Despite high abundances, total annual white perch consumption was relatively small compared to the other species in this study, typically ranging from 300-700 mt with no apparent trend over time (Figure A26 top panel). Polychaetes and crustaceans (mainly gammarid amphipods) were the two most dominant prey groups consumed, accounting for 15–50% and 5–53%, respectively, of the total consumption, depending on the year (Figure A26 bottom panel).

Spot

The mean weight of the stomach contents in both size classes of spot was low and averaged 0.04 g in small spot and <0.09 g in medium spot (Figure A27). Trends were relatively stable within the mean weight of the stomach contents as well as in the daily per capita consumption across the duration of the time-series (Figure A28). It should be noted that inconsistent analysis of stomach samples from 2002–2007 limited analyses of specific trends within that time period. Abundance of medium spot was steady from 2002–2009, ranging from 4–10 million fish (Figure A29). Beyond 2009, abundance has decreased to levels consistently below 4 million fish, reaching a time-series minimum in 2015 of <1 million individuals. Small spot abundance has oscillated throughout the time-series with relatively strong year classes in 2005 and 2010. Since 2011, abundance of small individuals has fallen below 2 million fish and reached a time-series low in 2015, similar to the medium size class. Population-level consumption during the six-month index period from 2002–2007 was primarily driven by trends in abundance for both size classes of spot due to the aforementioned issues associated with inconsistent dietary analyses (Figure A30). Beyond 2007, we observed a peak in 2010 for small spot that is correlated with a strong year class, but population-level consumption remained low thereafter. Medium spot contributed more to population-level consumption than small spot and was steady until 2010, after which a declining trend was observed.

Total annual consumption by spot fluctuated between 25–200 mt from 2002–2014 before reaching a time-series low in 2015 of approximately 1 mt (Figure A31 top panel), which was the lowest recorded population-level consumption value for any of the species analyzed in this study. After 2007, when inconsistencies in stomach content analyses ceased for spot, polychaetes were often the dominant component (50%) of annual consumption (Figure A31 bottom panel). Bivalves and crustaceans (mainly amphipods) were also periodically important to the annual consumption profile of biological material. The "other" prey category, which at times exceeded 50% of the annual spot consumption, was typically detritus consumed while sifting through benthic matter to locate prey.

Influence of fish size and seasonality on consumption patterns

The influence of fish size on the fraction of total consumption was readily apparent throughout this study (Figure A32 left panel). For all six predators, the small size class accounted for a relatively small proportion of the total consumption. White perch was the only predator that accounted for an appreciable amount of total consumption within a species (~40%). For striped bass and summer flounder, the large size class accounted for a significant component of total consumption (~35% for striped bass and ~70% for summer flounder). As expected, most of the consumption for all six predators occurred during the index period when predator abundance was at its highest in the mainstem of the Chesapeake Bay (Figure A32 right panel). The only exception was white perch, which consumed an excess of 75% during the non-index period. Similarly, striped bass total consumption was approximately 45% during the non-index period. For both species, the non-index period occurs during the summer months when evacuation rates, and therefore consumption rates, were higher due to warm water temperatures. Furthermore, both white perch and striped bass have resident populations throughout the year that likely account for greater consumption than the seasonal predators evaluated in this study.

Patterns in total consumption across predators

Predator consumption values for each of the predators were aggregated to evaluate the consumptive pressure of predator groups within the Chesapeake Bay mainstem. Piscivorous fishes (i.e., striped bass, summer flounder, and weakfish) showed a nearly three-fold decline in total consumption across the duration of this study (Figure A33a). The relative contributions of YOY Atlantic menhaden and bay anchovy to consumption by piscivorous fishes increased throughout the time-series (Figure A33b). Conversely, the relative contribution of mysids decreased throughout the time-series. The benthivorous predators (i.e., Atlantic croaker, white perch, and spot) demonstrated a greater than ten-fold decline in total consumption (Figure A34a), however the relative contributions of specific forage prey varied minimally (Figure A34b). The combined total annual consumption of all six predators declined by an order of magnitude from 13,000 mt in 2002 to 1,300 mt in 2015 (Figure A35a). Overall, benthivorous fishes had a higher total consumption than piscivorous fishes and this is reflected in the relative contributions of forage prey by all six predators (Figure A35b). However, the total amount of forage prey consumed by piscivores and benthivores was similar from 2008–2015. The relative contribution of forage prey by all six predators was commensurate across the time-series. Among forage prey polychaetes were the most important, although the relative contributions of YOY menhaden and bay anchovy increased due to consumption patterns of the piscivores. Periodic influxes of specific prey groups in the diets of the six predators highlighted the importance of annual pulses of prey in the Chesapeake Bay (e.g., mysids in 2002 and 2005, YOY spot in 2010).

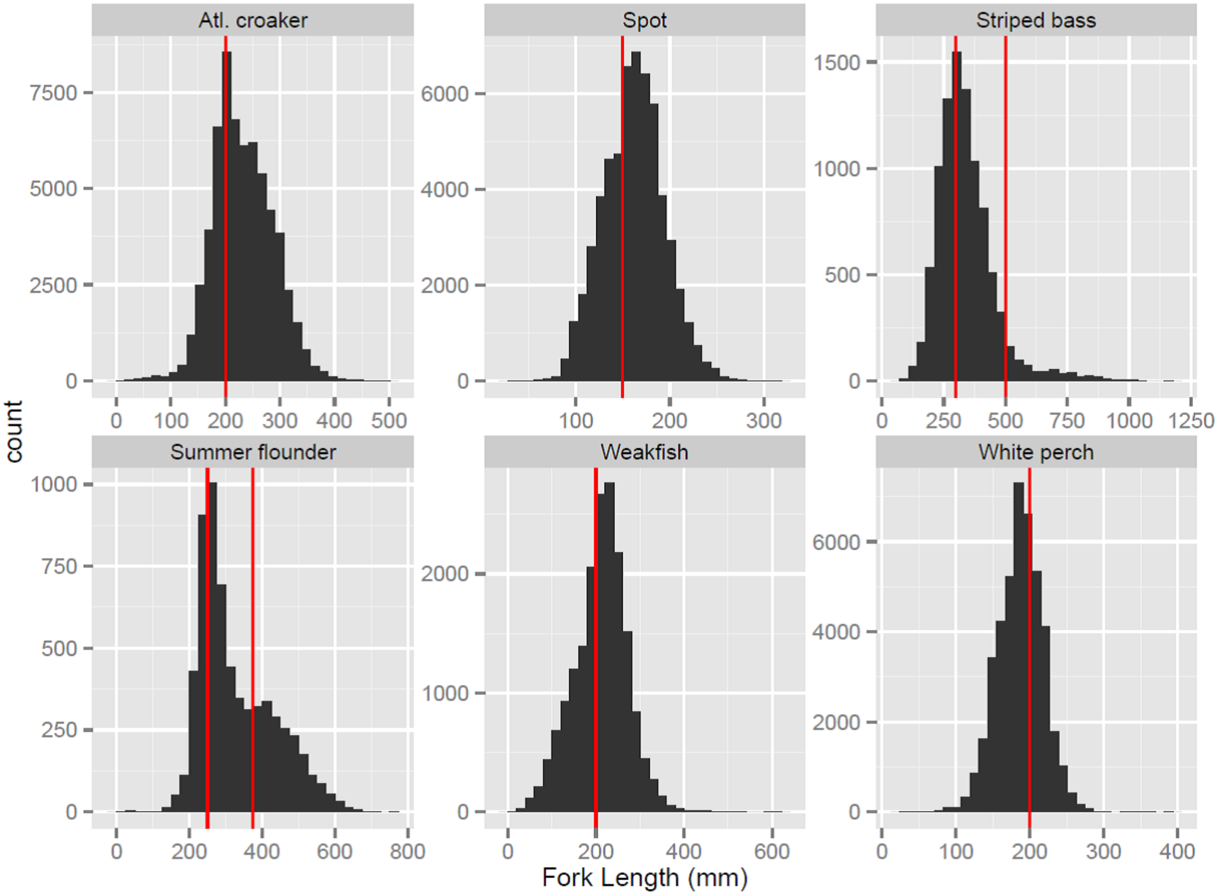


Figure A1. Length-frequency distributions of fish predators sampled by the ChesMMAP survey. Red lines mark the threshold used to define size classes of predators.

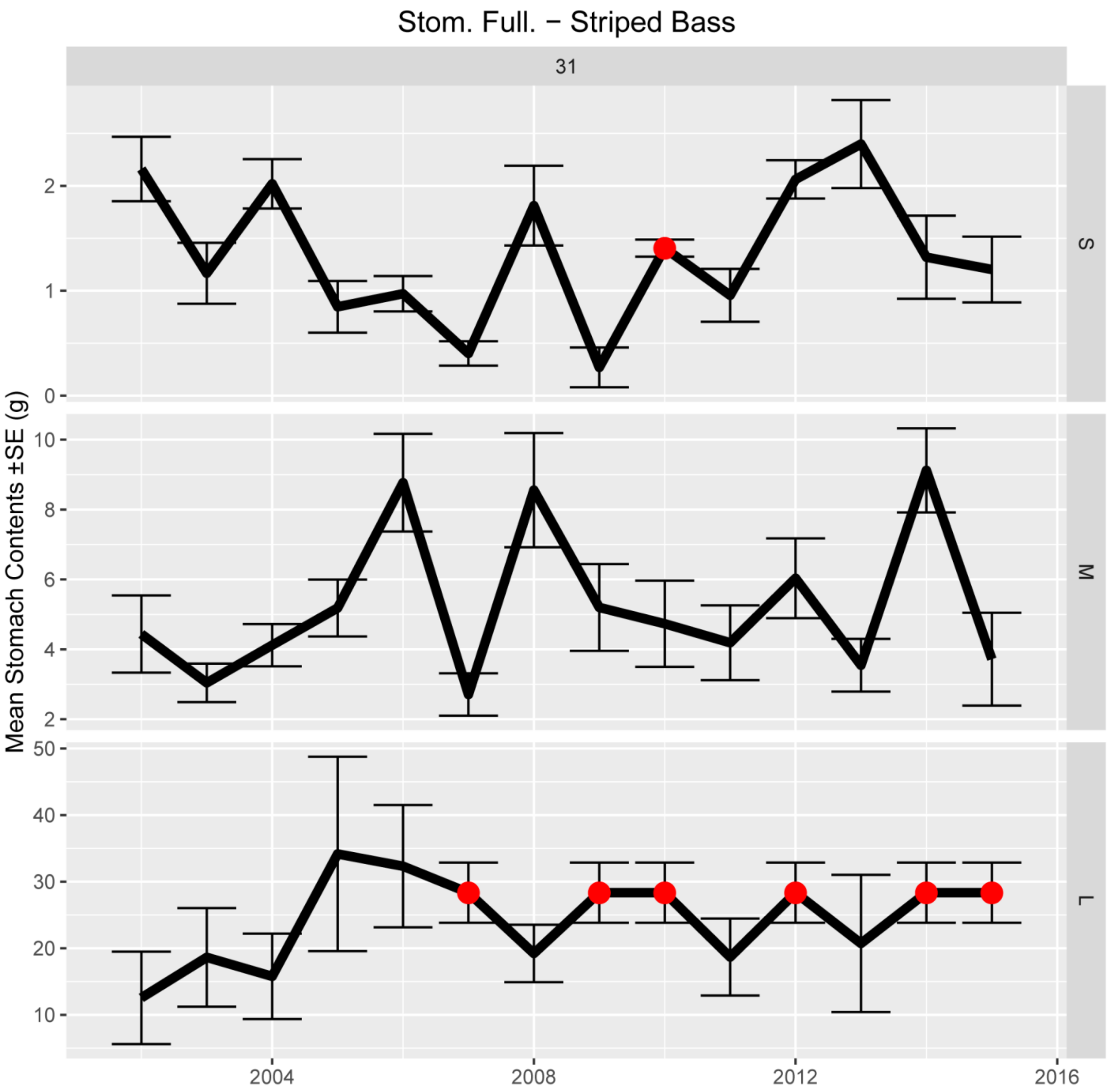


Figure A2. Mean weight of stomach contents (grams) for small (S), medium (M), and large (L) striped bass during the six-month index period. Error bars represent SE.

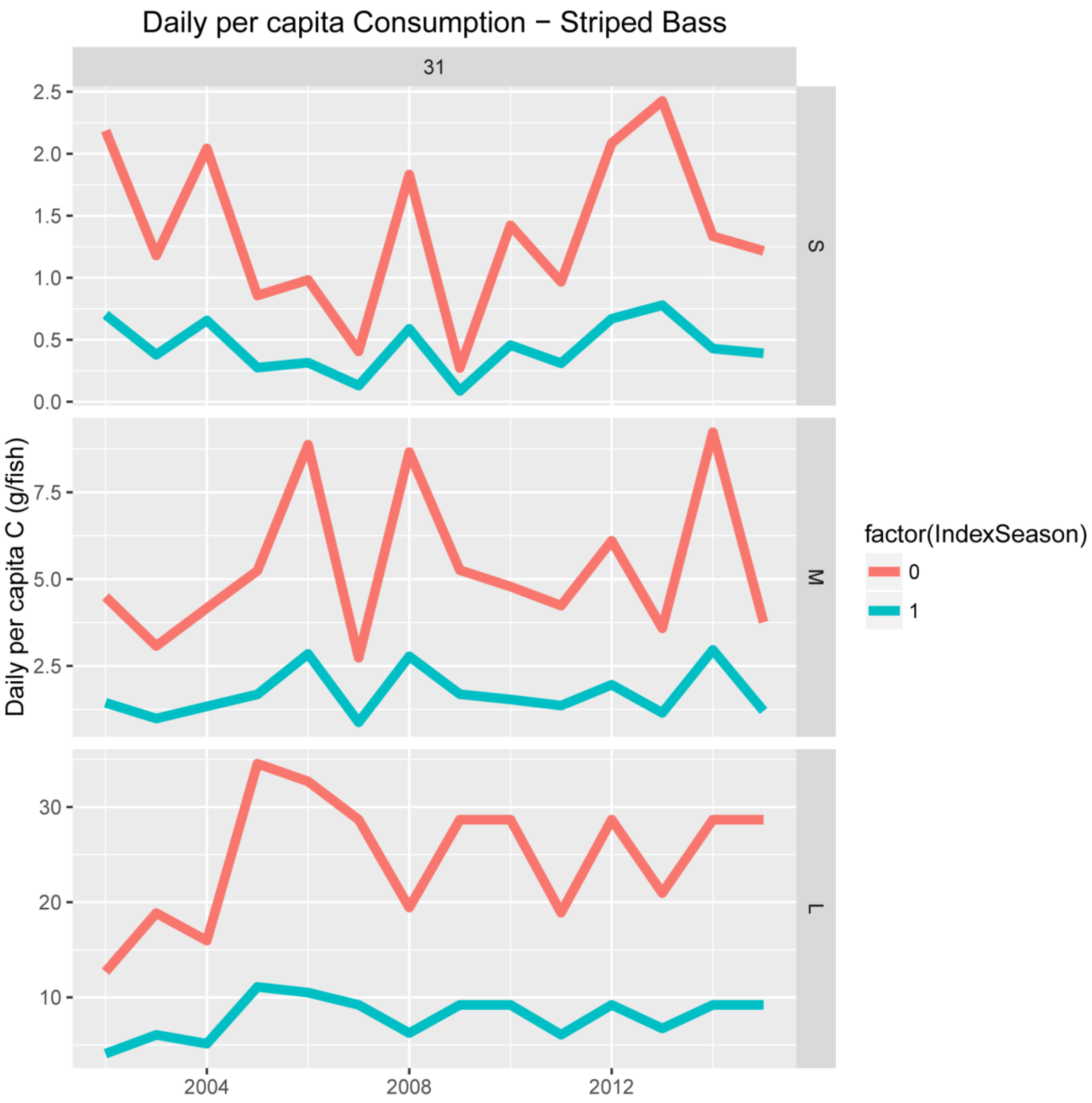


Figure A3. Daily per capita consumption (g/fish) during the non-index (red; factor = 0) and index (blue; factor = 1) period for small (S), medium (M), and large (L) striped bass.

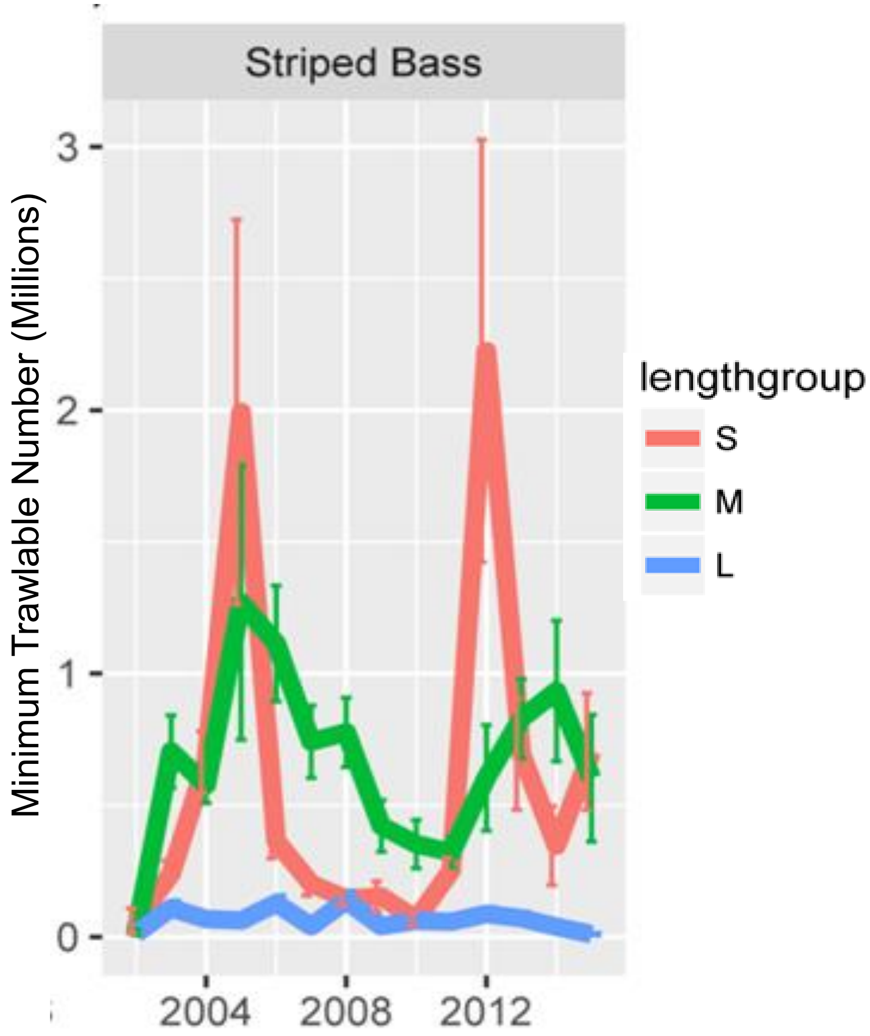


Figure A4. Minimum swept-area abundance of small (S), medium (M), and large (L) striped bass during the six-month index period. Error bars represent SE.

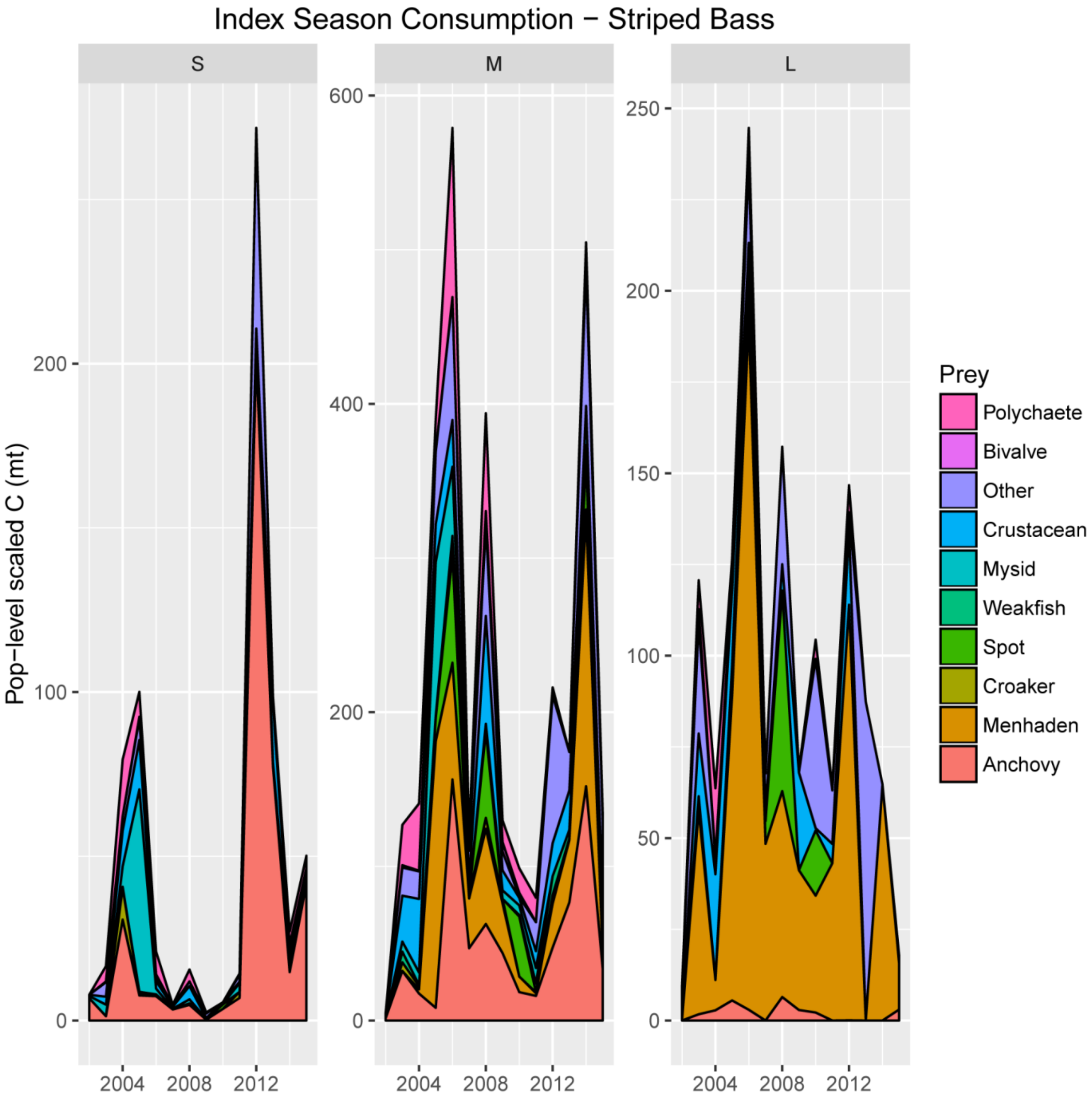


Figure A5. Population-level consumption (mt) of major forage prey groups during the six-month index period for small (S), medium (M), and large (L) striped bass.

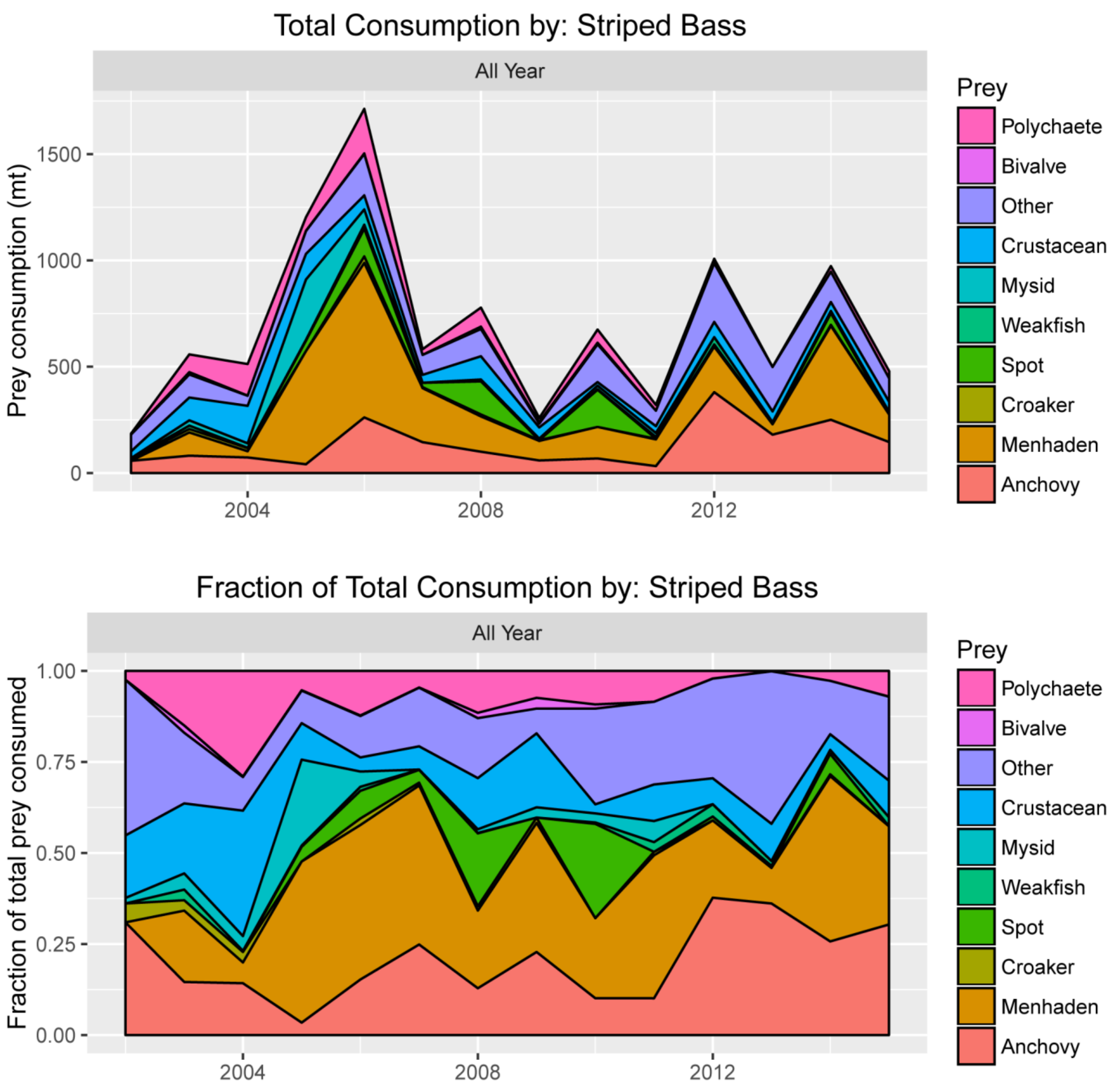


Figure A6. Striped bass total annual consumption (mt) of select forage prey groups. Top: total prey consumption by all size classes over the entire year. Bottom: relative contributions of each forage prey to the total amount consumed per year.

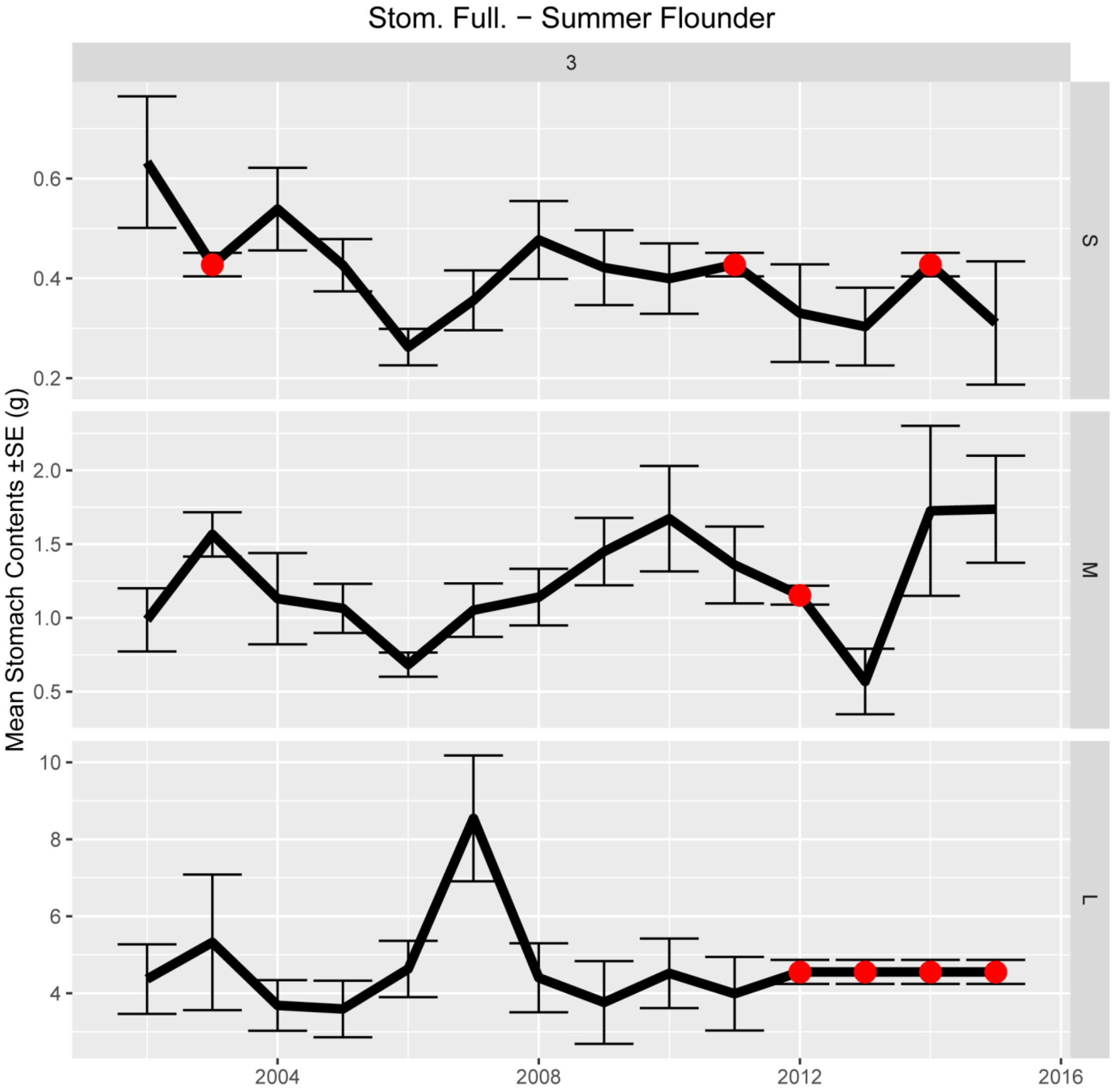


Figure A7. Mean weight (g) of stomach contents for small (S), medium (M), and large (L) summer flounder during the six-month index period. Error bars represent SE.

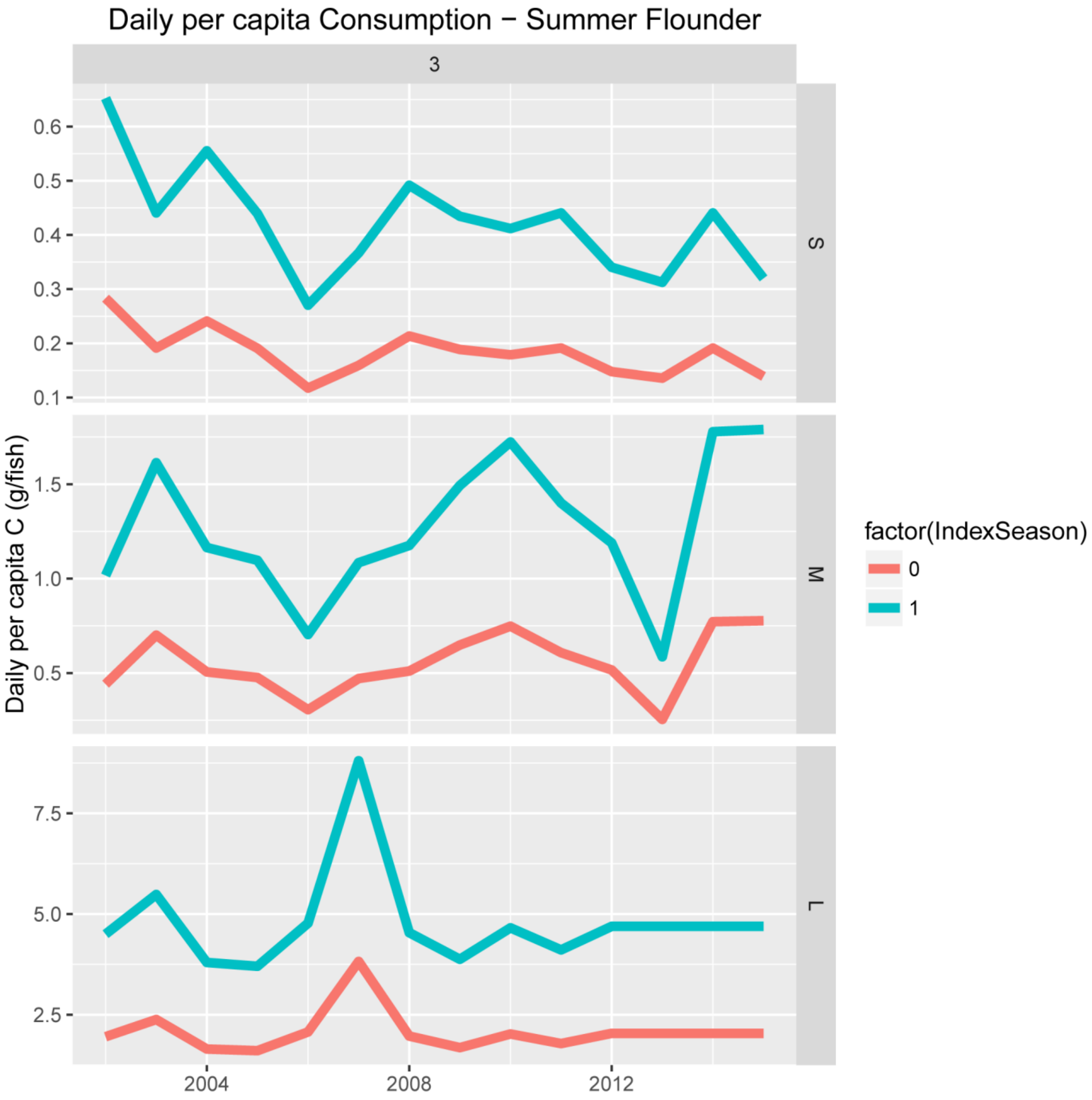


Figure A8. Daily per capita consumption (g/fish) during the non-index (red; factor = 0) and index (blue; factor = 1) period for small (S), medium (M), and large (L) summer flounder.

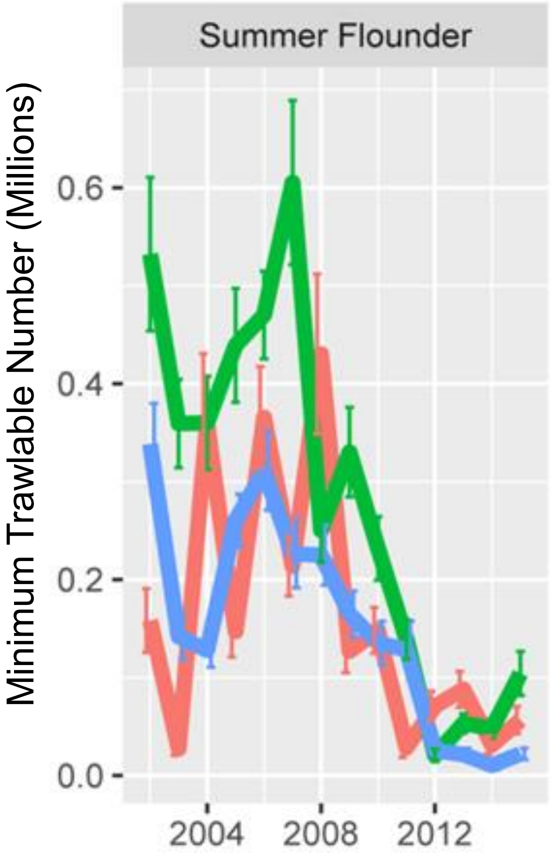


Figure A9. Minimum swept-area abundance of small (S), medium (M), and large (L) summer flounder during the six-month index period. Error bars represent SE.

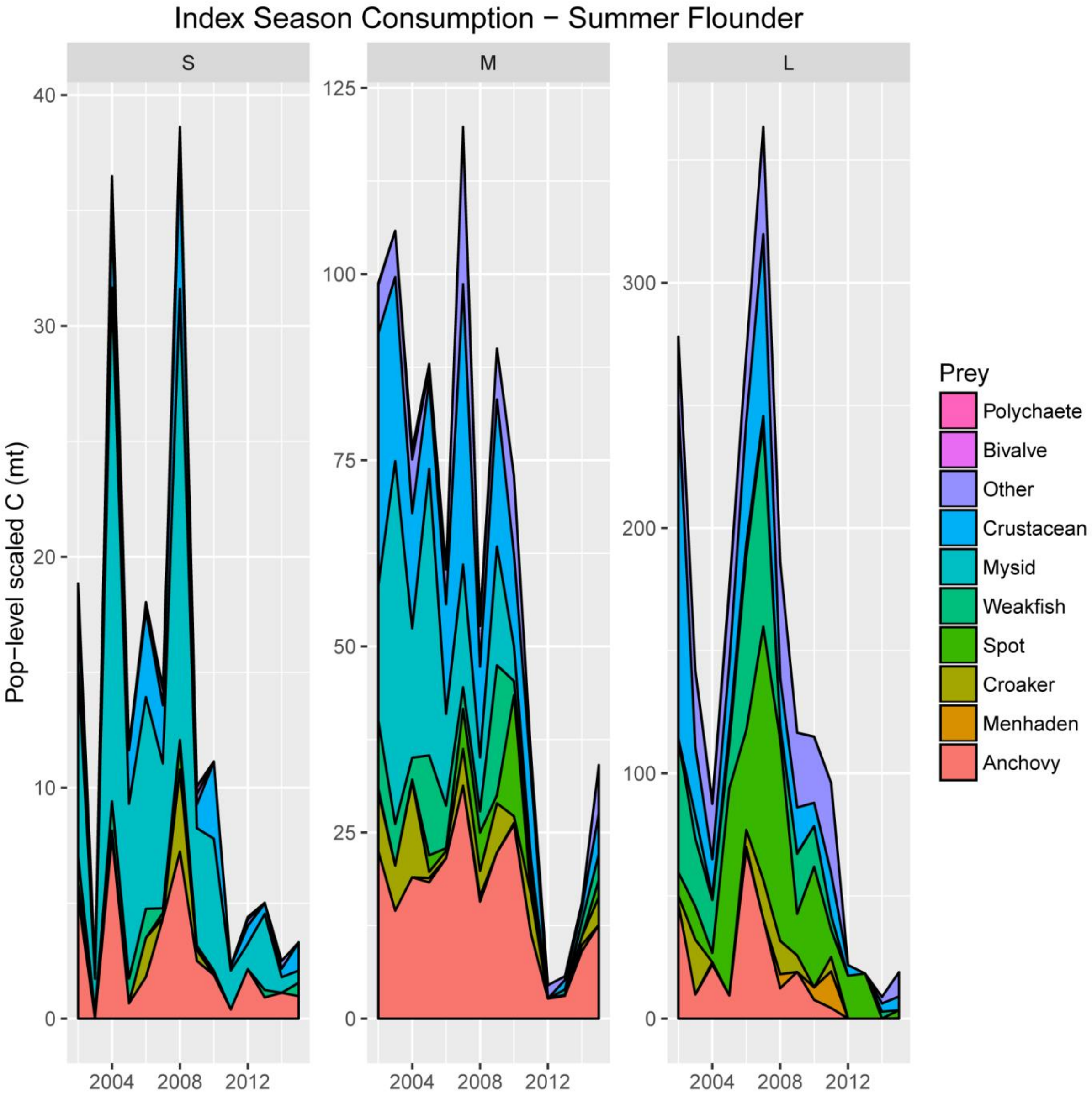


Figure A10. Population-level consumption (mt) of major forage prey groups for the six-month index period by small (S), medium (M), and large (L) summer flounder.

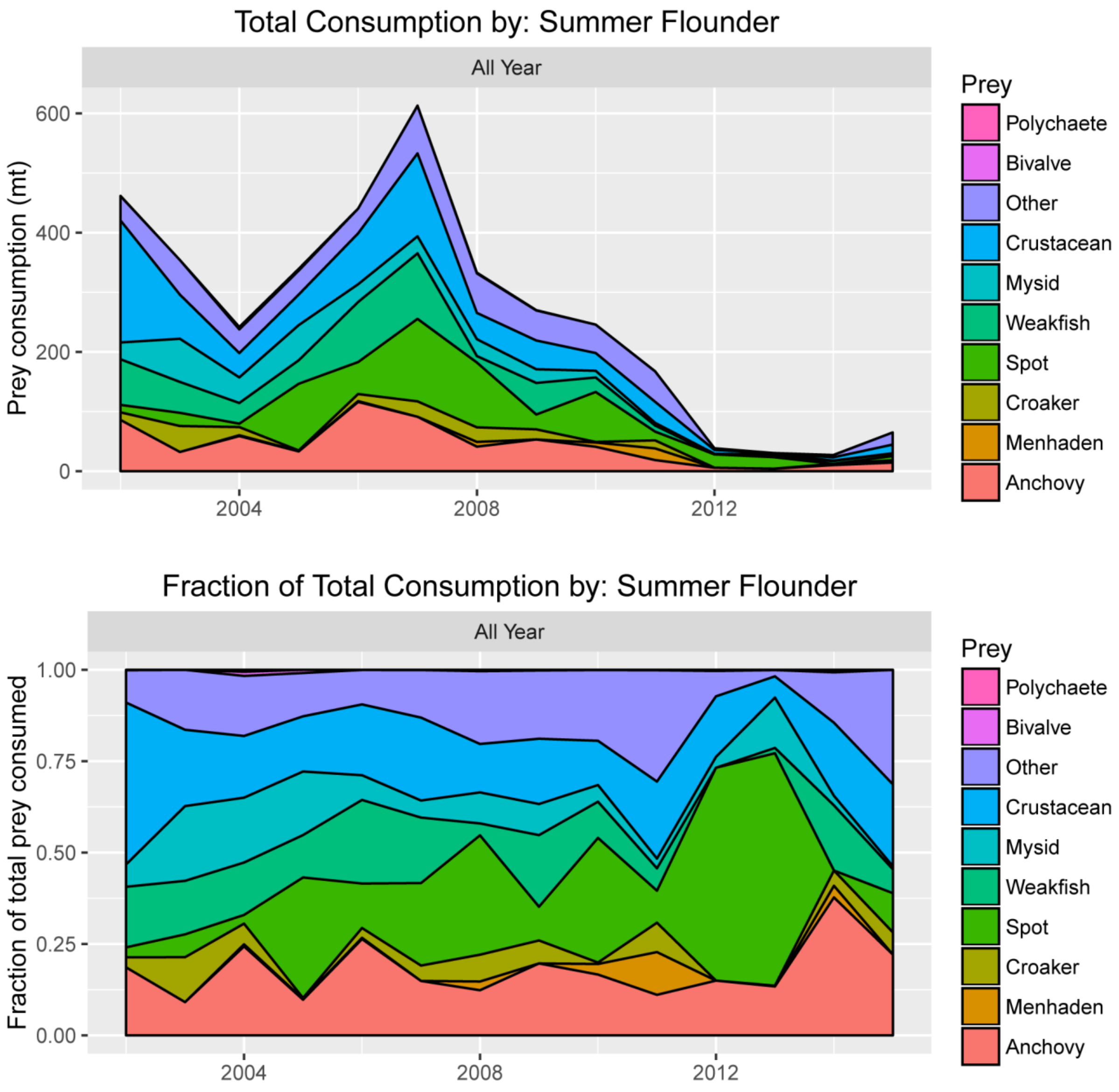


Figure A11. Summer flounder total annual consumption (mt) of select forage prey groups. Top: total prey consumption by all size classes over the entire year. Bottom: relative contributions of each forage prey to total annual consumption.

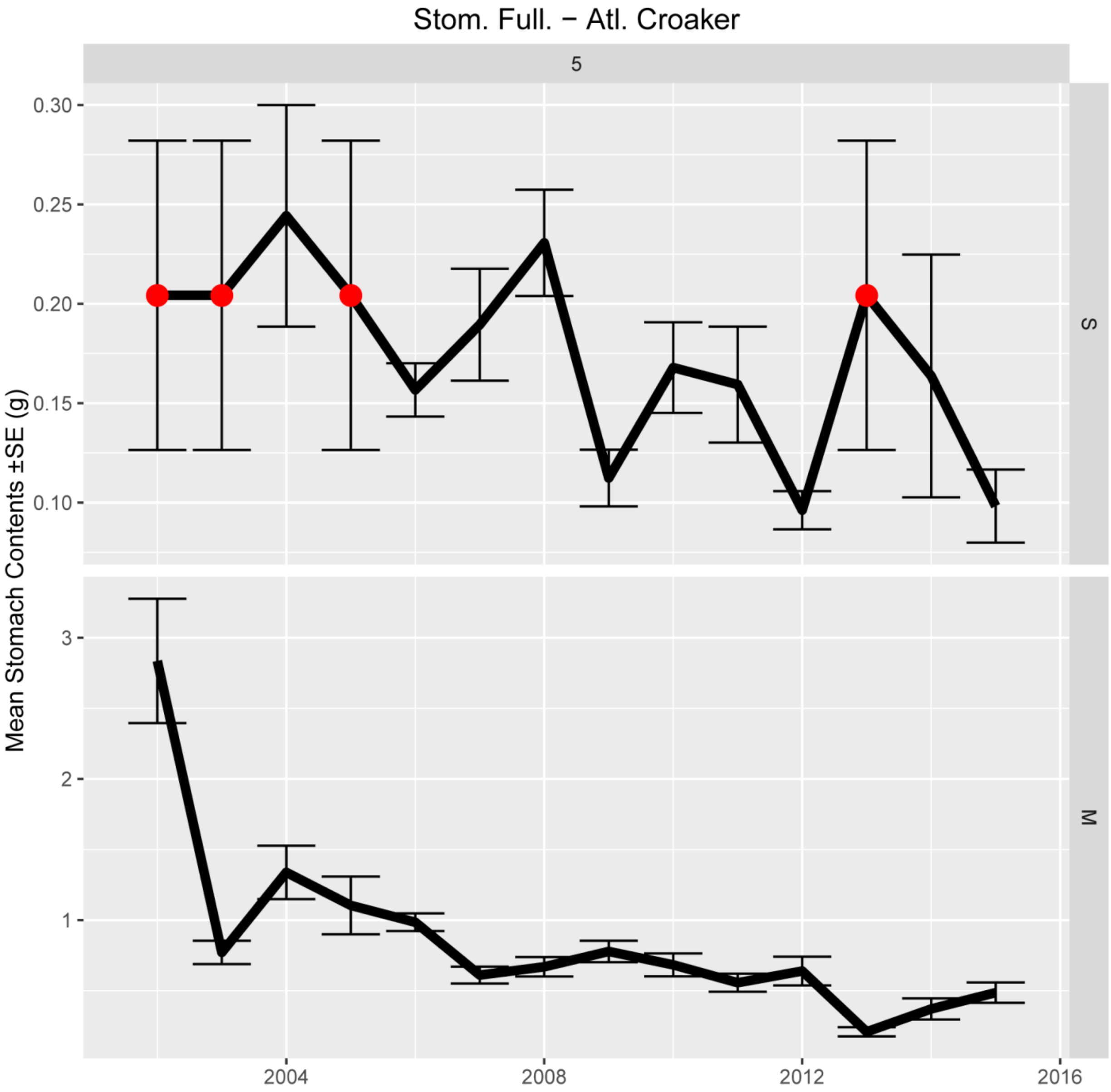


Figure A12. Mean weight (g) of stomach contents for small (S) and medium (M) Atlantic croaker during the six-month index period. Error bars represent SE.

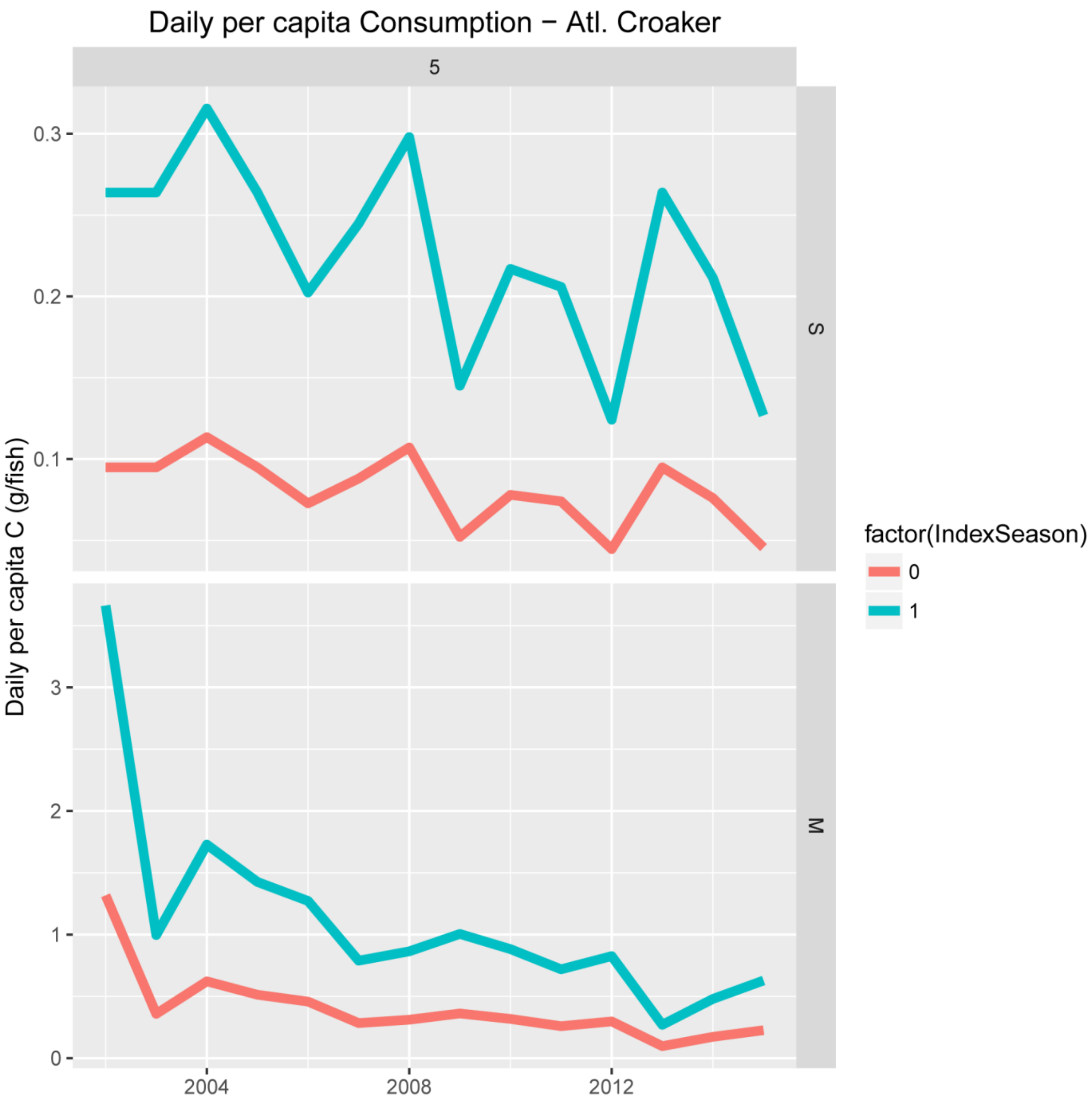


Figure A13. Daily per capita consumption (g/fish) during the non-index (red; factor = 0) and index (blue; factor = 1) period for small (S) and medium (M) Atlantic croaker.

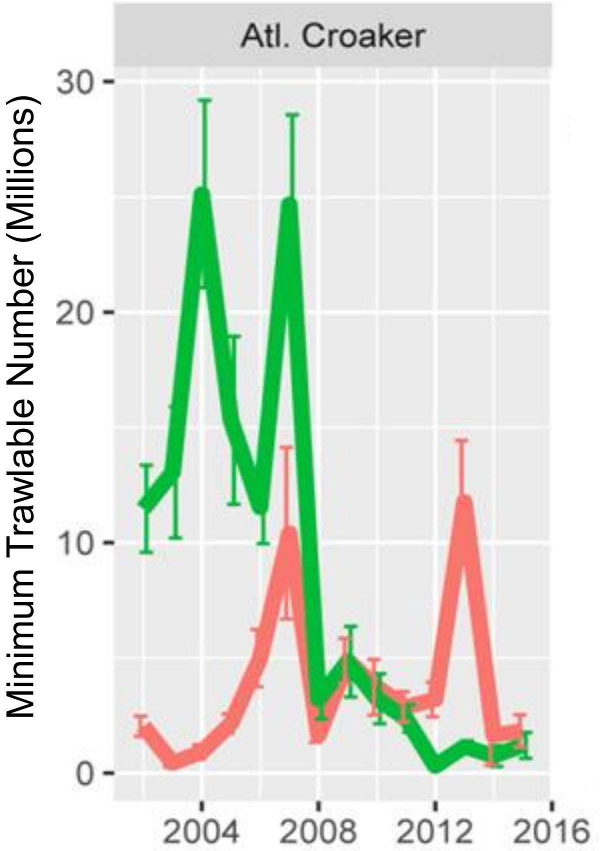


Figure A14. Minimum swept-area abundance of small (S) and medium (M) Atlantic croaker during the six-month index period. Error bars represent SE.

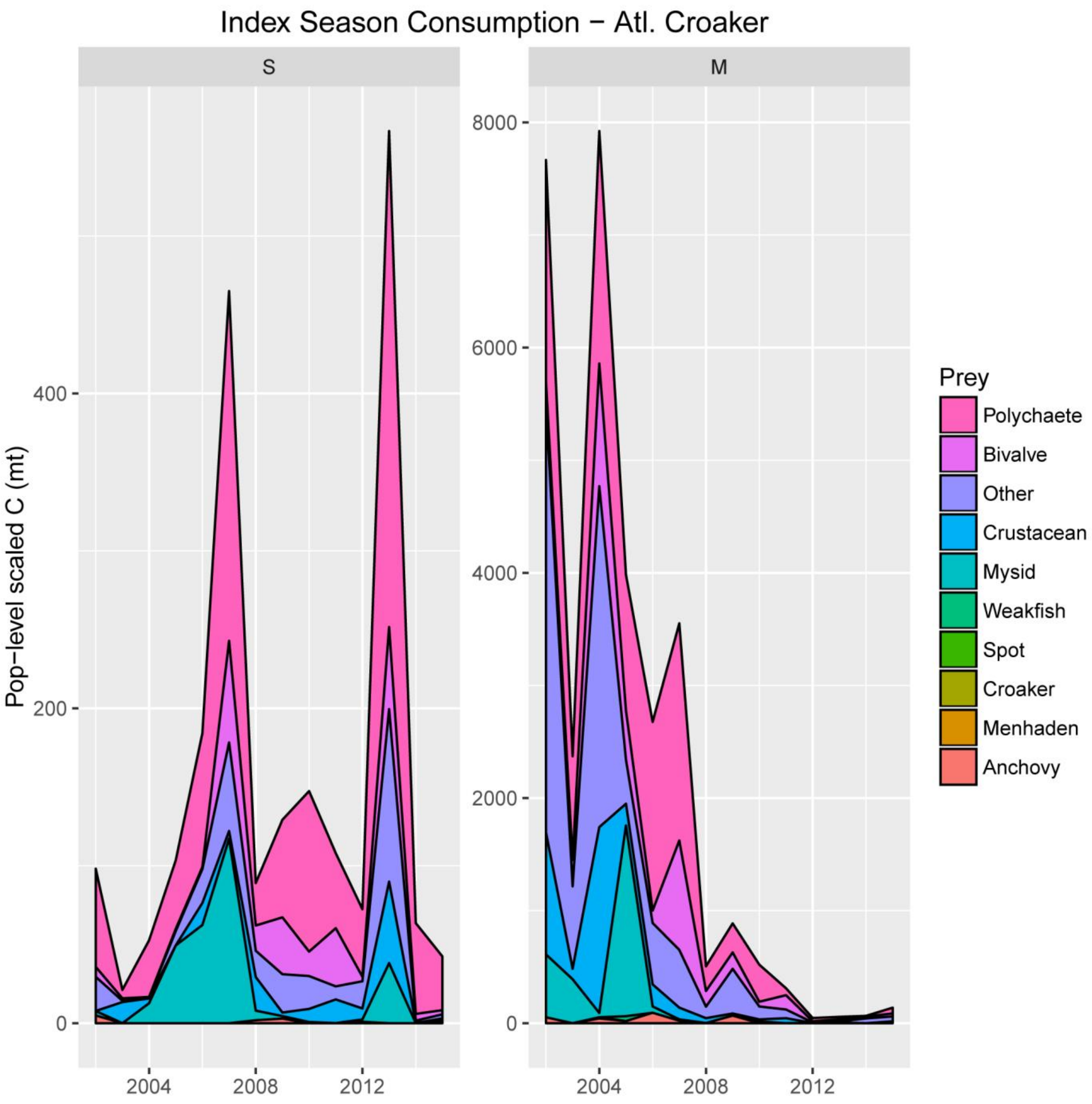


Figure A15. Population-level consumption (mt) of major forage prey groups for the six-month index period for small (S) and medium (M) Atlantic croaker.

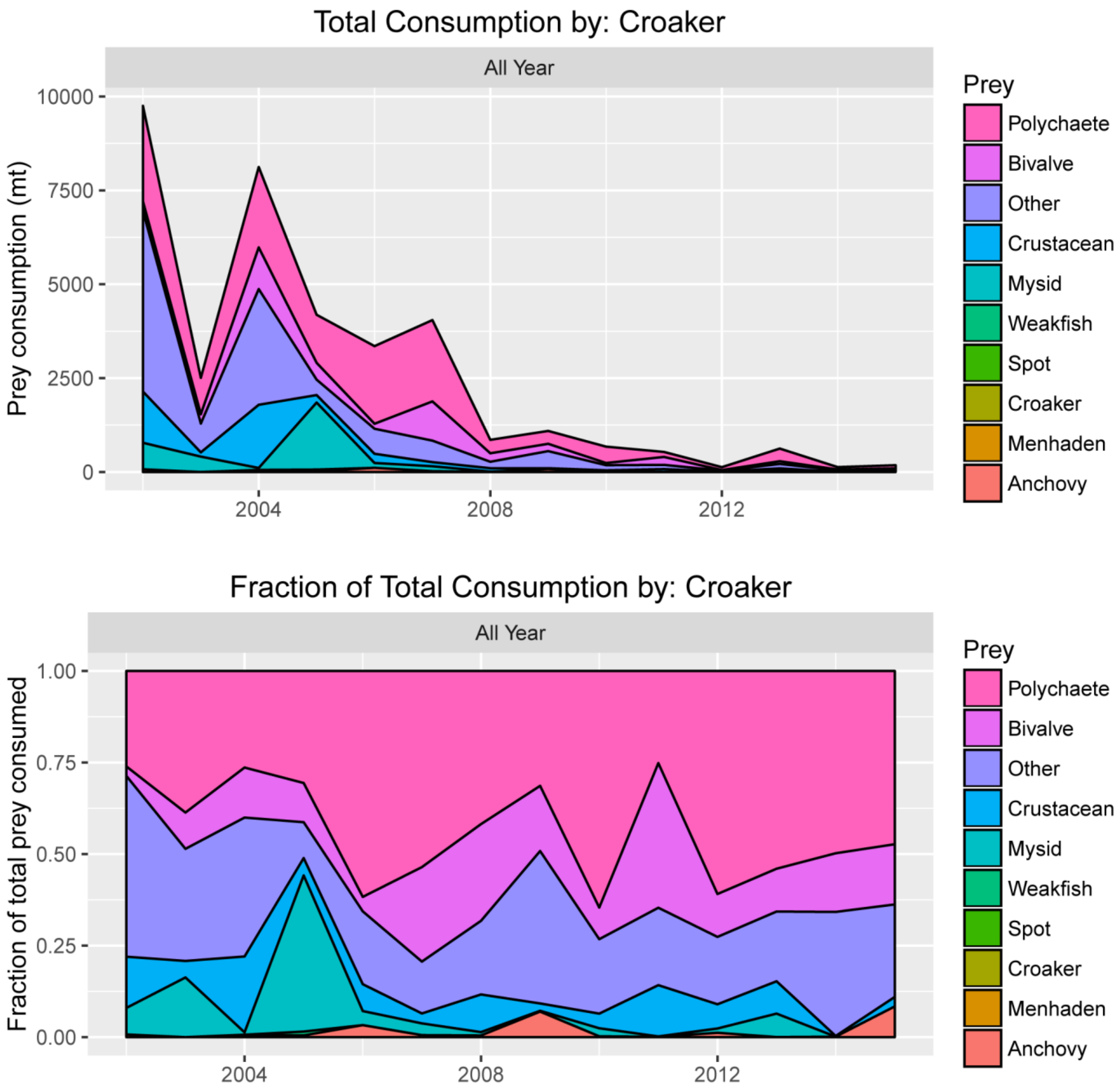


Figure A16. Atlantic croaker total annual consumption (mt) of select forage prey groups. Top: total prey consumption by all size classes over the entire year. Bottom: relative contributions of each forage prey to the total amount consumed per year.

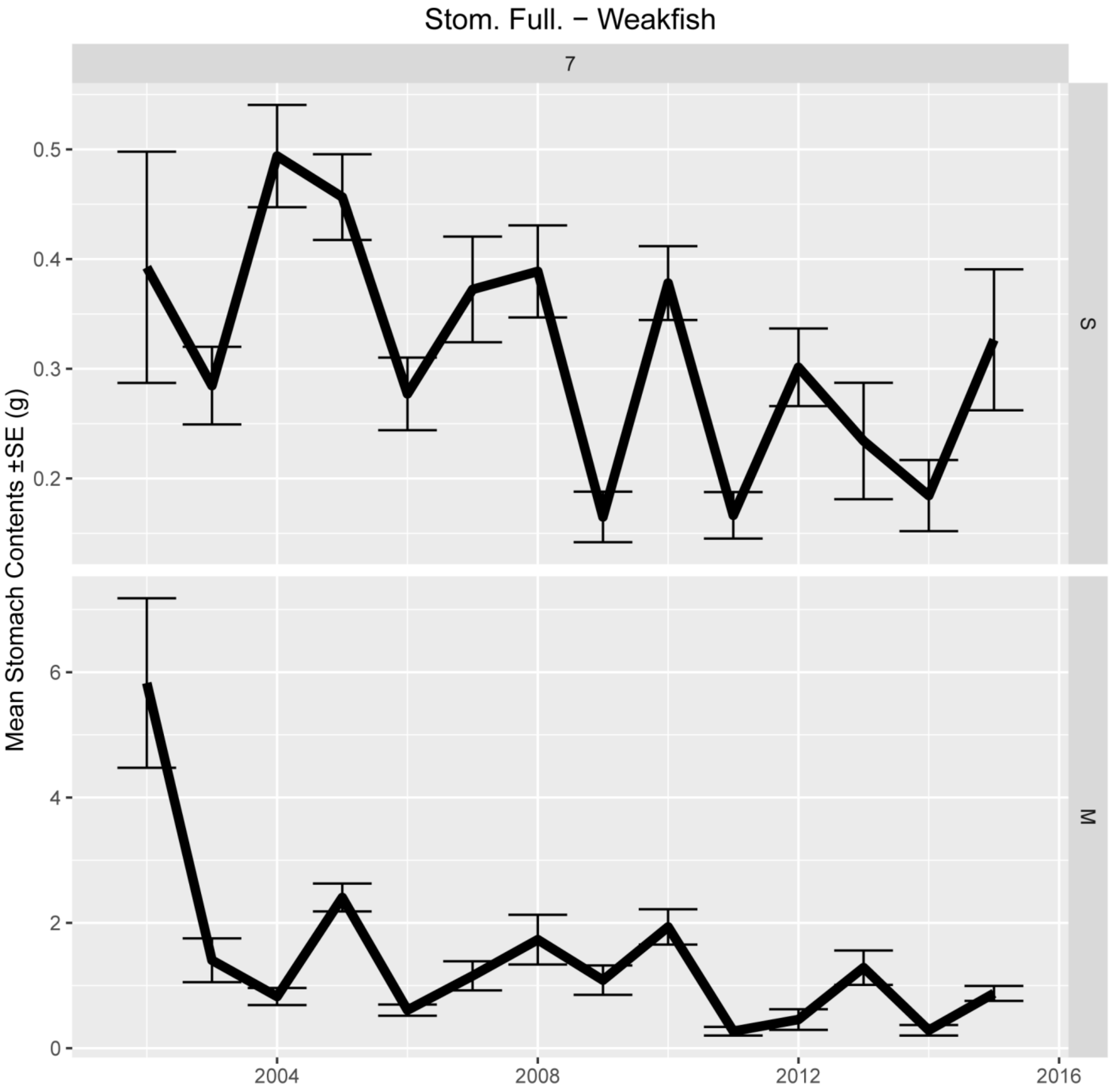


Figure A17. Mean weight (g) of stomach contents for small (S) and medium (M) weakfish during the six-month index period. Error bars represent SE.

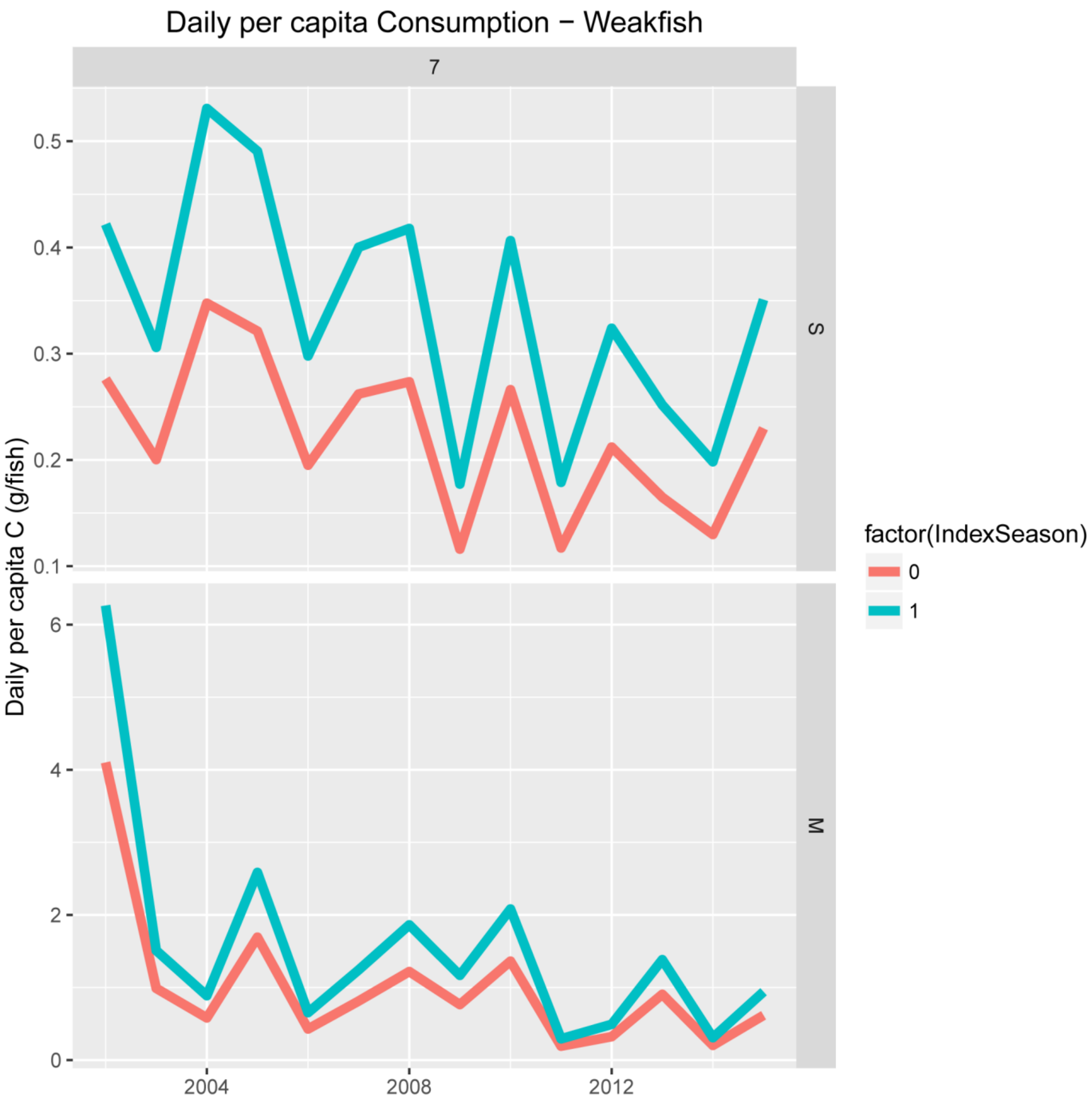


Figure A18. Daily per capita consumption (g/fish) during the non-index (red; factor = 0) and index (blue; factor = 1) period for small (S) and medium (M) weakfish.

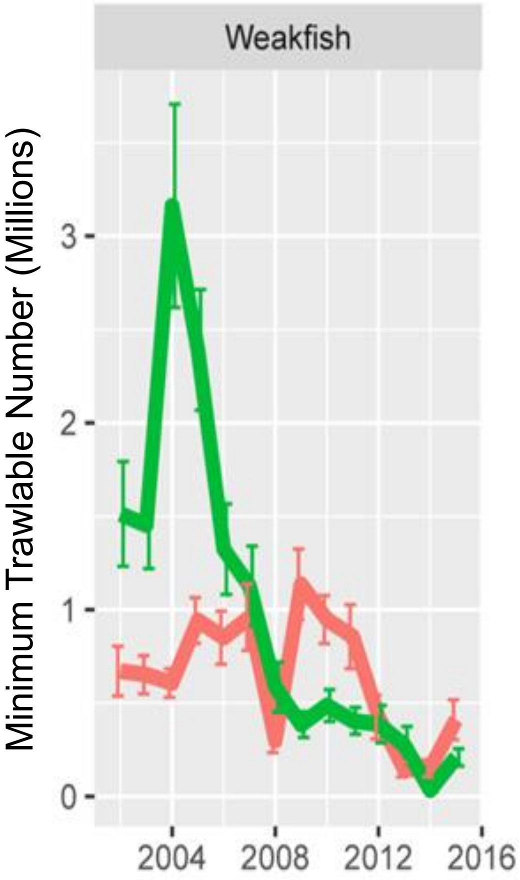


Figure A19. Minimum swept-area abundance of small (S) and medium (M) weakfish during the six-month index period. Error bars represent SE.

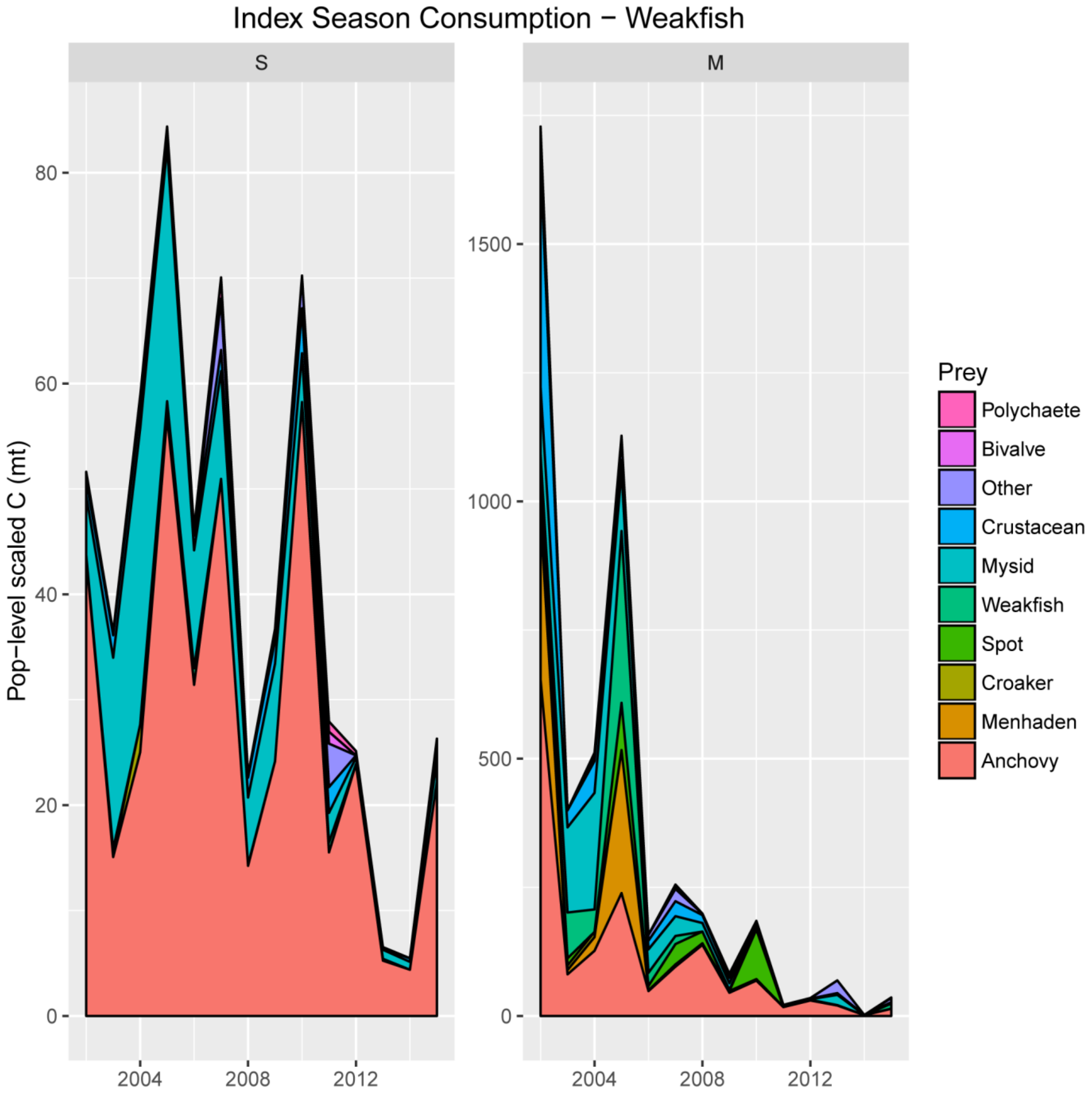


Figure A20. Population-level consumption (mt) of major forage prey groups during the six-month index period for small (S) and medium (M) weakfish.

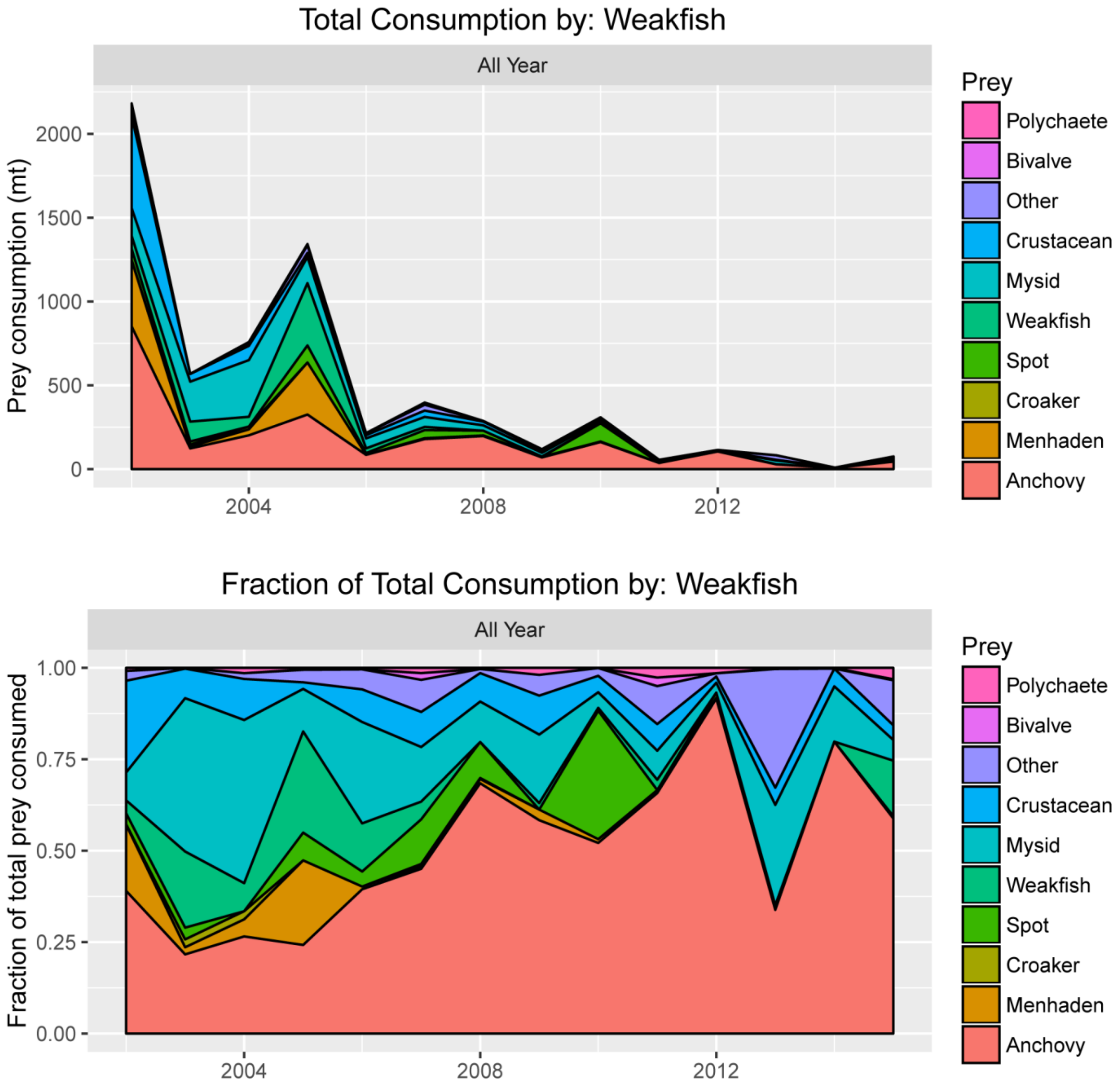


Figure A21. Weakfish total annual consumption (mt) of select forage prey groups. Top: total prey consumption by all size classes over the entire year. Bottom: relative contributions of each forage prey to the total amount consumed per year.

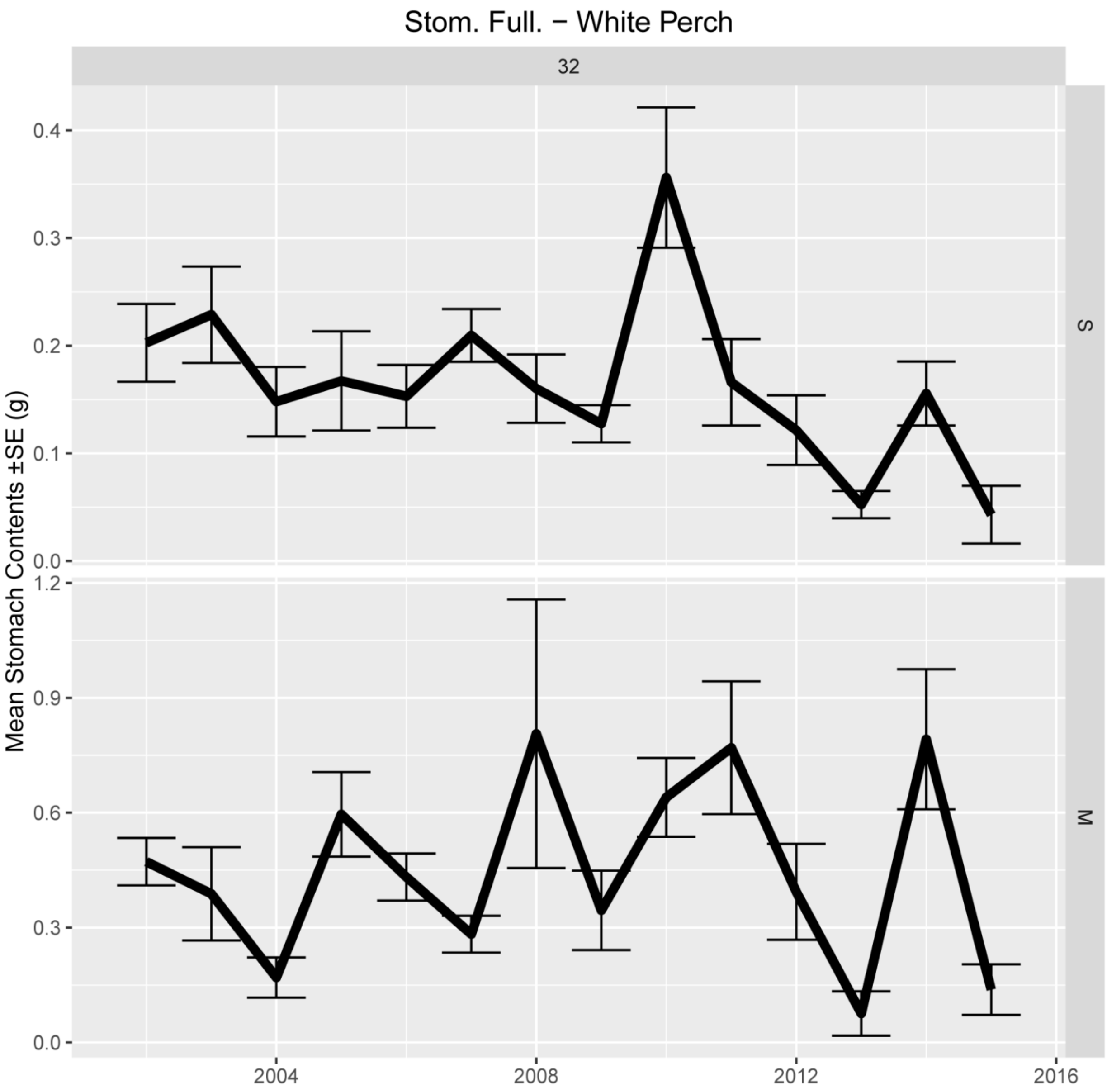


Figure A22. Mean weight (g) of stomach contents for small (S) and medium (M) white perch during the six-month index period. Error bars represent SE.

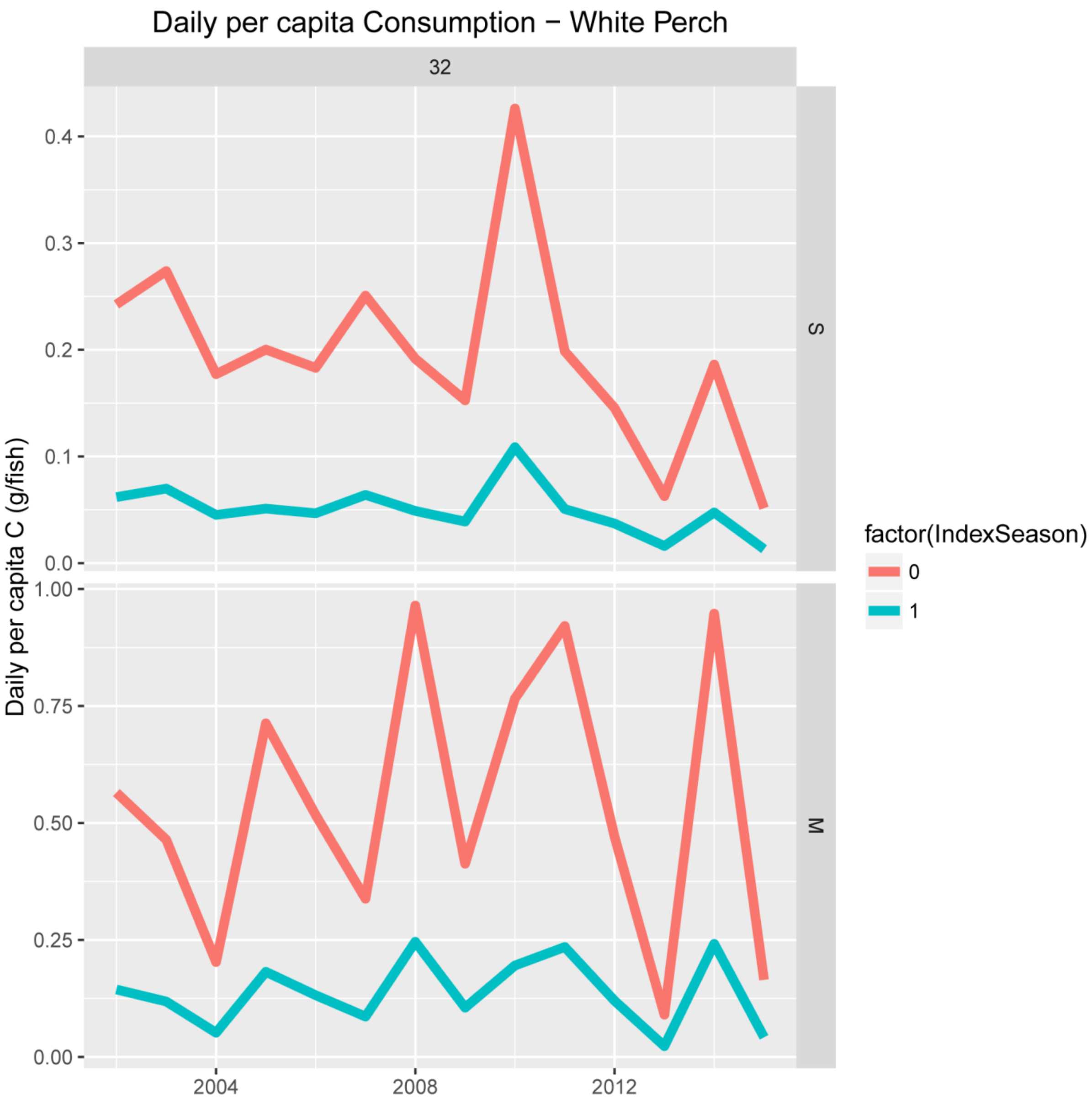


Figure A23. Daily per capita consumption (g/fish) during the non-index (red; factor = 0) and index (blue; factor = 1) period for small (S) and medium (M) white perch.

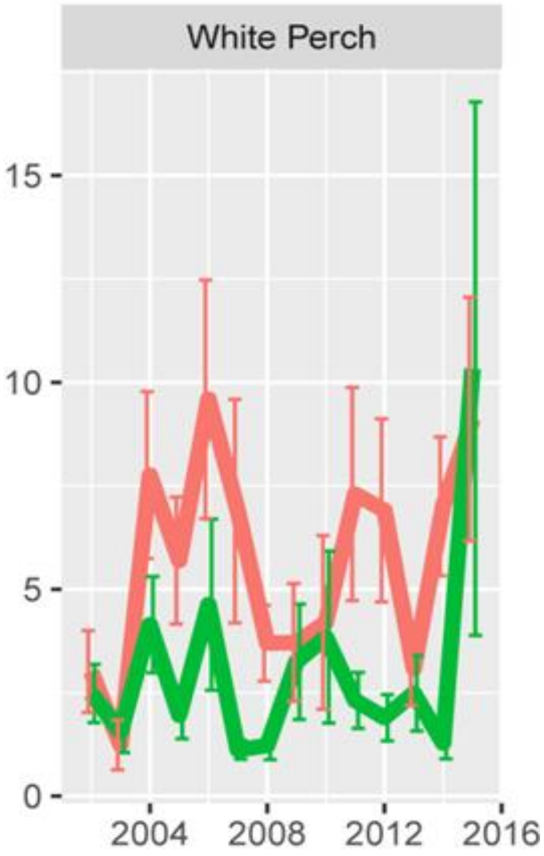


Figure A24. Minimum swept-area abundance of small (S) and medium (M) white perch during the six-month index period. Error bars represent SE.

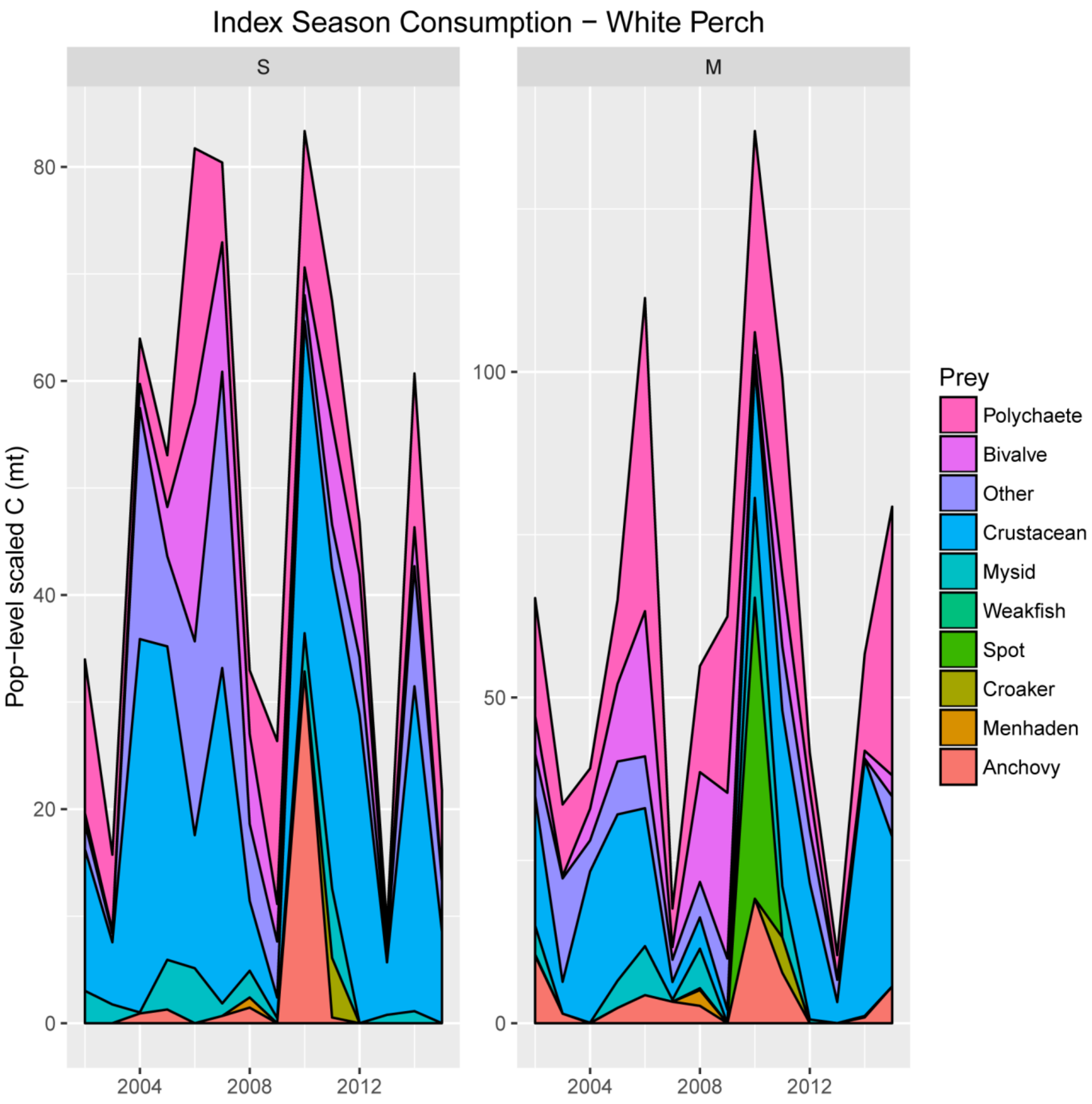


Figure A25. Population-level consumption (mt) of major forage prey groups during the six-month index period for small (S) and medium (M) white perch.

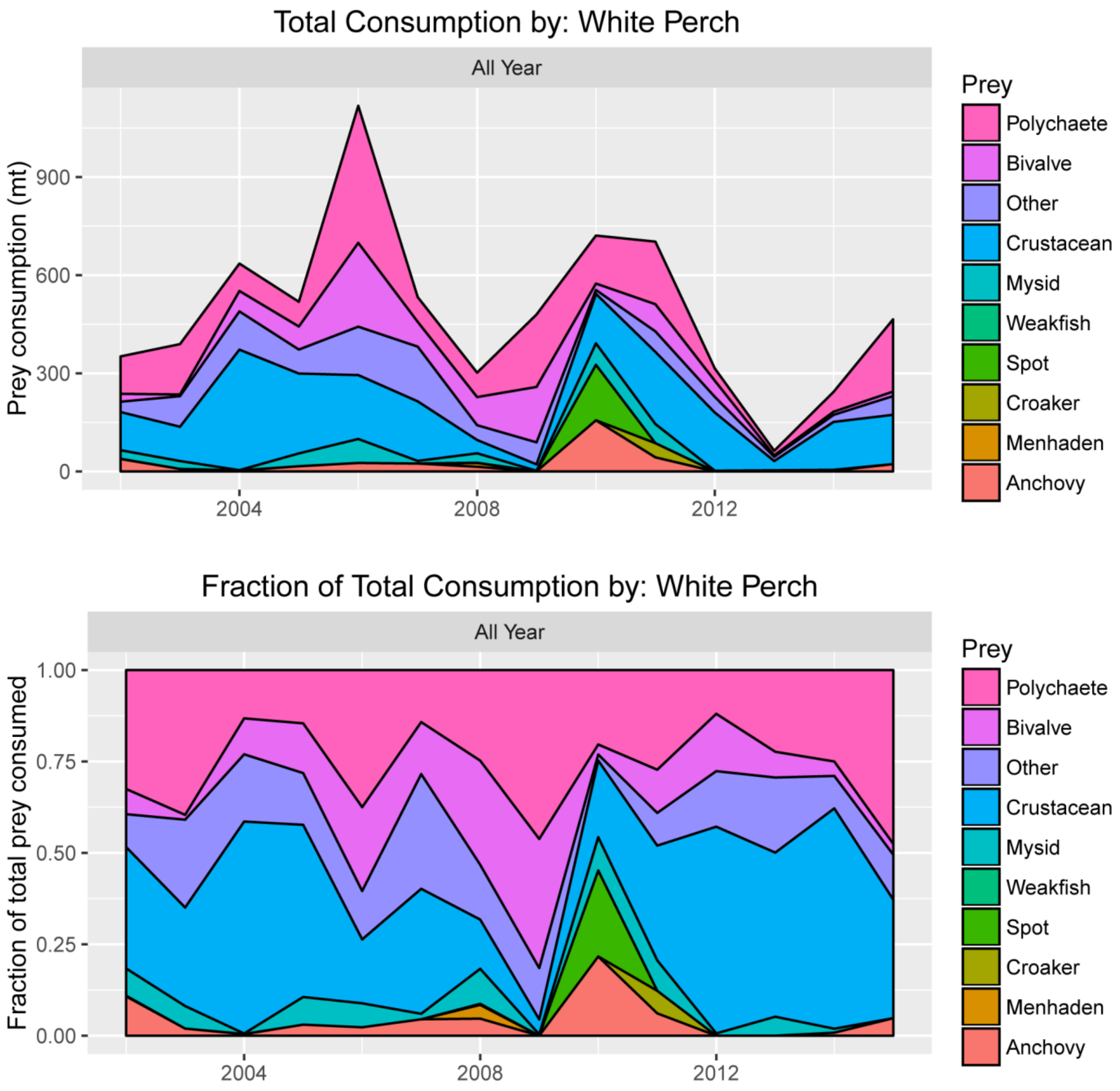


Figure A26. White perch total annual consumption (mt) of select forage prey groups. Top: total prey consumption by all size classes over the entire year. Bottom: relative contributions of each forage prey to the total amount consumed per year.

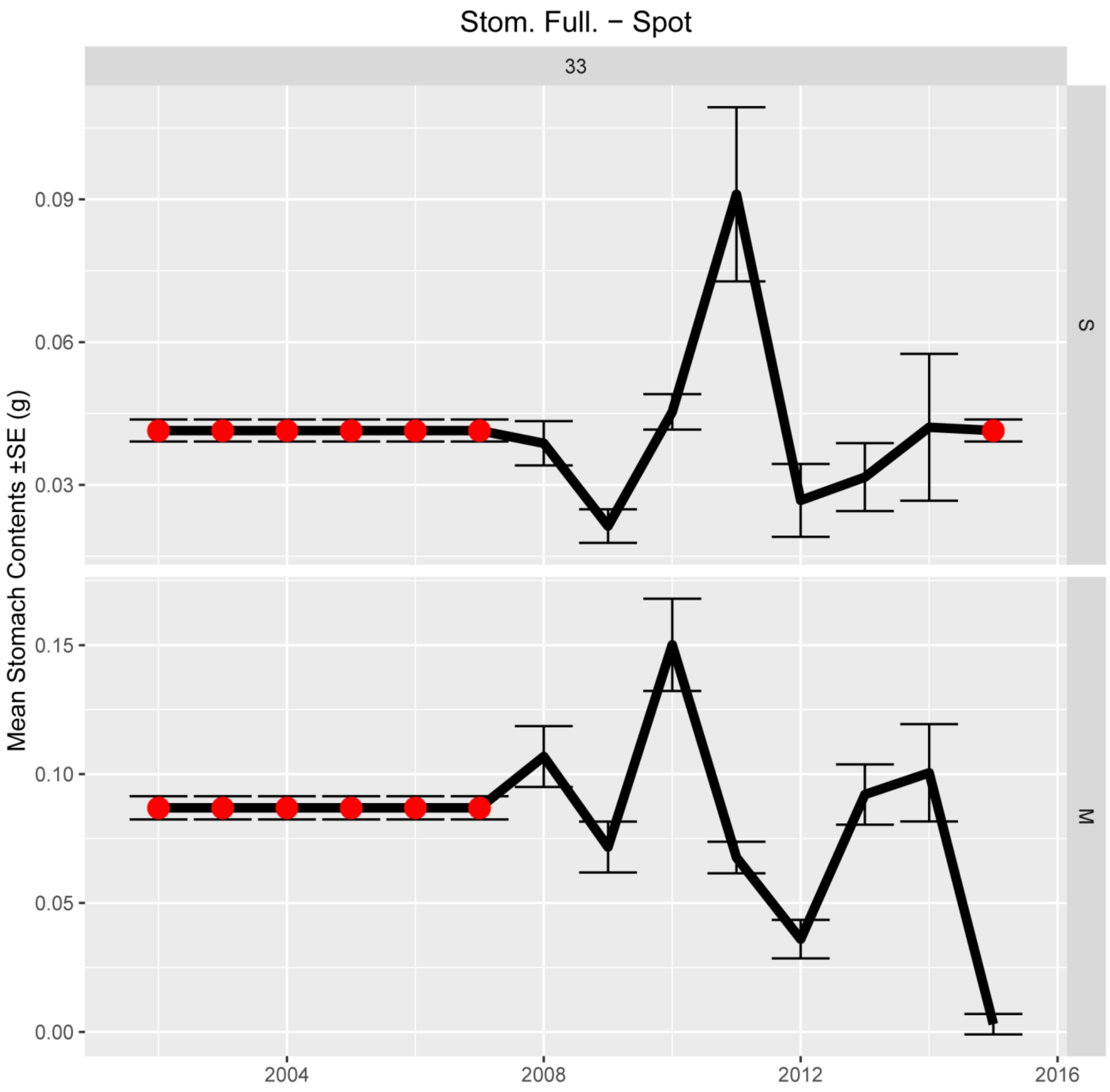


Figure A27. Mean weight (g) of stomach contents for small (S) and medium (M) spot during the six-month index period. Error bars represent SE.

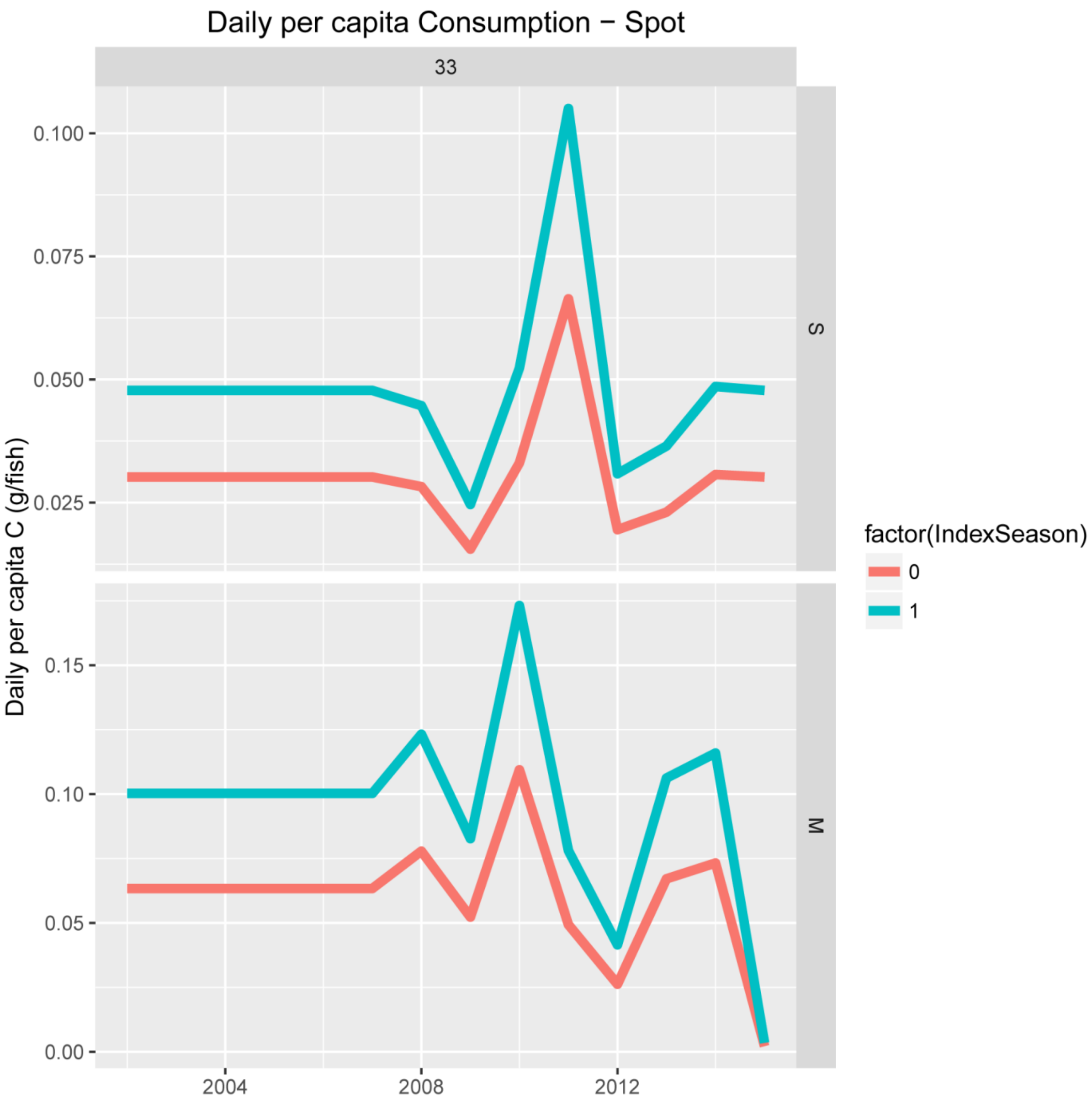


Figure A28. Daily per capita consumption (g/fish) during the non-index (red; factor = 0) and index (blue; factor = 1) period for small (S) and medium (M) spot.

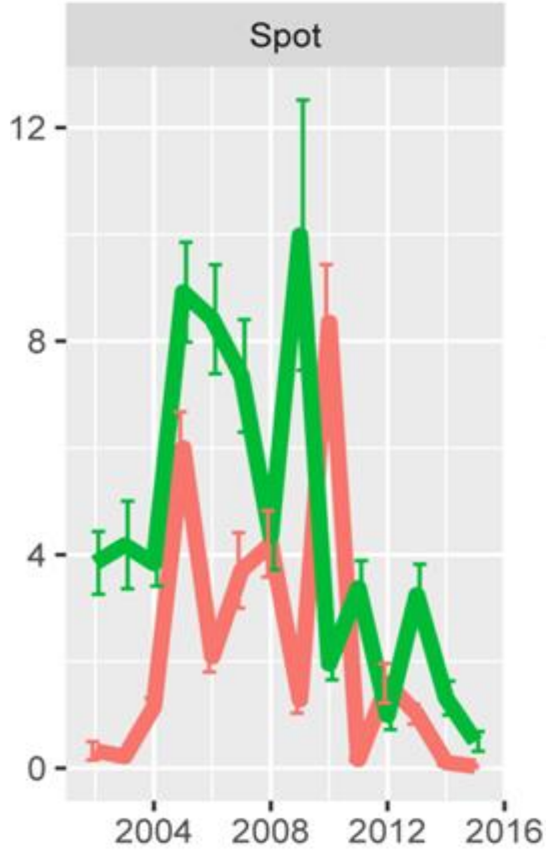


Figure A29. Minimum swept-area abundance of small (S) and medium (M) spot during the six-month index period. Error bars represent SE.

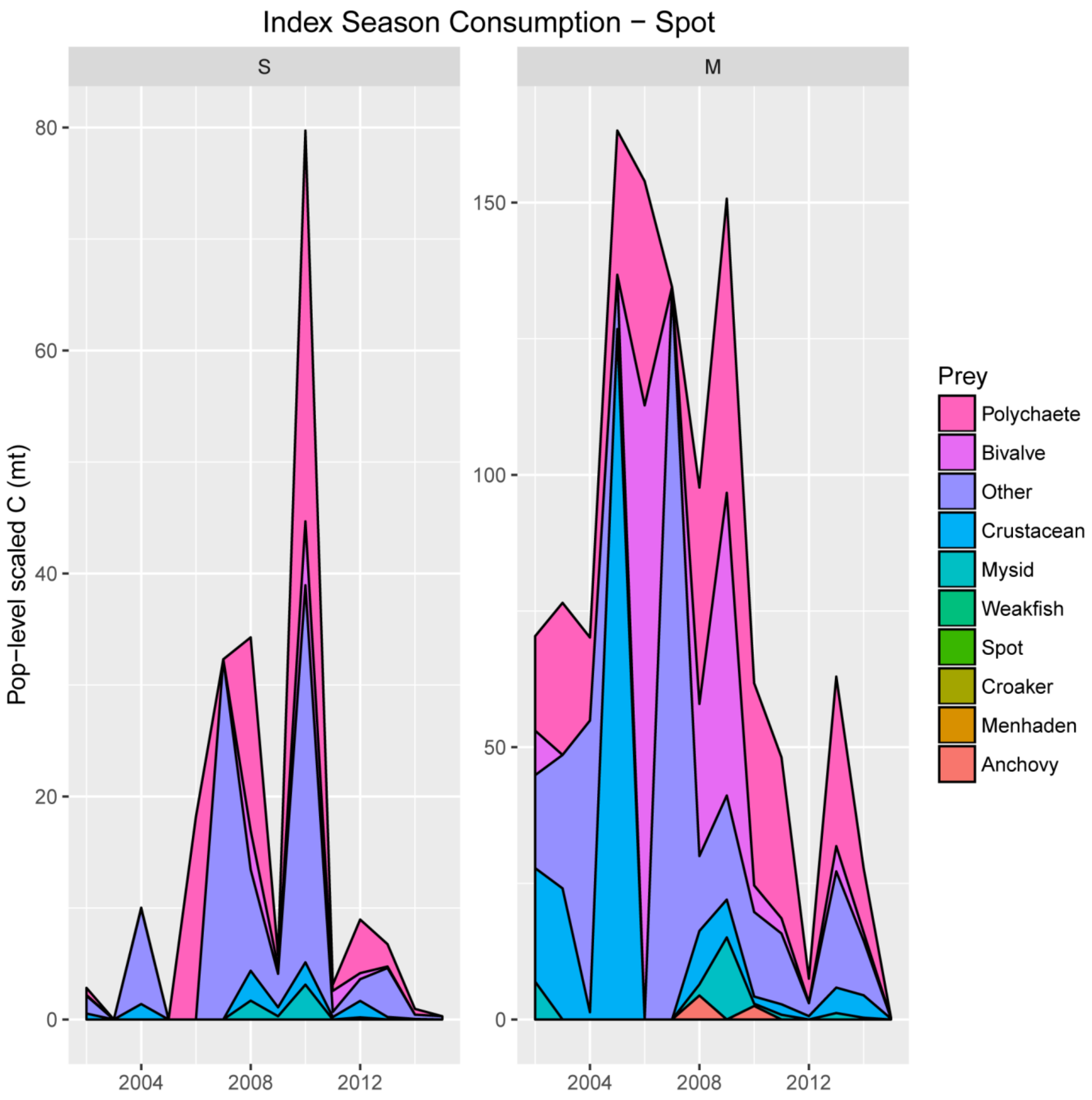


Figure A30. Population-level consumption (mt) of major forage prey groups during the six-month index period for small (S) and medium (M) spot.

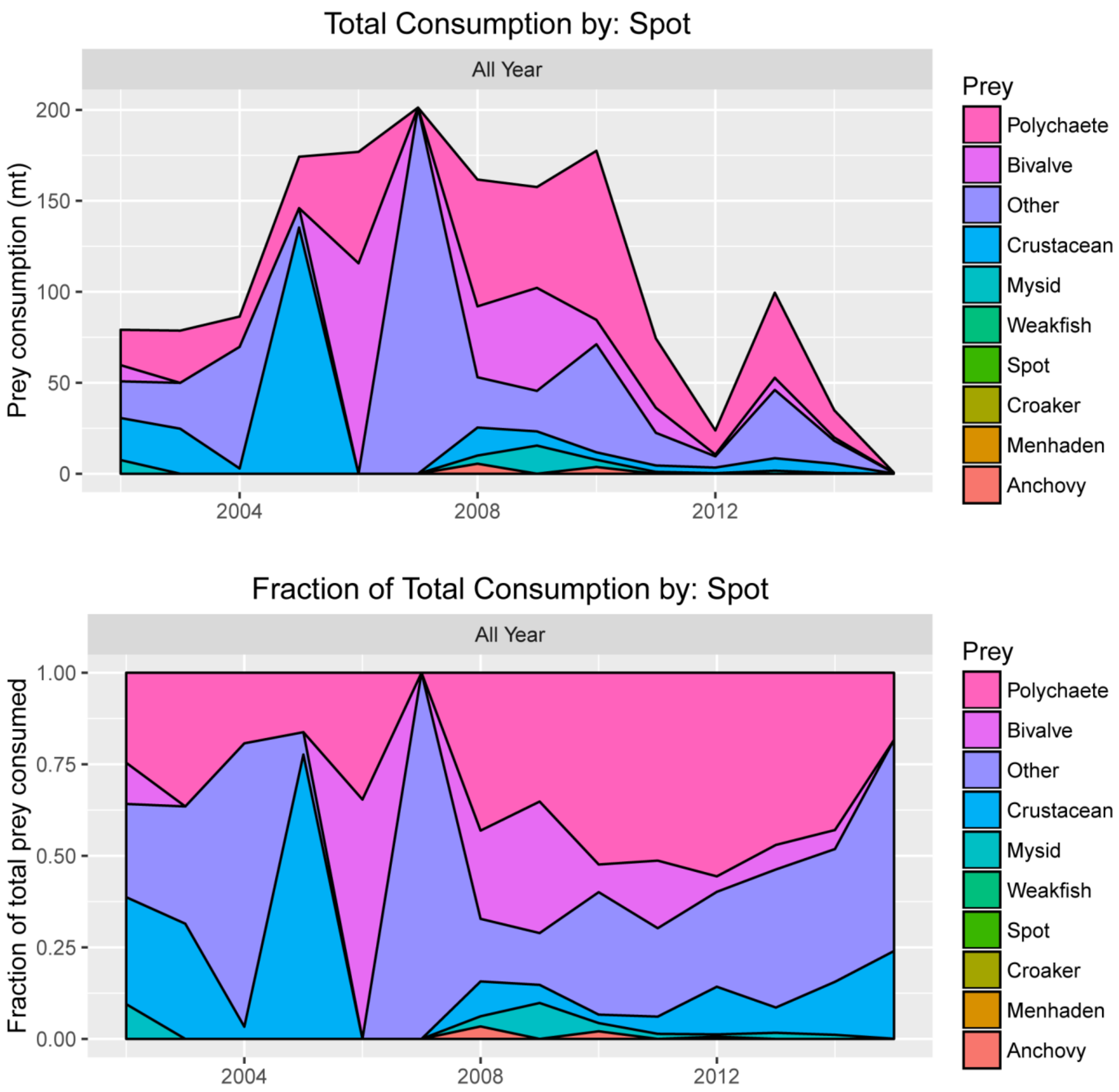


Figure A31. Spot total annual consumption (mt) of select forage prey groups. Top: total prey consumption by all size classes over the entire year. Bottom: relative contributions of each forage prey to the total amount consumed per year.

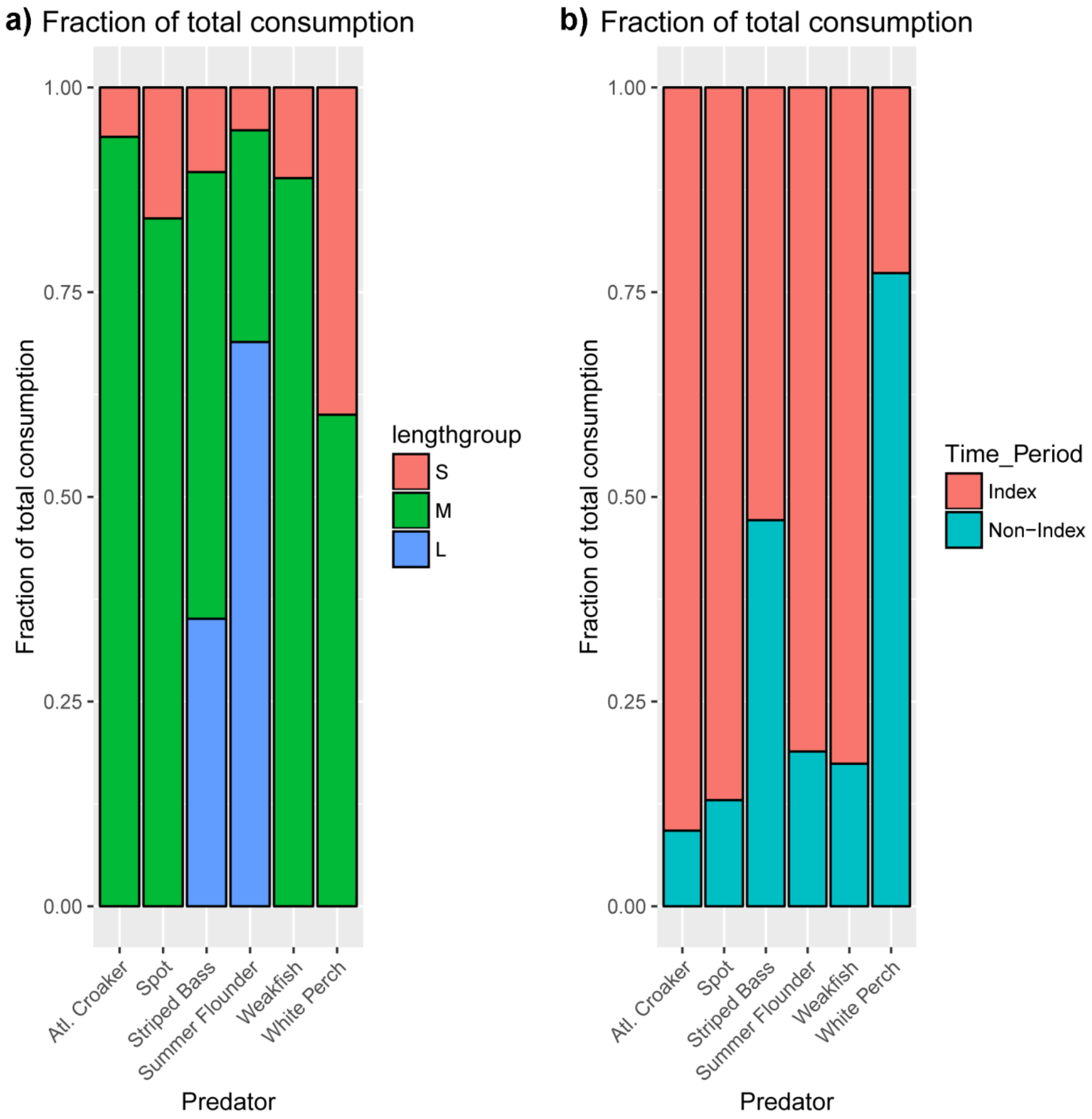


Figure A32. Fraction of total annual consumption by each predator based on a) length group (S-small, M-medium, L-large) and b) time period (Index – six-month period with highest abundance; Non-index – six-month period with lowest abundance).

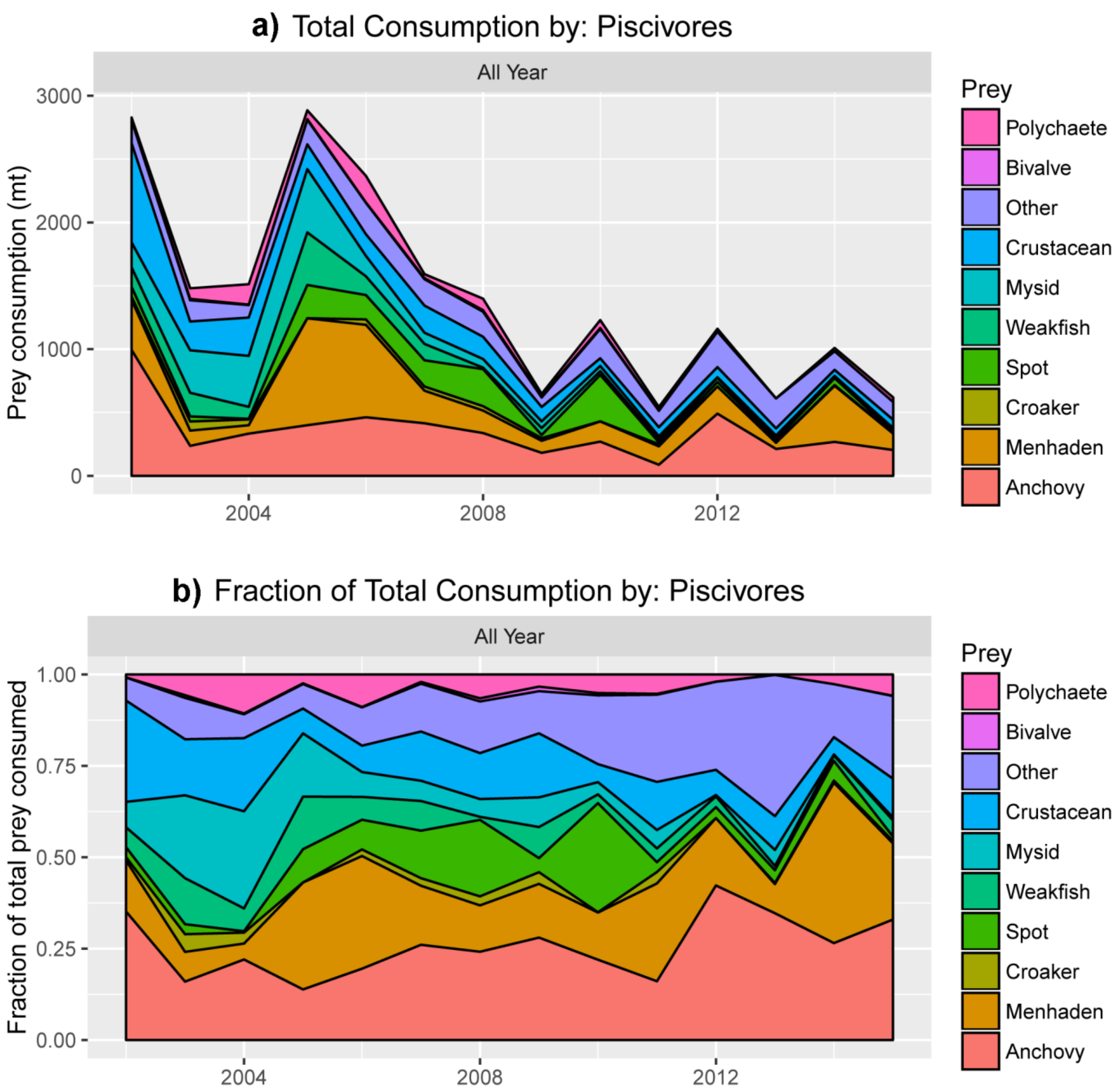
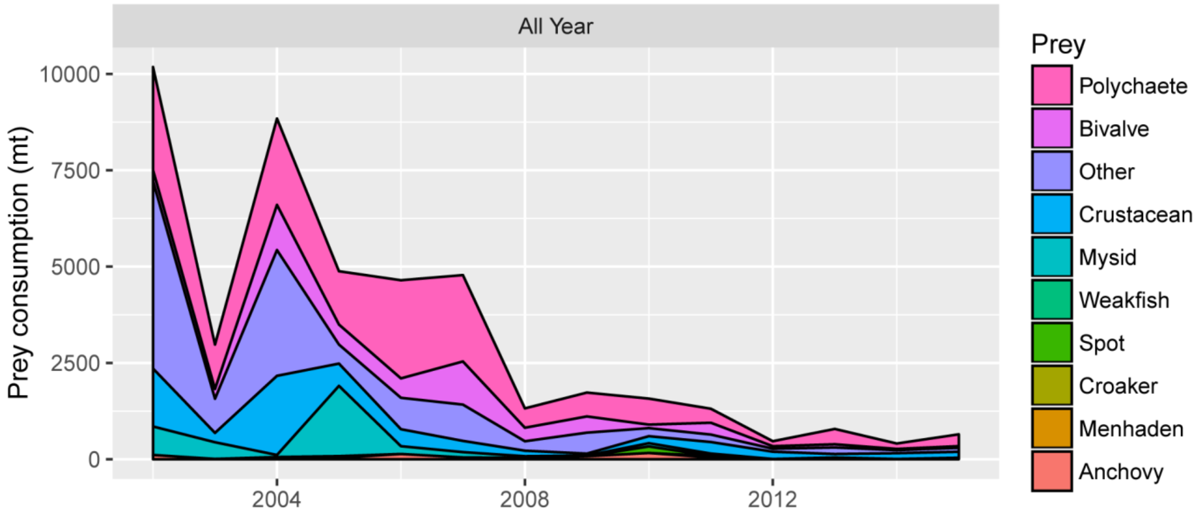


Figure A33. a) Total annual consumption by combined piscivorours predators (striped bass, summer flounder, and weakfish), and b) fraction of total consumption among the piscivorous predators.

a) Total Consumption by: Benthivores



b) Fraction of Total Consumption by: Benthivores

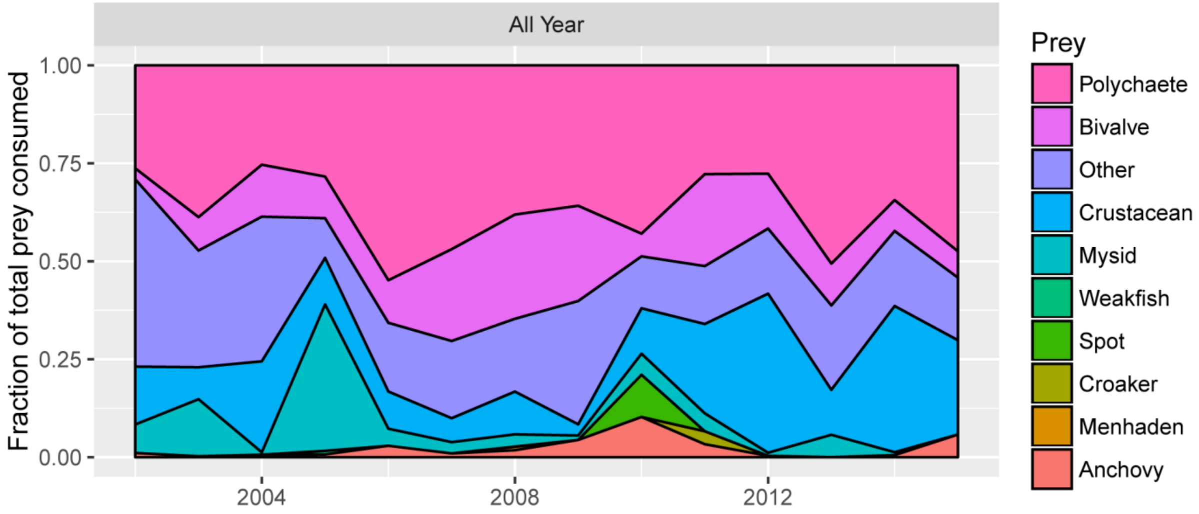


Figure A14. a) Total annual consumption (mt) by combined benthivorous predators (Atlantic croaker, white perch, and spot), and b) fraction of total consumption among the benthivorous predators.

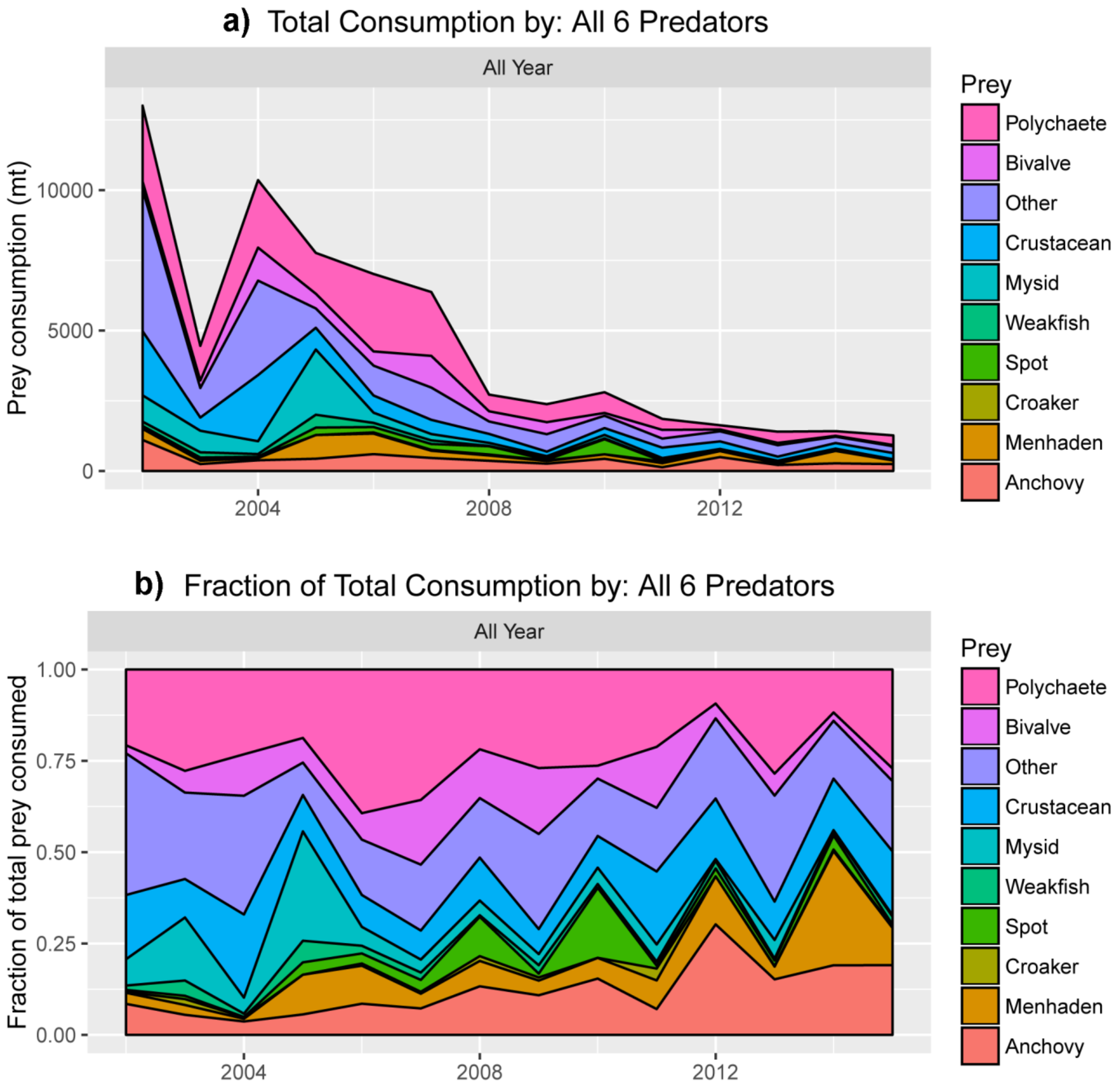


Figure A15. a) Total annual consumption by all six combined predators (striped bass, summer flounder, weakfish, Atlantic croaker, white perch, and spot), and b) fraction of total consumption among all six predators.