Ref. No. [UMCES]CBL 2016-001

Final Report

(Feb 1, 2015 – January 31, 2016)

Forage indicators and consumption profiles for Chesapeake Bay fishes

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Submitted on:	January 31, 2016
Sponsors Reference	NA
UMCES Project	CBL 2015-045CBT 07-5-25759

1. Abstract

Understanding predator-prey relationships and the status of the forage base is important to develop ecosystem approaches to fisheries management (EAFM). We analyzed data and synthesized results from eight existing (or historical) monitoring programs to assess trends in the Chesapeake Bay forage base using a combination of complementary indicators and approaches. Our first objective was to develop indicators for 14 dominant forage groups. We developed a suite of four indicators: 1) relative prey abundance or biomass, 2) diet-based indices, 3) prey-predator ratios, and 4) consumption-prey ratios. Forage taxa examined included eight fishes (e.g., young-of-year (YOY) Atlantic menhaden *Brevoortia tyrannus*, bay anchovy *Anchoa mitchilli*, YOY alewife *Alosa pseudoharengus*, YOY blueback herring *Alosa aestivalis*, Atlantic silverside *Menidia menidia*, YOY Atlantic croaker *Micropogonias undulatus*, YOY spot *Leiostomus xanthurus*, and YOY weakfish *Cynoscion regalis*) and six invertebrates (Mysidae, Bivalvia, Polychaeta, mantis shrimp *Squilla empusa*, sand shrimp *Crangon septemspinosa* and *Macoma spp.*). Our second objective was to develop consumption profiles to quantify the relative, bay-wide magnitude of prey consumed by six biomass-dominant predator fishes in the Bay. Gastric evacuation models and area-swept abundance estimates were used to estimate relative population-scale consumption for striped bass *Morone saxatilis*, summer flounder *Paralichthys dentatus*, weakfish, Atlantic croaker, white perch *Morone americana*, and spot.

The suite of forage indicators provided complementary perspectives on the status of the forage base not possible with a single metric. Some forage species (e.g., YOY Atlantic menhaden, YOY spot, and silversides) exhibited correlated shifts in abundance on decadal scales that could be indicative of alternative ecosystem states or broad-scale environmental drivers. Overall, forage indicators had a high degree of interannual variability that likely influences the opportunistic feeding exhibited by many predator fishes. For example, some years were characterized by pulses in availability and consumption of certain prey taxa. Although forage indices remained relatively stable from 2002-2014, total consumption by the six predators declined by more than an order of magnitude, primarily due to decreases in abundances of predators (especially Atlantic croaker). Our findings integrate data from multiple surveys and can be used to inform management decisions. Interpretation and application of this research is complicated by sampling uncertainties in the monitoring surveys and by the dynamic nature of predator-prey interactions in the Bay which, over the decades, has experienced dramatic shifts in relative abundance of its constituent fauna. The research represents a step towards understanding the forage base and consumption needs of predators, and it has the potential to support development of better monitoring programs and improved management of forage groups in Chesapeake Bay.

2. Introduction

Advances in ecosystem approaches to fisheries management (EAFM) require an adequate understanding of predator-prey relationships and the status of the forage base that supports predators. Part of the motivation for EAFM is to account for predator-prey interactions and environmental effects that are not readily addressed using single species management approaches (Link, 2002; Pikitch *et al.*, 2004). Understanding predator-prey dynamics can be particularly important in estuarine nursery and feeding grounds like the Chesapeake Bay, where many migratory predators reside during periods of accelerated growth (Hartman and Brandt, 1995a; Buchheister *et al.*, 2013).

The Chesapeake Bay supports numerous economically and ecologically valuable species and there has been increased acknowledgment of the need to better characterize and evaluate the forage base that supports predators. The recognition of the importance of prey has been formalized in an objective of the Chesapeake Bay Program's Watershed Agreement to develop a strategy for assessing the forage fish base available as food for predatory species in the Chesapeake Bay. In an evolving context, "forage fish" was interpreted broadly to include other forage taxa that are important, including invertebrates. A Forage Workshop, sponsored by the Chesapeake Bay Program's (CBP) Scientific and Technical Advisory Committee (STAC), was convened in November 2014 and brought together resource managers and regional experts to summarize current understanding and identify critical research needs (Ihde *et al.*, 2015). This workshop and a recent synthesis of Chesapeake Bay fish diet data (Buchheister and Latour, 2015) have identified dominant forage species in the Bay. However, despite availability of data from several monitoring surveys, there had not been a concerted effort to develop baywide indicators of forage availability that integrate the information across surveys. Also, population-scale measures of prey consumption had not been evaluated for aggregated predators.

Forage indicators are metrics developed to monitor the status of prey resources in a system, and they are important to facilitate EAFM (Methratta and Link, 2006; Link, 2010). Forage indicators can quantify different aspects of the prey base, for example, providing information on prey standing stock, relative prey availability, prey importance to predators, and predation intensity. Suites of indicators are generally more beneficial and informative than a single metric when developing ecological indicators, particularly for EAFM applications (Rice and Rochet, 2005; Methratta and Link, 2006). This is particularly true for forage in Chesapeake Bay, given the diversity of prey and predators and the complexity of ecological processes underlying predator-prey interactions. In a management context, forage indicators can monitor the supply of forage for managed (and unmanaged) predators and can inform fisheries management actions. Forage indicators have utility as 1) a foundation for developing target levels to guide management actions, 2) a potential warning mechanism to indicate poor conditions, 3) quantitative metrics to support and prioritize habitat conservation efforts, or 4) a means to prioritize research, management, or conservation efforts.

Information on the consumption of prey by predators is a valuable complement to other forage indicators. Consumption estimates characterize the relative importance of specific prey to individual predators and predator assemblages. They can identify predators having the strongest effect on prey populations, and they can be used to evaluate changes in relative predatory demand through time. Basic diet composition data provide a crucial but incomplete depiction of relative prey importance for predatory fishes. To evaluate large-scale patterns of forage status and importance, consumption should ideally be scaled to the predator population (Overholtz *et al.*, 2000; Link and Sosebee, 2008). In doing so, consumption profiles for predators can be generated that account for many factors that may influence the relative importance of different prey. For example, as predators increase in size or age, diets often shift and individuals can eat more, but their abundance declines due to mortality over time. Accordingly, there are complex interactions between predator abundances and per capita consumption that will influence total population-level consumption patterns.

In this research, we analyzed data and synthesized results from eight existing (or historical) monitoring programs to assess trends in the forage base from the Chesapeake Bay, using a combination of complementary indicators and approaches. Our two specific objectives were:

1. **Develop a suite of forage indicators for dominant prey species in Chesapeake Bay.** Forage groups evaluated included a diverse assemblage of invertebrates and vertebrates that have been identified as key forage in the Bay (Buchheister and Latour, 2015; Ihde *et al.*, 2015). Here, we provide indicators for 14 prey groups including various pelagic fishes, demersal fishes, small crustaceans, and other benthic invertebrates. To provide complementary perspectives on the forage base, we developed four types of indicators: 1) relative prey abundance or biomass, 2) diet-based indices, 3) prey-predator ratios, and 4) consumption-prey ratios.

2. **Develop consumption profiles for six biomass-dominant predatory fishes in the Bay.** Consumption profiles refer to the relative magnitude of prey consumed by predators, scaled to their bay-wide populations. Predators selected for the study represent three piscivores (striped bass *Morone saxatilis*, summer flounder *Paralichthys dentatus*, and weakfish *Cynoscion regalis*) and three benthivores (Atlantic croaker *Micropogonias undulatus*, white perch *Morone americana*, and spot *Leiostomus xanthurus*), which account for a combined total of nearly 80% of the fish fauna captured by a benthic trawl survey (Buchheister *et al.*, 2013).

This study provides valuable, foundational information on the status of numerous forage groups in Chesapeake Bay and addresses some of the principal research recommendations identified during the Forage Workshop (Ihde *et al.*, 2015). Specifically, we conducted a coordinated analysis of extant data and developed a suite of indicators that can support EAFM in Chesapeake Bay.

3. Methods

3.1. Objective 1 (Forage Indicators) Methods

We developed four types of forage indicators, each of which provides a different perspective on the status of forage in Chesapeake Bay (Table 1). The four indicator types are 1) relative prey abundance or biomass, 2) diet-based indices, 3) prey-predator ratios, and 4) consumption-prey ratios. These indicators were included in the list of candidate metrics recommended by the recent Forage Workshop (Ihde *et al.*, 2015). Details describing each indicator type are provided below. All indicators were obtained or calculated using data from existing monitoring surveys operated by the states or Chesapeake Bay Program. These surveys represent long-standing, reliable monitoring programs that use standardized protocols and that have broad spatial coverage in Chesapeake Bay and its tributaries. All indicators were developed at the annual scale, relying on time periods and spatial locations of reliable capture, largely following protocols described for existing trawl and seine surveys (Bonzek *et al.*, 2011; Tuckey and Fabrizio, 2012).

3.1.1. Relative Abundance and Biomass Indicators

3.1.1.1. Data Sources

Indices of relative forage fish abundance were obtained or developed for five surveys in the Chesapeake Bay that use various gears and sample multiple regions, seasons, and years (Table 2). The surveys used in our analyses were selected based on two criteria: 1) must be fishery independent and 2) must have been conducted for 10 yrs or longer. The longest survey in our analyses was the 55-year MD DNR Juvenile Striped Bass Index seine survey (MJS), 1959-2013. The MJS was conducted in four tributary systems (Head of Bay, Choptank, Nanticoke, and Potomac) in the Maryland portion of Chesapeake Bay (http://dnr2.maryland.gov/fisheries/Pages/striped-bass/juvenile-index.aspx). We analyzed 39 years of index-value data, 1968-73 & 1980-2012, from the Virginia Institute of Marine Science (VIMS) Juvenile Striped Bass Seine Survey (VJS) that was conducted in tributaries of the Virginia portion of Chesapeake Bay (http://hjort.cbl.umces.edu/chesfims.html). Twenty-seven years of Atlantic menhaden (*Brevoortia tyrannus*) annual indices, 1988-2014, were obtained from the VIMS Juvenile Fish and Blue Crab Trawl Survey (VJT) that is conducted in the main-stem and in tributaries of the Virginia portion of Chesapeake Bay (http://www.vims.edu/research/departments/fisheries/programs/juvenile_surveys/index.php). Our analyses included 26 years, 1989-2014, of data from the MD DNR Blue Crab Summer Trawl (MST) survey that is conducted in six systems: Chester, Patuxent, and Choptank rivers and Eastern Bay, Tangier Sound, and Pocomoke Sound (http://dnr2.maryland.gov/fisheries/Pages/blue-crab/trawl.aspx). The shortest survey used in in this study was 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 (http://hjort.cbl.umces.edu/chesfims.html). Both the TIES and CHESFIMS (CFT, collectively) surveys were conducted in the mainstem of Chesapeake Bay from near the bay mouth to the upper bay.

Metrics of benthic invertebrate biomass were obtained from surveys in the mainstem and in tributaries of the Chesapeake Bay's Maryland and Virginia regions; we collectively refer to the surveys as the Chesapeake Bay Benthic Monitoring Survey (CBMS) (http://www.baybenthos.versar.com/). These data contained measures of ash-free dry weight that catalog benthic invertebrate species for a period of 20 years, 1995-2014, in July, August, and September of each year.

3.1.1.2. Calculation of indicators

Indicators of relative forage abundance or biomass were developed using a multi-stage approach to integrate information from multiple surveys. First, survey-specific indices were developed or obtained for each species. Second, prey-specific indices were developed by pooling information across multiple surveys using a hierarchical Bayesian approach developed by Conn (2010). Third, the prey-specific indices were combined based on functional prey groups (pelagic fishes, demersal fishes, and benthic invertebrates) using biomass-weighted averages to generate more general forage indices of aggregate prey groups.

Indices of relative, annual young-of-the-year (YOY) forage fish abundance and coefficients of variation (CV) were provided by Drs. Mary Fabrizio and Troy Tuckey at VIMS for the VJS and VJT surveys. These measures of abundance were calculated as random stratified geometric means. Delta-lognormal generalized linear models (GLM) were applied to generate annual indices of abundance from the raw data for the remaining three surveys in our analyses. The delta-lognormal method estimates the probability of a non-zero occurrence, using a binomial distribution, and the positive catch rate independently (Maunder and Punt, 2004). The condition of a positive occurrence must be met before the positive index is formulated, using a lognormal distribution in our procedure. A seasonal effect was accounted for in each delta-lognormal GLM by including sampling month as a factor. Months with <2% positive observations were excluded from the index calculation to prevent convergence issues. Jack-knife estimates of error (CV and standard error, SE) were computed for each index. Of the three surveys for which we were able to obtain raw data, there were sufficient data from at least one or more of the surveys to generate delta-lognormal GLM annual indices of abundance for Atlantic menhaden, bay anchovy (*Anchoa mitchilli*), alewife (*Alosa pseudoharengus*), blueback herring (*Alosa aestivalis*), Atlantic silverside (*Menidia menidia*), Atlantic croaker, spot, and weakfish (Table 2).

For each forage fish species, a single index of abundance was calculated by combining survey indices using Conn's (2010) Bayesian hierarchical model. Conn (2010) developed this analytical approach to generate a single time series of relative abundance from multiple, noisy abundance indices. The method assumes that each survey index measures the same quantity (i.e., relative fish abundance), but each index has a different measure of process error estimated that could be caused for example by differences in catchability, spatial distribution, or gear selectivity (Conn, 2010). For each species index, we excluded surveys whose time series were missing 10% or more of the annual indices (due to null catches). The hierarchical index for each species was developed using multiple surveys; however, blueback herring was an exception because only one survey (MJS) met our criterion for inclusion. Hierarchical indices of abundance from the Conn (2010) approach are scaled to have a mean of one and thus are suitable for direct comparison among species. The hierarchical indices of forage fish abundance were included in a correlation analysis across species to identify similarities in annual trends.

The species-level data for benthic invertebrates were pooled into two broader groups: bivalves and polychaetes. Indices for crustacean invertebrates (e.g., mysids, sand shrimp, mantis shrimp) could not be reliably estimated from the survey data because these taxa are not sampled effectively by the survey gear. Given the expansive sampling domain for the benthic survey, the data were grouped into seven spatial 'regions': lower, mid, and upper mainstem; and lower and upper tributaries; and east-middle and west-middle tributaries. Delta-lognormal GLMs were used to estimate relative annual indices of biomass for each pooled benthic group. Season (month) and region were accounted for by including them as factors in each model. A jack-knife procedure was used to calculate estimates of error.

In addition to the individual forage-fish species and benthic group indicators we also calculated annual indices for functional prey groups of ecological relevance. These indicators were specified as pelagic, demersal, and benthic prey groups. For the pelagic prey group, we pooled Atlantic menhaden and bay anchovy hierarchical indices into a biomass-weighted mean index. Each index was weighted adjusted by relative biomass (Atlantic menhaden: 0.60; anchovy: 0.40), based on modeled total biomass for each species obtained from the Chesapeake Bay Fisheries Ecosystem Model (CBFEM) (Christensen *et al.*, 2009). The demersal prey group was also a biomass-weighted mean index for YOY Atlantic croaker, spot, and weakfish. Atlantic croaker and spot had a relative biomass weight of 0.39 and weakfish a weight of 0.22, based on the CBFEM (Christensen *et al.*, 2009). Model-based biomass estimates from the CBFEM were used in the absence of direct bay-wide biomass estimates for each species. Unlike the fish species, the indices for the polychaete and bivalve benthic groups were based on biomass. For this reason, rather than calculating a biomass-weighted benthic prey index we estimated a Delta-lognornal GLM annual index using benthic group as a factor in the model. This pooled benthic index of abundance was scaled to have a mean of one for consistency with the methods used with the other functional prey group indices.

3.1.2. Diet-based indicators

Previous work conducted in Chesapeake Bay (Buchheister and Latour, 2016) demonstrated the utility of using predator diet data to infer patterns of prey availability for prey groups for which there is little monitoring information. As opportunistic feeders, the average mass and occurrence of prey found in the stomach of a given predator can be an indicator of relative prey availability. For this study, we followed the methods detailed in Buchheister and Latour (2016) to calculate diet-based prey indices. The authors provide details of their methodology; we provide a synopsis here.

All diet data were obtained from the ChesMMAP trawl survey. Details of the ChesMMAP diet sampling are provided below in the methods for Objective 2 and in ChesMMAP survey reports (e.g., Bonzek *et al.*, 2008). We focused on analyzing diets of 12 predator species for which there were sufficient numbers of stomach samples. The predators were Atlantic croaker, clearnose skate *Raja eglanteria*, kingfish *Menticirrhus spp*., Northern puffer *Sphoeroides maculatus*, Northern searobin *Prionotus carolinus*, scup *Stenotomus chrysops*, spot, spotted hake *Urophycis regia*, striped bass, summer flounder, weakfish, and white perch. The predators represent a range of different body morphologies, feeding modes, preferred habitats, and life histories that combine to provide diverse and comprehensive perspectives on the consumed prey. We focused on 6 prey groups for this analysis: 1) mysid shrimp (primarily *Neomysis americana*), 2) bay anchovy (*Anchoa mitchilli*, with minor contribution by *Anchoa hepsetus*), 3) bivalves (dominant species included *Ensis directus*, *Gemma gemma*, *Macoma spp*., *Mercenaria mercenaria*, *Mya arenaria*, and *Tagelus plebeius*), 4) polychaete worms (including families Capitellidae, Chaetopteridae, Glyceridae, Maldanidae, Nereidae, Pectinariidae, Terebellidae), 5) mantis shrimp (*Squilla empusa*), and 6) sand shrimp (*Crangon septemspinosa*). Bivalves and polychaetes were analyzed at a coarser taxonomic resolution relative to the other prey groups because identification to genus and species was often not possible (Buchheister and Latour, 2016). Predators of these 6 prey groups were restricted to those that had a minimum frequency of occurrence of 10% and a minimum of 150 stomachs containing the prey. However, the 10% criterion was relaxed to 8% to allow summer flounder to be included as a predator on mantis shrimp because summer flounder had a large number of stomachs (n=235) containing mantis shrimp.

For each combination of predator and prey with sufficient data, a delta-generalized additive mixed model (delta-GAMM) was used to model the consumption of the prey by the predator. This modeling approach allowed us to 1) account for the high occurrence of zero values, 2) standardize the consumption results for the effects of significant covariates, 3) model covariate effects as non-linear functions based on the observed patterns, and 4) account for the non-independence of predator fishes that were captured in the same station. The statistical model was comprised of two parts: the "binomial" model and the "positive" model. The binomial model estimated the probability that a stomach contained the prey of interest using a GAMM with a binomial distribution and a logit link. The positive model excluded all zeros and modeled the natural log-transformed biomass of prey consumed using a GAMM with a Gaussian distribution and an identity link. Both models took the form:

$$Y_{ij} = \alpha + \beta(YR_i) + \mathrm{f}_1(L_i) + \mathrm{f}_2(LA_i) + \mathrm{f}_3(T_i) + \mathrm{f}_4(D_i) + b_j + \varepsilon_{ij}$$

where Y is the response variable for either the binomial or positive model. For the binomial model, Y_{ij} = logit(p_{ij}) = log(p_{ij}/(1-p_{ij})), where p_{ij} is the expected probability that fish *i* from station *j* contains the prey of interest. For the positive model, Y_{ij} = log(μ_{ij}), where μ_{ij} is the expected mass (in g) of a prey group in the stomach of fish *i* from station *j*. In this equation, α is the overall intercept, β is a vector of parametric effects for the categorical year (*YR*) factor, and $\mathrm{f}_{1\text{-}4}$ are smoothing functions for each covariate (Wood, 2006; Zuur *et al.*, 2009). The continuous covariates included predator length (*L*) in mm, latitude (*LA*) in decimal degrees, water temperature (*T*) in °C, and water depth (*D*) in m. The b_j term is the independent and identically distributed random station effect which is assumed to be normally distributed with mean of zero and variance of σ_b^2. The residual error ε_{ij} for each predator fish and station was assumed to be normally distributed with a mean of zero and variance of σ_ε^2 (Wood, 2006; Zuur *et al.*, 2009).

GAMMs were fitted to all of the predator-prey combinations. Models with all possible combinations of the continuous covariates (*L*, *LA*, *T*, and *D*) were fitted and the best fixed effects structure was determined using Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002). Year was retained in all models to generate the desired annual indices. Due to low sample sizes of stomachs, some years were excluded for certain predator-prey combinations.

Year-specific, diet-based indices were developed for each predator-prey combination using two approaches. First, an index of mean prey mass consumed by an individual predator was calculated by multiplying the estimates of both the binomial and positive models together. This value was calculated as $C_y = p_y \times \mu_y$, where p_y is the expected probability that a predator from year *y* consumed a given prey, and μ_y is the expected mass of the prey in a predator's stomach in year *y*. Second, an index of the occurrence probability of a prey in the stomach of a predator was taken to be the estimate p_y. All estimates were standardized for predator length, latitude, depth, and water temperature using the predator-specific means for each covariate in the statistical models.

3.1.3. Prey to predator ratios

Prey to predator ratios (PPR) were calculated by dividing a prey abundance index by a predator abundance index and then scaling the indicator to its mean. Methods for developing the prey indices are described in section 3.1.1. Random-stratified geometric mean annual indices of predator abundance were generated for six species (striped bass, Atlantic croaker, summer flounder, weakfish, spot, and white perch) from the CHESMMAP survey (2002-2013). Recognizing that diets of predator fishes during earlier life stages differ from the diets in later stages for most of these species (Buchheister and Latour, 2015), we excluded the youngest age classes of predators from the calculation of the predator abundance indices. Specifically, we only included age-2+ striped bass and age 1+ spot, Atlantic croaker, summer flounder, and weakfish in the predator index calculations. All ages of white perch were retained given their more consistent diet at the ages and sizes sampled by the gear (Buchheister and Latour, 2015). PPR indices were calculated only for taxa that commonly have trophic interactions based on the diet analyses and consumption profiles conducted for this study. For striped bass, we developed PPR indices using Atlantic menhaden, bay anchovy, and the pelagic forage fish indices as prey. Polychaete, bivalve, and benthic forage were the examined prey for Atlantic croaker and white perch PPR indices. Bay anchovy and spot were the prey used for the summer flounder PPR indices. Atlantic menhaden and bay anchovy were the prey used for the weakfish PPR indices, and polychates were the only prey used for the spot PPR index.

3.1.4. Consumption to prey ratios

Consumption to prey ratios (CPR) are an index of predation pressure, and they were calculated as the total consumption of each prey group divided by each prey group's abundance, then scaling this relationship to its mean. The total, population-scale consumption estimate was obtained using the methods described in section 3.2, summing across the six fish predators. The prey index methodology is described in section 3.1.1. CPR indices were calculated for seven prey groups (YOY Atlantic menhaden, bay anchovy, YOY Atlantic croaker, YOY spot, YOY weakfish, benthic polychaetes, and bivalves) from 2002-2014.

3.2. Objective 2 (Consumption Profiles) Methods

3.2.1. Data sources

Estimates of consumption relied on data collected by the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP). Details on the survey methodology and protocols are reported by Bonzek et al. (2011). Briefly, the survey relies on a random-stratified design, sampling in five latitudinal regions of the bay and in three depth strata. 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 bottom trawl to collect late juvenile and adult fishes. 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. Subsamples are selected for stomach removals and gut-content analysis in the laboratory. In the laboratory, stomach contents are identified to the lowest possible taxon, enumerated, and weighed.

Each predator species was divided into multiple size classes (designated as S: small, M: medium, L: large) to account for ontogenetic shifts in diets (Buchheister and Latour, 2015) and differences in presumed sampling-gear selectivity by size (Table 3). Information on gear selectivity by size is not available for the survey; therefore, we defined the S size class cutoff as the mode of the length-frequency distribution (rounded to the nearest 5 cm) for each predator (Figure 1). 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 cutoffs for the large size classes were selected to balance the number of available samples among the M and L size classes and to approximate the sizes where dietary breaks are the strongest (Buchheister and Latour, 2015).

3.2.2. Calculations

Mean weight of stomach contents – The mean mass of stomach contents (in grams) was calculated for each predator size class at each sampled station. The mean was then calculated across stations, by weighting each station and size-class combination by the number of fish caught in the tow. Any stomachs determined to be empty either in the field or in the lab were included in the calculation. If fewer than 30 stomachs were sampled in a year for a given size class of a predator (which occurred in 10% of all years), the mean stomach content weight across years was used in order to minimize error and excessive variability caused by low sample sizes. The global mean was also used for spot from 2002-2007 due to inconsistent analysis of stomach samples during this time period. 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, gravimetric diet composition (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 hauls containing the predator, n_h = the number of individuals of the predator collected at sampling site *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 site *h*; and m_{hk} = the total mass of prey group *k* occurring in the predator stomachs from sampling site *h*. This cluster sampling estimator accounts for the lack of independence among sampled predators from the same station, and it provides a more reliable description of the diet at the population level (by weighting by the catch).

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 were defined as: bay anchovy, YOY Atlantic menhaden, mysids, bivalves, polychaetes, YOY spot, YOY croaker, YOY weakfish, crustaceans, and “other” prey. Differences in taxonomic resolution of prey groups was in part a logistical limitation of diet analysis, where identification of polychaetes and bivalves to the species or genus level is often not possible due to digestion and a lack of identifiable hard parts.

Consumption rates – Daily per capita consumption (c) was estimated using a gastric evacuation rate model (Eggers, 1977; Elliott and Persson, 1978). This method is of intermediate complexity relative to alternative approaches such as a simple % body weight method and a more complex bioenergetics model that requires substantial laboratory research. 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) commonly used in similar studies (Overholtz *et al.*, 2000). 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 annual 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 (ie "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 g to mt. 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, annual consumption was calculated as the sum of the consumption for two semi-year (ie 6-month) periods. Use of a 6-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 6 month period in which predator abundances are highest (Table 3), based on ChesMMAP data and historical ChesMMAP reporting (Bonzek *et al.*, 2008).

Estimates for trawl-survey catchability are not currently available to adjust (i.e., scale up) the minimum swept-area estimates of abundance. Catchability for each predator and size class would largely be a function of sampling gear efficiency for each predator and size selectivity for each predator's size class. In the absence of this information, we conducted sensitivity analyses exploring the effect of different size-selectivity parameters for S and L size classes (25, 50, and 100%), assuming a selection of 1 for M-sized fish. Generally, selectivity parameters had a larger effect on the magnitude of consumption than on the interannual patterns of consumption, and the relative importance of prey types was not strongly affected.

4. Results

4.1. Objective 1 Results

4.1.1. Forage abundance indices

Each of the eight forage species included in the hierarchical-index analysis experienced considerable year-to-year variability in abundance, but identifiable patterns were observed (Figure 2). Atlantic menhaden and spot both experienced a period of relatively high abundance from 1970 to 1995. Their annual abundances were positively correlated (ρ = 0.74; Figure 3). Atlantic croaker and weakfish abundances also were positively correlated (ρ = 0.70; Figure 3) being relatively abundant in recent years. Abundance of bay anchovy was relatively low and stable in recent years following a decline in the mid-1990s.

For the forage fishes, considerable variability was observed among survey abundances in years when surveys overlapped (Figure 4). The hierarchical index tended to resemble the trend and pattern of abundances in the longest survey included in its calculation, but in years when multiple surveys overlapped, observable deviations often indicated influence of other surveys (Figure 4). For each species, process errors, reflective of error from catchability, spatial distribution, or gear selectivity for example, tended to be consistent among surveys, except that the highest errors occurred in the shortest surveys in the analysis (e.g., CFT), indicative of either higher variability or incongruous patterns with the other time series (Figure 5).

For benthic bivalves and polychaetes, the delta-lognormal GLM indices of biomass were generally less variable during the 18-yr time series than were the indices for YOY forage fishes (Figure 6). The peak biomass of bivalves occurred in 2009 but that peak was only 1.5 times higher than the time-series mean. Low variability was observed throughout the 18-yr time series for the polychaete and overall benthic indices of biomass (Figure 6).

4.1.2. Diet-based indices

Diet-based indices of consumed prey biomass exhibited similarities across diverse predator species. For example, consumption of mysids by 5 of the 7 fish predators demonstrated a distinct peak in mysid biomass consumed per individual predator in 2003 followed by a decline over the course of the time series (Figure 7a); only striped bass and spotted hake, which have greater residence in the bay during colder months, did not show this pattern. Diet-based indices for bay anchovy tended to increase over the time series, along with interannual variability in its consumption (Figure 7b). Indices for bivalves had a coherent peak in 2008 shared by several predators (despite different preferred habitats and life histories), and they were also higher towards the end of the time series (Figure 7c). For other prey groups (polychaetes, sand shrimp, and mantis shrimp), consumption patterns tended to be less coherent across predators, with the following primary exceptions: 2010 was a strong year for the polychaete index (shared by Atlantic croaker, spot, white perch, kingfish, and scup); 2003 was a strong year for the sand shrimp index (shared by kingfish, summer flounder, and clearnose skate); and 2002 was a strong year for mantis shrimp (shared by clearnose skate and summer flounder) (Figure 7d-f).

Patterns in probability of prey occurrence in predator stomachs highlighted differences among years, predators, and prey. Occurrence of mysids exhibited the strongest coherent pattern across predators, with all but one predator (spotted hake) having a strong decline in mysid occurrence over the years (Figure 8a). For example, mysid occurrence in summer flounder stomachs peaked at nearly 100% in 2003 and declined to ~18% by 2014. And, 2003 was indicative of high probability of occurrence of sand shrimp, noted for several predators (Figure 8e). For a given prey (e.g., bay anchovy, bivalve, polychaete, and mantis shrimp), strong differences in probability of occurrence were detected across predator species, apparently caused by different feeding behaviors and, potentially, prey preferences. However, differences among the predators was also influenced by the size of predators used to standardize the delta GAMM models. For example, if larger summer flounder had been used for the standardization, the probability level of mysid occurrence would decline while that of bay anchovy would increase, but the interannual patterns and trends would remain identical for the predator.

4.1.3. Prey to predator ratio (PPR) indices

Ratios of prey to predator abundances for each of the six fish predators and corresponding prey were variable within the 13 year time-series with relatively large confidence intervals (Figure 9). Peaks in PPR indices were driven by high prey abundances or low predator abundance. For example, several peaks in PPR for striped bass resulted from high abundance of YOY Atlantic menhaden prey in 2005, 2009, and 2010 and high abundance of bay anchovy prey in 2012 when striped bass abundance was relatively stable (Figure 9, Figure 10). These increases in prey abundance translated into PPR being ~2.4 and 2.8 times greater than the overall mean during those years (Figure 9). Dominant patterns in PPR indices for other predators were largely influenced by changes in predator abundance. For Atlantic croaker, PPR indices with polychaete, bivalve, and benthic prey index were 27, 11, and 18 times greater, respectively, than the mean PPR index for each prior to 2008 (Figure 9), due to the dramatic decline in Atlantic croaker abundance following 2008 (Figure 10). Similarly, weakfish, summer flounder, and spot also experienced declines in abundance during the time series with strong effects on PPR indices for their respective prey. For weakfish, the peak PPR indices were 32 and 72 times greater for menhaden and anchovy prey, respectively, than the mean value prior to 2005, the year when weakfish abundance declined. Summer flounder PPR indices peaked in 2012 with values 57 times (anchovy) and 25 times (spot) greater than the mean index for each prior to 2006, the year when summer flounder abundance declined. PPR indices for white perch remained relatively stable over the time series except for slightly higher values in 2002 and 2003 when white perch abundance was relatively low.

4.1.4. Consumption to prey ratio (CPR) indices

CPR indices were variable over the 13 year time series, and the major patterns were more strongly driven by changes in consumption of prey as opposed to prey abundance. For example, the high CPR index for Atlantic menhaden in 2006 (Figure 11) resulted from notably high consumption of YOY Atlantic menhaden in that year (see Objective 2 results; Figure 23) relative to overall YOY Atlantic menhaden abundance (Figure 2), indicating relatively high predation pressure on YOY Atlantic menhaden in 2006 by the six predator fishes in our analysis. The CPR indices for YOY spot and polychaetes also peaked in that same year (Figure 11) due to high overall demand by an abundant predator suite (e.g., see Objective 2 results, Figure 24). The peak in the bay anchovy CPR index in 2002 was an example of the CPR index being influenced by low prey abundance as opposed to high consumption by predators, but the CPR index for bay anchovy remained relatively stable thereafter (Figure 11). CPR indices for bay anchovy, YOY weakfish, polychaetes, and bivalves were relatively lower towards the end of the time series (Figure 11), corresponding to lower total consumption by predators that was driven by lower predator abundance (see Objective 2 results).

4.2. Objective 2 Results

4.2.1. Predator-specific consumption patterns

Striped Bass

The mean stomach contents of striped bass were relatively consistent over the time series. Mean contents were, on average, 20-30 g higher in L individuals compared to S individuals (Figure 12a). Daily per capita consumption patterns for the six-month index period (Figure 12b) were identical to mean stomach contents, but the magnitude was different because the stomach evacuation rate model took into account the slower digestion of prey in the cold index months. Striped bass abundances did not indicate a trend over time (Figure 12c), and abundances of M striped bass tended to be greater than abundances of the other size classes, except in 2005 and 2012 when S striped bass (primarily ages 1 and 2) were more abundant due to strong recruitment events (Figure 12c). Population-level consumption for the six-month index period, tended to be dominated by M striped bass, primarily due to their greater abundances, but the observed peaks in consumption in 2006, 2008 and 2014 were driven mostly by greater stomach contents (Figure 12d). Population consumption by S striped bass was of low magnitude, except during the strong recruitment years. Large striped bass had levels of population consumption that were intermediate between the L and S individuals (Figure 12d).

The total annual consumption by striped bass over the index and non-index seasons fluctuated around 500 mt, but reached a value of more than 1600 mt in 2006 (Figure 13a), due primarily to consumption by M and L striped bass (Figure 12). Overall, YOY Atlantic menhaden and bay anchovy were the two most important prey items, each accounting for up to 40% of the total annual consumption, depending on the year (Figure 13b).

Summer Flounder

The stomach contents of summer flounder were also relatively consistent over time, aside from a peak in 2007 for L fish. The S, M, and L fish contained, on average, approximately 0.4, 1.2, and 4.5 g of stomach contents, respectively (Figure 14a). Daily per capita consumption patterns and magnitudes for the six-month index period (Figure 14b) were nearly identical to mean stomach contents. The magnitudes of stomach contents and daily per capita consumption were similar (unlike for striped bass as shown in Figure 12) because gut evacuation occurs more rapidly at the warmer summer and fall temperatures in the index period. Summer flounder abundances were of similar magnitude across size classes, with all sizes declining after 2007 (Figure 14c). The six-month scaled population consumption highlighted the greater consumption by L summer flounder and the decline in consumption in the later years (Figure 14d).

Total annual consumption, considering the index and non-index periods, by all summer flounder size classes peaked near 600 mt and declined to low levels by 2012 (Figure 15a). Relative contribution of prey types through time was largely consistent and relatively well distributed among prey types (Figure

15b). The apparent increased importance of YOY spot in recent years was biased by the low sample sizes for diet analyses.

Atlantic Croaker

The mean stomach contents and per capita consumption of S Atlantic croaker was stable over time (0.18 g), whereas M Atlantic croaker mean stomach contents declined through time (Figure 16a,b). Abundance of M Atlantic croaker showed a distinct shift to lower numbers following 2007, whereas the abundance of S Atlantic croaker remained stable, aside from strong year classes in 2007 and 2013 (Figure 16c). The six-month scaled population consumption highlighted the large consumptive decline by M Atlantic croaker, falling below the low values of the S Atlantic croakers in the most recent years (Figure 16d).

Total annual consumption by Atlantic croaker fluctuated between 2500 and nearly 10,000 mt from 2002 to 2007 before dropping to values as low as 127 mt in 2012 (Figure 17a). Polychaetes often comprised >50% of the annual consumption, with bivalves and other prey also being periodically important (Figure 17b). Interestingly, mysids contributed substantially to consumption in 2005 (40%) and moderately in 2003 (18%), despite Atlantic croaker typically focusing on benthic infauna (e.g., polychaetes and bivalves) as opposed to small zooplankton like mysids.

White Perch

During the 6-month index period, white perch had stable but low mean stomach contents (<0.9 g) and per capita consumption (<0.25 g) (Figure 18a,b). Abundance of S white perch was typically greater than for M fish, and neither group showed trends or shifts in abundance through the time series (Figure 18c). Six-month scaled population consumption was similar between size classes and stable through time (Figure 18d).

Despite high abundances, total annual white perch consumption was relatively small, typically ranging from 200-700 mt with no obvious trend over time (Figure 19a). Polychaetes and crustaceans were the two most significant prey groups consumed, accounting for 5-60% and 12-45%, respectively, of total consumption, depending on the year (Figure 19b).

The general pattern for the six fish predators was that the small size class accounted for a relatively small proportion of the total consumption, with white perch being the only exception (small white perch accounted for ~40% of total white perch consumption) (Figure 20a). For the two predators with a large size class (striped bass and summer flounder), the large size class accounted for appreciable fractions of total consumption, as much as ~70% for summer flounder (Figure 20a). Most of the consumption by the 6 predators occurred during their 6-month index periods of higher abundance in Chesapeake Bay (Figure 20b). Here, the exceptions were striped bass and white perch whose non-index period consumption accounted for up to 75% in the case of white perch and >40% in the case of striped bass (Figure 20b). For those two species, their non-index period occurs during the warmer summer months when consumption rates are higher due to higher temperatures, but it also is true that striped bass and white perch maintain relatively higher abundances throughout the year in the Bay compared to the other more seasonal predators.

4.2.2. Patterns in total consumption across predators

The individual predator consumptions were summed to evaluate the combined consumptive pressure of predator groups in the Chesapeake Bay mainstem. Piscivores (i.e., striped bass, summer flounder, and weakfish) showed a nearly three-fold decline in total consumption Figure 21a. Relative contributions of YOY Atlantic menhaden and bay anchovy to consumption by piscivores increased while relative contribution of mysids to consumption by piscivores decreased during the time series (Figure 21b). Benthivores (i.e., Atlantic croaker, white perch, and spot) exhibited an even more drastic decline (> ten-fold) in total consumption, although the relative contributions of particular prey varied little. The combined consumption of all six predators declined by nearly an order of magnitude from values as high as 13,000 mt in 2002 to 1400 mt in 2014 (Figure 21a). The similarity in consumption patterns of benthivores and all predators seen in Figure 21 reflects the overall higher consumption by benthivores relative to piscivores. However, from 2008-2014, the amounts consumed by piscivores and benthivores has been similar (Figure 21a). That shift in total consumption by all predators after 2007 (Figure 21a) was driven mostly by the trends in Atlantic croaker consumption (Figure 17a). Relative contributions of prey groups to total consumption by the six predators remained similar over the time series, with polychaetes being most important overall, although relative contributions of YOY Atlantic menhaden and bay anchovy increased in response to patterns in consumption by piscivores (Figure 21b). Periodically, particular prey had pulses of increased importance, for example mysids in 2003 and 2005, and YOY spot in 2010 (Figure 21b).

4.2.3. Patterns in predatory removals of key prey groups

Estimates of the combined, total prey removals by the six predators declined after 2007 (Figure 22a). The decline in Atlantic croaker consumption was particularly notable. During the 13-yr time series, the relative contribution of Atlantic croaker to total consumption declined from nearly 75% to ~10% of the total. In that period, relative contribution to consumption by striped bass increased from near zero to 63% (Figure 22b).

Consumption by striped bass was a relatively important contribution to total consumption of YOY Atlantic menhaden and bay anchovy, with a dramatic increase in relative contribution of striped bass to bay anchovy consumption from <25% prior to 2011 to ~90% by 2014 (Figure 23). YOY Atlantic menhaden were primarily consumed by striped bass, although in earlier years (2002-2005) weakfish also consumed a large fraction (37-64%; Figure 23). Consumption of mysids by five predators (excluding Atlantic croaker) declined steeply after 2006 to near zero in 2014 (Figure 23).

Consumption of three key benthic invertebrate groups (bivalves, crustaceans, and polychaetes) demonstrate the major effect that the decline in Atlantic croaker consumption has had on removals of these benthic prey by the six predators (Figure 24). Magnitudes of removals for the three benthic prey groups varied interannually more than 10-fold (Figure 24a); the declining consumption by Atlantic croaker had the largest effect on consumption patterns. The relative contributions by Atlantic croaker to crustacean and polychaete removals also declined substantially over the time series (Figure 24b).

5. Discussion

We developed several complementary forage indicators to examine abundance patterns in 13 prey types and consumption by six biomass-dominant fish predators in Chesapeake Bay. Examination of the many indicators in aggregate yields some significant conclusions. First, abundances of some of the forage species with the longest time series (e.g., YOY Atlantic menhaden, YOY spot, and silversides) exhibited correlated shifts on decadal scales that could be indicative of alternative ecosystem states or broad-scale environmental drivers. Second, although forage indices remained relatively stable during the past 13 years, results indicate that total consumption by the six predators declined, predominantly due to decreases in predator abundances, especially Atlantic croaker. Third, the development of multiple forage indicators and analyses highlighted different perspectives of forage that would not have been adequately captured by relative prey abundance trends alone. A suite of metrics is advantageous in untangling complex interactions in fisheries systems where prey, predators, and environmental conditions are changing dynamically to significantly affect predator and prey relationships. Fourth, indicator trends had a high degree of interannual variability that likely contributes to the observed opportunistic feeding by many predator fish species and complicates management utility. These four synthetic conclusions pertaining to 1) multispecies shifts, 2) declines in predatory consumption, 3) suite of metrics, and 4) interannual variability are discussed below, followed by comments on sources of uncertainty and the utility of indicators for management.

5.1. Multispecies shifts

Several forage species exhibited long-term changes in abundance that were correlated with one another. For example, the period of high YOY Atlantic menhaden and YOY spot abundance in the 1970s and 1980s has been documented by other authors who analyzed some of the same data sets (Wingate and Secor, 2008; Wood and Austin, 2009; Buchheister *et al.*, 2016). Wood and Austin (2010) linked the correlated patterns of recruitment (YOY abundances) for fish species assemblages to life history traits; specifically, coastal shelf-spawning species (e.g., Atlantic menhaden, spot) had correlated recruitments that were inversely related to recruitments of anadromous species (e.g., white perch and striped bass). The mechanisms driving such decadal-scale patterns remain unclear, but studies suggest potential links to climate (Wood and Austin, 2009; Buchheister *et al.*, 2016) and environmental factors, particularly during winter (Wingate and Secor, 2008).

5.2. Declines in predator abundance and consumption

Two, related and striking conclusions from our analyses were the substantial declines in abundance and prey consumption by multiple predators (Atlantic croaker, summer flounder, weakfish, and spot). Atlantic croaker, in particular, was responsible for a large but declining fraction of the total consumption of prey in Chesapeake Bay due to large declines in its abundance after 2007. These declines may be related to shifts in distribution of the coastwide population. Atlantic croaker have been shown to have decadal-scale periods of population outbursts along the coast, in which the population distribution expands to more northerly states (e.g., NJ) during periods of warmer winters due to enhanced overwinter survival (Hare and Able, 2007). For example, commercial landings of Atlantic croaker were particularly high in MD, VA, and NJ in the 1970s and again in the 1990s to the early 2000s (Hare and Able, 2007). Although the Atlantic croaker stock assessment (ASMFC, 2010) estimated that biomass increased rapidly from 1990 to 2008 (which was the last year in the assessment), coast-wide landings and the multiple trawl-survey indices for Atlantic croaker have been declining from the mid-2000s by as much as 50% (Figure 16; A. Buchheister, unpublished data), suggesting that the last population outburst may have ended.

Declines in abundance and total consumption of forage taxa from 2002-2014 must be viewed within a broader temporal context that includes substantial changes in predator abundances. Striped bass and summer flounder experienced stock recoveries from low levels in recent decades (NEFSC, 2013a, 2013b), whereas weakfish declined dramatically since the 1980s. Thus, our 13-yr time period of consumption estimates are representative of the current ecosystem state, but may not be representative of historical conditions when predator and prey abundances could have been vastly different.

Any large-scale shifts in stock biomass or distribution of Atlantic croaker or other predator species could have large impacts on predator-prey and forage dynamics in Chesapeake Bay. For example, the decline in Atlantic croaker abundance and its large consumptive demand on the benthos could potentially release prey from predation pressure and alleviate competition among other benthivores (for example, spot and white perch). Although weights of stomach contents could be a metric for assessing density-dependent benefits of reduced Atlantic croaker abundance, no such trends were apparent in mean stomach contents of the three benthivores species. The decline in Atlantic croaker stomach contents through time appears to be primarily related to the decrease in mean sizes of Atlantic croaker. Changes to food web structure and energy flows are hard to predict, but the order-of-magnitude decline of medium-sized Atlantic croaker abundance (Figure 16) certainly had a substantial effect on the predatory removals of polychaetes and bivalves in the Bay.

5.3. Suite of metrics

As we had anticipated, developing a suite of forage indicators was important to provide different perspectives on forage and predator-prey dynamics that would not have been possible with a single indicator. For example, some indicators were useful to identify years or periods of increased prey availability, while other indicators and analyses identified periods of lower predator abundance and lower consumptive demand. Considered holistically, our suite of indicators was successful in capturing complex patterns in system-wide biotic conditions that could not have been achieved using a single indicator approach.

Development of the four forage indicators and the consumption profiles focused on 2002-2014 as a case study period, where ChesMMAP data allowed for calculation of the diet and consumption-related indicators. The lack of historical diet data hinders long-term comparisons of diet-related indicators, but the case study highlighted the value of the more comprehensive approach. PPR indicators potentially are more informative when there is greater contrast in the data set, as was demonstrated by Jim Uphoff and colleagues (MD DNR, 2015), who calculated the ratio indicators for striped bass and various prey, showing significant changes associated with striped bass recovery in the Bay. Multiple indicators of forage and predator abundances and predatory consumption will be necessary for monitoring and for informing management, given the complexity of the system and interactions.

5.4. Interannual variability

There was high interannual variability for many indicators, particularly the abundance indicators, highlighting the dynamic nature of the forage base and predator-prey interactions in the bay. The use of multiple metrics can help alleviate some of the challenges to interpretation of predator-prey interactions caused by this variability. Recruitment in many fishes is notoriously variable, fluctuating by an order of magnitude or more due to variability in environmental and ecological conditions (Houde et al., in review). Some years were particularly favorable for availability of certain prey, resulting in "pulses" of prey consumption by predators, as seen for consumption of mysids, bivalves, spot, and sand shrimp. Simulations suggest that such pulses in prey production could theoretically have substantial impacts on predator populations (Buchheister *et al.*, 2015). Variability caused by observation and process errors in fisheries survey sampling can also be substantial if catchability is strongly affected by environmental conditions, spatial changes in distribution, and variability in growth and mortality.

5.5. Sources of uncertainty

We acknowledge that there are different sources of uncertainty that influenced our results, but the analyses provide important insights into trends and patterns. Sources of uncertainty include: differences in catchability among sizes and species for both predators and prey groups; spatiotemporal and environmental effects on measured variables, and general sampling error. To minimize such effects, we used fishery-independent survey data from reliable and relatively long-standing programs. We applied methods developed for dealing with some of these difficulties (e.g., the Bayesian hierarchical analysis for Objective 1). We conducted sensitivity analyses for Objective 2, which indicated that interannual trends in consumption of prey were not particularly sensitive to gear size selectivity of sampled predators. And, we focused our attention on patterns and trends with the strongest signals that would likely be more robust to the different sources of uncertainty. However, care is always needed in interpreting data that can be noisy and influenced by complex technical, environmental, and ecological interactions. Additionally, findings are restricted to the time periods examined, which does not capture dramatic changes in fish populations that have occurred over the past century or even longer periods and may not reveal shifting baselines that could be important in restoration efforts (Jackson *et al.*, 2001; Kemp *et al.*, 2005). The analyses we conducted also highlighted some research needs to reduce uncertainty in multispecies studies in Chesapeake Bay. Specifically, estimation of gear efficiency and size selectivity for the ChesMMAP survey would help to increase precision and accuracy of any future estimates.

It is probable that we underestimated the magnitude of prey consumption, likely due to underestimates in predator abundances and mean stomach contents, but our relative abundance and consumption estimates portray the trends and patterns in Chesapeake Bay. Our estimates of total bay anchovy consumption (0.25-1.25 kmt) were approximately two orders of magnitude lower than estimates of baywide bay anchovy biomass (27-192 kmt) (Jung and Houde, 2004), and we expected that consumption would be a greater fraction of the standing stock, given the high natural mortality of bay anchovy (Newberger and Houde, 1995; Jung and Houde, 2004). Our per capita annual consumption estimates were lower than bioenergetics modeling estimates for striped bass and weakfish by a factor of ~5 (Hartman and Brandt, 1995b). These comparisons suggest that our low estimates are predominantly attributable to 1) underestimates in surveyed predator abundances due to size and gear selectivity, 2) underestimates in mean per capita consumption caused by high frequency of empty stomachs and low mean stomach contents, and 3) lack of sampling of predators in other habitats (e.g., shallow water, midwater, and tributaries) where predators also reside. Given the probable underestimated total consumption, we chose to not make any comparisons of predator consumption to fisheries yields (e.g., for Atlantic menhaden), but instead we focused on relative consumption which we believe to be representative of temporal patterns and trends in the Bay.

5.6. Utility for managers

Our findings provide useful information to managers as they deliberate on approaches for integrating forage considerations into management. For Objective 1, we provide basic information on the interannual patterns and variability in the relative abundance, availability, importance, and predation intensity for key forage taxa and groups. For species monitored by more than one survey, our research integrated information from multiple sources to develop more comprehensive metrics. For some prey groups (e.g., mysids, sand shrimp, mantis shrimp), our results apparently are the longest time series developed for these key forage groups in Chesapeake Bay. The observed similarities in abundance trends of important forage groups was an important outcome of taking a more holistic, multispecies approach to developing forage indicators, including and emphasis on forage assemblages. However, the shifts in YOY abundances of forage fishes and their potential link to climatic or bottom-up drivers raises questions about what historical target levels may be appropriate benchmarks or reference points if these indicators are to be used for management. For example, the high levels of YOY Atlantic menhaden recruitment seen historically may not be achievable now, regardless of management action, if those levels were driven by climate and environmental conditions that no longer prevail.

Although beyond the scope of this project, our forage indicators could be used as a foundation for developing future management target values (i.e. reference points) to inform management decisions (e.g., target levels of forage abundance). Such targets would likely be based on historical levels that are deemed acceptable or desirable, but three difficulties are that 1) historical baselines can shift, potentially caused by factors outside of management control (e.g., climate, environment), 2) the Chesapeake Bay ecosystem is complex and predators often are generalists such that ideal forage conditions may be dynamic, and 3) some of the time series and available survey data sets are not sufficiently long to make inferences about historical conditions and targets. Generally, the forage indicators could have utility as a warning system to identify periods when forage conditions may be unfavorable for managed predators. As highlighted in the Forage Workshop, there are also constraints on what actions managers can undertake to affect the state of the forage base, with the two most likely avenues being fishing regulations on managed species and actions aimed at maintaining or improving forage habitats (Ihde *et al.*, 2015).

For Objective 2, our findings have provided additional information on the most important forage groups for the six predators (at the sizes analyzed). Our analyses identified predators that are likely to have the largest consumption effect on each of the prey groups; for example, our results emphasize the probable importance of a species like Atlantic croaker on the benthos. The analyses can help managers to prioritize prey groups that are most important to predators, which could inform and support decisions on habitat protection or water quality improvements. Fundamentally, the consumption information is also valuable for managers to share with concerned stakeholders to inform them of the relative importance of prey groups that should be conserved in Chesapeake Bay.

5.7. Conclusions

Our findings represent an important, foundational step in the process of assessing the status of forage in Chesapeake Bay. Our analyses address several of the prioritized recommendations from the Forage Workshop and thus help address needs identified by managers, stakeholders, and scientists (Ihde *et al.*, 2015). We strategically integrated data from the most reliable and longstanding fish and forage surveys in the Chesapeake Bay, and we developed a suite of forage indicators to track forage abundance, forage availability, prey importance, and predation intensity. With the PPR indices and the consumption profile analyses, we described relationships between forage trends and predator trends through time. The analyses lend insight into patterns in relative predator demand and forage supply for a 13-year period. The research has improved understanding of forage dynamics and trends in Chesapeake Bay and produced novel information for some prey groups (e.g., mysids, sand shrimp, polychaetes) that previously had received less attention than forage fishes. Interpretation and application of this research is complicated by the dynamic nature of predator-prey interactions in the Bay (which over the decades has experienced dramatic changes in relative abundance of its constituent fauna) and by the sampling uncertainties of the monitoring surveys. Although drivers of the observed changes in prey abundance and consumptive trends remain to be fully explored, this research is a step towards understanding complex dynamics that can lead to better monitoring and management of critical forage groups in Chesapeake Bay.

6. Acknowledgments

We thank the researchers, staff, volunteers, institutions, and funding agencies that are responsible for conducting and supporting the many fisheries-independent surveys that were used in the analyses. We are particularly grateful to RJ Latour, CF Bonzek, and J Gartland for supplying ChesMMAP data; M Fabrizio and T Tuckey for indices from the VIMS trawl and seine surveys; E Durrell for data from the MD DNR seine survey; M Lane for data from the CBP Benthic Survey; TJ Miller for TIES/CHESFIMS data; and C Walstrum for MD DNR summer trawl survey data. We thank TF Ihde for his management and oversight of the project. We thank the Chesapeake Bay Trust and the Chesapeake Bay Program’s Fisheries Goal Implementation Team for funding support.

7. Literature cited

ASMFC. 2010. Atlantic croaker 2010 benchmark stock assessment. Atlantic States Marine Fisheries Commission.

Bonzek, C. F., Gartland, J., and Latour, R. J. 2011. Data collection and analysis in support of single and multispecies stock assessments in Chesapeake Bay: The Chesapeake Bay Multispecies Monitoring and Assessment Program. Report to VA Marine Resources Commission and U.S. Fish & Wildlife Service: 1–155.

Bonzek, C. F., Latour, R. J., and Gartland, J. 2008. Data collection and analysis in support of single and multispecies stock assessments in Chesapeake Bay: The Chesapeake Bay Multispecies Monitoring and Assessment Program. Report to VA Marine Resources Commission: 1–191. Virginia Institute of Marine Science, Gloucester Point, VA.

Buchheister, A., Bonzek, C. F., Gartland, J., and Latour, R. J. 2013. Patterns and drivers of the demersal fish community of Chesapeake Bay. Marine Ecology Progress Series, 481: 161–180.

Buchheister, A., and Latour, R. J. 2015. Diets and trophic guild structure of a diverse fish assemblage in Chesapeake Bay, USA. Journal of Fish Biology, 86: 967–992.

Buchheister, A., and Latour, R. J. 2016. Dynamic trophic linkages in a large estuarine system — support for supply-driven dietary changes using delta generalized additive mixed models. Canadian Journal of Fisheries and Aquatic Sciences, 73:5-17.

Buchheister, A., Miller, T. J., Houde, E. D., Secor, D. H., and Latour, R. J. 2016. Spatial and temporal dynamics of Atlantic menhaden (*Brevoortia tyrannus*) recruitment in the Northwest Atlantic Ocean. ICES Journal of Marine Science. doi: 10.1093/icesjms/fsv260.

Buchheister, A., Wilberg, M. J., Miller, T. J., and Latour, R. J. 2015. Simulating bottom-up effects on predator productivity and consequences for the rebuilding timeline of a depleted population. Ecological Modelling, 311: 48–62.

Burnham, K. P., and Anderson, D. R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York, New York. 488 pp.

Christensen, V., Beattie, A., Buchanan, C., Ma, H., Martell, S. J. D., Latour, R. J., Preikshot, D., et al. 2009. Fisheries ecosystem model of the Chesapeake Bay: methodology, parameterization, and model exploration. U.S. Department of Commerce, NOAA Technical Memorandum, NMFS-F/SPO: 1–146. U.S. Department of Commerce.

Conn, P. B. 2010. Hierarchical analysis of multiple noisy abundance indices. Canadian Journal of Fisheries and Aquatic Sciences, 67: 108–120.

Durbin, E. G., Durbin, A. G., Langton, R. W., and Bowman, R. E. 1983. Stomach contents of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus morhua*, and estimation of their daily rations. Fishery Bulletin, 81: 437–454.

Eggers, D. 1977. The nature of prey selection by planktivorous fish. Ecology, 58: 46–59.

Elliott, J. M., and Persson, L. 1978. The estimation of daily rates of food consumption for fish. Journal of Animal Ecology, 47: 977–991.

Hare, J. A., and Able, K. W. 2007. Mechanistic links between climate and fisheries along the east coast of the United States: explaining population outbursts of Atlantic croaker (*Micropogonias undulatus*). Fisheries Oceanography, 16: 31–45.

Hartman, K. J., and Brandt, S. B. 1995a. Trophic resource partitioning, diets, and growth of sympatric estuarine predators. Transactions of the American Fisheries Society, 124: 520–537.

Hartman, K. J., and Brandt, S. B. 1995b. Predatory demand and impact of striped bass, bluefish, and weakfish in the Chesapeake Bay: applications of bioenergetics models. Canadian Journal of Fisheries and Aquatic Sciences, 52: 1667–1687.

Houde, E. D., A. Annis, L. W. Harding, Jr., M. Mallonee and M. J. Wilberg. In Review. Factors affecting abundance of age-0 Atlantic menhaden (*Brevoortia tyrannus*) in Chesapeake Bay. ICES Journal of Marine Science.

Ihde, T. F., Houde, E. D., Bonzek, C. F., and Franke, E. 2015. Assessing the Chesapeake Bay forage base: Existing data and research priorities. 198 pp.

Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science, 293: 629–638.

Jung, S., and Houde, E. D. 2004. Recruitment and spawning-stock biomass distribution of bay anchovy (*Anchoa mitchilli*) in Chesapeake Bay. Fishery Bulletin, 102: 63–77.

Kemp, W. M., Boynton, W. R., Adolf, J. E., Boesch, D. F., Boicourt, W. C., Brush, G., Cornwell, J. C., et al. 2005. Eutrophication of Chesapeake Bay: historical trends and ecological interactions. Marine Ecology Progress Series, 303: 1–29.

Link, J. S. 2002. Ecological considerations in fisheries management: When does it matter? Fisheries, 27: 10–17.

Link, J. S. 2010. Ecosystem-based fisheries management: confronting tradeoffs. Cambridge University Press, New York. 207 pp.

Link, J. S., and Sosebee, K. 2008. Estimates and implications of skate consumption in the Northeast U.S. Continental Shelf ecosystem. North American Journal of Fisheries Management, 28: 649–662.

Maunder, M. N., and Punt, A. E. 2004. Standardizing catch and effort data: a review of recent approaches. Fisheries Research, 70: 141–159.

Methratta, E., and Link, J. 2006. Evaluation of quantitative indicators for marine fish communities. Ecological Indicators, 6: 575–588.

MD DNR. 2015. Marine and estuarine finfish ecological and habitat investigations. Performance report for federal aid grant F-63-R, Segment 5. Maryland Department of Natural Resources (MD DNR). 173 pp.

NEFSC. 2013a. Striped bass stock assessment for 2013. Northeast Fisheries Science Center Reference Document 13-16: 492–966.

NEFSC. 2013b. Summer flounder stock assessment for 2013. Northeast Fisheries Science Center Reference Document 13-16: 1–491.

Newberger, T. A., and Houde, E. D. 1995. Population biology of bay anchovy *Anchoa mitchilli* in the mid Chesapeake Bay. Marine Ecology Progress Series, 116: 25–37.

Overholtz, W. J., Link, J. S., and Suslowicz, L. E. 2000. Consumption of important pelagic fish and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparisons. ICES Journal of Marine Science, 57: 1147–1159.

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., et al. 2004. Ecosystem-based fishery management. Science, 305: 346–347.

Rice, J., and Rochet, M. 2005. A framework for selecting a suite of indicators for fisheries management. ICES Journal of Marine Science, 62: 516–527.

Sparre, P., and Venema, S. 1998. Introduction to tropical fish stock assessment - Part 1: Manual. Rome. FAO Fisheries Technical Paper 306/1 Rev. 2. 407 pp.

Tuckey, T. D., and Fabrizio, M. C. 2012. Estimating Relative Juvenile Abundance of Ecologically Important Finfish in the Virginia Portion of Chesapeake Bay. Gloucester Point, VA. 1-96 pp.

Wingate, R. L., and Secor, D. H. 2008. Effects of Winter Temperature and Flow on a Summer-Fall Nursery Fish Assemblage in the Chesapeake Bay, Maryland. Transactions of the American Fisheries Society, 137: 1147–1156.

Wood, R. J., and Austin, H. M. 2009. Synchronous multidecadal fish recruitment patterns in Chesapeake Bay, USA. Canadian Journal of Fisheries and Aquatic Sciences, 66: 496–508.

Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman & Hall/CRC, Boca Raton, FL. 391 pp.

Zuur, A. F., Ieno, Elena, N., Walker, N. J., Saveliev, A. A., and Smith, G. M. 2009. Mixed effects models and extensions in ecology with R. Springer, New York. 574 pp.

8. Tables

Table 1. Description of forage indicators.

Forage indicators	Description/justification
Relative prey abundance or biomass	Survey-based estimates of relative prey abundance or biomass. Metric of prey standing stock in system.
Diet-based indices	Predators viewed as prey "samplers", diets used to develop an index of relative prey importance and availability. Particularly useful for poorly sampled prey groups (e.g., mysids).
Prey-predator ratios (PPR)	Ratio of prey abundance (or biomass) index to predator index. Index of relative prey availability, accounting for relative abundance of predators and prey.
Consumption-prey ratios (CPR)	Ratio of population-scaled consumption to index of relative prey abundance or biomass. Index of predation intensity.

Table 2. Summary of surveys used for developing different forage indicators for fish, crustacean (Crust.), and benthic invertebrate (Bent.) prey groups. Indices included relative prey abundance or biomass, diet-based indices, prey to predator ratios (PPR), and consumption to prey ratios (CPR). Sampling regions for each survey were in the Maryland (MD) and Virginia (VA) tributaries (trib) or along the mainstem of Chesapeake Bay. Asterisks denote that ChesMMAP sampling occurred bimonthly from March to November. Gears used in the fish surveys were: 1) beach seine (BS), 2) semi-balloon otter trawl (OT), 3) midwater trawl (MT), and 4) bottom trawl (BT). 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 indicator development.

							Fishes								Crust.			Bent.	
Index	Survey	Regions	Years	n_{years}	Months	Gear	YOY Menhaden	Bay anchovy	YOY alewife	YOY blueback	Atl. silverside	YOY croaker	YOY weakfish	YOY spot	Mysid	Mantis shrimp	Sand shrimp	Polychaete	Bivalve
Abundance	MD DNR Seine (MJS)	MD trib	1959-2013	55	Jul-Sep	BS	■	■	■	■	■			■					
	MD DNR Sum. Trawl (MST)	MD trib, VA eastern trib	1989-2013	26	May-Oct	OT	■												
	VIMS Juv. Trawl (VJT)	VA trib & mainstem	1988-2013	27	Apr-Dec	OT	■	■				■	■	■					
	VIMS Seine (VJS)	VA trib	1968-73, 1980-2013	39	Jul-Sep	BS	■	■						■					
	TIES/CHESFIMS (CFT)	Mainstem	1995-2007	13	Jan, Mar-Nov	MT	■	■	■		■	■	■	■					
	ChesMMAP	Mainstem	2002-2014	13	Mar-Nov*	BT						■	■	■					
Biomass	CBP Benthos (CBMS)	Trib, mainstem	1995-2014	20	Jan-Dec	BG												■	■
Diet-based	ChesMMAP	Mainstem	2002-2014	13	Mar-Nov*	BT	■								■	■	■	■	■
PPR	ChesMMAP	Mainstem	2002-2014	13	Mar-Nov*	BT	■	■										■	■
CPR	ChesMMAP	Mainstem	2002-2014	13	Mar-Nov*	BT						■	■	■					

Table 3. 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 ($n_{sampled}$) and for non-empty samples ($n_{non\text{-}empty}$) that were used for diet analysis. Predators were divided into two 6-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	1343	494	895	394	Nov-Apr	10.5	May-Oct	20.3
	M	300-500	2773	973	1929	789	Nov-Apr	10.5	May-Oct	20.3
	L	>500	537	330	267	204	Nov-Apr	10.5	May-Oct	20.3
Summer Flounder	S	<250	1061	595	777	470	Jun-Nov	20.6	Dec-May	13.2
	M	250-375	2261	1053	1463	785	Jun-Nov	20.6	Dec-May	13.2
	L	>375	1827	967	739	539	Jun-Nov	20.6	Dec-May	13.2
Weakfish	S	<200	3112	958	2487	859	Jun-Nov	20.9	Dec-May	17.1
	M	≥200	4230	1035	2973	910	Jun-Nov	20.9	Dec-May	17.1
Atlantic Croaker	S	<200	1363	639	1071	567	May-Oct	22.5	Nov-Apr	13.7
	M	≥200	2743	960	2369	871	May-Oct	22.5	Nov-Apr	13.7
White Perch	S	<200	1519	477	958	377	Nov-Apr	10.0	May-Oct	21.8
	M	≥200	1835	616	1110	483	Nov-Apr	10.0	May-Oct	21.8
Spot	S	<150	1270	598	814	449	Jun-Nov	21.5	Dec-May	17.5
	M	≥150	2050	913	1272	639	Jun-Nov	21.5	Dec-May	17.5

9. Figures

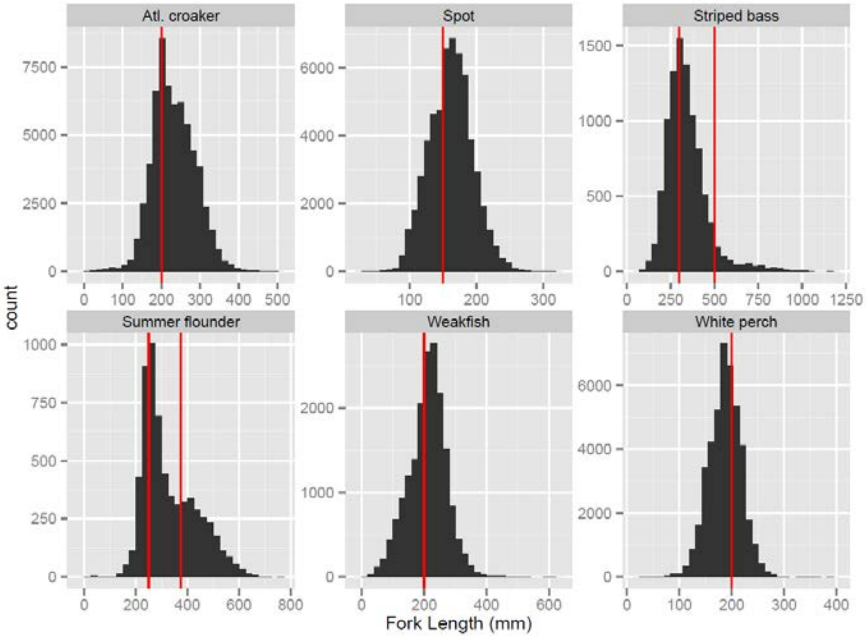


Figure 1. Length-frequency distributions of fish predators from the ChesMMAP survey. Red lines mark the threshold lengths used to define size classes of predators.

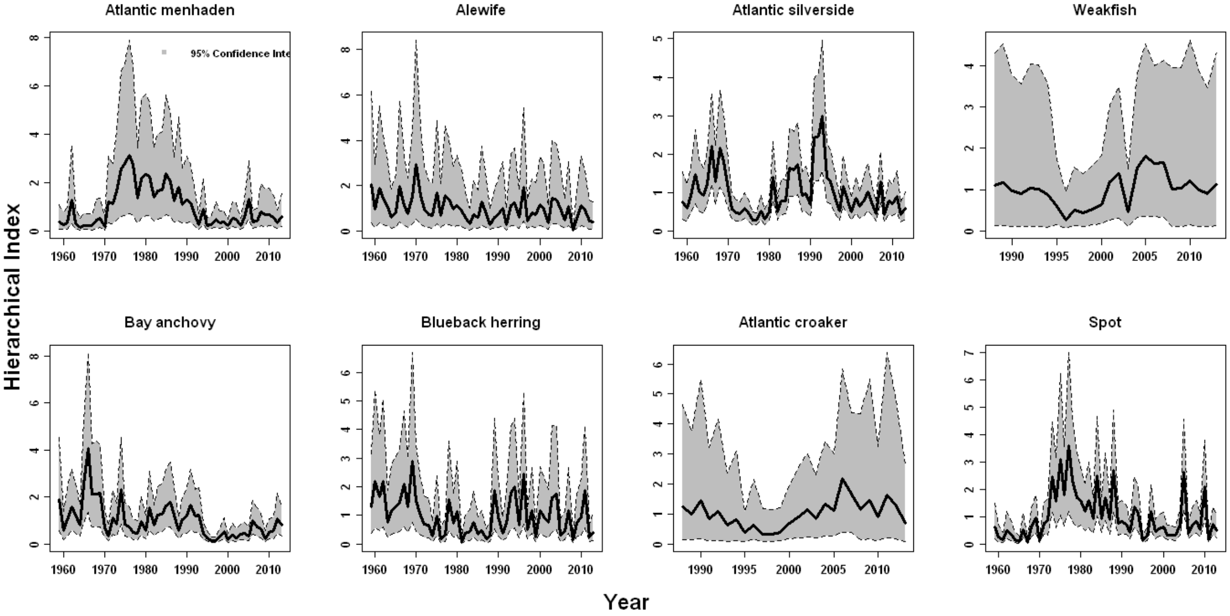


Figure 2. Forage fish abundances indices for eight fish species. Indices of relative YOY fish abundance (black lines) were derived using data from multiple surveys (see Table 1) using a hierarchical Bayesian analysis and they are standardized to have a mean of 1. Gray shading represents the 95% confidence interval for the index values.

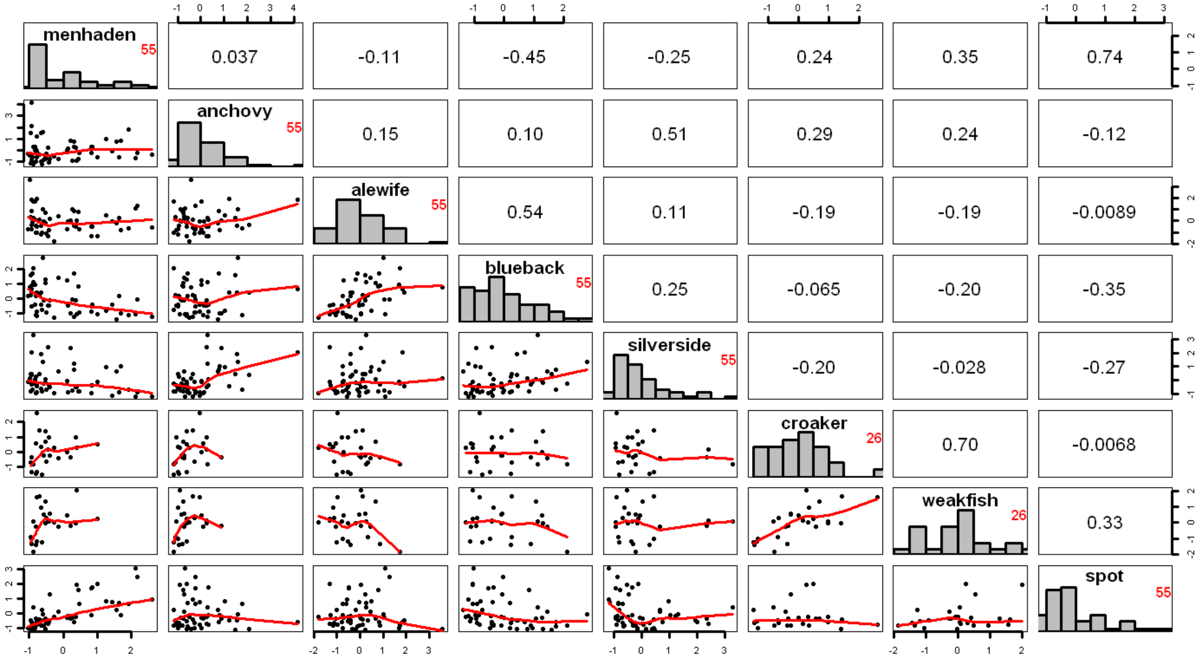


Figure 3. Relationships among hierarchical indices of YOY forage fish abundances. Upper panels show the Pearson correlation coefficients. Diagonal panels show the frequency distributions of index values for each species and the red numbers indicate the number of years in each time series. The bottom panels are scatterplots of each paired relationship fitted iwith a smooth spline for visual reference.

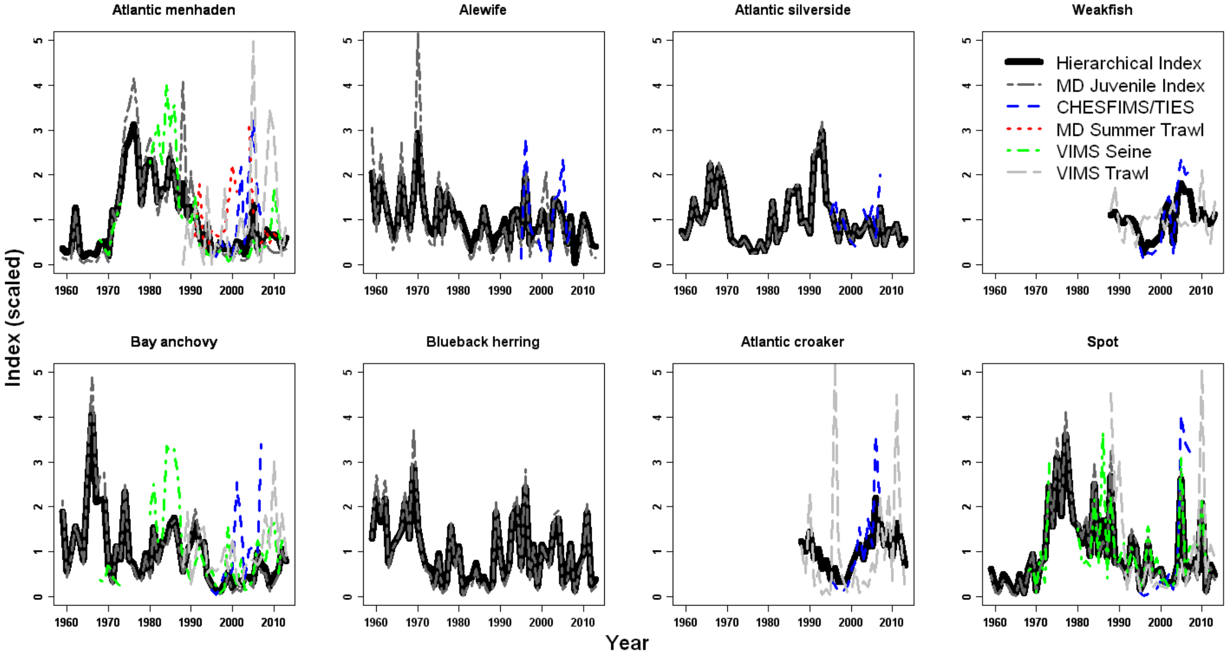


Figure 4. Survey-specific and hierarchical forage indices for eight prey fishes. Survey-specific indices for each fish species are identified by color and line type (see legend). For each species, the survey-specific indices were combined into a hierarchical index (thick, solidblack line) using the methods of Conn (2010). All index values are scaled to have a mean of one.

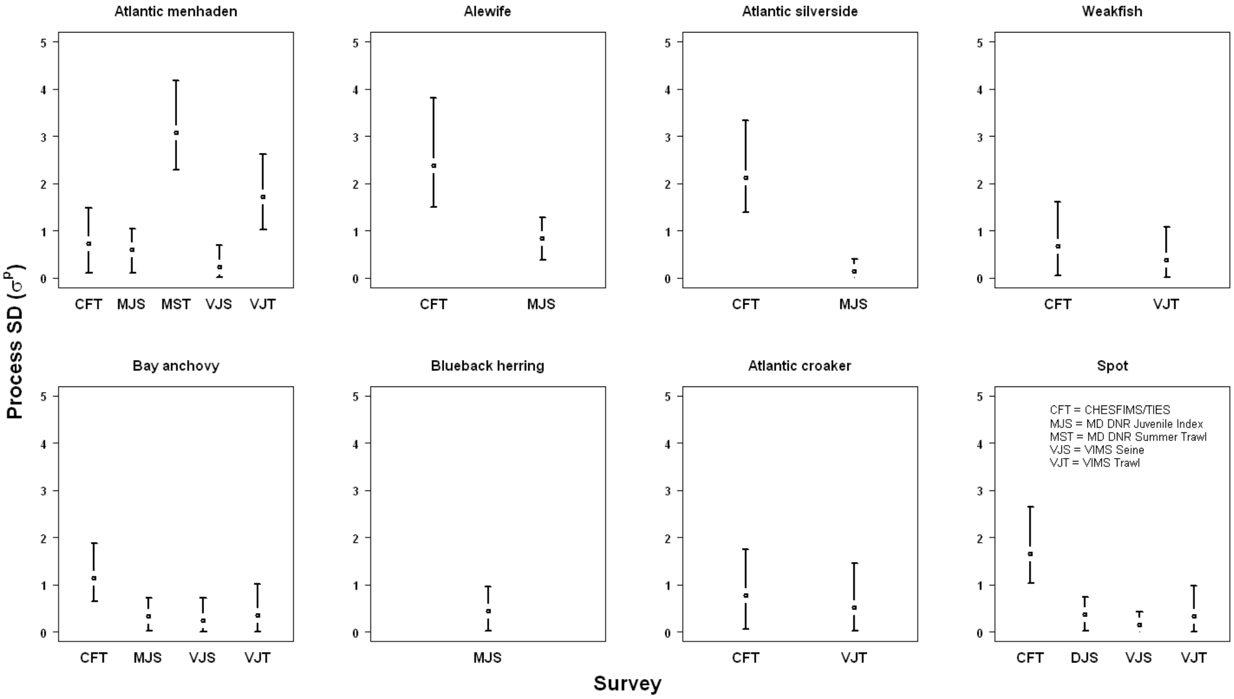


Figure 5. Posterior means and 95% credible intervals for the standard deviation of process error (σ^P) for each index used to derive hierarchical indices of abundance for each forage species. For index definitions, see (Table 2).

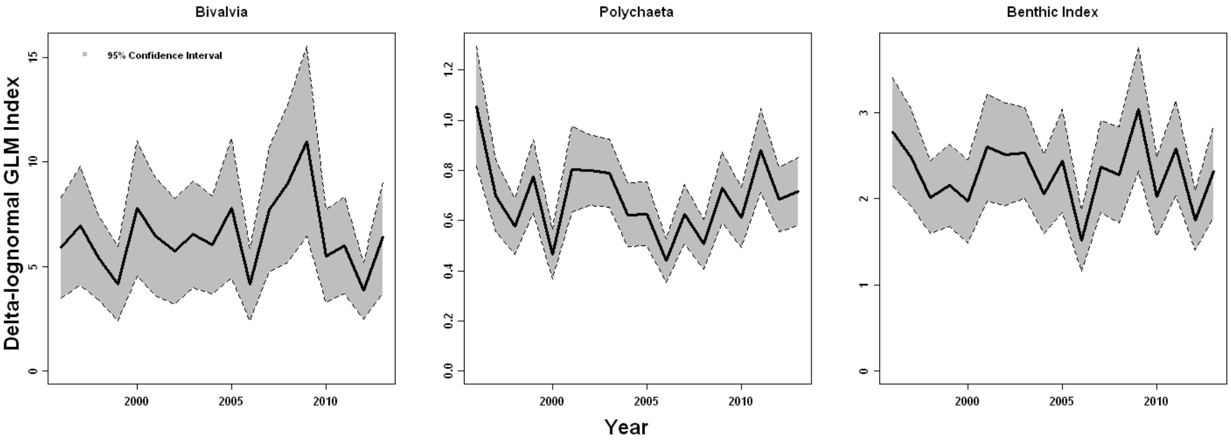


Figure 6. Delta-lognormal GLM indices of relative biomass of bivalve, polychaete, and overall benthic prey. The overall benthic index is a relative biomass index for bivalves and polychaetes combined. Index units are grams ash-free dry weight per square meter.

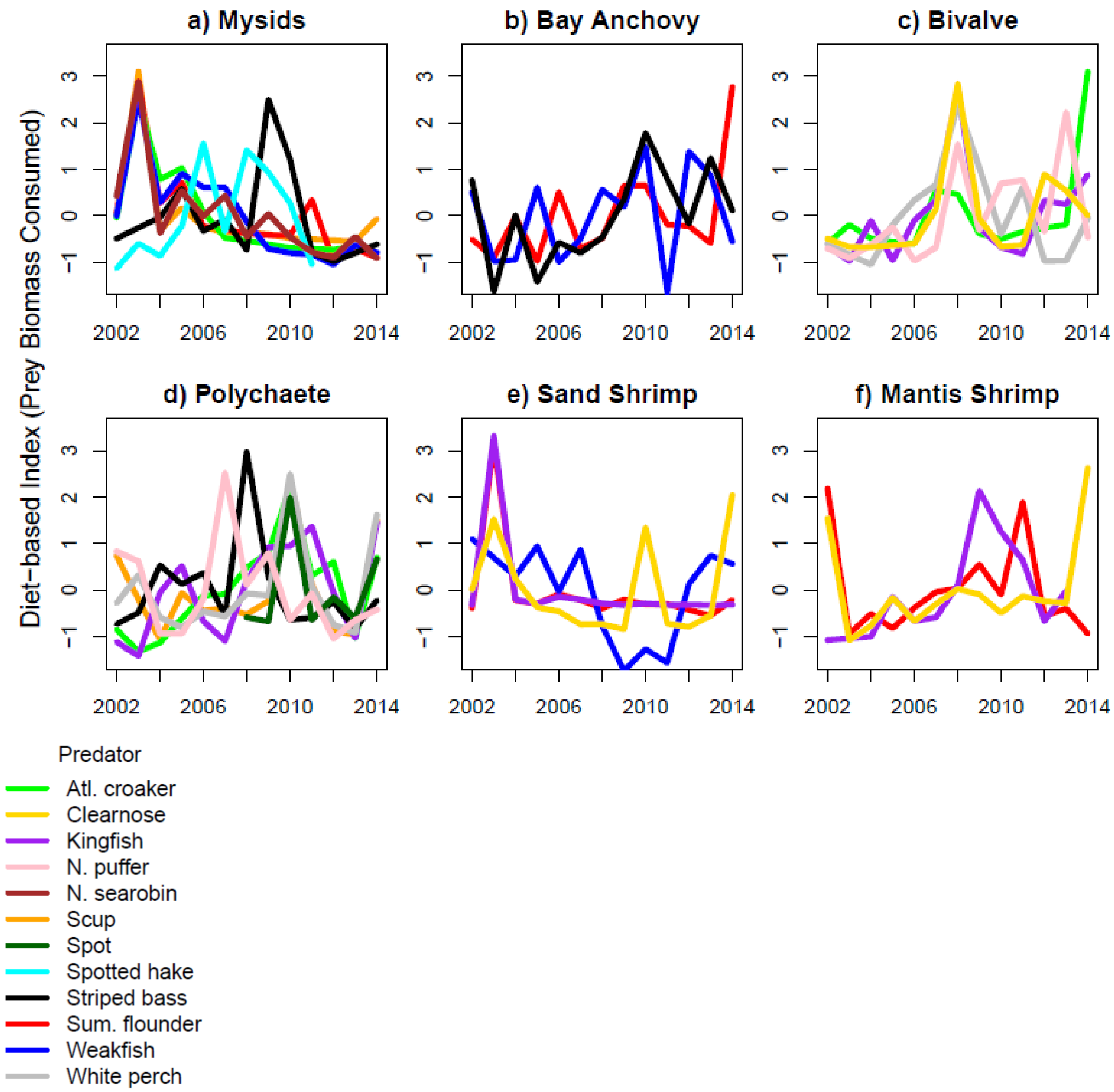


Figure 7. Diet-based indices of prey biomass consumed by twelve predator fishes over time. Each panel represents a different prey group (as labeled). Consumption of each prey by a predator (colored lines; see legend) was estimated using a delta GAMM, and standardized to a mean of zero and standard deviation of one. Predators with insufficient consumption of a particular prey were excluded from analysis.

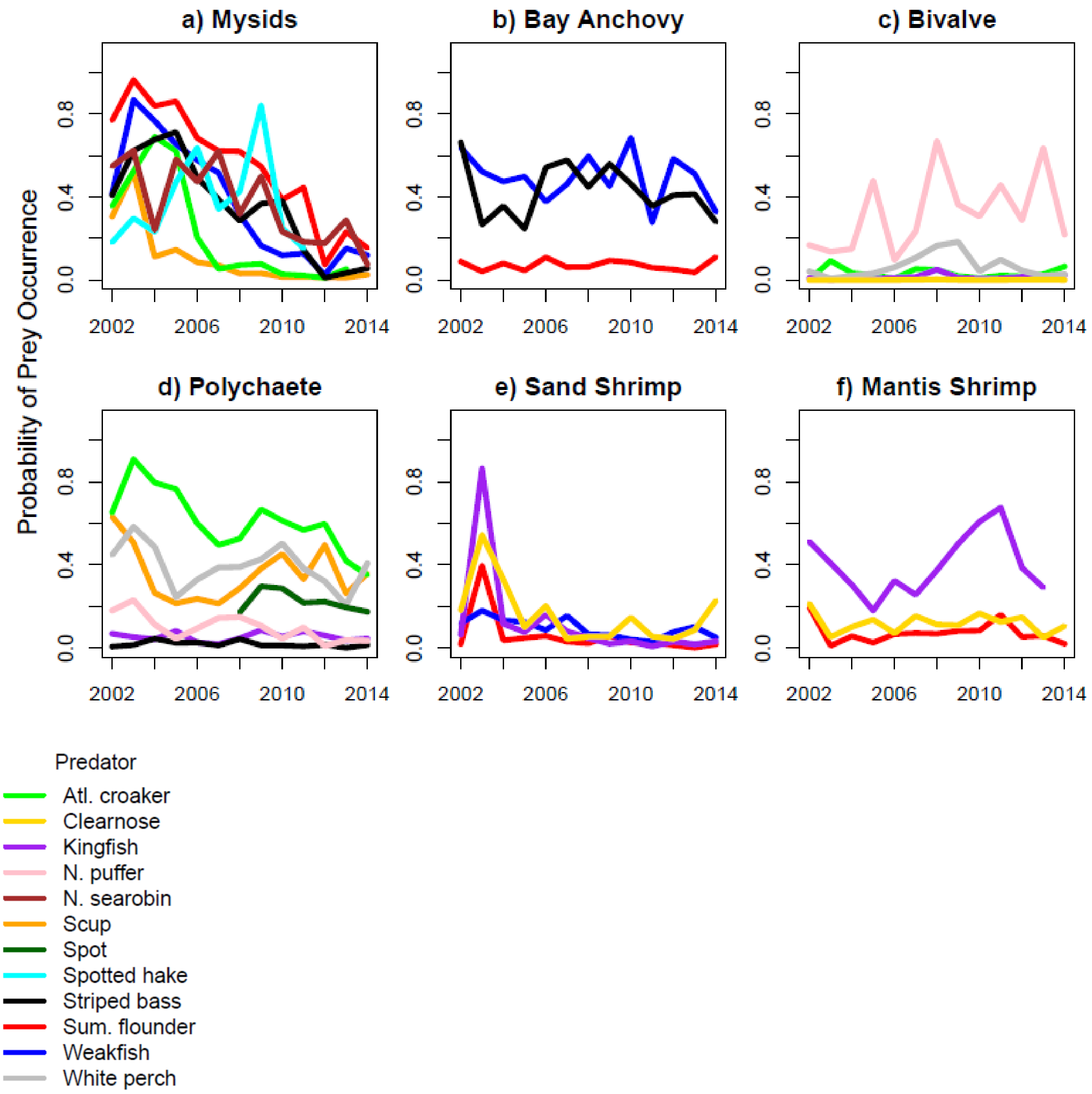


Figure 8. Diet-based indices of probability of annual prey occurrence in the stomachs of twelve fish predators. Each panel represents a prey group (as labeled). Prey occurrence for each predator-prey combination was estimated using a delta GAMM. Predators with insufficient consumption of a particular prey were excluded from analysis.

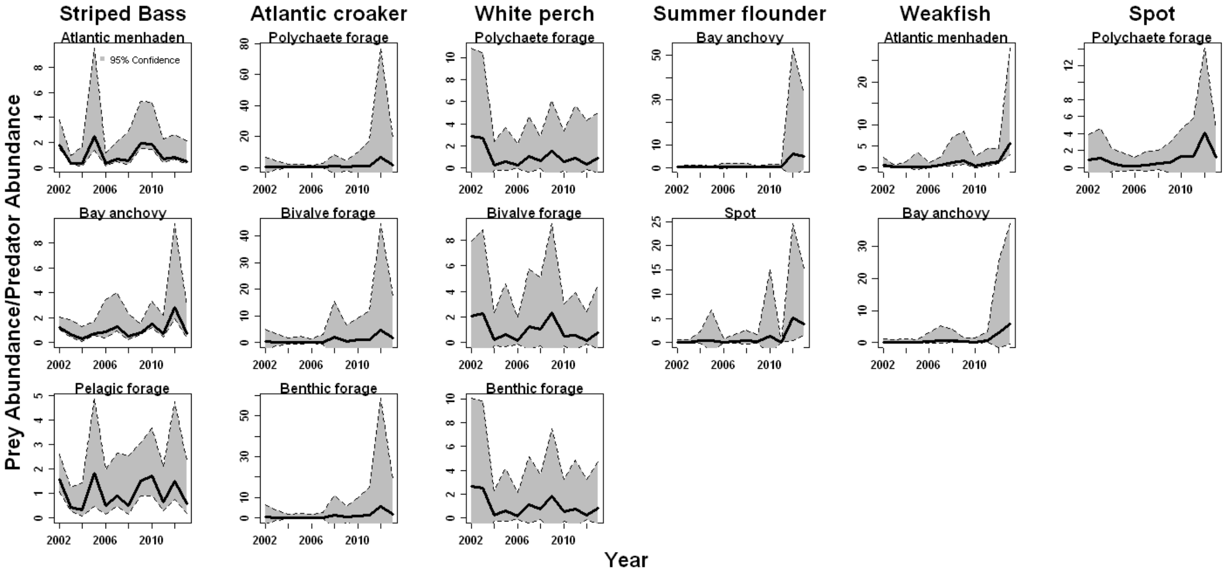


Figure 9. Prey to predator ratio (PPR) indices. Each column of plots presents the ratios of prey to predator abundances for the six predators and their corresponding prey. The PPR indices (continuous black lines) represent a measure of relative prey availability with the associated 95% confidence interval for the metric (shading). Values in each panel were standardized to have a mean of one.

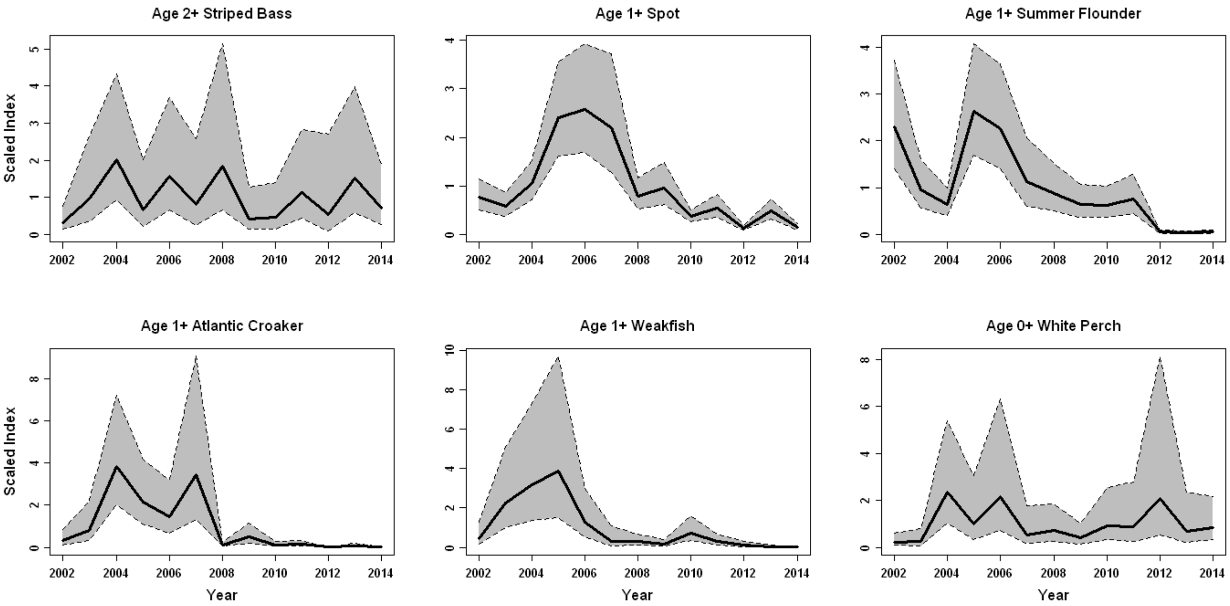


Figure 10. Predator abundance indices. Random stratified geometric mean indices of abundance (black continuous line) with associated 95% confidence intervals (grey shading).

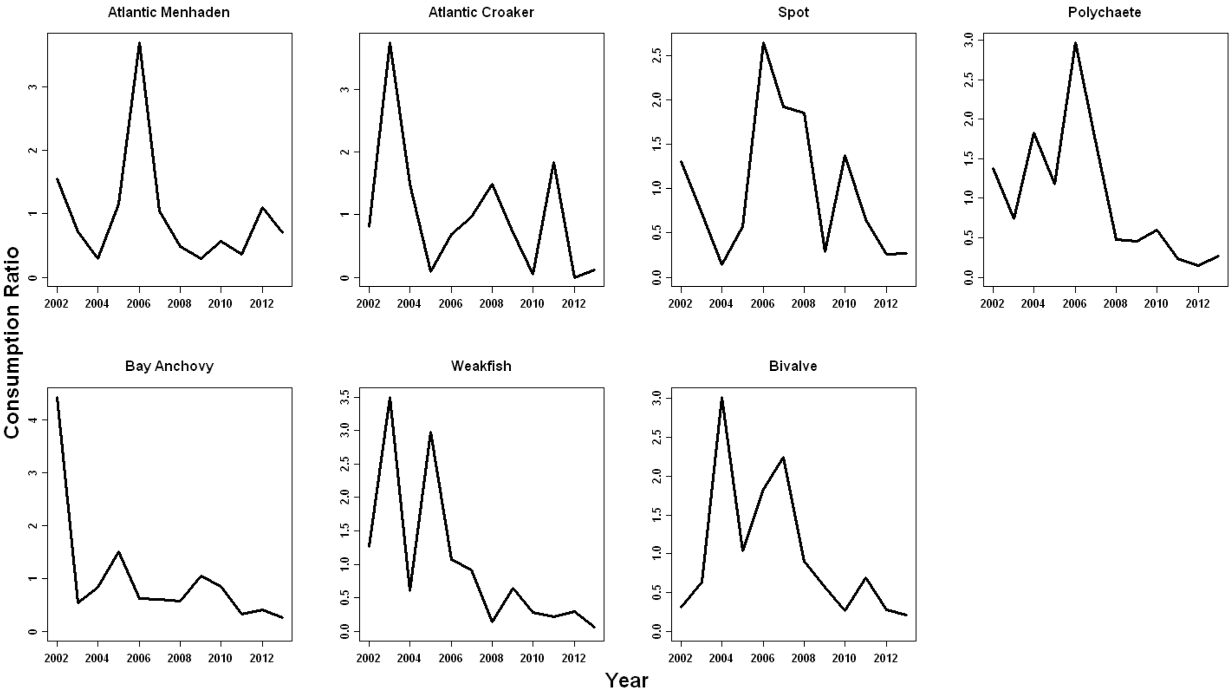


Figure 11. Prey consumption to prey abundance ratios for five YOY forage fishes and two categories of benthic invertebrate prey.

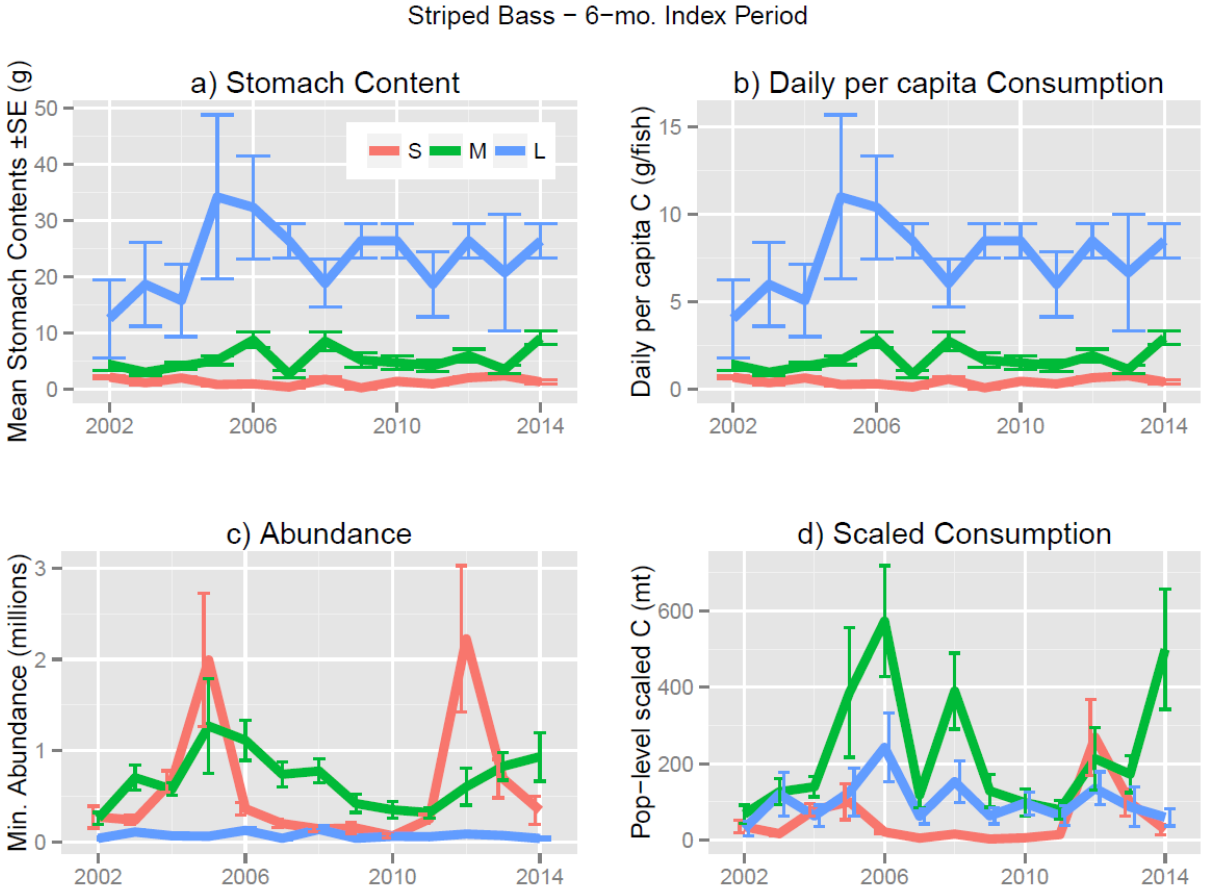


Figure 12. Consumption results for small (S), medium (M), and large (L) striped bass during the 6-month index period. a) Mean stomach contents, b) daily per capita consumption (C), c) minimum swept-area abundance, and d) consumption scaled to the population for the 6-month period. Line colors represent the size classes as indicated in the legend of panel a, and error bars are for SE.

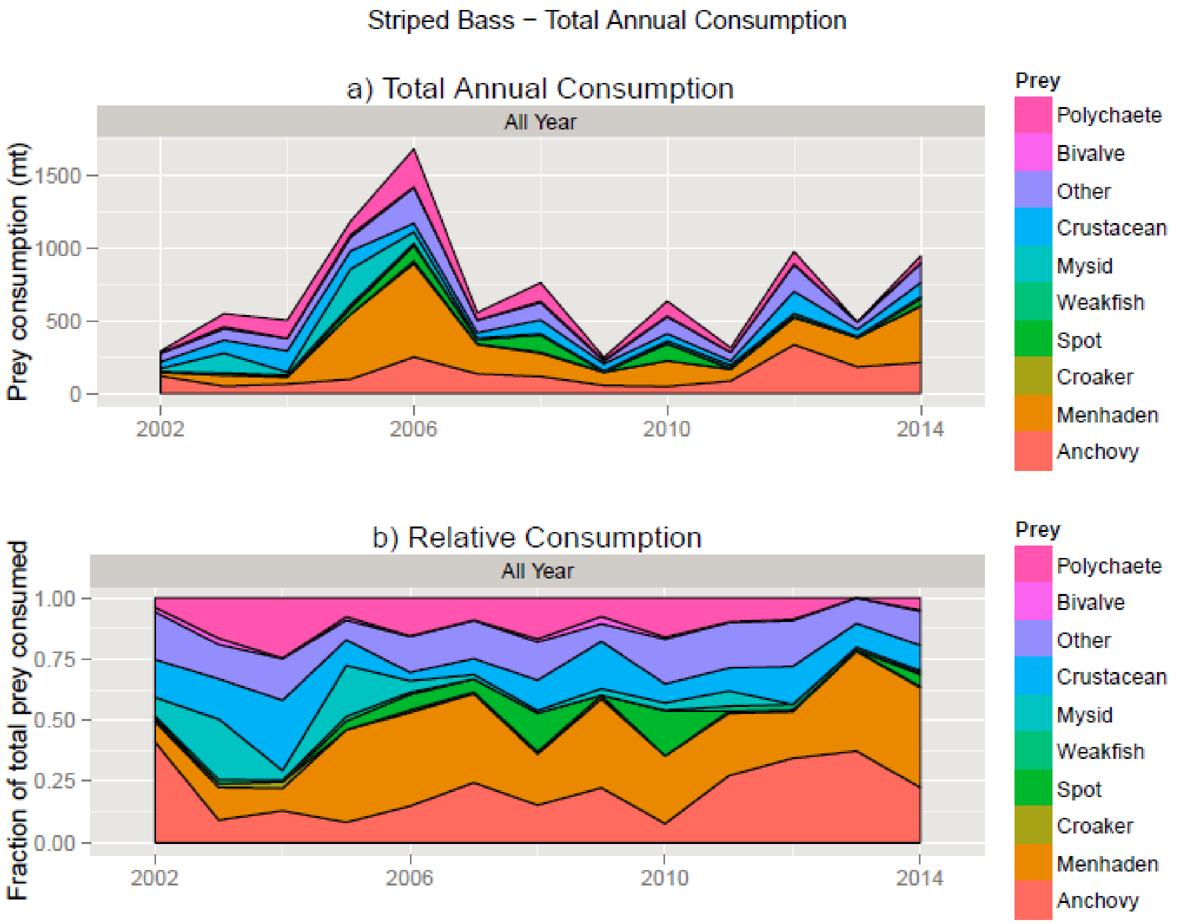


Figure 13. Striped bass total annual consumption of select prey groups. a) Total prey consumption by all size classes of striped bass over the entire year. b) Relative contributions of each prey to the total amount consumed per year.

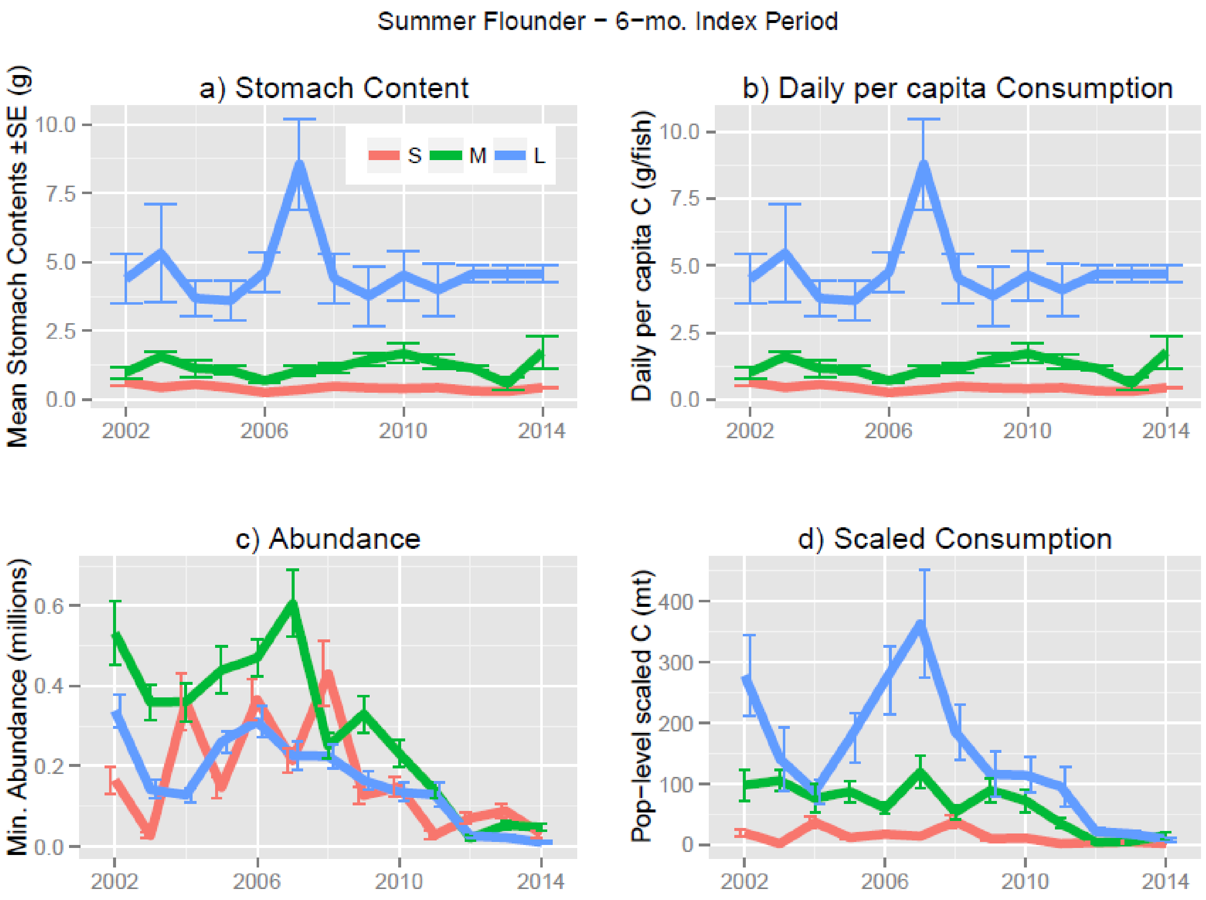


Figure 14. Consumption results for small (S), medium (M), and large (L) summer flounder during the 6-month index period. a) Mean stomach contents, b) daily per capita consumption (C), c) minimum swept-area abundance, and d) consumption scaled to the population for the 6-month period. Line colors represent the size classes as indicated in the legend of panel a, and error bars are for SE.

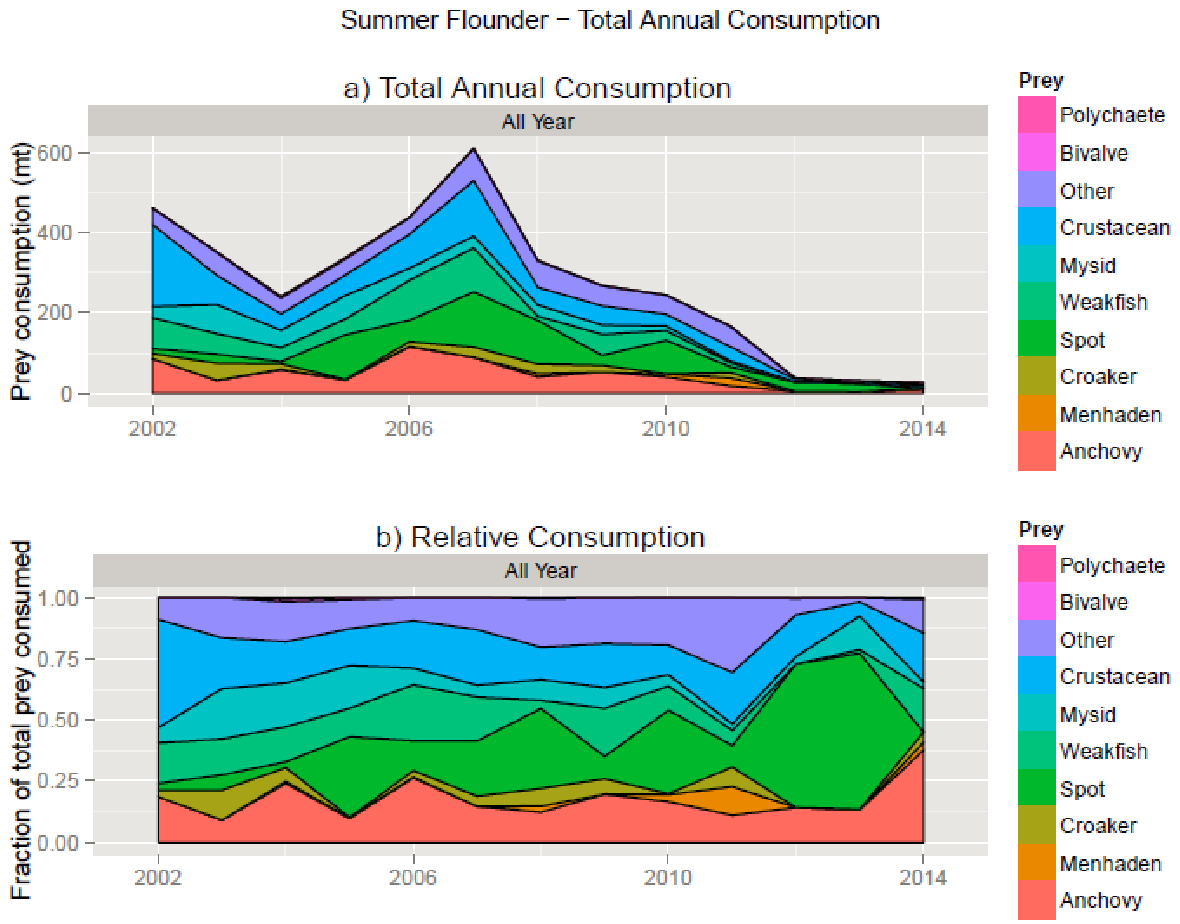


Figure 15. Summer flounder total annual consumption of select prey groups. a) Total prey consumption by all summer flounder size classes over the entire year. b) Relative contributions of each prey to the total amount consumed per year.

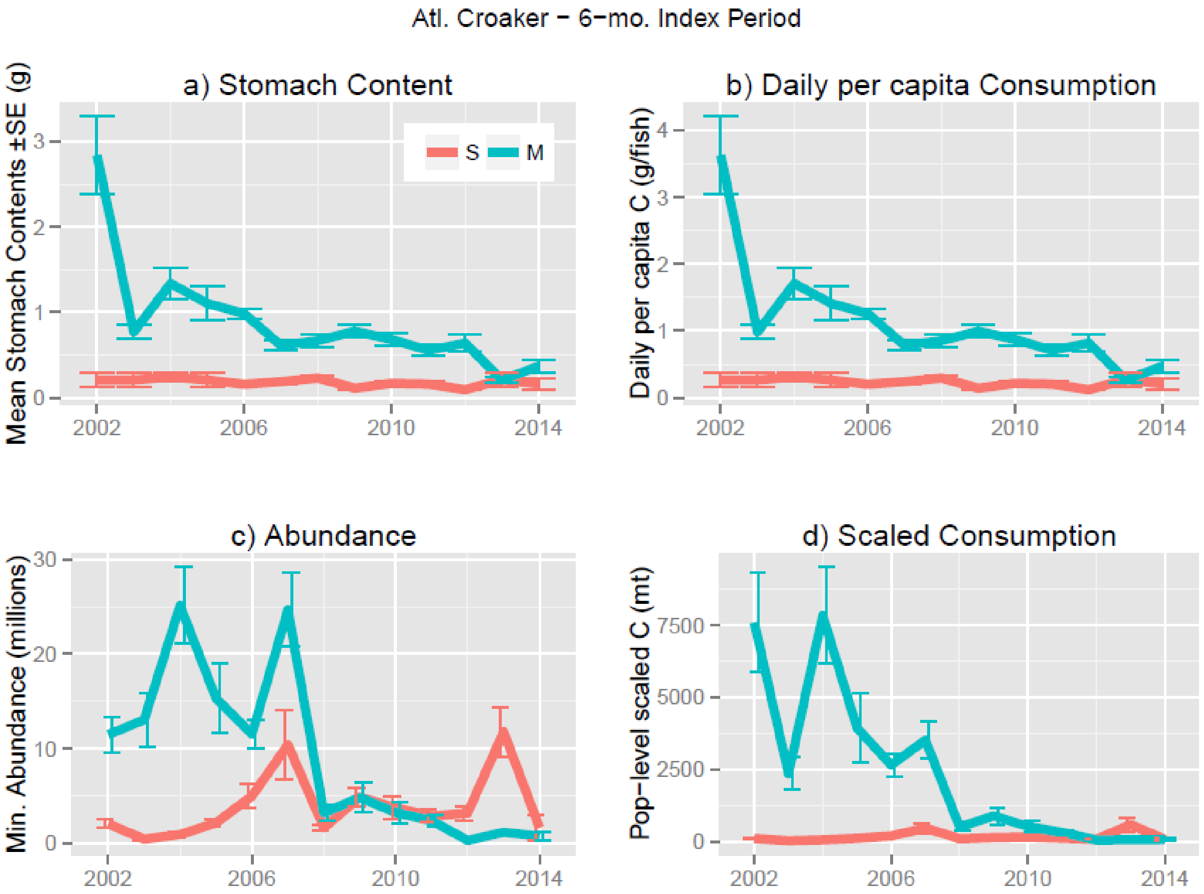


Figure 16. Consumption results for small (S) and medium (M) Atlantic croaker during the 6-month index period. a) Mean stomach contents, b) daily per capita consumption (C), c) minimum swept-area abundance, and d) consumption scaled to the population for the 6-month period. Line colors represent the size classes as indicated in the legend of panel a, and error bars are for SE.

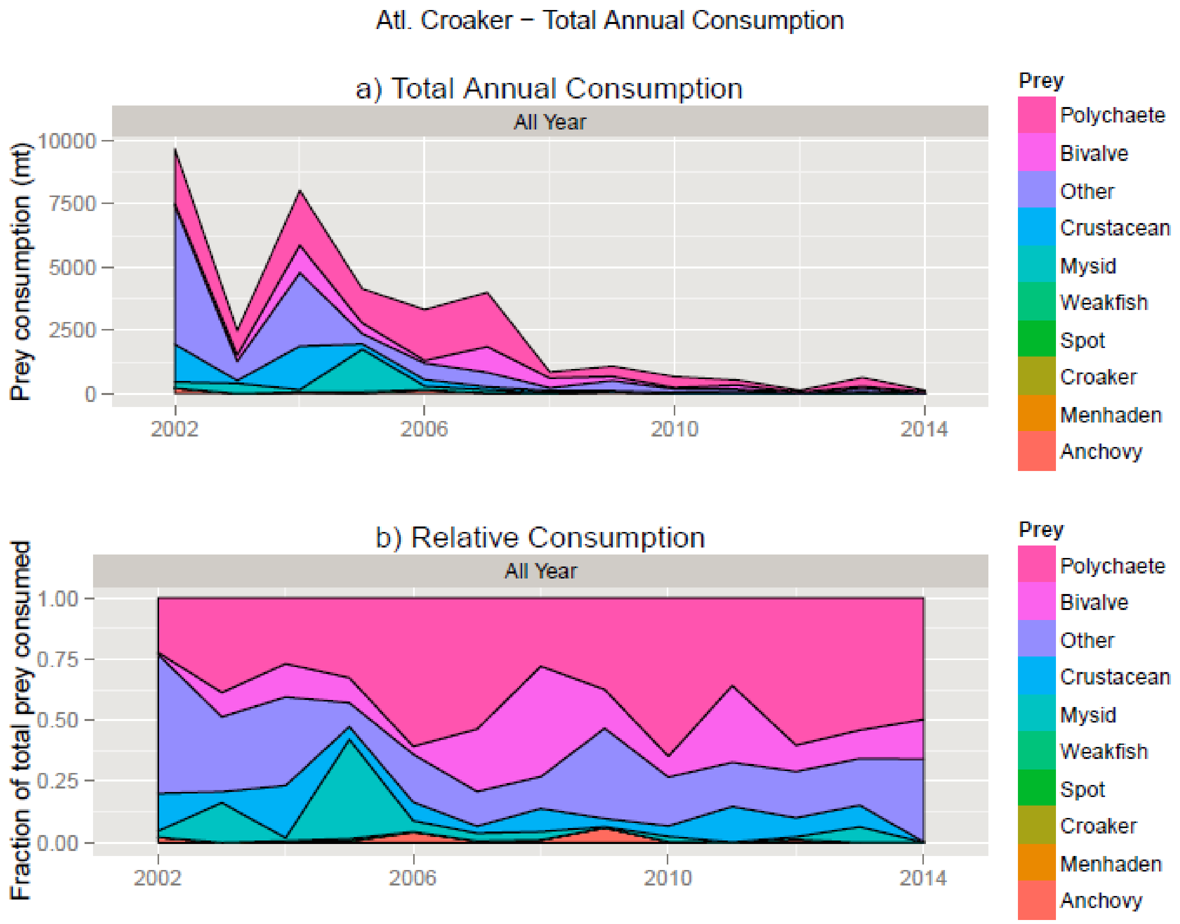


Figure 17. Atlantic croaker total annual consumption of select prey groups. a) Total prey consumption by all Atlantic croaker size classes over the entire year. b) Relative contributions of each prey to the total amount consumed per year.

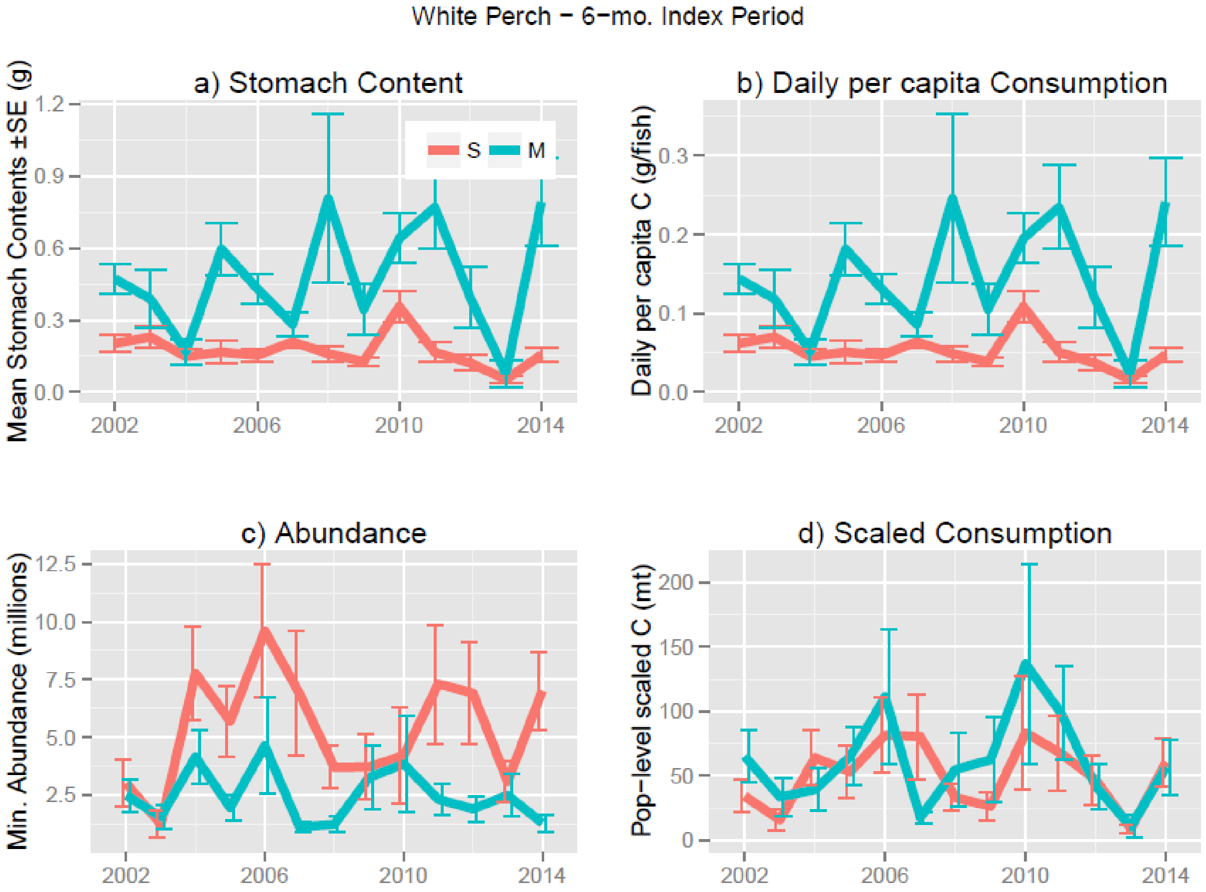


Figure 18. Consumption results for small (S) and medium (M) white perch during the 6-month index period. a) Mean stomach contents, b) daily per capita consumption (C), c) minimum swept-area abundance, and d) consumption scaled to the population for the 6-month period. Line colors represent the size classes as indicated in the legend of panel a, and error bars are for SE.

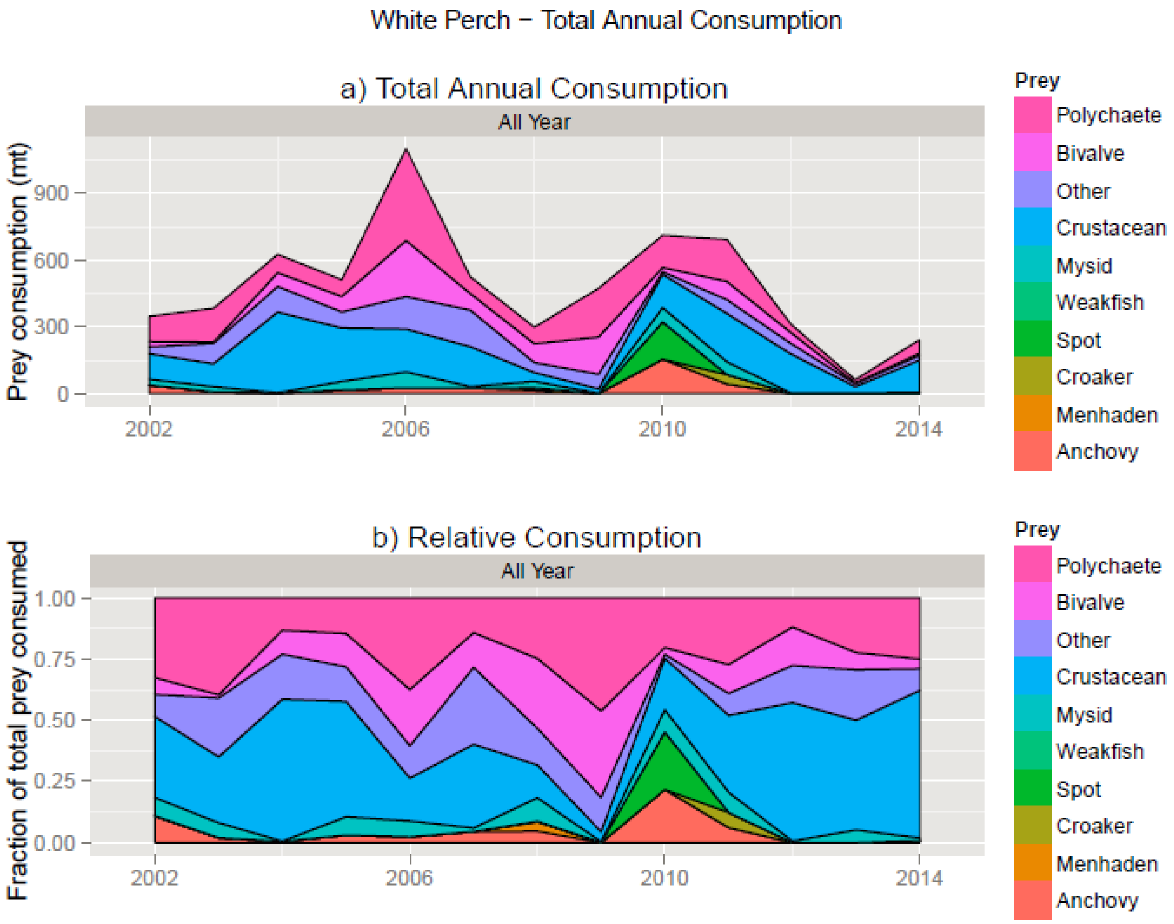


Figure 19. White perch total annual consumption of select prey groups. a) Total prey consumption by all white perch size classes over the entire year. b) Relative contributions of each prey to the total amount consumed per year.

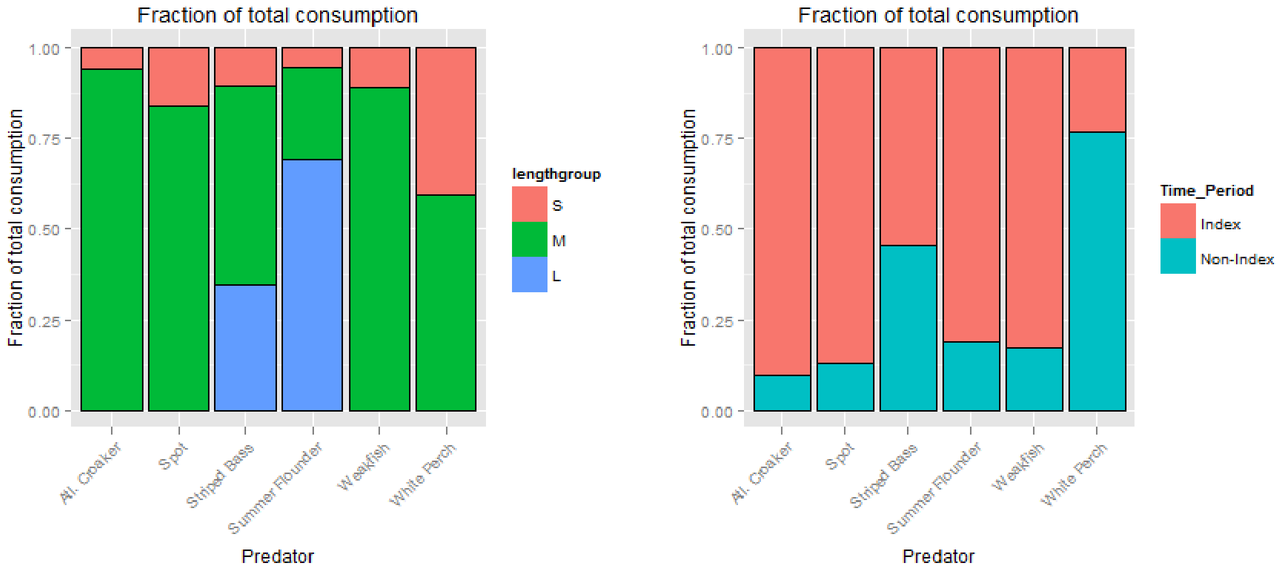
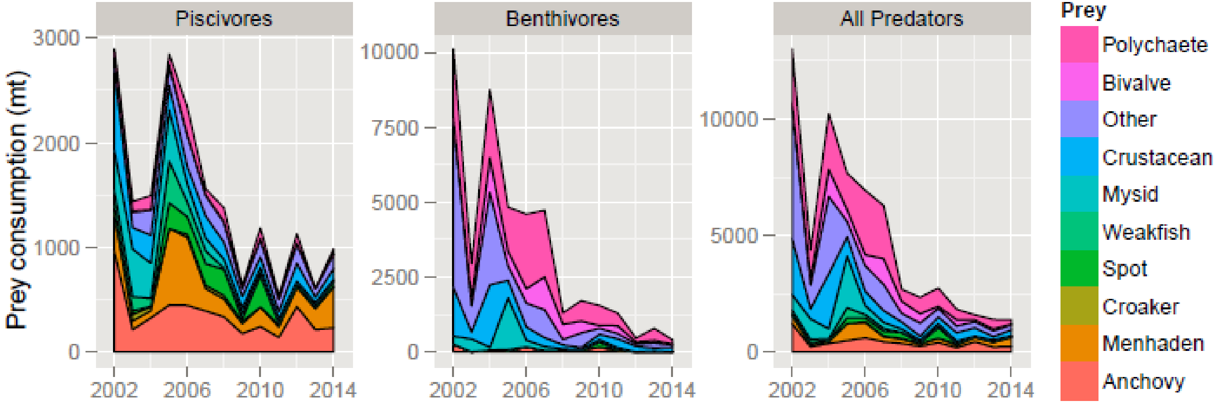


Figure 20. Fraction of total annual consumption by each predator based on a) lengthgroup (S-small, M-medium, L-large) and b) time period (Index – 6-month period with highest abundance, Non-Index – 6-month period with lowest abundance).

a) Total Annual Consumption



b) Relative Consumption

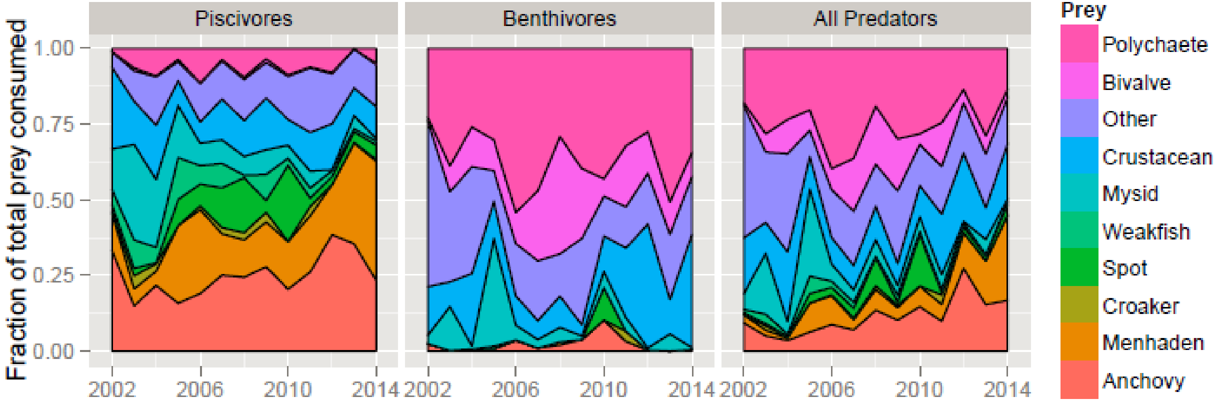


Figure 21. Combined consumption by groups of predators. a) Total annual consumption by predator combinations (piscivores: striped bass, summer flounder, weakfish; benthivores: white perch, and spot; and all six predators). b) Fraction of total consumption for each of the three predator groups.

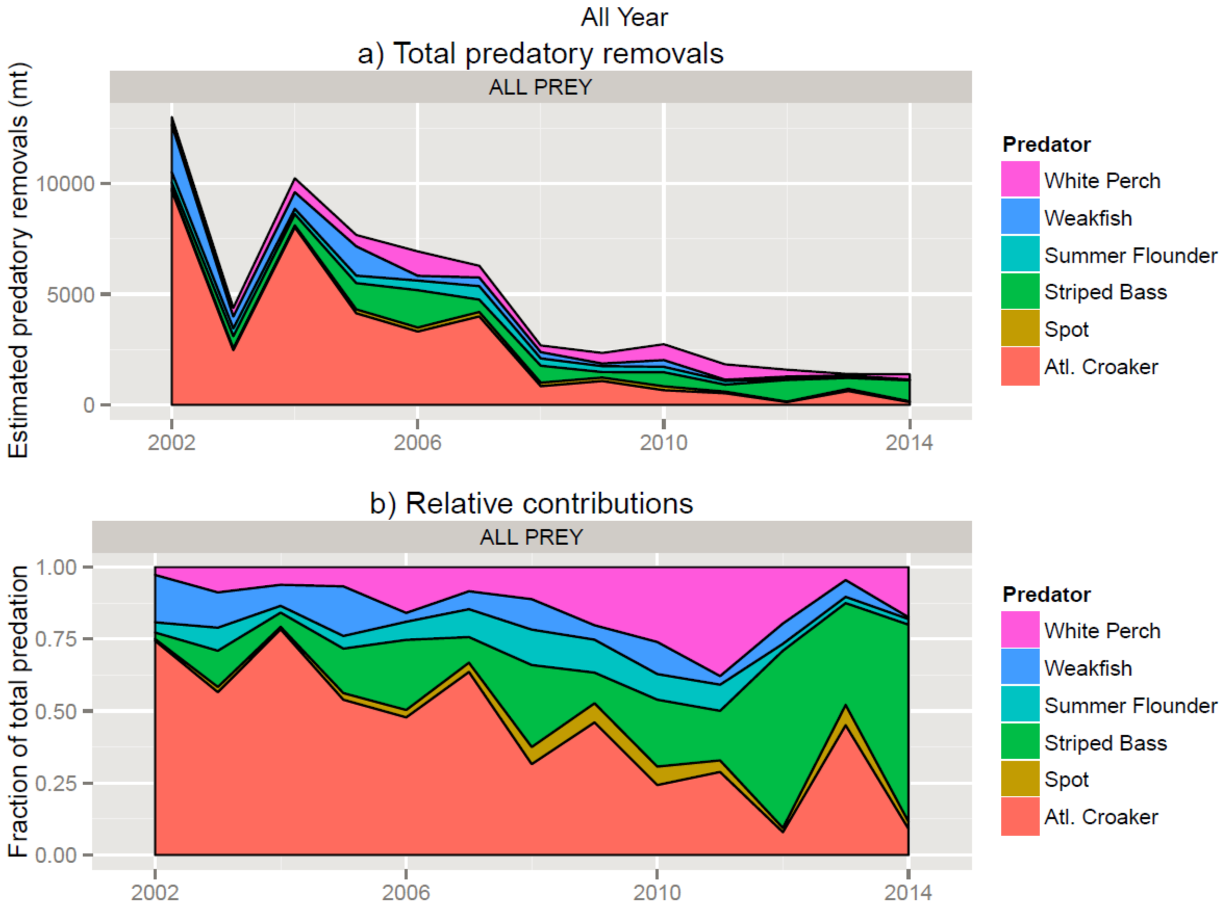


Figure 22. Relative contributions of the six fish predators to total predatory removals. a) Total annual predatory removals (mt). b) Relative contributions of individual predators to total removals.

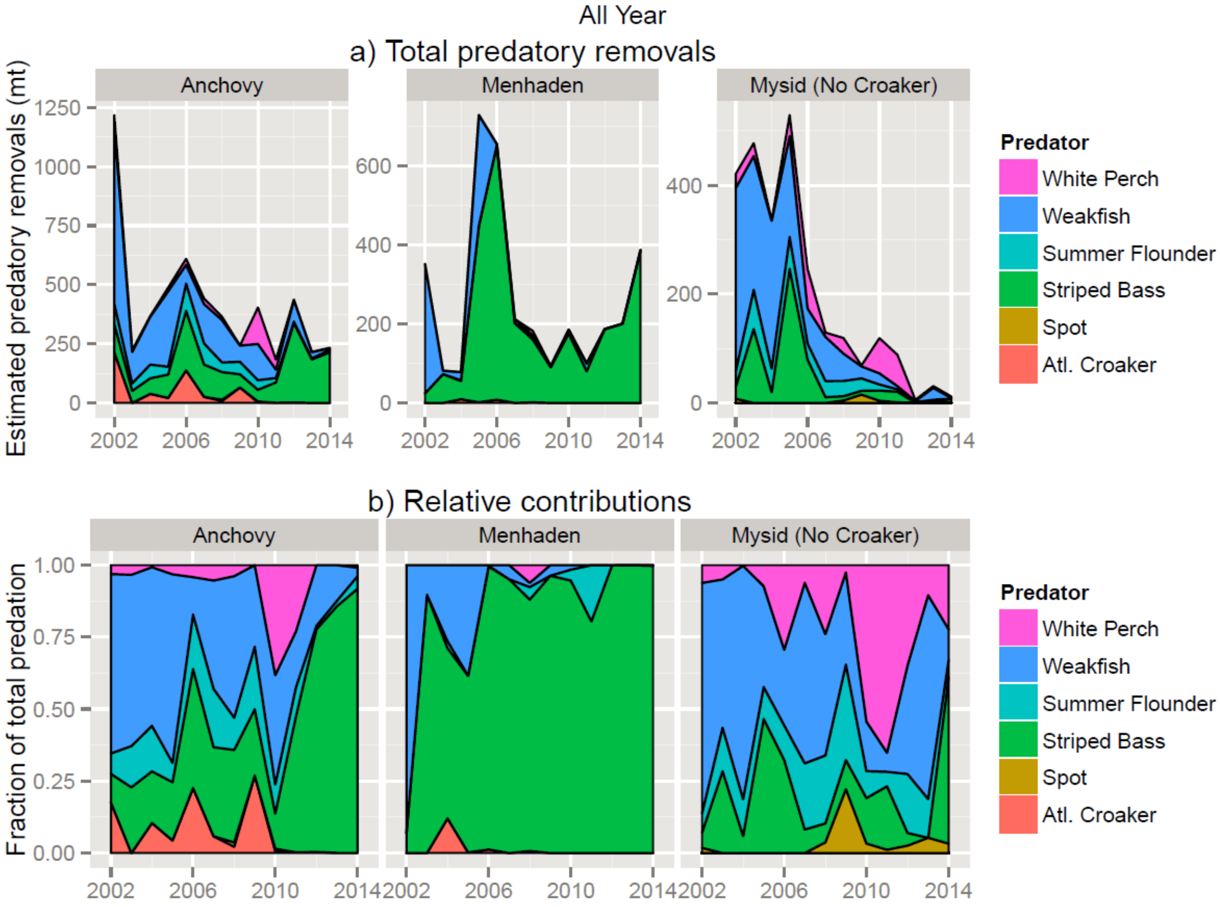


Figure 23. Consumptive removals of three key prey (bay anchovy, YOY Atlantic menhaden, and mysids) of piscivorous predators. a) Total annual removals of the three prey (mt). b) Relative contributions of each predator to the total removals of each. Note: for the mysid panels, consumption by Atlantic croaker was excluded because high consumption by Atlantic croaker in 2005 (1650 mt) obscured the scale and patterns.

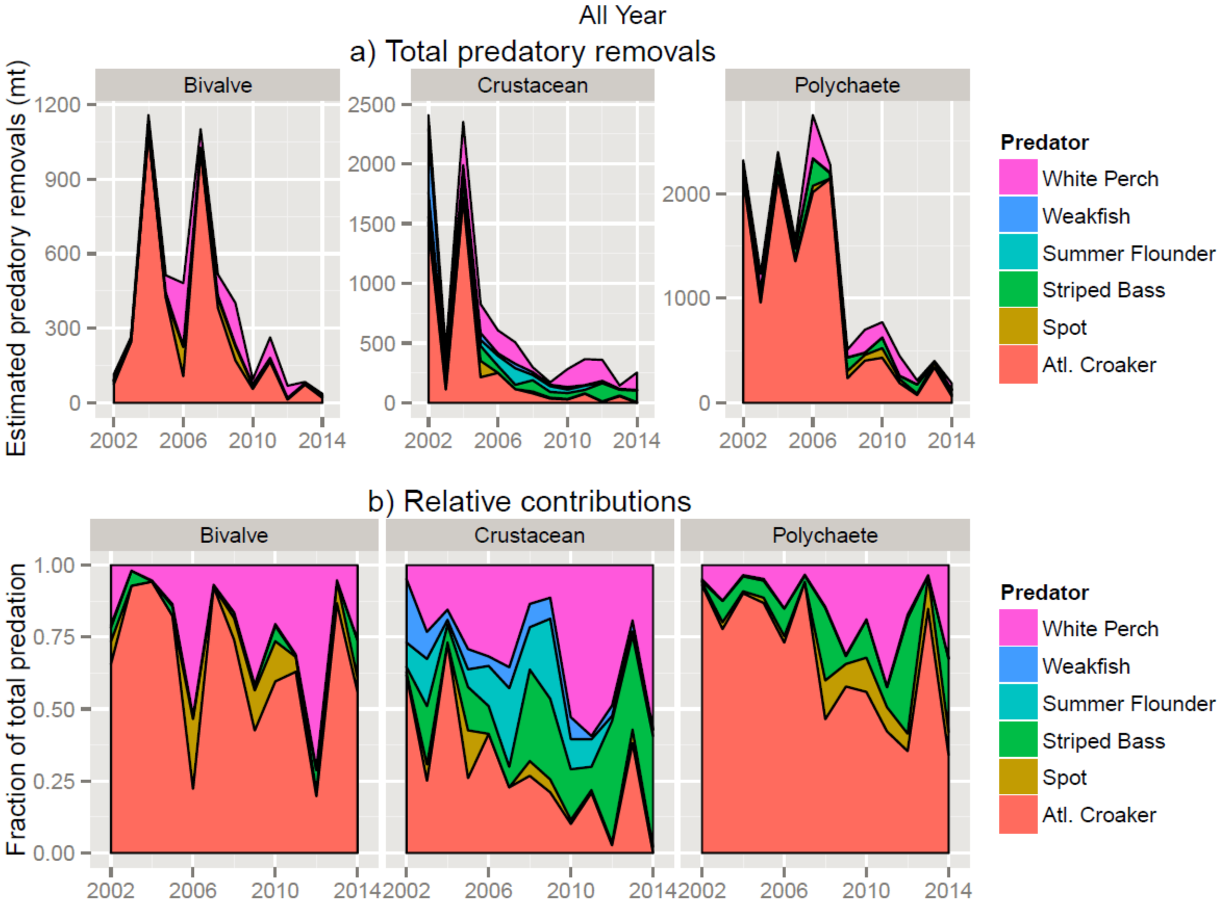


Figure 24. Consumptive removals of three key invertebrate prey groups (bivalves, crustaceans, polychaetes) by the six fish predators. a) Total annual removals of the three prey groups (mt). b) Relative contributions of each predator to the total removals of each prey group.