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Dynamic trophic linkages in a large estuarine system – support for supply-driven dietary changes using delta generalized additive mixed models

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Abstract: Trophic dynamics within aquatic systems are a predominant regulator of fish production and an important consideration for implementing ecosystem approaches to fisheries management. We analyzed ten years of fish diet data from Chesapeake Bay, USA to 1) evaluate the effects of environmental variables on trophic interactions of 12 common predatory fishes, 2) infer dynamics of four key prey groups (mysids, bay anchovy, bivalves, and polychaetes), and 3) evaluate whether interannual dietary trends were coherent among predators and regulated by prey availability. Based on delta generalized additive mixed models (delta-GAMM), predator length was the most important covariate in modeling prey consumption. When significant, latitude, temperature, and depth effects were largely similar across predators for a given prey. Annual patterns of mysid and bivalve consumption each showed a single, dramatic peak shared by multiple predators with varied feeding preferences and distributional characteristics, but annual trends were not correlated with available survey-based measures of prey availability likely due to methodological differences. Overall, the coherence in consumption patterns across predators was consistent with supply-driven dynamics controlled by regional and annual changes in prey availability. Also, the novel application of delta-GAMM to fish diet data was useful in characterizing the dynamics of poorly sampled prey groups and the trophic interactions for ubiquitous species from the Northwest Atlantic Ocean.

Keywords: trophic ecology, diet analysis, fish stomach contents, statistical methods, environmental effects
Introduction

Trophic dynamics have been described as one of the three principal drivers of fisheries production (Link 2010; Gaichas et al. 2012). Trophic dynamics control not only the direct consequences of predation (e.g., mortality, survival, growth, changes in population biomass, and modified size structure) but also a myriad of indirect ecological effects (e.g., changes in behavior, distribution, habitat utilization, foraging, and competition), all of which are critical to governing the structure and function of aquatic food webs (Carpenter et al. 1985; Whipple et al. 2000). Consequently, understanding the factors regulating predator-prey interactions is an important consideration in applying a more holistic, ecosystem-based approach to managing fisheries resources (Link 2002; Latour et al. 2003). One of the challenges to advancing knowledge on predator-prey interactions is to continue moving beyond basic diet descriptions by evaluating the factors regulating the dynamics of food web linkages, including how environmental conditions and prey availability alter foraging patterns (Link 2002; Hunsicker et al. 2011).

Chesapeake Bay is one model system where researchers and managers are interested in understanding how the environment and prey availability regulate dynamic predator-prey interactions, in part to facilitate ecosystem-based fisheries management (EBFM) efforts (Houde 2006; Christensen et al. 2009). Chesapeake Bay is the largest juvenile nursery and estuarine foraging ground in the northwest Atlantic Ocean, supporting many fish stocks and their commercial and recreational fisheries (Able and Fahay 2010). Consequently, variability in predator-prey interactions in the bay can influence recruitment, growth, mortality, and production of many valuable fishes. Mysids, bay anchovy, bivalves, and polychaetes, in particular, are four key prey groups in Chesapeake Bay that have a proportionately large
influence on the bay’s diverse fish assemblage (Buchheister and Latour 2015). However, there is limited information on the basic biological and ecological characteristics of these prey groups (particularly mysids) and their trophic interactions with predators at larger spatiotemporal scales in estuaries. The availability of extensive fish diet data in Chesapeake Bay (Buchheister and Latour 2015) provides a unique opportunity for obtaining some of this information.

Fishes are biological samplers of their environment and thus predator diets can be used as indicators of prey dynamics and availability, particularly for cryptic or poorly sampled prey groups. Generally, prey consumption rate for an un-satiated predator increases with the prey’s density (Holling 1959), and many fishes are generalist or opportunistic feeders whose foraging is strongly regulated by prey encounter rates (Gerking 1994; Juanes 1994). These density-dependent foraging characteristics have allowed scientists to use predator diets to estimate prey distributions (Fahrig et al. 1993; Link 2004), derive annual indices of relative prey abundance (Link 2004; Mills et al. 2007), and corroborate long term changes in prey availability (Dwyer et al. 2010; Pálsson and Björnsson 2011).

Making inferences on prey availability from predator diets can be biased by environmental conditions, prey selectivity, and foraging efficiency (Eggers 1977; Juanes 1994). These potential biases are analogous to difficulties faced in deriving indices of relative abundance from traditional fish survey gears, and two approaches are useful in that context. First, statistical models can standardize indices by partitioning variability and accounting for the effects of different covariates (Maunder and Punt 2004; Kimura and Somerton 2006) and second, multiple gear types with different sampling properties can be used synoptically to derive more robust estimates of a desired response variable. Extension of this reasoning to trophic studies suggests that indices of prey consumption would be more representative of prey availability once
standardized for heterogeneous environmental conditions that introduce variability into predator-prey interactions, and also that synchronous patterns across multiple predators would strengthen the robustness of conclusions for individual prey. An added benefit of this prey-centric analytical approach is that when limited biological data exist for the prey, the effects of modeled covariates can be used to draw inference on prey distribution, availability, and dynamics.

In this study, we evaluate the trophic interactions among several dominant fishes and key prey groups in Chesapeake Bay. We used diet composition data from an extensive, multi-seasonal bottom trawl survey of Chesapeake Bay fishes to address three objectives: 1) evaluate the influence of predator length, spatiotemporal factors, and environmental drivers on prey consumption by 12 common Chesapeake Bay predators, 2) compare diet patterns across predators to infer basic dynamics of four key prey groups, and 3) evaluate whether interannual consumption trends were coherent among predators and correlated with annual prey abundance. We detail the trophic dynamics for several predators and prey groups that occur ubiquitously in estuarine and nearshore coastal waters throughout the Atlantic, contributing to ongoing efforts in ecosystem modeling and EBFM in Chesapeake Bay and the continental shelf (Latour et al. 2003; Houde 2006; Link et al. 2011). From a methodological perspective, this work is a novel application of delta generalized additive mixed models to draw ecological inference from dietary data while addressing several statistical problems common in trophic studies.

**Methods**

**Field and laboratory methods**

Data were obtained from the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP), operated by the Virginia Institute of Marine Science. Since 2002, this bottom trawl survey has sampled the Chesapeake Bay mainstem using a random-stratified design.
with stations stratified by depth and latitude (Fig. 1). Typically, five cruises were conducted per year (bimonthly from March to November), with approximately 80 stations sampled per cruise. Data on latitude, longitude, water depth, bottom temperature, salinity, and dissolved oxygen were collected at each station. After catches were sorted, species with broad length distributions or discrete length groups were further sorted into 2-4 size classes, random individual subsamples from the species-size-class groups were processed for weight and length (fork length for teleosts; disc width for batoids), and stomachs were removed for diet analysis. If stomachs were visually confirmed to be empty in the field, additional specimens (when available) were processed to obtain 3-5 nonempty stomachs per species and size class. In the laboratory, contents from preserved stomachs were sorted by trained technicians, identified to the lowest possible taxon using dissection microscopes, and prey categories weighed to the nearest 0.001 g.

We focused on four prey groups for this study: 1) mysid shrimp (primarily *Neomysis americana*), 2) bay anchovy (*Anchoa mitchilli*, with very minor contribution of *Anchoa hepsetus*), 3) bivalves (dominant species included *Ensis directus*, *Gemma gemma*, *Macoma spp.*, *Mercenaria mercenaria*, *Mya arenaria*, and *Tagelus plebeius*), and 4) polychaete worms (including families Capitellidae, Chaetopteridae, Glyceridae, Maldanidae, Nereidae, Pectinariidae, Terebellidae). These four prey groups were chosen because they represent relatively unique functional morphologies and are largely responsible for differentiating among fish trophic guilds within Chesapeake Bay (Buchheister and Latour 2015). The bivalve and polychaete groups were defined at a coarse taxonomic level because 1) prey were often not identifiable to greater taxonomic resolution due to digestion, 2) sample sizes were relatively low for predators with identifiable bivalve and polychaete taxa. Predators for each of the four prey groups were restricted to species with >15% frequency occurrence and a minimum sample size.
of 140 stomachs that contained the prey group. These two criteria excluded predators that rarely consumed a given prey group and omitted predators with low sample sizes. These restrictions yielded a total of 12 predator species with a total of 29,350 analyzed stomachs (Table 1). Depending on the species, 9-42% of sampled fish stomachs were empty (27% overall). Each predator-prey combination was represented by at least 146 fish and up to 2,301 fish that contained the prey of interest. Summaries of general diet compositions (% weight) for the selected predators were calculated using a cluster sampling estimator by pooling across all available non-empty stomachs (see Buchheister and Latour 2015 for equations).

**Delta generalized additive mixed models**

Statistical analysis of stomach content data is often complicated by three statistical issues. First, diet data often suffer from an overabundance of zero values that does not conform to standard statistical distributions. Second, samples of fish stomachs often violate the assumption of independence when multiple individuals are captured at the same location or when individuals are sampled repeatedly through time (e.g., in experimental studies) because samples will be auto-correlated in time and space (Hurlbert 1984; Bogstad et al. 1995; Millar and Anderson 2004). Third, the effects of covariates (e.g., temperature, predator size) on diets are often non-linear.

To account for these three complications, we applied delta generalized additive mixed models (delta-GAMM) to model the consumption of a prey group by an individual predator species. This approach built on the methods promoted by Stefánsson and Pállsson (1997) by accounting for the non-independence of the diet samples using random effects. Delta-GAMM combines statistical aspects of delta models (also known as two-part, hurdle, or zero-altered models), generalized additive models (GAM), and mixed effects models. The use of a GAM
allows for the effect of covariates to take flexible, nonlinear forms that are dictated by a
smoothing function (Wood 2006), but GAMs rely on the assumptions of independent and
identically distributed errors with constant variance. To account for the violation of the
independence assumption caused by the intra-station (i.e., intra-haul) correlation and by the
nested nature of the sampling design, we included station as a random effect in a mixed model
(Wood 2006; Zuur et al. 2009). To deal with the high frequency of zero values, the delta
approach was used to model the data in two parts: first, the presence-absence of a given prey in
the stomachs of a predator was modeled (termed the “binomial” model henceforth); and second,
the weight of prey consumed was modeled, provided that the prey occurred in the stomach
(termed the “positive” model henceforth). All models were fitted to individual predator-prey
combinations.

The binomial models estimated the probability that a stomach contains the prey of
interest, analogous to modeling the frequency of occurrence of a given prey. The first, binomial
stage of the delta-GAMM modeled presence absence data ($a_{ij}$) as $a_{ij} \sim \text{binomial}(1, p_{ij})$ with

$$\logit(p_{ij}) = \alpha + \beta(YR_i) + f_1(L_i) + f_2(LA_i) + f_3(T_i) + f_4(D_i) + b_j$$

where $\logit(p_{ij}) = \log(p_{ij}/(1-p_{ij}))$, $p_{ij}$ is the expected probability that fish $i$ from station $j$ contains
the prey of interest, $\alpha$ is the overall intercept, $\beta$ is a vector of parametric effects for the
categorical year ($YR$) factor, and $f_{1-4}$ are smooth 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 $\sigma_b^2$. Available data on longitude, salinity, dissolved
oxygen, and month were not included in the model to avoid convergence issues resulting from
overly complex models and to avoid slight collinearity among some variables. Models with interactions among variables (including variable coefficient GAMM; Wood 2006) were not formally evaluated because 1) graphical analyses did not indicate the presence of strong interactions (Zuur et al. 2010), 2) they would decrease sample sizes and precision of covariate effects, and 3) they often prohibited model convergence based on preliminary analyses.

The second, positive component of the delta-GAMM excludes all zeros and models the quantity of prey consumed, relying on an appropriate data distribution. We chose to model the biomass of prey consumed because this measure is more meaningful than prey counts in dictating the transfer of energy through food webs (e.g., Pauly et al. 2000). Also, prey abundance could not always be quantified due to digestion. We did not back-calculate the fresh weights of consumed prey, but instead assumed that the modeled covariate effects on the measured weights would be representative of the processes regulating consumption of fresh prey. Prey biomass was not modeled with a gamma distribution as done by Stefánsson and Pálsson (1997) because this distribution resulted in convergence issues for most predator-prey combinations in the GAMMs. Instead, we used a log-transformation of the biomass data in conjunction with a Gaussian distribution to alleviate convergence issues and homogenize the originally heteroscedastic residuals. The model for the second stage of the delta-GAMM, restricted to fish stomachs that contained a given prey, was defined as:

\[
\log(\mu_{ij}) = \alpha + \beta(YR_i) + f_1(L_i) + f_2(LA_i) + f_3(T_i) + f_4(D_i) + b_j + \varepsilon_{ij}
\]

where \(\mu_{ij}\) is the expected mass (in g) of a prey group in the stomach of fish \(i\) from station \(j\) given the random effect \(b_j\), and \(\varepsilon_{ij}\) is the residual error for each fish and station assumed to be normally distributed with a mean of zero and variance of \(\sigma^2\) (Wood 2006; Zuur et al. 2009). Definitions for all remaining components of the model are identical to those for equation 1.
All GAMMs were fitted to data from each of the 22 predator-prey combinations (Table 1), and Akaike’s Information Criterion (AIC) was used to select the optimal fixed effects structure (Burnham and Anderson 2002). Models with all possible combinations of explanatory variables were evaluated, with the exception that $YR$ was retained in all iterations to evaluate interannual consumption trends (objective 3). Partial effects plots for the best-fit models were used to demonstrate the effect of each covariate on the response after accounting for all other covariates in the model, and they were presented on the scale of the linear predictor (logit scale for binomial model results; log scale for positive model results). Goodness-of-fit measures (e.g., percent of deviance explained or $R^2$) are still being developed for mixed models (Nakagawa and Schielzeth 2013) and there is no standard summary statistic for overall GAMM fit, so these measures were not estimated. However, as a general proxy for overall goodness of fit, a fixed-effects version of each model (without the random station effect) was fitted to estimate the percent of deviance explained by the model. We fitted all statistical models with the gamm4 package (Wood 2012) in R 3.0.1 (R Core Team 2013).

**Annual trends in consumption**

A combined index of prey consumption for year $y$ ($C_y$) was obtained for each predator-prey combination by multiplying predictions for the binomial and positive components of the best-fit delta-GAMMs. The consumption index was calculated as $C_y = p_y \cdot \mu_y$ where $p_y$ is the expected probability that a predator from year $y$ consumed a given prey, and $\mu_y$ is the expected mass of the prey in a predator’s stomach in year $y$. Predictions were standardized for the other covariates by holding them constant at the mean values observed for each predator species (e.g.,
see Table 1 for mean predator lengths). All \( \mu_y \) values were bias-corrected for back transformation from lognormal space (Sprugel 1983).

To evaluate the similarity in prey consumption patterns across predators and the influence of prey availability, Pearson correlations (R) were calculated among predator estimates of logged \( C_y \) and indices of prey abundance. Logging of consumption indices was needed to normalize the data distributions and to prevent biased correlations due to outlier values. Indices of annual biomass for polychaetes and bivalves were calculated as geometric means (mean of \( \log(x+0.001) \), where \( x = \) biomass density in g m\(^{-2}\)) using data from the Chesapeake Bay Benthic Monitoring Program for the randomly selected stations surveyed within the bay mainstem (Versar, Inc., [www.baybenthos.versar.com](http://www.baybenthos.versar.com)). Bivalves from this dataset were restricted to the most common species found in predator stomachs (\( Ensis \) directus, \( Gemma \) gemma, \( Macoma \) spp., \( Mercenaria \) mercenaria, \( Mya \) arenaria, and \( Tagelus \) spp.), but only \( Macoma \) spp. and \( Gemma \) gemma were regularly sampled (occurring in 49% and 13% of stations, respectively). Annual abundance indices for bay anchovy were obtained from the Virginia Institute of Marine Science Juvenile Fish and Blue Crab Trawl Survey (Tuckey and Fabrizio 2012). Data on patterns of mysid annual abundance were not available from any existing Chesapeake Bay monitoring program. Significance of Pearson correlations were determined from critical R values based on Bonferroni-adjusted \( \alpha \) values (\( \alpha_{\text{adjusted}} = 0.05/n \), where \( n \) is the number of pairwise correlations for a given prey group). Spot were omitted from correlation analysis due to lack of stomach content data from 2002-2007. To facilitate visual comparison of annual consumption and prey indices across predators, all \( C_y \) values and prey indices were standardized to range from 0-1. These standardized \( C_y \) values were calculated as \( (C_y - C_{\text{min}})/(C_{\text{max}} - C_{\text{min}}) \), where \( C_{\text{min}} \) and \( C_{\text{max}} \) are the minimum and maximum values for \( C_y \) across the time series.
Results

The four prey groups of focus contributed substantially to predator diets. Collectively, bay anchovy, mysids, bivalves, and polychaetes accounted for large fractions of the fish diets (13-64%), reinforcing the broad importance of these prey to the examined predators (Fig. 2). Individual prey groups contributed as much as 41% to the overall diet of a predator, though these dietary contributions can be greater for specific predator size classes (Buchheister and Latour 2015).

Generalized additive mixed modeling

The best-fitting binomial and positive GAMMs included various combinations of the explanatory variables, ranging from all variables to none of the variables (except YR, which was forced; Table 2). Generally, the binomial models were more complex than the positive models; however, this may be partially attributed to lower samples sizes for positive models which may have restricted the ability to detect significant covariate effects. Proxies for the deviance explained by models varied among predator-prey combinations, ranging from 4.3-36.7% (mean 14.1%) for binomial models and 5.4-49.3% (mean 19.6%) for positive models. These goodness of fit values are comparable to other dietary studies that employed additive models and reflect the relatively large amount of variability inherent in diet composition data (Stefánsson and Pálsson 1997; Santos et al. 2013).

Length and latitude were typically the two most important covariates in the models (Table 2), indicating the importance of both size limitation and spatial dynamics in trophic
interactions. Most binomial models of prey consumption included length and latitude as significant covariates; best-fitting models that did not include length were typically for predators with relatively smaller length ranges. Significance of depth and temperature varied by prey; depth was not important for bivalves, and temperature was typically excluded from polychaete models. For the positive models, predator length was again a consistently important covariate, yet few models included latitude or temperature. Only two positive models revealed significant effects of water depth.

Consumption of mysids by predators was strongly influenced by the modeled covariates. Predator length produced the strongest effect on the probability of mysids being consumed, with larger individuals far less likely to consume this small-bodied prey (Fig. 3). The prey biomass consumed tended to increase across predators at smaller sizes prior to declining, with this transition occurring between ~150-300 mm (Fig. 3). Both the occurrence and the biomass consumed indicated greater mysid availability at lower latitudes for the predators with the largest sample sizes (Fig. 3). Temperature effects on mysid occurrence and biomass were inconsistent across predators, preventing clear conclusions regarding the influence of temperature on mysid dynamics. Mysid occurrences in stomachs were slightly greater at shallower depths, but weakfish contradicted this pattern.

Bay anchovy consumption was strongly influenced by predator length (Fig. 4). The parabolic shape for the binomial model indicates a strong peak in prey occurrence at sizes ~175-300 mm, with weakfish targeting bay anchovy at slightly smaller sizes than summer flounder and striped bass. The mass of bay anchovy found in stomachs increased with predator size until leveling off at sizes that corresponded to the peaks in bay anchovy occurrence (Fig. 4). A size effect on biomass consumed was not detected for striped bass. Effects of latitude on the
probability of bay anchovy consumption differed by predator, with striped bass opposing the
trend of greater bay anchovy occurrence at higher latitudes. Temperature effects varied by
 predator, and again striped bass opposed the general trend detected for the other species.
Weakfish and summer flounder results indicated greater probability of bay anchovy consumption
at lower temperatures. Depth effects on occurrence were negligible, although there was some
evidence for increased bay anchovy occurrence in shallower water.

Consumption of bivalves by Chesapeake Bay predators was strongly influenced by
predator length and latitude (Fig. 5). Dietary occurrence of bivalves increased with length for
Atlantic croaker, white perch, and northern puffer, but appeared to reach an asymptote for
Atlantic croaker. The biomass consumed also increased steeply with predator size. When viewed
in unison, the latitude effects for all predators demonstrated a decreased occurrence of bivalves
in stomachs at mid-latitudes, with increases in both the lower and upper bays (Fig. 5). For
Atlantic croaker, the mass of consumed bivalves also supported this parabolic latitudinal trend in
prey availability. Water temperature had a positive effect on bivalve occurrence in fish stomachs
for three species, but only white perch showed a similar positive relationship when modeling
prey biomass. Depth was not a significant covariate for any of the bivalve GAMMs.

Patterns of polychaete consumption showed varied responses to covariates depending on
the predator. Dietary occurrence of polychaetes varied greatly by predator length depending on
the species, but tended to increase with size before decreasing at larger sizes (Fig. 6). The biggest
exception to this pattern was for kingfish for which occurrence decreased monotonically. The
biomass of consumed polychaetes increased with predator length at similar rates across
predators, with only striped bass showing a reliable indication of saturation at larger sizes (Fig.
6). Latitudinal effects on the probability of polychaete consumption tended to show an inverse
pattern to bivalve occurrence by latitude (Figs. 5, 6). Polychaete occurrences were generally greatest in mid-latitudes, but latitude did not have significant effects on biomass of consumed polychaetes for the majority of modeled predators (Fig. 6). Temperature effects on polychaete occurrence and biomass were largely negligible across the majority of predators (Fig. 6). Depth effects on polychaete occurrence were inconclusive as a whole at shallow depths, but most fishes indicated decreasing occurrence as depth increased beyond ~10 m (Fig. 6).

**Annual trends in consumption indices**

Standardized indices of annual prey consumption varied through the time-series but demonstrated some synchronous and coherent trends across predators. Generation of the annual consumption index clarified the interpretation of the year effects from individual binomial and positive GAMM models (Fig. S1). Five of seven predators (Atlantic croaker, northern searobin, scup, summer flounder, weakfish) exhibited a distinct annual peak in consumption of mysids in 2003, with a magnitude dramatically greater than other years (Fig. 7). Correlations among annual trends for these five species were strong and ranged from 0.56-0.90, with 3 of 10 values being significant (R>0.84, Bonferroni-corrected p<0.05; Table 3). Only striped bass and spotted hake did not conform to this pattern. Consumption of bay anchovy by summer flounder and striped bass exhibited largely synchronous changes in directionality (Fig. 7) and were strongly correlated (R=0.71), though not significantly. Although consumption indices were not correlated with the bay anchovy index (Table 3), the highest consumption values for summer flounder and weakfish (and second highest value for striped bass) were obtained in 2010 when the prey index was at its highest. Bivalve consumption had a peak in 2008 that was shared by all predators (Fig. 7). Although some bivalve trends were strongly correlated with one another or with the prey...
index (R=0.69-0.74), none were significant (Table 3). Consumption indices of polychaetes were highly variable among predators; however, the highest values occurred in the last five years of the time series, and four of the seven predators (Atlantic croaker, scup, spot, and white perch) consumed the greatest amount of polychaetes in 2010 (Fig. 7). None of the pairwise polychaete correlations among predators and the prey index were significant (Table 3).

Discussion

Biological, environmental, and spatiotemporal factors strongly regulated predatory consumption of four key prey groups in Chesapeake Bay. Despite the notorious variability of fish diet data generated from the complex processes that influence trophic dynamics (Gerking 1994; Wootton 1998), the use of an extensive data set, multiple opportunistic predators, and the novel application of delta-GAMMs aided in illuminating more robust commonalities in feeding patterns that appear to be linked to prey availability at both small and large scales. Predator length and latitude were particularly important covariates influencing many predator-prey interactions. Coherent annual peaks in mysid, bay anchovy, and bivalve consumption were suggestive of episodic, annual pulses in prey productivity that may be mediated by bottom-up processes. These dynamic changes in consumptive patterns have the potential to influence regional and annual patterns in fish productivity (e.g., Buchheister et al. in review) and are thus an important consideration in managing fisheries in a broader, ecosystem context (Link 2010).
Predator length as a strong determinant of diet

Predator length was the most consistently important determinant of prey consumption, supporting a vast literature that emphasizes the significance of body size in structuring trophic interactions (e.g., Juanes 1994; Scharf et al. 2000; Kerr & Dickie 2001). Among other things, body size regulates the foraging process by controlling the physical constraints on the size and types of prey that can be ingested, the speed and endurance of a predator, the relative success of foraging attacks, and the visual limit for prey detection (Eggers 1977; Scharf et al. 2002). In this study, the binomial GAMM effects for predator length provide information on the continuous functional forms of relative prey occurrence in predators of varying sizes. The forms of these size-based occurrence curves were either linear, asymptotic, or dome-shaped (which translate to sigmoidal, asymptotic, and dome shapes when converted to the 0-1 probability scale). The sigmoidal decline in consumption of mysids supports their greater importance to juveniles and smaller sized individuals (Mauchline 1980; Hostens and Mees 1999), while the sigmoidal or asymptotic increase in bivalve consumption suggests this prey is a “terminal” prey for which occurrence is greatest at the most advanced ages and sizes that were sampled (Buchheister and Latour 2015). The dome shapes for bay anchovy and polychaetes identified these prey as being transitional forage resources as predators grew (through the examined sizes), reaching consumption optima at intermediate sizes. Generally, these bay anchovy optima corresponded with significant shifts in diet composition based on discrete size-class cutoffs (Latour et al. 2008; Buchheister and Latour 2015), and they also corresponded with published distributions of predator-prey size ratios for summer flounder and weakfish (Scharf et al. 2000). The empirically-derived occurrence curves may be useful in informing the parameterization of size-based
components of prey suitability functions that are used in foraging or multispecies models (Garrison et al. 2010).

**Prey dynamics**

Predator diets contributed to the basic understanding of mysid distribution and abundance. Despite the importance of mysids in estuarine and marine food webs (Mauchline 1980, Jumars 2007), relatively little is known about basic mysid dynamics in Chesapeake Bay and similar estuaries. Our diet analysis suggests mysid availability and presumably density was highest at lower latitudes in the Chesapeake Bay’s polyhaline region near the mouth. In contrast, densities of *N. americana*, the predominant mysid in local fish diets (Buchheister and Latour 2015), peaked at mesohaline salinities ~50-90 km away from the mouth of Delaware Bay (Hulburt 1957, Cronin et al. 1962). These trends are consistent with the hypothesis that coastal waters act as the major source for estuarine mysid populations (Whitely 1948; Hulburt 1957; Hopkins 1965), and they suggest that physical advection and distance from the coastal population source may be more important than specific salinity regimes in dictating estuarine mysid distributions in large estuaries like Chesapeake Bay. However, mysid consumption did occur throughout the entire sampled area, likely supported by local estuarine reproduction that can occur through their hypothesized 2-3 annual reproductive cycles (Hulburt 1957) and their tolerance for a broad range of salinities (Mauchline 1980). Although mysid populations tend to peak in summer months with warmer temperatures, mysids can be found throughout the year in Mid-Atlantic estuaries (Hulburt 1957; Hopkins 1965). This seasonal ubiquity contributed to the lack of consistent dietary occurrence trends with temperature, and supports the importance of mysids as a food resource throughout the year to a variety of resident and seasonally migrating
predators (Buchheister and Latour 2015). Analyses suggested greater mysid availability in relatively shallower bay areas (4-15 m) based on the diets, contrary to trends in Delaware Bay where Hulburt (1957) noted low mysid concentration in areas <5.5 m. However, his study sampled during daylight hours in surface waters when mysids typically reside on the benthos (Herman 1963).

Bay anchovy are the most abundant fish in the Chesapeake Bay and they contribute substantially to the production of commercially and recreationally important piscivorous species like striped bass, summer flounder, weakfish, and bluefish (Baird and Ulanowicz 1989; Houde and Zastrow 1991). For many piscivores, bay anchovy acts as a key forage species that bridges the transition from small zooplanktonic and benthic prey to larger forage fishes (Buchheister and Latour 2015, this study). The conflicting latitudinal and temperature trends in bay anchovy consumption between striped bass and the other predators were likely related to spatiotemporal differences in predator-prey overlap. Bay anchovy tend to be more abundant in the mid-bay in the summer months, prior to moving to the lower bay and inner continental shelf to overwinter (Wang and Houde 1995; Jung and Houde 2004). Summer flounder and weakfish, exhibit life history strategies that favor use of the lower bay during warmer months (Latour et al. 2008; Able and Fahay 2010), opposing the distributional patterns of the anadromous striped bass that tends to favors the upper bay with higher densities in cold months. Thus, use of diets to infer relative prey availability is challenging when both the prey and its predators exhibit different migratory life histories. Regarding depth, the observed dietary trends correspond with previous work suggesting that, although bay anchovy occur at a variety of depths, they tend to be more rare in deeper waters >25 m (Houde and Zastrow 1991).
The trends of bivalve and polychaete consumption revealed broad-scale patterns in the availability of macrobenthic prey for demersal fishes in Chesapeake Bay. These patterns were detected within each of the two general prey groups, despite the need to aggregate numerous taxa for logistical reasons. The decline of bivalve consumption and increase of polychaete consumption in mid-latitude, mesohaline waters could be influenced by two principal mechanisms relating to prey availability. First, regional biogeography and physico-chemical preferences (e.g., salinity, sediment type) largely dictate the bay regions in which individual macrobenthic species reside (Holland et al. 1987; Diaz and Schaffner 1990). For example, *Macoma* and *Gemma* clams favor the more moderate salinities of the mid- to upper-bay, while *Ensis* and *Tagelus* reside in more polyhaline, low-latitude waters (Diaz and Schaffner 1990). Thus, latitudinal trends of bivalve and polychaete prey are an amalgamation of effects generated from individual species that comprise each of the macrobenthic prey groups. A second potential mechanism relates to chronic and acute habitat degradation. Extensive seasonal hypoxia caused by eutrophication, physical stratification, and bacterial remineralization of organic matter is a dominant environmental feature in the bay from June to August, persisting up to 3 months in some areas (Murphy et al. 2011). Hypoxia diminishes macrobenthic productivity and biomass more strongly in deeper mid-bay waters relative to upper and lower bay regions during the summer months (Holland et al. 1987; Kemp et al. 2005). This decreased production may have contributed to the declines in mid-bay bivalve consumption, whereas the increased dietary occurrence of polychaetes in the mid-bay could be attributed to their greater tolerance of low oxygen conditions relative to bivalves (Vaquer-Sunyer and Duarte 2008; Sturdivant et al. 2013) or their tendency to more quickly recolonize benthic habitats once waters become re-oxygenated (Rosenberg et al. 2002). Effects of hypoxia on mid-bay macrobenthic prey availability are not
isolated to summer, as habitat degradation and seasonal hypoxia-induced mortality have shifted
the annual benthic community to smaller, shorter-lived species with lower standing stock
biomass (Holland et al. 1987; Kemp et al. 2005). Indeed, the latitudinal trend in bivalve
consumption was detected in all sampled months (A. Buchheister, unpublished data), suggesting
that species biogeographical distributions and long-term degradation of mid-bay habitats may be
more influential on macrobenthic consumption than direct seasonal hypoxic effects, particularly
considering that fishes avoid the low oxygen waters (Buchheister et al. 2013).

**Annual patterns in prey consumption**

Despite the lack of concordance between indices of prey abundance and consumption
overall, there was strong evidence of prey availability regulating annual consumption indices of
individual Chesapeake Bay predators, as supported in many other systems (Fahrig et al. 1993;
Mills et al. 2007; Dwyer et al. 2010; Pálsson and Björnsson 2011). The strongest empirical
indication that prey availability was involved in the annual trends was the coherence in peak
consumption of mysids, bivalves, and bay anchovy by predators with varied feeding preferences,
foraging modes, and distributional patterns. For example, two benthivorous species (Atlantic
croaker and scup) exhibited the same 2003 peak in mysid consumption as other zooplanktivorous
and piscivorous species (Northern searobin, summer flounder, weakfish), despite having diets
that do not typically target mysids (Buchheister and Latour 2015). Also, an upper bay species
(white perch) demonstrated a similar bivalve consumption peak as other lower bay predators,
even though the bivalve genera that predominate in these regions differ with *Macoma* clams in
the mid and upper bay and *Ensis* and *Tagelus* clams in the lower bay. These synchronous dietary
patterns likely relate to 1) the density-dependent feeding behavior of animals (Holling 1959), and
2) the opportunistic feeding strategies that evolved to allow fishes to exploit spatiotemporally-patchy prey resources in dynamic, heterogeneous environments (Gerking 1994).

Presumably, different environmental or ecological conditions supported large pulses in prey production during certain years (mysids – 2003; bivalves – 2008; bay anchovy – 2010) that were utilized by a variety of predators that adapted to the greater prey availability. For example, mysid consumption was correlated with mean annual spring temperature, spring salinity, and surface chlorophyll-a (A. Buchheister, unpublished data), with 2003 being a distinct year in the environmental time series as with the annual consumption indices. Those conditions could have contributed to greater mysid production through bottom-up processes including improved local reproduction during the spring spawning event, greater overall phytoplankton food availability that improved juvenile or adult survival, or greater immigration of mysids from coastal waters (Hopkins 1965, Ezzack and Corey 1979). Indeed, bottom-up mechanisms have been implicated as drivers of ecosystem structure, fish recruitment, and fisheries landings in the Chesapeake Bay and Mid-Atlantic Bight (Frank et al. 2007; Hare and Able 2007), and the dietary trends documented are consistent with such donor control in food webs. However, any speculations on specific mechanisms driving pulses in production of mysids, bay anchovy, or bivalves require more directed and targeted research.

The general lack of concordance between prey abundance indices and the consumption indices can be partially explained by 1) biases in prey sampling (whether by survey gear or by predators) and 2) the different spatiotemporal scales represented by each index. First, possible survey biases include: the long-term benthic monitoring program excluding Maryland waters (>12 m; that survey only sampling from July to September (after the macrobenthic biomass is affected by summertime hypoxia); and the bay anchovy index being derived from a bottom trawl
survey that is not optimal for sampling pelagic species. Predator consumption biases largely take the form of prey selectivity (Eggers 1977; Juanes 1994), but annual consumption trends were mirrored by the annual effects from the binomial models, whose presence/absence data tend to be less biased by prey selectivity than gravimetric diet estimates (Link 2004; Baker et al. 2014).

Second, inference at the broad, annual scale can be obfuscated by variation in distributional changes and spatiotemporal overlap of predators and prey. For example, the absence of peaks in mysid consumption by striped bass and spotted hake in 2003 is likely due to the absence of these predators in lower latitudes from July to September, where mysids appear more concentrated and when mysid biomass peaks (Hulburt 1957; Hopkins 1965). Use of multiple predators with contrasting life histories helped identify incongruous overlap situations such as this, but interpretation of patterns is more challenging when both predator and prey are highly mobile (as was the case for bay anchovy and their predators). Inadequate contrast in annual prey densities has been identified as another complicating factor in detecting density-dependent diet signals (Pinnegar et al. 2003). Also, indices of prey standing stocks may not be fully representative of prey production rates, particularly for shorter lived prey groups with multiple or continuous recruitment events throughout the year.

Methodological considerations

When modeling the consumption of an individual prey group, there is a potential for interactions among prey caused largely by prey selectivity and prey switching (Eggers 1977; Juanes 1994; Stefánsson and Pálsson 1997), such that the consumption of one prey influences the consumption of another. There is some evidence of prey interaction between mysids and bay anchovy (Buchheister 2013), but the interaction is confounded by the strong opposing
ontogenetic trends in consumption for these two prey. The decreased likelihood of mysid consumption when bay anchovy are present in a stomach (Buchheister 2013) could be driven more by the size-based shifts in feeding as opposed to active prey selection (Juanes 1994), or by patchiness of prey that can reduce the likelihood of joint occurrence of prey. Undoubtedly, prey selectivity and the choices predators make at small scales can influence broader consumptive trends of multiple prey, but disentangling these effects from other system interactions, indirect food web effects, and spatiotemporal changes in predator-prey overlap require continued research.

Generalized additive mixed effects models provided a powerful and flexible approach for drawing more robust statistical inferences from stomach content data. The biggest advantages of these models included the ability to 1) appropriately handle the excessive number of zeros in an approach that is ecologically meaningful, 2) account for the correlation structure of the hierarchical sampling design that is common in fisheries surveys, 3) incorporate a variety of categorical and continuous explanatory variables, 4) account for nonlinear effects of covariates on the response, and 5) maintain diet information at the individual fish level, to avoid pooling data as is needed for average-based analytical methods (e.g., pooling predators into size classes was not required). However, as with other statistical modeling, GAMM convergence was largely predicated on having sufficient sample sizes for models of greater complexity. Proxies for goodness of fit and precision of covariate effects were poor in some cases, but this is largely attributable to the large variability in ecological datasets that are typically noisy. The major dietary patterns and general conclusions of the study where not altered by the exclusion of the random station effect (nor replacing it with a random stratum effect), but accounting for the non-independence of fish is more statistically valid and helps avoid erroneous conclusions (Hurlbert...
1984, Millar and Anderson 2004). Although GAMMs have been described as being on “the frontier of statistical research” (Zuur et al. 2009), these and related methods are being advanced quickly and are becoming more accessible to researchers (Wood 2006; Zuur et al. 2009); thus, they are rapidly being integrated into the statistical toolboxes of many ecologists and fisheries scientists (e.g., Venables and Dichmont 2004; Ciannelli et al. 2008).

Implications

Comprehensive, spatiotemporally-extensive trophic studies such as this work help elucidate the trophic relationships and drivers that structure ecosystems, and can contribute to implementation of EBFM. The coherence in annual prey consumption indices of multiple predators supports their utility as indicators of relative prey abundance that could augment current prey sampling surveys (e.g., Mills et al. 2007), and such diet metrics may be particularly useful for monitoring or hindcasting key prey groups, such as mysids, for which systematic sampling does not exist. EBFM applications of this type of research include parameterization of multispecies and ecosystem models (Pauly et al. 2000), use of dietary indices as ecosystem indicators (Dwyer et al. 2010), empirical information for helping parameterize prey vulnerabilities within foraging sub-models (Garrison et al. 2010), fitting of functional response curves if consumptions are expressed as rates (Moustahfid et al. 2010), and potentially the use of diet time-series as additional tuning indices for ecosystem models. Continued research on trophic dynamics, particularly focused on long time periods and broader spatial extents, will provide valuable information on fish and food web ecology to support EBFM at the scales most pertinent to resource management.
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anchovy *Anchoa mitchilli* to bluefish predation: Does large body size always provide a

marine fish predators: interspecific variation and effects of ontogeny and body size on


Table 1. Sample summaries for Chesapeake Bay predators collected for dietary analysis. Length measurements were recorded as fork length (teleosts) or disc width (batoids). \(N_s\) = Number of stations with predator captured, \(N_f\) = Number of individual fish sampled for stomachs, \(P_e\) = percentage of fish stomachs that were empty. Numbers of fish containing key prey groups are indicated.

<table>
<thead>
<tr>
<th>Predator</th>
<th>Range (mm)</th>
<th>Length (mm)</th>
<th>(N_s)</th>
<th>(N_f)</th>
<th>(P_e)</th>
<th>Any Prey</th>
<th>Mysid</th>
<th>Anchovy</th>
<th>Bivalve</th>
<th>Polychaete</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atlantic croaker ((\textit{Micropogonias undulatus}))</td>
<td>20 - 478</td>
<td>242</td>
<td>977</td>
<td>3374</td>
<td>14</td>
<td>2914</td>
<td>458</td>
<td>--</td>
<td>550</td>
<td>1753</td>
</tr>
<tr>
<td>Clearnose skate ((\textit{Raja eglanteria}))</td>
<td>84 - 519</td>
<td>412</td>
<td>355</td>
<td>941</td>
<td>13</td>
<td>821</td>
<td>--</td>
<td>--</td>
<td>146</td>
<td>--</td>
</tr>
<tr>
<td>Kingfishes ((\textit{Menticirrhus spp.})*)</td>
<td>45 - 383</td>
<td>236</td>
<td>399</td>
<td>1077</td>
<td>18</td>
<td>882</td>
<td>--</td>
<td>--</td>
<td>179</td>
<td>178</td>
</tr>
<tr>
<td>Northern puffer ((\textit{Sphoeroides maculatus}))</td>
<td>49 - 272</td>
<td>156</td>
<td>407</td>
<td>1087</td>
<td>9</td>
<td>990</td>
<td>--</td>
<td>--</td>
<td>292</td>
<td>180</td>
</tr>
<tr>
<td>Northern searobin ((\textit{Prionotus carolinus}))</td>
<td>40 - 223</td>
<td>127</td>
<td>387</td>
<td>941</td>
<td>20</td>
<td>751</td>
<td>381</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Scup ((\textit{Stenotomus chrysops}))</td>
<td>69 - 223</td>
<td>123</td>
<td>347</td>
<td>879</td>
<td>17</td>
<td>732</td>
<td>150</td>
<td>--</td>
<td>--</td>
<td>268</td>
</tr>
<tr>
<td>Spot ((\textit{Leiostomus xanthurus}))</td>
<td>40 - 311</td>
<td>156</td>
<td>616</td>
<td>2217</td>
<td>29</td>
<td>1581</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>556</td>
</tr>
<tr>
<td>Spotted hake ((\textit{Urophycis regia}))</td>
<td>50 - 318</td>
<td>147</td>
<td>244</td>
<td>609</td>
<td>19</td>
<td>491</td>
<td>323</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Striped bass ((\textit{Morone saxatilis}))</td>
<td>92 - 1051</td>
<td>372</td>
<td>1005</td>
<td>3868</td>
<td>33</td>
<td>2590</td>
<td>549</td>
<td>638</td>
<td>--</td>
<td>707</td>
</tr>
<tr>
<td>Summer flounder ((\textit{Paralichthys dentatus}))</td>
<td>129 - 750</td>
<td>344</td>
<td>1501</td>
<td>4874</td>
<td>42</td>
<td>2828</td>
<td>1119</td>
<td>663</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Weakfish ((\textit{Cynoscion regalis}))</td>
<td>15 - 616</td>
<td>211</td>
<td>1128</td>
<td>6699</td>
<td>25</td>
<td>4994</td>
<td>2301</td>
<td>1951</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>White perch ((\textit{Morone americana}))</td>
<td>68 - 351</td>
<td>202</td>
<td>524</td>
<td>2784</td>
<td>38</td>
<td>1739</td>
<td>--</td>
<td>--</td>
<td>278</td>
<td>510</td>
</tr>
</tbody>
</table>

*\textit{Menticirrhus saxatilis} and \textit{M. americanus} combined.
Table 2. Best binomial and positive generalized additive mixed models (GAMM) for each predator-prey combination. Inclusion (+) and exclusion (blank) of covariates for the best fit models were determined through model selection using Akaike’s Information Criterion ($YR = \text{Year}; \ L = \text{Length}; \ LA = \text{Latitude}; \ T = \text{Temperature}; \ D = \text{Depth}$). Inclusion of $YR$ was forced in all models. A proxy for the deviance explained (% Dev) by each model was determined by fitting a fixed-effects generalized additive model with the specified covariates.

<table>
<thead>
<tr>
<th>Prey</th>
<th>Predator</th>
<th>Binomial GAMM</th>
<th>Positive GAMM</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$YR \ L \ LA \ T \ D$</td>
<td>$YR \ L \ LA \ T \ D$</td>
</tr>
<tr>
<td>Bay anchovy</td>
<td>Summer flounder</td>
<td>+ + + + +</td>
<td>+ +</td>
</tr>
<tr>
<td></td>
<td>Striped bass</td>
<td>+ + + + +</td>
<td>+ +</td>
</tr>
<tr>
<td></td>
<td>Weakfish</td>
<td>+ + + +</td>
<td>+ +</td>
</tr>
<tr>
<td>Bivalve</td>
<td>Atlantic croaker</td>
<td>+ +</td>
<td>+ + +</td>
</tr>
<tr>
<td></td>
<td>Clearnose skate</td>
<td>+ +</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Kingfish</td>
<td>+ +</td>
<td>+ +</td>
</tr>
<tr>
<td></td>
<td>Northern puffer</td>
<td>+ + + +</td>
<td>+ +</td>
</tr>
<tr>
<td></td>
<td>White perch</td>
<td>+ + + +</td>
<td>+ +</td>
</tr>
<tr>
<td>Mysid</td>
<td>Atlantic croaker</td>
<td>+ +</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>Northern searobin</td>
<td>+ +</td>
<td>+ + +</td>
</tr>
<tr>
<td></td>
<td>Scup</td>
<td>+ +</td>
<td>+ +</td>
</tr>
<tr>
<td></td>
<td>Spotted hake</td>
<td>+ +</td>
<td>+ + +</td>
</tr>
<tr>
<td></td>
<td>Striped bass</td>
<td>+ + + +</td>
<td>+ +</td>
</tr>
<tr>
<td></td>
<td>Summer flounder</td>
<td>+ + + + +</td>
<td>+ + +</td>
</tr>
<tr>
<td></td>
<td>Weakfish</td>
<td>+ + + + +</td>
<td>+ + +</td>
</tr>
<tr>
<td>Polychaete</td>
<td>Atlantic croaker</td>
<td>+ + + + +</td>
<td>+ +</td>
</tr>
<tr>
<td></td>
<td>Kingfish</td>
<td>+ +</td>
<td>+ +</td>
</tr>
<tr>
<td></td>
<td>Northern puffer</td>
<td>+ + +</td>
<td>+ +</td>
</tr>
<tr>
<td></td>
<td>Scup</td>
<td>+ + +</td>
<td>+ +</td>
</tr>
<tr>
<td></td>
<td>Spot</td>
<td>+ + +</td>
<td>+ +</td>
</tr>
<tr>
<td></td>
<td>Striped bass</td>
<td>+ + + +</td>
<td>+ +</td>
</tr>
<tr>
<td></td>
<td>White perch</td>
<td>+ + + +</td>
<td>+ + +</td>
</tr>
</tbody>
</table>

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Table 3. Pearson correlations among annual predator consumption indices and prey abundance indices (when available) for each of four prey groups (a – bay anchovy; b – mysids; c – bivalves; d – polychaetes). Correlations were calculated from logged values of annual consumption indices. Gray shading used to denote significance (alpha=0.05) without Bonferroni correction; bold used to denote significance with Bonferroni correction. Spot were omitted from polychaete correlations due to lack of sampling over the whole time series.

<table>
<thead>
<tr>
<th>a. Mysids</th>
<th>Scup</th>
<th>Flounder</th>
<th>Croaker</th>
<th>Weakfish</th>
<th>N. searobin</th>
<th>Str. bass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flounder</td>
<td>0.79</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Croaker</td>
<td>0.88</td>
<td>0.69</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weakfish</td>
<td>0.83</td>
<td>0.58</td>
<td>0.90</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N. searobin</td>
<td>0.88</td>
<td>0.56</td>
<td>0.75</td>
<td>0.78</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Str. bass</td>
<td>0.05</td>
<td>-0.15</td>
<td>0.11</td>
<td>-0.07</td>
<td>0.33</td>
<td></td>
</tr>
<tr>
<td>Sp. Hake</td>
<td>-0.14</td>
<td>-0.45</td>
<td>-0.09</td>
<td>0.03</td>
<td>0.33</td>
<td>0.33</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>b. Bay anchovy</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Str. bass</td>
<td>0.71</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weakfish</td>
<td>-0.01</td>
<td>0.03</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Index</td>
<td>0.41</td>
<td>0.34</td>
<td>0.42</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>c. Bivalves</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Cl. skate</td>
<td>0.69</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>W. perch</td>
<td>0.41</td>
<td>0.72</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Croaker</td>
<td>0.20</td>
<td>0.49</td>
<td>0.31</td>
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Fig. 1. Map of Chesapeake Bay mainstem areas sampled by the Chesapeake Bay Multispecies Monitoring and Assessment Program. Survey area is divided into 1 km² grid cells and classified into three depth strata. Areas in white are not sampled by the survey.
Fig. 2. Composition of predator diets (as % of stomach content weight) for twelve Chesapeake Bay fishes consuming four key prey groups (bay anchovy, mysids, bivalves, and polychaetes). The remainder of stomach contents were comprised of other prey.
Fig. 3. Modeled effects of continuous covariates on consumption of mysids based on delta generalized additive mixed-effects models (GAMMs) for multiple Chesapeake Bay predators. Upper panels depict covariate effects on the relative probability (on the logit scale) of a predator stomach containing a mysid, based on a binomial GAMM. Lower panels depict covariate effects on the relative amount of mysids consumed (log of biomass) based on a positive GAMM. Dashed lines represent 95% confidence limits for the estimated effects. Predator curves are not plotted if a covariate was not included in the best model.
Fig. 4. Modeled effects of continuous covariates on consumption of bay anchovy based on delta generalized additive mixed-effects models (GAMMs) for multiple Chesapeake Bay predators. See Figure 3 for full description of plot.
Fig. 5. Modeled effects of continuous covariates on consumption of bivalves based on delta generalized additive mixed-effects models (GAMMs) for multiple Chesapeake Bay predators. See Figure 3 for full description of plot.
Fig. 6. Modeled effects of continuous covariates on consumption of polychaetes based on delta generalized additive mixed-effects models (GAMMs) for multiple Chesapeake Bay predators. See Figure 3 for full description of plot.
Fig. 7. Annual indices of prey consumption derived from the delta generalized additive mixed-effects models. Consumption of each prey by a predator was standardized to range from 0-1 (solid, colored lines). Standardized prey abundance index denoted with dashed line, but not available for mysids.