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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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Manuscripts

1   **Dynamic trophic linkages in a large estuarine system – support for supply-**

2   **driven dietary changes using delta generalized additive mixed models**

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15   **Abstract:** Trophic dynamics within aquatic systems are a predominant regulator of fish

16   production and an important consideration for implementing ecosystem approaches to fisheries

17   management. We analyzed ten years of fish diet data from Chesapeake Bay, USA to 1) evaluate

18   the effects of environmental variables on trophic interactions of 12 common predatory fishes, 2)

19   infer dynamics of four key prey groups (mysids, bay anchovy, bivalves, and polychaetes), and 3)

20   evaluate whether interannual dietary trends were coherent among predators and regulated by

21   prey availability. Based on delta generalized additive mixed models (delta-GAMM), predator

22   length was the most important covariate in modeling prey consumption. When significant,

23   latitude, temperature, and depth effects were largely similar across predators for a given prey.

24   Annual patterns of mysid and bivalve consumption each showed a single, dramatic peak shared

25   by multiple predators with varied feeding preferences and distributional characteristics, but

26   annual trends were not correlated with available survey-based measures of prey availability

27   likely due to methodological differences. Overall, the coherence in consumption patterns across

28   predators was consistent with supply-driven dynamics controlled by regional and annual changes

29   in prey availability. Also, the novel application of delta-GAMM to fish diet data was useful in

30   characterizing the dynamics of poorly sampled prey groups and the trophic interactions for

31   ubiquitous species from the Northwest Atlantic Ocean.

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33   **Keywords**: trophic ecology, diet analysis, fish stomach contents, statistical methods,

34   environmental effects

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Introduction

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37   Trophic dynamics have been described as one of the three principal drivers of fisheries

38   production (Link 2010; Gaichas et al. 2012). Trophic dynamics control not only the direct

39   consequences of predation (e.g., mortality, survival, growth, changes in population biomass, and

40   modified size structure) but also a myriad of indirect ecological effects (e.g., changes in

41   behavior, distribution, habitat utilization, foraging, and competition), all of which are critical to

42   governing the structure and function of aquatic food webs (Carpenter et al. 1985; Whipple et al.

43   2000). Consequently, understanding the factors regulating predator-prey interactions is an

44   important consideration in applying a more holistic, ecosystem-based approach to managing

45   fisheries resources (Link 2002; Latour et al. 2003). One of the challenges to advancing

46   knowledge on predator-prey interactions is to continue moving beyond basic diet descriptions by

47   evaluating the factors regulating the dynamics of food web linkages, including how

48   environmental conditions and prey availability alter foraging patterns (Link 2002; Hunsicker et

49   al. 2011).

50   Chesapeake Bay is one model system where researchers and managers are interested in

51   understanding how the environment and prey availability regulate dynamic predator-prey

52   interactions, in part to facilitate ecosystem-based fisheries management (EBFM) efforts (Houde

53   2006; Christensen et al. 2009). Chesapeake Bay is the largest juvenile nursery and estuarine

54   foraging ground in the northwest Atlantic Ocean, supporting many fish stocks and their

55   commercial and recreational fisheries (Able and Fahay 2010). Consequently, variability in

56   predator-prey interactions in the bay can influence recruitment, growth, mortality, and

57   production of many valuable fishes. Mysids, bay anchovy, bivalves, and polychaetes, in

58   particular, are four key prey groups in Chesapeake Bay that have a proportionately large

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59   influence on the bay's diverse fish assemblage (Buchheister and Latour 2015). However, there is

60   limited information on the basic biological and ecological characteristics of these prey groups

61   (particularly mysids) and their trophic interactions with predators at larger spatiotemporal scales

62   in estuaries. The availability of extensive fish diet data in Chesapeake Bay (Buchheister and

63   Latour 2015) provides a unique opportunity for obtaining some of this information.

64   Fishes are biological samplers of their environment and thus predator diets can be used as

65   indicators of prey dynamics and availability, particularly for cryptic or poorly sampled prey

66   groups. Generally, prey consumption rate for an un-satiated predator increases with the prey's

67   density (Holling 1959), and many fishes are generalist or opportunistic feeders whose foraging is

68   strongly regulated by prey encounter rates (Gerking 1994; Juanes 1994). These density-

69   dependent foraging characteristics have allowed scientists to use predator diets to estimate prey

70   distributions (Fahrig et al. 1993; Link 2004), derive annual indices of relative prey abundance

71   (Link 2004; Mills et al. 2007), and corroborate long term changes in prey availability (Dwyer et

72   al. 2010; Pálsson and Björnsson 2011).

73   Making inferences on prey availability from predator diets can be biased by

74   environmental conditions, prey selectivity, and foraging efficiency (Eggers 1977; Juanes 1994).

75   These potential biases are analogous to difficulties faced in deriving indices of relative

76   abundance from traditional fish survey gears, and two approaches are useful in that context.

77   First, statistical models can standardize indices by partitioning variability and accounting for the

78   effects of different covariates (Maunder and Punt 2004; Kimura and Somerton 2006) and second,

79   multiple gear types with different sampling properties can be used synoptically to derive more

80   robust estimates of a desired response variable. Extension of this reasoning to trophic studies

81   suggests that indices of prey consumption would be more representative of prey availability once

82   standardized for heterogeneous environmental conditions that introduce variability into predator-

83   prey interactions, and also that synchronous patterns across multiple predators would strengthen

84   the robustness of conclusions for individual prey. An added benefit of this prey-centric analytical

85   approach is that when limited biological data exist for the prey, the effects of modeled covariates

86   can be used to draw inference on prey distribution, availability, and dynamics.

87   In this study, we evaluate the trophic interactions among several dominant fishes and key

88   prey groups in Chesapeake Bay. We used diet composition data from an extensive, multi-

89   seasonal bottom trawl survey of Chesapeake Bay fishes to address three objectives: 1) evaluate

90   the influence of predator length, spatiotemporal factors, and environmental drivers on prey

91   consumption by 12 common Chesapeake Bay predators, 2) compare diet patterns across

92   predators to infer basic dynamics of four key prey groups, and 3) evaluate whether interannual

93   consumption trends were coherent among predators and correlated with annual prey abundance.

94   We detail the trophic dynamics for several predators and prey groups that occur ubiquitously in

95   estuarine and nearshore coastal waters throughout the Atlantic, contributing to ongoing efforts in

96   ecosystem modeling and EBFM in Chesapeake Bay and the continental shelf (Latour et al. 2003;

97   Houde 2006; Link et al. 2011). From a methodological perspective, this work is a novel

98   application of delta generalized additive mixed models to draw ecological inference from dietary

99   data while addressing several statistical problems common in trophic studies.

100
101   **Methods**

102   **Field and laboratory methods**

103   Data were obtained from the Chesapeake Bay Multispecies Monitoring and Assessment

104   Program (ChesMMAP), operated by the Virginia Institute of Marine Science. Since 2002, this

105   bottom trawl survey has sampled the Chesapeake Bay mainstem using a random-stratified design

106   with stations stratified by depth and latitude (Fig. 1). Typically, five cruises were conducted per

107   year (bimonthly from March to November), with approximately 80 stations sampled per cruise.

108   Data on latitude, longitude, water depth, bottom temperature, salinity, and dissolved oxygen

109   were collected at each station. After catches were sorted, species with broad length distributions

110   or discrete length groups were further sorted into 2-4 size classes, random individual subsamples

111   from the species-size-class groups were processed for weight and length (fork length for teleosts;

112   disc width for batoids), and stomachs were removed for diet analysis. If stomachs were visually

113   confirmed to be empty in the field, additional specimens (when available) were processed to

114   obtain 3-5 nonempty stomachs per species and size class. In the laboratory, contents from

115   preserved stomachs were sorted by trained technicians, identified to the lowest possible taxon

116   using dissection microscopes, and prey categories weighed to the nearest 0.001 g.

117   We focused on four prey groups for this study: 1) mysid shrimp (primarily *Neomysis*

118   *americana*), 2) bay anchovy (*Anchoa mitchilli*, with very minor contribution of *Anchoa*

119   *hepsetus*), 3) bivalves (dominant species included *Ensis directus*, *Gemma gemma*, *Macoma spp.*,

120   *Mercenaria mercenaria*, *Mya arenaria*, and *Tagelus plebeius*), and 4) polychaete worms

121   (including families Capitellidae, Chaetopteridae, Glyceridae, Maldanidae, Nereidae,

122   Pectinariidae, Terebellidae). These four prey groups were chosen because they represent

123   relatively unique functional morphologies and are largely responsible for differentiating among

124   fish trophic guilds within Chesapeake Bay (Buchheister and Latour 2015). The bivalve and

125   polychaete groups were defined at a coarse taxonomic level because 1) prey were often not

126   identifiable to greater taxonomic resolution due to digestion, 2) sample sizes were relatively low

127   for predators with identifiable bivalve and polychaete taxa. Predators for each of the four prey

128   groups were restricted to species with >15% frequency occurrence and a minimum sample size

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129   of 140 stomachs that contained the prey group. These two criteria excluded predators that rarely

130   consumed a given prey group and omitted predators with low sample sizes. These restrictions

131   yielded a total of 12 predator species with a total of 29,350 analyzed stomachs (Table 1).

132   Depending on the species, 9-42% of sampled fish stomachs were empty (27% overall). Each

133   predator-prey combination was represented by at least 146 fish and up to 2,301 fish that

134   contained the prey of interest. Summaries of general diet compositions (% weight) for the

135   selected predators were calculated using a cluster sampling estimator by pooling across all

136   available non-empty stomachs (see Buchheister and Latour 2015 for equations).

137

138   **Delta generalized additive mixed models**

139   Statistical analysis of stomach content data is often complicated by three statistical issues.

140   First, diet data often suffer from an overabundance of zero values that does not conform to

141   standard statistical distributions. Second, samples of fish stomachs often violate the assumption

142   of independence when multiple individuals are captured at the same location or when individuals

143   are sampled repeatedly through time (e.g., in experimental studies) because samples will be auto-

144   correlated in time and space (Hurlbert 1984; Bogstad et al. 1995; Millar and Anderson 2004).

145   Third, the effects of covariates (e.g., temperature, predator size) on diets are often non-linear.

146   To account for these three complications, we applied delta generalized additive mixed

147   models (delta-GAMM) to model the consumption of a prey group by an individual predator

148   species. This approach built on the methods promoted by Stefánsson and Pálsson (1997) by

149   accounting for the non-independence of the diet samples using random effects. Delta-GAMM

150   combines statistical aspects of delta models (also known as two-part, hurdle, or zero-altered

151   models), generalized additive models (GAM), and mixed effects models. The use of a GAM

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152   allows for the effect of covariates to take flexible, nonlinear forms that are dictated by a

153   smoothing function (Wood 2006), but GAMs rely on the assumptions of independent and

154   identically distributed errors with constant variance. To account for the violation of the

155   independence assumption caused by the intra-station (i.e., intra-haul) correlation and by the

156   nested nature of the sampling design, we included station as a random effect in a mixed model

157   (Wood 2006; Zuur et al. 2009). To deal with the high frequency of zero values, the delta

158   approach was used to model the data in two parts: first, the presence-absence of a given prey in

159   the stomachs of a predator was modeled (termed the "binomial" model henceforth); and second,

160   the weight of prey consumed was modeled, provided that the prey occurred in the stomach

161   (termed the "positive" model henceforth). All models were fitted to individual predator-prey

162   combinations.

163   The binomial models estimated the probability that a stomach contains the prey of

164   interest, analogous to modeling the frequency of occurrence of a given prey. The first, binomial

165   stage of the delta-GAMM modeled presence absence data (a_{ij}) as $a_{ij} \sim$ binomial($1, p_{ij}$) with

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

167   where $\text{logit}(p_{ij}) = \log(p_{ij}/(1-p_{ij}))$, p_{ij} is the expected probability that fish i from station j contains

168   the prey of interest, α is the overall intercept, β is a vector of parametric effects for the

169   categorical year (*YR*) factor, and f_{1-4} are smooth functions for each covariate (Wood 2006; Zuur

170   et al. 2009). The continuous covariates included predator length (*L*) in mm, latitude (*LA*) in

171   decimal degrees, water temperature (*T*) in °C, and water depth (*D*) in m. The b_j term is the

172   independent and identically distributed random station effect which is assumed to be normally

173   distributed with mean of zero and variance of σ_b^2. Available data on longitude, salinity, dissolved

174   oxygen, and month were not included in the model to avoid convergence issues resulting from

175   overly complex models and to avoid slight collinearity among some variables. Models with

176   interactions among variables (including variable coefficient GAMM; Wood 2006) were not

177   formally evaluated because 1) graphical analyses did not indicate the presence of strong

178   interactions (Zuur et al. 2010), 2) they would decrease sample sizes and precision of covariate

179   effects, and 3) they often prohibited model convergence based on preliminary analyses.

180   The second, positive component of the delta-GAMM excludes all zeros and models the

181   quantity of prey consumed, relying on an appropriate data distribution. We chose to model the

182   biomass of prey consumed because this measure is more meaningful than prey counts in

183   dictating the transfer of energy through food webs (e.g., Pauly et al. 2000). Also, prey abundance

184   could not always be quantified due to digestion. We did not back-calculate the fresh weights of

185   consumed prey, but instead assumed that the modeled covariate effects on the measured weights

186   would be representative of the processes regulating consumption of fresh prey. Prey biomass was

187   not modeled with a gamma distribution as done by Stefánsson and Pálsson (1997) because this

188   distribution resulted in convergence issues for most predator-prey combinations in the GAMMs.

189   Instead, we used a log-transformation of the biomass data in conjunction with a Gaussian

190   distribution to alleviate convergence issues and homogenize the originally heteroscedastic

191   residuals. The model for the second stage of the delta-GAMM, restricted to fish stomachs that

192   contained a given prey, was defined as:

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

194   where μ_{ij} is the expected mass (in g) of a prey group in the stomach of fish i from station j given

195   the random effect b_j, and ε_{ij} is the residual error for each fish and station assumed to be normally

196   distributed with a mean of zero and variance of σ_ε^2 (Wood 2006; Zuur et al. 2009). Definitions

197   for all remaining components of the model are identical to those for equation 1.

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198   All GAMMs were fitted to data from each of the 22 predator-prey combinations (Table

199   1), and Akaike's Information Criterion (AIC) was used to select the optimal fixed effects

200   structure (Burnham and Anderson 2002). Models with all possible combinations of explanatory

201   variables were evaluated, with the exception that *YR* was retained in all iterations to evaluate

202   interannual consumption trends (objective 3). Partial effects plots for the best-fit models were

203   used to demonstrate the effect of each covariate on the response after accounting for all other

204   covariates in the model, and they were presented on the scale of the linear predictor (logit scale

205   for binomial model results; log scale for positive model results). Goodness-of-fit measures (e.g.,

206   percent of deviance explained or R^2) are still being developed for mixed models (Nakagawa and

207   Schielzeth 2013) and there is no standard summary statistic for overall GAMM fit, so these

208   measures were not estimated. However, as a general proxy for overall goodness of fit, a fixed-

209   effects version of each model (without the random station effect) was fitted to estimate the

210   percent of deviance explained by the model. We fitted all statistical models with the gamm4

211   package (Wood 2012) in R 3.0.1 (R Core Team 2013).

212

213   **Annual trends in consumption**

214   A combined index of prey consumption for year y (C_y) was obtained for each predator-

215   prey combination by multiplying predictions for the binomial and positive components of the

216   best-fit delta-GAMMs. The consumption index was calculated as $C_y = p_y * \mu_y$ where p_y is the

217   expected probability that a predator from year y consumed a given prey, and μ_y is the expected

218   mass of the prey in a predator's stomach in year y. Predictions were standardized for the other

219   covariates by holding them constant at the mean values observed for each predator species (e.g.,

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220　　see Table 1 for mean predator lengths). All μ_y values were bias-corrected for back transformation

221　　from lognormal space (Sprugel 1983).

222　　　　　To evaluate the similarity in prey consumption patterns across predators and the influence

223　　of prey availability, Pearson correlations (R) were calculated among predator estimates of logged

224　　C_y and indices of prey abundance. Logging of consumption indices was needed to normalize the

225　　data distributions and to prevent biased correlations due to outlier values. Indices of annual

226　　biomass for polychaetes and bivalves were calculated as geometric means (mean of

227　　log(x+0.001), where x = biomass density in g m^{-2}) using data from the Chesapeake Bay Benthic

228　　Monitoring Program for the randomly selected stations surveyed within the bay mainstem

229　　(Versar, Inc., www.baybenthos.versar.com). Bivalves from this dataset were restricted to the

230　　most common species found in predator stomachs (*Ensis directus*, *Gemma gemma*, *Macoma*

231　　*spp.*, *Mercenaria mercenaria*, *Mya arenaria*, and *Tagelus spp.*), but only *Macoma spp.* and

232　　*Gemma gemma* were regularly sampled (occurring in 49% and 13% of stations, respectively).

233　　Annual abundance indices for bay anchovy were obtained from the Virginia Institute of Marine

234　　Science Juvenile Fish and Blue Crab Trawl Survey (Tuckey and Fabrizio 2012). Data on patterns

235　　of mysid annual abundance were not available from any existing Chesapeake Bay monitoring

236　　program. Significance of Pearson correlations were determined from critical R values based on

237　　Bonferroni-adjusted α values ($\alpha_{adjusted}$ = 0.05/n, where n is the number of pairwise correlations

238　　for a given prey group). Spot were omitted from correlation analysis due to lack of stomach

239　　content data from 2002-2007. To facilitate visual comparison of annual consumption and prey

240　　indices across predators, all C_y values and prey indices were standardized to range from 0-1.

241　　These standardized C_y values were calculated as $(C_y - C_{min})/(C_{max} - C_{min})$, where C_{min} and C_{max}

242　　are the minimum and maximum values for C_y across the time series.

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243

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Results

246   The four prey groups of focus contributed substantially to predator diets. Collectively,

247 bay anchovy, mysids, bivalves, and polychaetes accounted for large fractions of the fish diets

248 (13-64%), reinforcing the broad importance of these prey to the examined predators (Fig. 2).

249 Individual prey groups contributed as much as 41% to the overall diet of a predator, though these

250 dietary contributions can be greater for specific predator size classes (Buchheister and Latour

251 2015).

252

Generalized additive mixed modeling

254   The best-fitting binomial and positive GAMMs included various combinations of the

255 explanatory variables, ranging from all variables to none of the variables (except *YR*, which was

256 forced; Table 2). Generally, the binomial models were more complex than the positive models;

257 however, this may be partially attributed to lower samples sizes for positive models which may

258 have restricted the ability to detect significant covariate effects. Proxies for the deviance

259 explained by models varied among predator-prey combinations, ranging from 4.3-36.7% (mean

260 14.1%) for binomial models and 5.4-49.3% (mean 19.6%) for positive models. These goodness

261 of fit values are comparable to other dietary studies that employed additive models and reflect

262 the relatively large amount of variability inherent in diet composition data (Stefánsson and

263 Pálsson 1997; Santos et al. 2013).

264   Length and latitude were typically the two most important covariates in the models

265 (Table 2), indicating the importance of both size limitation and spatial dynamics in trophic

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266   interactions. Most binomial models of prey consumption included length and latitude as

267   significant covariates; best-fitting models that did not include length were typically for predators

268   with relatively smaller length ranges. Significance of depth and temperature varied by prey;

269   depth was not important for bivalves, and temperature was typically excluded from polychaete

270   models. For the positive models, predator length was again a consistently important covariate,

271   yet few models included latitude or temperature. Only two positive models revealed significant

272   effects of water depth.

273   Consumption of mysids by predators was strongly influenced by the modeled covariates.

274   Predator length produced the strongest effect on the probability of mysids being consumed, with

275   larger individuals far less likely to consume this small-bodied prey (Fig. 3). The prey biomass

276   consumed tended to increase across predators at smaller sizes prior to declining, with this

277   transition occurring between ~150-300 mm (Fig. 3). Both the occurrence and the biomass

278   consumed indicated greater mysid availability at lower latitudes for the predators with the largest

279   sample sizes (Fig. 3). Temperature effects on mysid occurrence and biomass were inconsistent

280   across predators, preventing clear conclusions regarding the influence of temperature on mysid

281   dynamics. Mysid occurrences in stomachs were slightly greater at shallower depths, but weakfish

282   contradicted this pattern.

283   Bay anchovy consumption was strongly influenced by predator length (Fig. 4). The

284   parabolic shape for the binomial model indicates a strong peak in prey occurrence at sizes ~175-

285   300 mm, with weakfish targeting bay anchovy at slightly smaller sizes than summer flounder and

286   striped bass. The mass of bay anchovy found in stomachs increased with predator size until

287   leveling off at sizes that corresponded to the peaks in bay anchovy occurrence (Fig. 4). A size

288   effect on biomass consumed was not detected for striped bass. Effects of latitude on the

289   probability of bay anchovy consumption differed by predator, with striped bass opposing the

290   trend of greater bay anchovy occurrence at higher latitudes. Temperature effects varied by

291   predator, and again striped bass opposed the general trend detected for the other species.

292   Weakfish and summer flounder results indicated greater probability of bay anchovy consumption

293   at lower temperatures. Depth effects on occurrence were negligible, although there was some

294   evidence for increased bay anchovy occurrence in shallower water.

295   Consumption of bivalves by Chesapeake Bay predators was strongly influenced by

296   predator length and latitude (Fig. 5). Dietary occurrence of bivalves increased with length for

297   Atlantic croaker, white perch, and northern puffer, but appeared to reach an asymptote for

298   Atlantic croaker. The biomass consumed also increased steeply with predator size. When viewed

299   in unison, the latitude effects for all predators demonstrated a decreased occurrence of bivalves

300   in stomachs at mid-latitudes, with increases in both the lower and upper bays (Fig. 5). For

301   Atlantic croaker, the mass of consumed bivalves also supported this parabolic latitudinal trend in

302   prey availability. Water temperature had a positive effect on bivalve occurrence in fish stomachs

303   for three species, but only white perch showed a similar positive relationship when modeling

304   prey biomass. Depth was not a significant covariate for any of the bivalve GAMMs.

305   Patterns of polychaete consumption showed varied responses to covariates depending on

306   the predator. Dietary occurrence of polychaetes varied greatly by predator length depending on

307   the species, but tended to increase with size before decreasing at larger sizes (Fig. 6). The biggest

308   exception to this pattern was for kingfish for which occurrence decreased monotonically. The

309   biomass of consumed polychaetes increased with predator length at similar rates across

310   predators, with only striped bass showing a reliable indication of saturation at larger sizes (Fig.

311   6). Latitudinal effects on the probability of polychaete consumption tended to show an inverse

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312   pattern to bivalve occurrence by latitude (Figs. 5, 6). Polychaete occurrences were generally

313   greatest in mid-latitudes, but latitude did not have significant effects on biomass of consumed

314   polychaetes for the majority of modeled predators (Fig. 6). Temperature effects on polychaete

315   occurrence and biomass were largely negligible across the majority of predators (Fig. 6). Depth

316   effects on polychaete occurrence were inconclusive as a whole at shallow depths, but most fishes

317   indicated decreasing occurrence as depth increased beyond ~10 m (Fig. 6).

318

319   **Annual trends in consumption indices**

320   Standardized indices of annual prey consumption varied through the time-series but

321   demonstrated some synchronous and coherent trends across predators. Generation of the annual

322   consumption index clarified the interpretation of the year effects from individual binomial and

323   positive GAMM models (Fig. S1). Five of seven predators (Atlantic croaker, northern searobin,

324   scup, summer flounder, weakfish) exhibited a distinct annual peak in consumption of mysids in

325   2003, with a magnitude dramatically greater than other years (Fig. 7). Correlations among annual

326   trends for these five species were strong and ranged from 0.56-0.90, with 3 of 10 values being

327   significant (R>0.84, Bonferroni-corrected p<0.05; Table 3). Only striped bass and spotted hake

328   did not conform to this pattern. Consumption of bay anchovy by summer flounder and striped

329   bass exhibited largely synchronous changes in directionality (Fig. 7) and were strongly

330   correlated (R=0.71), though not significantly. Although consumption indices were not correlated

331   with the bay anchovy index (Table 3), the highest consumption values for summer flounder and

332   weakfish (and second highest value for striped bass) were obtained in 2010 when the prey index

333   was at its highest. Bivalve consumption had a peak in 2008 that was shared by all predators (Fig.

334   7). Although some bivalve trends were strongly correlated with one another or with the prey

15

335   index (R=0.69-0.74), non were significant (Table 3). Consumption indices of polychaetes were

336   highly variable among predators; however, the highest values occurred in the last five years of

337   the time series, and four of the seven predators (Atlantic croaker, scup, spot, and white perch)

338   consumed the greatest amount of polychaetes in 2010 (Fig. 7). None of the pairwise polychaete

339   correlations among predators and the prey index were signficant (Table 3).

340

341

342   **Discussion**

343   Biological, environmental, and spatiotemporal factors strongly regulated predatory

344   consumption of four key prey groups in Chesapeake Bay. Despite the notorious variability of

345   fish diet data generated from the complex processes that influence trophic dynamics (Gerking

346   1994; Wootton 1998), the use of an extensive data set, multiple opportunistic predators, and the

347   novel application of delta-GAMMs aided in illuminating more robust commonalities in feeding

348   patterns that appear to be linked to prey availability at both small and large scales. Predator

349   length and latitude were particularly important covariates influencing many predator-prey

350   interactions. Coherent annual peaks in mysid, bay anchovy, and bivalve consumption were

351   suggestive of episodic, annual pulses in prey productivity that may be mediated by bottom-up

352   processes. These dynamic changes in consumptive patterns have the potential to influence

353   regional and annual patterns in fish productivity (e.g., Buchheister et al. in review) and are thus

354   an important consideration in managing fisheries in a broader, ecosystem context (Link 2010).

355

Predator length as a strong determinant of diet

356

357   Predator length was the most consistently important determinant of prey consumption,

358 supporting a vast literature that emphasizes the significance of body size in structuring trophic

359 interactions (e.g., Juanes 1994; Scharf et al. 2000; Kerr & Dickie 2001). Among other things,

360 body size regulates the foraging process by controlling the physical constraints on the size and

361 types of prey that can be ingested, the speed and endurance of a predator, the relative success of

362 foraging attacks, and the visual limit for prey detection (Eggers 1977; Scharf et al. 2002). In this

363 study, the binomial GAMM effects for predator length provide information on the continuous

364 functional forms of relative prey occurrence in predators of varying sizes. The forms of these

365 size-based occurrence curves were either linear, asymptotic, or dome-shaped (which translate to

366 sigmoidal, asymptotic, and dome shapes when converted to the 0-1 probability scale). The

367 sigmoidal decline in consumption of mysids supports their greater importance to juveniles and

368 smaller sized individuals (Mauchline 1980; Hostens and Mees 1999), while the sigmoidal or

369 asymptotic increase in bivalve consumption suggests this prey is a "terminal" prey for which

370 occurrence is greatest at the most advanced ages and sizes that were sampled (Buchheister and

371 Latour 2015). The dome shapes for bay anchovy and polychaetes identified these prey as being

372 transitional forage resources as predators grew (through the examined sizes), reaching

373 consumption optima at intermediate sizes. Generally, these bay anchovy optima corresponded

374 with significant shifts in diet composition based on discrete size-class cutoffs (Latour et al. 2008;

375 Buchheister and Latour 2015), and they also corresponded with published distributions of

376 predator-prey size ratios for summer flounder and weakfish (Scharf et al. 2000). The empirically-

377 derived occurrence curves may be useful in informing the parameterization of size-based

378   components of prey suitability functions that are used in foraging or multispecies models

379   (Garrison et al. 2010).

380

381   **Prey dynamics**

382   Predator diets contributed to the basic understanding of mysid distribution and

383   abundance. Despite the importance of mysids in estuarine and marine food webs (Mauchline

384   1980, Jumars 2007), relatively little is known about basic mysid dynamics in Chesapeake Bay

385   and similar estuaries. Our diet analysis suggests mysid availability and presumably density was

386   highest at lower latitudes in the Chesapeake Bay's polyhaline region near the mouth. In contrast,

387   densities of *N. americana*, the predominant mysid in local fish diets (Buchheister and Latour

388   2015), peaked at mesohaline salinities ~50-90 km away from the mouth of Delaware Bay

389   (Hulburt 1957, Cronin et al. 1962). These trends are consistent with the hypothesis that coastal

390   waters act as the major source for estuarine mysid populations (Whitely 1948; Hulburt 1957;

391   Hopkins 1965), and they suggest that physical advection and distance from the coastal

392   population source may be more important than specific salinity regimes in dictating estuarine

393   mysid distributions in large estuaries like Chesapeake Bay. However, mysid consumption did

394   occur throughout the entire sampled area, likely supported by local estuarine reproduction that

395   can occur through their hypothesized 2-3 annual reproductive cycles (Hulburt 1957) and their

396   tolerance for a broad range of salinities (Mauchline 1980). Although mysid populations tend to

397   peak in summer months with warmer temperatures, mysids can be found throughout the year in

398   Mid-Atlantic estuaries (Hulburt 1957; Hopkins 1965). This seasonal ubiquity contributed to the

399   lack of consistent dietary occurrence trends with temperature, and supports the importance of

400   mysids as a food resource throughout the year to a variety of resident and seasonally migrating

401   predators (Buchheister and Latour 2015). Analyses suggested greater mysid availability in

402   relatively shallower bay areas (4-15 m) based on the diets, contrary to trends in Delaware Bay

403   where Hulburt (1957) noted low mysid concentration in areas <5.5 m. However, his study

404   sampled during daylight hours in surface waters when mysids typically reside on the benthos

405   (Herman 1963).

406   Bay anchovy are the most abundant fish in the Chesapeake Bay and they contribute

407   substantially to the production of commercially and recreationally important piscivorous species

408   like striped bass, summer flounder, weakfish, and bluefish (Baird and Ulanowicz 1989; Houde

409   and Zastrow 1991). For many piscivores, bay anchovy acts as a key forage species that bridges

410   the transition from small zooplanktonic and benthic prey to larger forage fishes (Buchheister and

411   Latour 2015, this study). The conflicting latitudinal and temperature trends in bay anchovy

412   consumption between striped bass and the other predators were likely related to spatiotemporal

413   differences in predator-prey overlap. Bay anchovy tend to be more abundant in the mid-bay in

414   the summer months, prior to moving to the lower bay and inner continental shelf to overwinter

415   (Wang and Houde 1995; Jung and Houde 2004). Summer flounder and weakfish, exhibit life

416   history strategies that favor use of the lower bay during warmer months (Latour et al. 2008; Able

417   and Fahay 2010), opposing the distributional patterns of the anadromous striped bass that tends

418   to favors the upper bay with higher densities in cold months. Thus, use of diets to infer relative

419   prey availability is challenging when both the prey and its predators exhibit different migratory

420   life histories. Regarding depth, the observed dietary trends correspond with previous work

421   suggesting that, although bay anchovy occur at a variety of depths, they tend to be more rare in

422   deeper waters >25 m (Houde and Zastrow 1991).

19

423   The trends of bivalve and polychaete consumption revealed broad-scale patterns in the

424   availability of macrobenthic prey for demersal fishes in Chesapeake Bay. These patterns were

425   detected within each of the two general prey groups, despite the need to aggregate numerous taxa

426   for logistical reasons. The decline of bivalve consumption and increase of polychaete

427   consumption in mid-latitude, mesohaline waters could be influenced by two principal

428   mechanisms relating to prey availability. First, regional biogeography and physico-chemical

429   preferences (e.g., salinity, sediment type) largely dictate the bay regions in which individual

430   macrobenthic species reside (Holland et al. 1987; Diaz and Schaffner 1990). For example,

431   *Macoma* and *Gemma* clams favor the more moderate salinities of the mid- to upper-bay, while

432   *Ensis* and *Tagelus* reside in more polyhaline, low-latitude waters (Diaz and Schaffner 1990).

433   Thus, latitudinal trends of bivalve and polychaete prey are an amalgamation of effects generated

434   from individual species that comprise each of the macrobenthic prey groups. A second potential

435   mechanism relates to chronic and acute habitat degradation. Extensive seasonal hypoxia caused

436   by eutrophication, physical stratification, and bacterial remineralization of organic matter is a

437   dominant environmental feature in the bay from June to August, persisting up to 3 months in

438   some areas (Murphy et al. 2011). Hypoxia diminishes macrobenthic productivity and biomass

439   more strongly in deeper mid-bay waters relative to upper and lower bay regions during the

440   summer months (Holland et al. 1987; Kemp et al. 2005). This decreased production may have

441   contributed to the declines in mid-bay bivalve consumption, whereas the increased dietary

442   occurrence of polychaetes in the mid-bay could be attributed to their greater tolerance of low

443   oxygen conditions relative to bivalves (Vaquer-Sunyer and Duarte 2008; Sturdivant et al. 2013)

444   or their tendency to more quickly recolonize benthic habitats once waters become re-oxygenated

445   (Rosenberg et al. 2002). Effects of hypoxia on mid-bay macrobenthic prey availability are not

446   isolated to summer, as habitat degradation and seasonal hypoxia-induced mortality have shifted

447   the annual benthic community to smaller, shorter-lived species with lower standing stock

448   biomass (Holland et al. 1987; Kemp et al. 2005). Indeed, the latitudinal trend in bivalve

449   consumption was detected in all sampled months (A. Buchheister, unpublished data), suggesting

450   that species biogeographical distributions and long-term degradation of mid-bay habitats may be

451   more influential on macrobenthic consumption than direct seasonal hypoxic effects, particularly

452   considering that fishes avoid the low oxygen waters (Buchheister et al. 2013).

453

454   **Annual patterns in prey consumption**

455   Despite the lack of concordance between indices of prey abundance and consumption

456   overall, there was strong evidence of prey availability regulating annual consumption indices of

457   individual Chesapeake Bay predators, as supported in many other systems (Fahrig et al. 1993;

458   Mills et al. 2007; Dwyer et al. 2010; Pálsson and Björnsson 2011). The strongest empirical

459   indication that prey availability was involved in the annual trends was the coherence in peak

460   consumption of mysids, bivalves, and bay anchovy by predators with varied feeding preferences,

461   foraging modes, and distributional patterns. For example, two benthivorous species (Atlantic

462   croaker and scup) exhibited the same 2003 peak in mysid consumption as other zooplanktivorous

463   and piscivorous species (Northern searobin, summer flounder, weakfish), despite having diets

464   that do not typically target mysids (Buchheister and Latour 2015). Also, an upper bay species

465   (white perch) demonstrated a similar bivalve consumption peak as other lower bay predators,

466   even though the bivalve genera that predominate in these regions differ with *Macoma* clams in

467   the mid and upper bay and *Ensis* and *Tagelus* clams in the lower bay. These synchronous dietary

468   patterns likely relate to 1) the density-dependent feeding behavior of animals (Holling 1959), and

21

469   2) the opportunistic feeding strategies that evolved to allow fishes to exploit spatiotemporally-

470   patchy prey resources in dynamic, heterogeneous environments (Gerking 1994).

471   Presumably, different environmental or ecological conditions supported large pulses in

472   prey production during certain years (mysids – 2003; bivalves – 2008; bay anchovy – 2010) that

473   were utilized by a variety of predators that adapted to the greater prey availability. For example,

474   mysid consumption was correlated with mean annual spring temperature, spring salinity, and

475   surface chlorophyll-a (A. Buchheister, unpublished data), with 2003 being a distinct year in the

476   environmental time series as with the annual consumption indices. Those conditions could have

477   contributed to greater mysid production through bottom-up processes including improved local

478   reproduction during the spring spawning event, greater overall phytoplankton food availability

479   that improved juvenile or adult survival, or greater immigration of mysids from coastal waters

480   (Hopkins 1965, Ezzack and Corey 1979). Indeed, bottom-up mechanisms have been implicated

481   as drivers of ecosystem structure, fish recruitment, and fisheries landings in the Chesapeake Bay

482   and Mid-Atlantic Bight (Frank et al. 2007; Hare and Able 2007), and the dietary trends

483   documented are consistent with such donor control in food webs. However, any speculations on

484   specific mechanisms driving pulses in production of mysids, bay anchovy, or bivalves require

485   more directed and targeted research.

486   The general lack of concordance between prey abundance indices and the consumption

487   indices can be partially explained by 1) biases in prey sampling (whether by survey gear or by

488   predators) and 2) the different spatiotemporal scales represented by each index. First, possible

489   survey biases include: the long-term benthic monitoring program excluding Maryland waters

490   >12 m; that survey only sampling from July to September (after the macrobenthic biomass is

491   affected by summertime hypoxia); and the bay anchovy index being derived from a bottom trawl

492   survey that is not optimal for sampling pelagic species. Predator consumption biases largely take

493   the form of prey selectivity (Eggers 1977; Juanes 1994), but annual consumption trends were

494   mirrored by the annual effects from the binomial models, whose presence/absence data tend to

495   be less biased by prey selectivity than gravimetric diet estimates (Link 2004; Baker et al. 2014).

496   Second, inference at the broad, annual scale can be obfuscated by variation in distributional

497   changes and spatiotemporal overlap of predators and prey. For example, the absence of peaks in

498   mysid consumption by striped bass and spotted hake in 2003 is likely due to the absence of these

499   predators in lower latitudes from July to September, where mysids appear more concentrated and

500   when mysid biomass peaks (Hulburt 1957; Hopkins 1965). Use of multiple predators with

501   contrasting life histories helped identify incongruous overlap situations such as this, but

502   interpretation of patterns is more challenging when both predator and prey are highly mobile (as

503   was the case for bay anchovy and their predators). Inadequate contrast in annual prey densities

504   has been identified as another complicating factor in detecting density-dependent diet signals

505   (Pinnegar et al. 2003). Also, indices of prey standing stocks may not be fully representative of

506   prey production rates, particularly for shorter lived prey groups with multiple or continuous

507   recruitment events throughout the year.

508

509   **Methodological considerations**

510   When modeling the consumption of an individual prey group, there is a potential for

511   interactions among prey caused largely by prey selectivity and prey switching (Eggers 1977;

512   Juanes 1994; Stefánsson and Pálsson 1997), such that the consumption of one prey influences the

513   consumption of another. There is some evidence of prey interaction between mysids and bay

514   anchovy (Buchheister 2013), but the interaction is confounded by the strong opposing

515   ontogenetic trends in consumption for these two prey. The decreased likelihood of mysid

516   consumption when bay anchovy are present in a stomach (Buchheister 2013) could be driven

517   more by the size-based shifts in feeding as opposed to active prey selection (Juanes 1994), or by

518   patchiness of prey that can reduce the likelihood of joint occurrence of prey. Undoubtedly, prey

519   selectivity and the choices predators make at small scales can influence broader consumptive

520   trends of multiple prey, but disentangling these effects from other system interactions, indirect

521   food web effects, and spatiotemporal changes in predator-prey overlap require continued

522   research.

523   Generalized additive mixed effects models provided a powerful and flexible approach for

524   drawing more robust statistical inferences from stomach content data. The biggest advantages of

525   these models included the ability to 1) appropriately handle the excessive number of zeros in an

526   approach that is ecologically meaningful, 2) account for the correlation structure of the

527   hierarchical sampling design that is common in fisheries surveys, 3) incorporate a variety of

528   categorical and continuous explanatory variables, 4) account for nonlinear effects of covariates

529   on the response, and 5) maintain diet information at the individual fish level, to avoid pooling

530   data as is needed for average-based analytical methods (e.g., pooling predators into size classes

531   was not required). However, as with other statistical modeling, GAMM convergence was largely

532   predicated on having sufficient sample sizes for models of greater complexity. Proxies for

533   goodness of fit and precision of covariate effects were poor in some cases, but this is largely

534   attributable to the large variability in ecological datasets that are typically noisy. The major

535   dietary patterns and general conclusions of the study where not altered by the exclusion of the

536   random station effect (nor replacing it with a random stratum effect), but accounting for the non-

537   independence of fish is more statistically valid and helps avoid erroneous conclusions (Hurlbert

538   1984, Millar and Anderson 2004). Although GAMMs have been described as being on "the

539   frontier of statistical research" (Zuur et al. 2009), these and related methods are being advanced

540   quickly and are becoming more accessible to researchers (Wood 2006; Zuur et al. 2009); thus,

541   they are rapidly being integrated into the statistical toolboxes of many ecologists and fisheries

542   scientists (e.g., Venables and Dichmont 2004; Ciannelli et al. 2008).

543

544   **Implications**

545   Comprehensive, spatiotemporally-extensive trophic studies such as this work help

546   elucidate the trophic relationships and drivers that structure ecosystems, and can contribute to

547   implementation of EBFM. The coherence in annual prey consumption indices of multiple

548   predators supports their utility as indicators of relative prey abundance that could augment

549   current prey sampling surveys (e.g., Mills et al. 2007), and such diet metrics may be particularly

550   useful for monitoring or hindcasting key prey groups, such as mysids, for which systematic

551   sampling does not exist. EBFM applications of this type of research include parameterization of

552   multispecies and ecosystem models (Pauly et al. 2000), use of dietary indices as ecosystem

553   indicators (Dwyer et al. 2010), empirical information for helping parameterize prey

554   vulnerabilities within foraging sub-models (Garrison et al. 2010), fitting of functional response

555   curves if consumptions are expressed as rates (Moustahfid et al. 2010), and potentially the use of

556   diet time-series as additional tuning indices for ecosystem models. Continued research on trophic

557   dynamics, particularly focused on long time periods and broader spatial extents, will provide

558   valuable information on fish and food web ecology to support EBFM at the scales most pertinent

559   to resource management.

560

Acknowledgements

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765 **Table 1.** Sample summaries for Chesapeake Bay predators collected for dietary analysis. Length measurements were recorded as fork

766 length (teleosts) or disc width (batoids). N_s = Number of stations with predator captured, N_f = Number of individual fish sampled for

767 stomachs, P_e = percentage of fish stomachs that were empty. Numbers of fish containing key prey groups are indicated.

	Length (mm)					No. fish containing prey				
Predator	Range	Mean	N_s	N_f	P_e	Any Prey	Mysid	Anchovy	Bivalve	Polychaete
Atlantic croaker (*Micropogonias undulatus*)	20 - 478	242	977	3374	14	2914	458	--	550	1753
clearnose skate (*Raja eglanteria*)	84 - 519	412	355	941	13	821	--	--	146	--
kingfishes (*Menticirrhus spp.*)*	45 - 383	236	399	1077	18	882	--	--	179	178
northern puffer (*Sphoeroides maculatus*)	49 - 272	156	407	1087	9	990	--	--	292	180
northern searobin (*Prionotus carolinus*)	40 - 223	127	387	941	20	751	381	--	--	--
scup (*Stenotomus chrysops*)	69 - 223	123	347	879	17	732	150	--	--	268
spot (*Leiostomus xanthurus*)	40 - 311	156	616	2217	29	1581	--	--	--	556
spotted hake (*Urophycis regia*)	50 - 318	147	244	609	19	491	323	--	--	--
striped bass (*Morone saxatilis*)	92 - 1051	372	1005	3868	33	2590	549	638	--	707
summer flounder (*Paralichthys dentatus*)	129 - 750	344	1501	4874	42	2828	1119	663	--	--
weakfish (*Cynoscion regalis*)	15 - 616	211	1128	6699	25	4994	2301	1951	--	--
white perch (*Morone americana*)	68 - 351	202	524	2784	38	1739	--	--	278	510

768 *Menticirrhus saxatilis* and *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* = Year; *L* = Length; *LA* = Latitude; *T* = Temperature; *D* = 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.

Prey	Predator	Binomial GAMM						Positive GAMM					
		YR	*L*	*LA*	*T*	*D*	% Dev	*YR*	*L*	*LA*	*T*	*D*	% Dev
Bay anchovy	Summer flounder	+	+	+	+	+	13.5	+	+				5.4
	Striped bass	+	+	+	+	+	17.0	+		+			9.4
	Weakfish	+	+	+	+		8.7	+	+				7.6
Bivalve	Atlantic croaker	+	+	+			13.5	+	+	+			24.6
	Clearnose skate	+		+			16.9	+					22.3
	Kingfish	+		+	+		22.6	+	+				35.4
	Northern puffer	+	+	+	+		15.0	+	+				20.0
	White perch	+	+	+	+		12.6	+	+				15.0
Mysid	Atlantic croaker	+	+		+		16.5	+					8.8
	Northern searobin	+		+			6.8	+	+		+	+	15.7
	Scup	+			+	+	13.5	+					6.0
	Spotted hake	+	+		+	+	19.3	+	+		+	+	29.1
	Striped bass	+	+	+	+		19.0	+	+	+			24.3
	Summer flounder	+	+	+	+	+	36.7	+	+	+			9.1
	Weakfish	+	+	+	+	+	18.8	+	+				12.8
Polychaete	Atlantic croaker	+	+	+	+	+	8.9	+	+				28.5
	Kingfish	+	+				6.9	+	+				49.3
	Northern puffer	+		+		+	9.5	+	+				32.4
	Scup	+	+	+		+	8.0	+	+				22.8
	Spot	+	+	+			4.3	+	+				16.7
	Striped bass	+	+	+		+	13.5	+	+				10.6
	White perch	+	+	+		+	8.2	+	+	+			25.5

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.

a. Mysids	Scup	Flounder	Croaker	Weakfish	N. searobin	Str. bass
Flounder	0.79					
Croaker	**0.88**	0.69				
Weakfish	0.83	0.58	**0.90**			
N. searobin	**0.88**	0.56	0.75	0.78		
Str. bass	0.05	-0.15	0.11	-0.07	0.33	
Sp. Hake	-0.14	-0.45	-0.09	0.03	0.03	0.33

b. Bay anchovy	Flounder	Str. bass	Weakfish
Str. bass	0.71		
Weakfish	-0.01	0.03	
Index	0.41	0.34	0.42

c. Bivalves	Kingfish	Cl. skate	W. perch	Croaker	N. puffer
Cl. skate	0.69				
W. perch	0.41	0.72			
Croaker	0.20	0.49	0.31		
N. puffer	0.23	0.30	0.40	0.35	
Index	-0.12	-0.13	-0.10	0.18	0.74

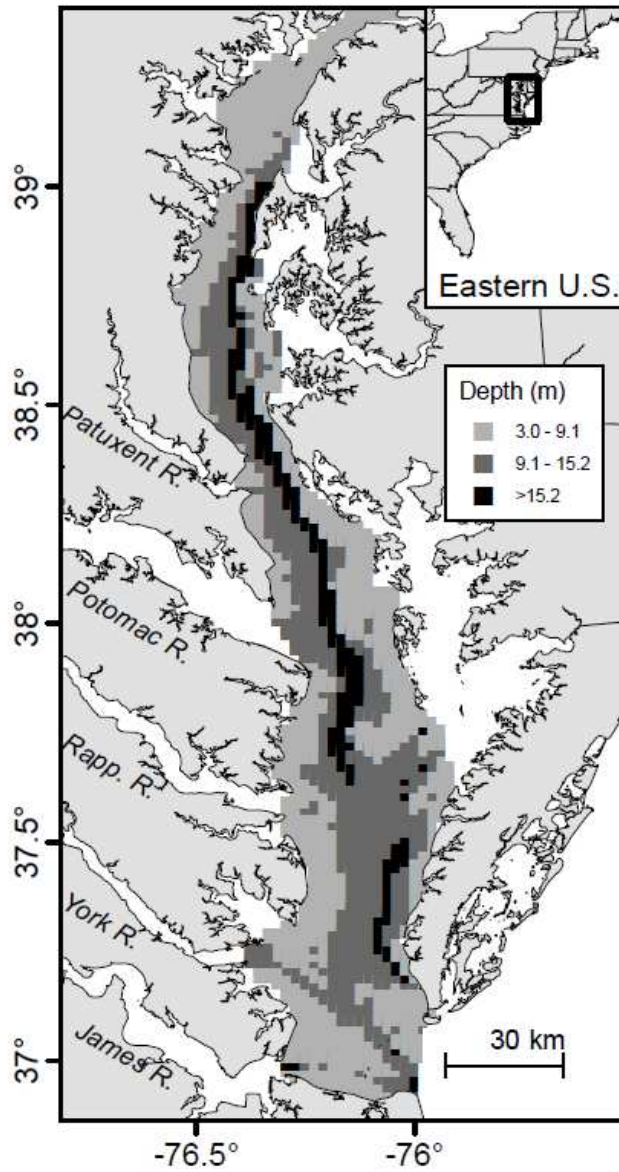| d. Polychaetes	Scup	Kingfish	W. perch	Croaker	N. puffer	Str. bass
Kingfish	0.05					
W. perch	0.66	0.14				
Croaker	0.50	0.67	0.58			
N. puffer	0.23	-0.40	0.23	0.10		
Str. bass	-0.67	0.33	-0.34	0.04	-0.36	
Index	0.49	0.33	0.37	0.22	0.14	-0.69

Fig. 1. Map of Chesapeake Bay mainstem areas sampled by the Chesapeake Bay Multispecies Monitoring and Assessment Program. Survey area is divided into 1 km^2 grid cells and classified into three depth strata. Areas in white are not sampled by the survey.
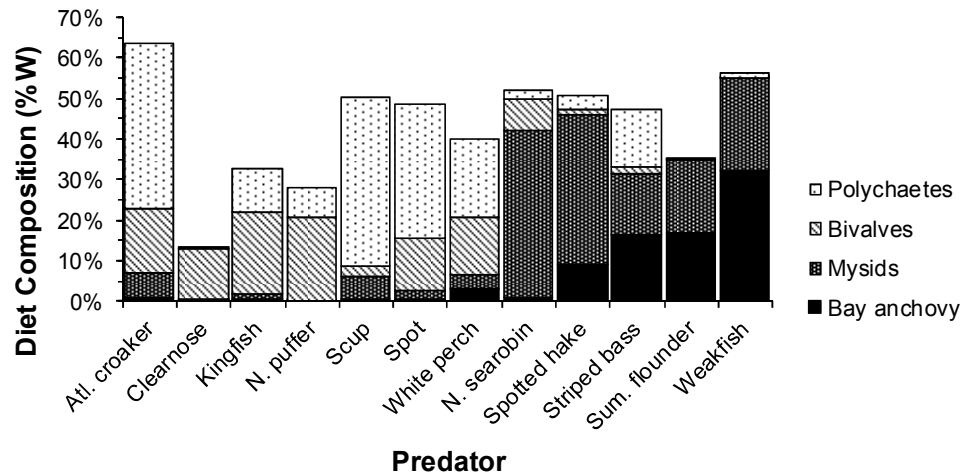
Fig. 2. Composition of predator diets (as % of stomach content weight) for twelve

Chesapeake Bay fishes consuming four key prey groups (bay anchovy, mysids, bivalves,

and polychaetes). The remainder of stomach contents were comprised of other prey.

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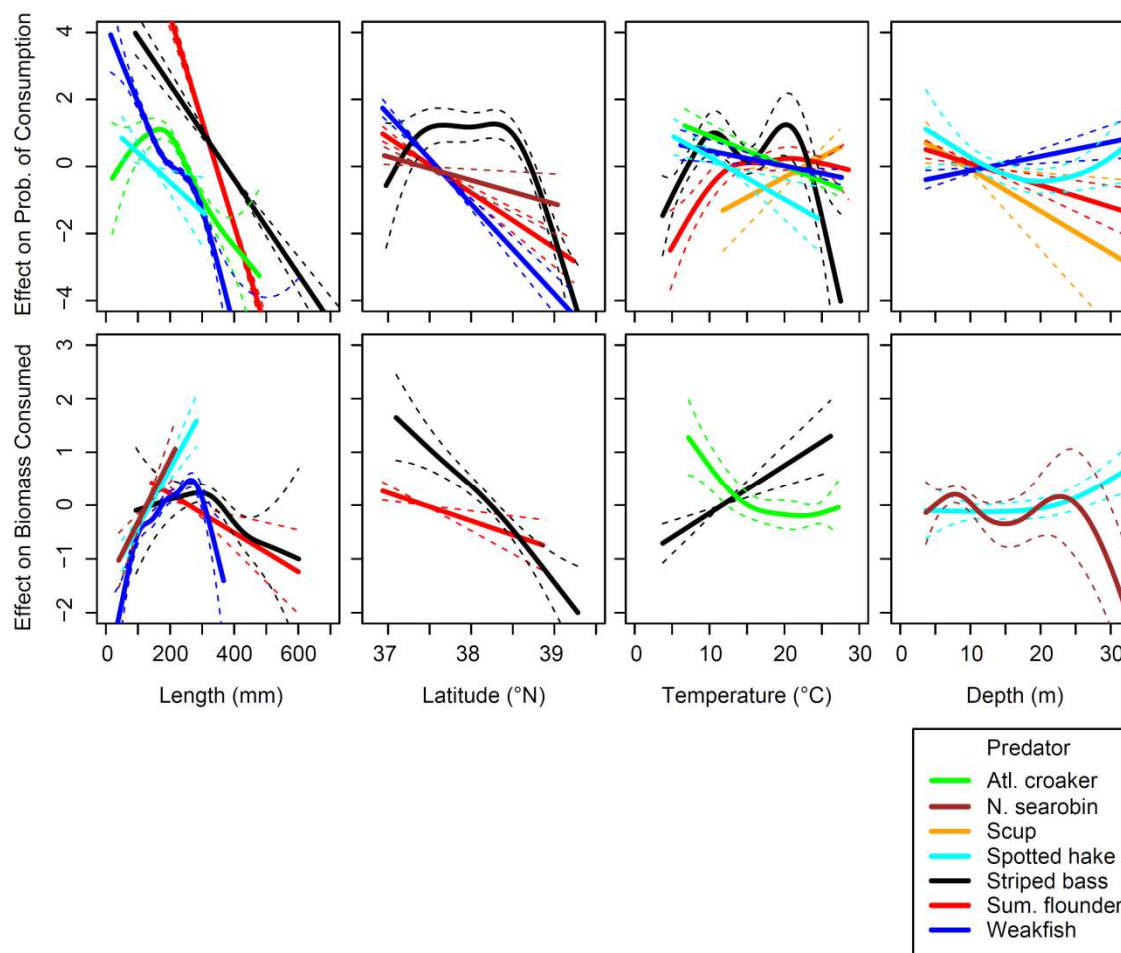
Fig. 3. Modeled effects of continuous covariates on consumption of mysids based on delta generalized additive mixed-effects models (GAMMs) for multiple Chesapeake Bay predators. Upper panels depict covariate effects on the relative probability (on the logit scale) of a predator stomach containing a mysid, 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.

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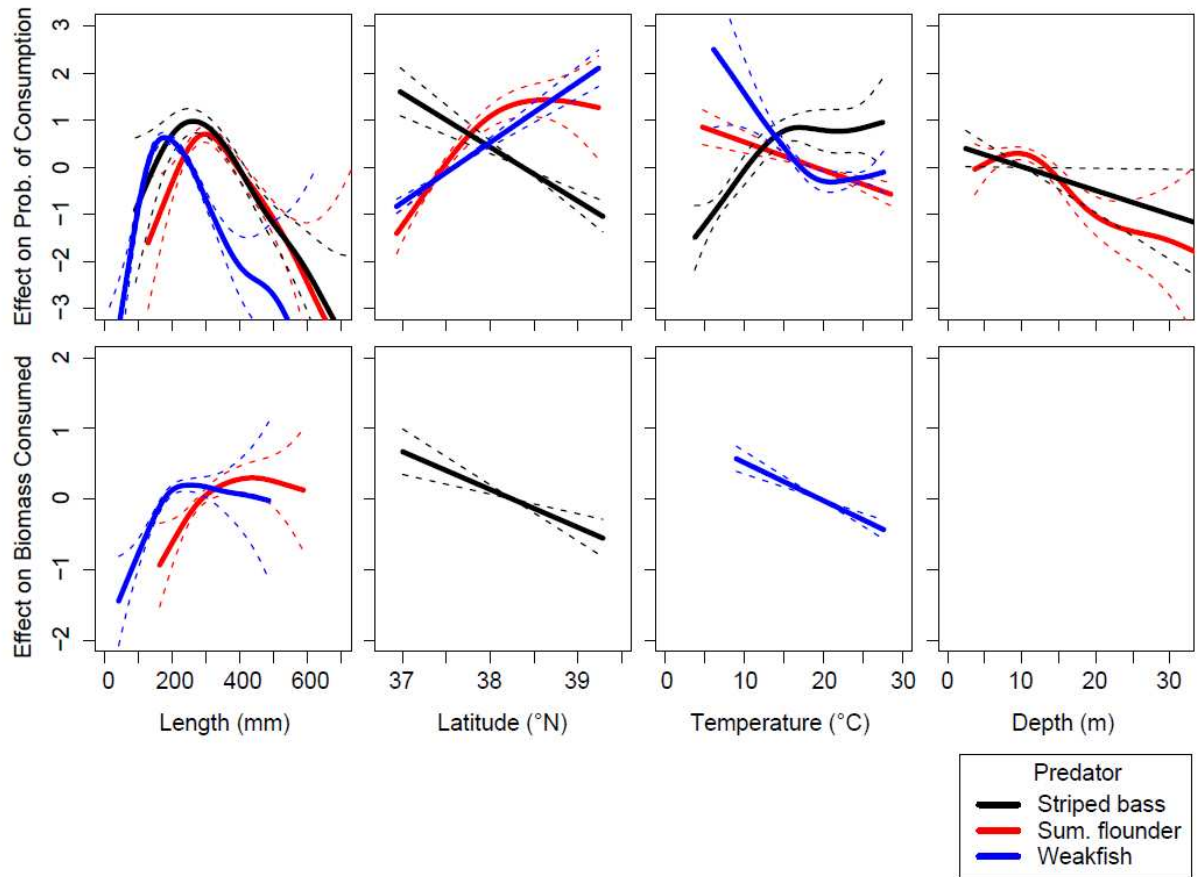
Fig. 4. Modeled effects of continuous covariates on consumption of bay anchovy based on delta generalized additive mixed-effects models (GAMMs) for multiple Chesapeake Bay predators. See Figure 3 for full description of plot.
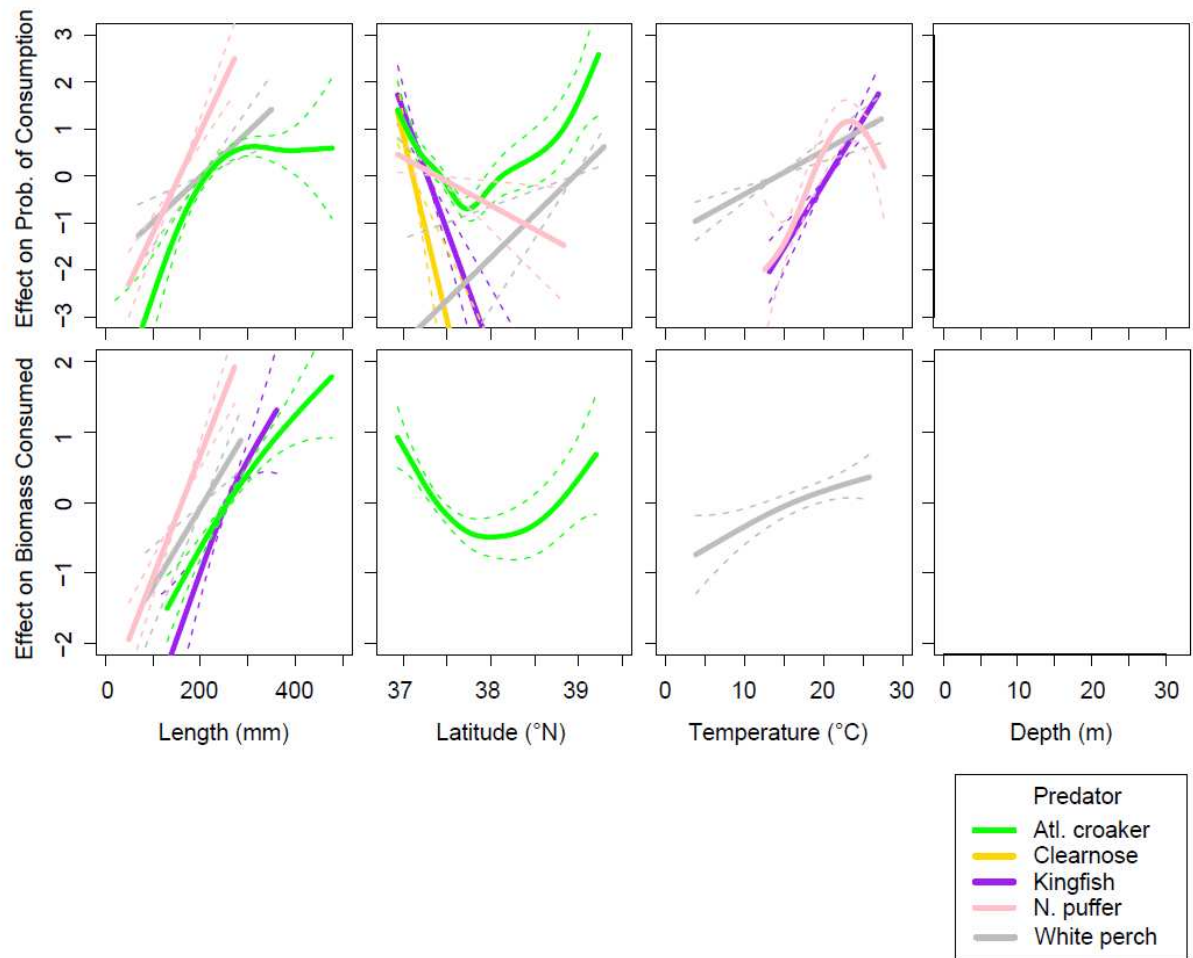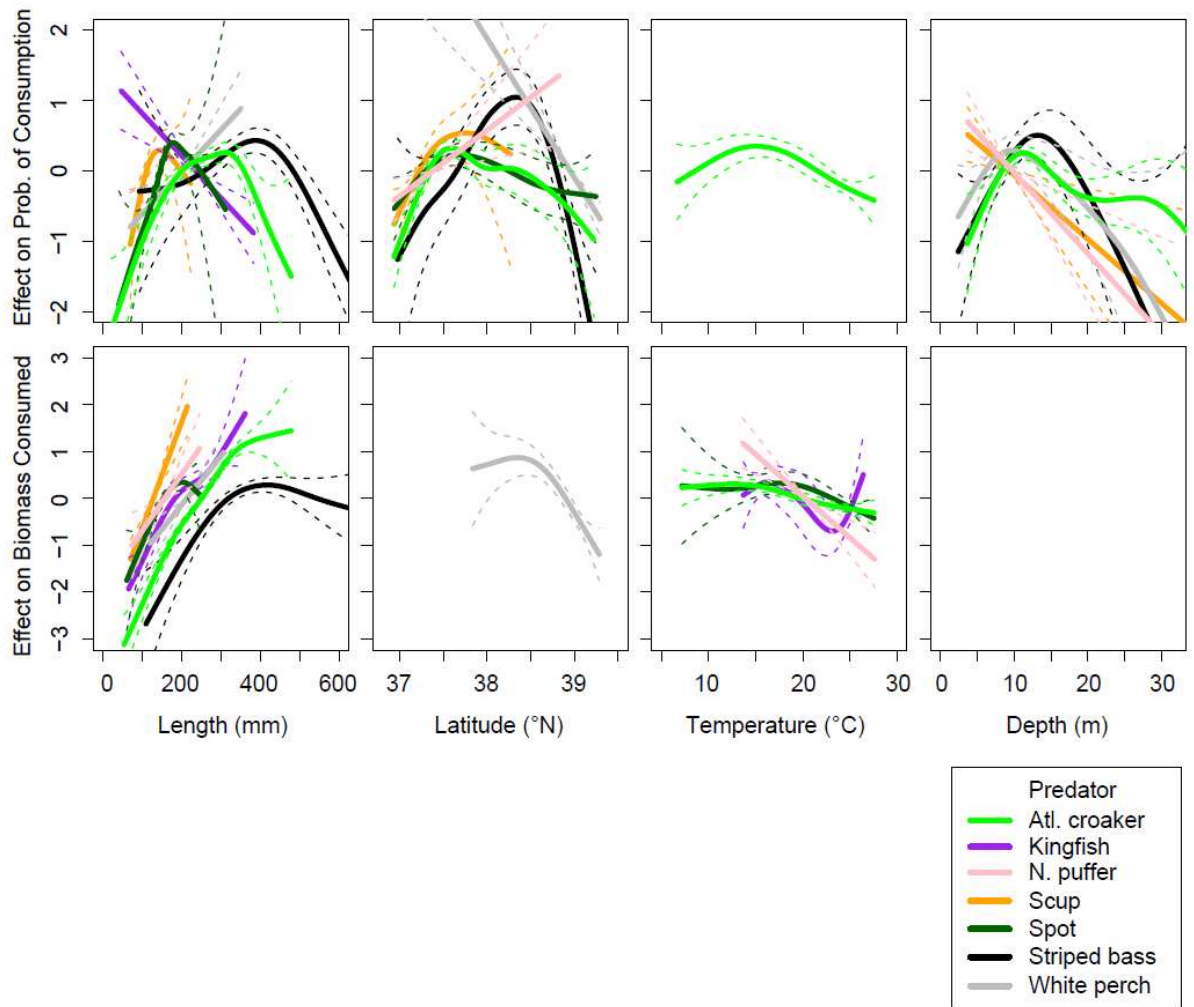
Fig. 5. Modeled effects of continuous covariates on consumption of bivalves based on delta generalized additive mixed-effects models (GAMMs) for multiple Chesapeake Bay predators. See Figure 3 for full description of plot.

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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.
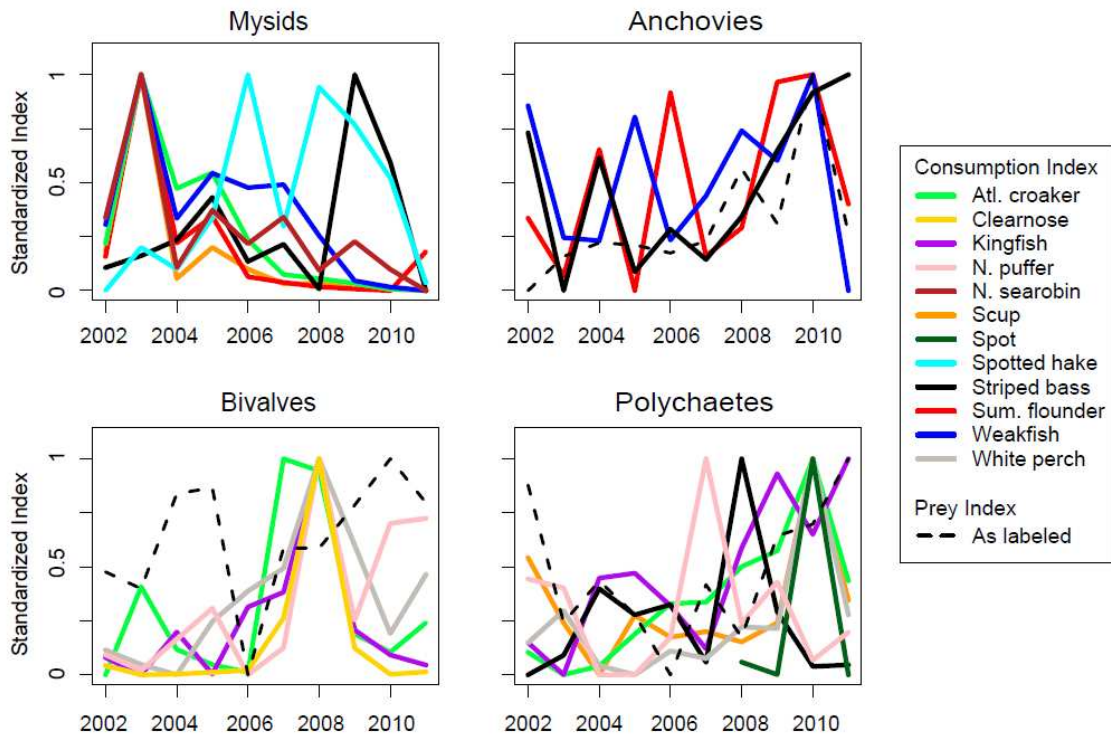
Fig. 7. Annual indices of prey consumption derived from the delta generalized additive mixed-effects models. Consumption of each prey by a predator was standardized to range from 0-1 (solid, colored lines). Standardized prey abundance index denoted with dashed line, but not available for mysids.