1 Simulating bottom-up effects on predator productivity and consequences for
2 the rebuilding timeline of a depleted population
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16 Abstract

17 Bottom-up control within ecosystems is characterized, in part, by predator populations
18 exhibiting growth and recruitment changes in response to variability in prey density or
19 production. Annual prey availability can vary more than 10-fold in marine ecosystems,
20 with prey experiencing a dramatic increase or pulse in production within some years. To
21 assess the bottom-up effects of such pulses on predator growth, production, and fisheries
22 management, we developed an age-specific, predator-prey simulation model
23 (parameterized for summer flounder, *Paralichthys dentatus*) based on simple
24 hypothesized mechanisms for consumption, growth, and population dynamics. Pulses in
25 each of the three modeled prey groups (small crustaceans, forage fish, larger fish prey)
26 generated different magnitudes of change in predator weight-at-age (w), spawning stock
27 biomass (S), fishery yield (Y), and recruitment (R), due to ontogenetic differences in
28 growth potential and dietary composition across predator age classes. Increases in
29 productivity of small forage fishes generated the greatest gains in predator w , S , Y , and
30 R , relative to pulses of the other prey groups. Median increases in R following a prey
31 pulse were minimal ($<4\%$) except under high fishing rates that stimulated a stronger
32 compensatory response in the population (8-11% increase in R), demonstrating the
33 interactive role of top-down and bottom-up effects on predator productivity. Seasonal
34 migration patterns determined the degree of spatiotemporal overlap of predators with the
35 spatially constrained pulses in prey production. Prey pulses reduced the median time
36 required for depleted populations to be rebuilt by 0-5% following declines in fishing
37 pressure. Reductions in time to recovery were highly variable due to recruitment
38 stochasticity, but stock recovery was more sensitive to the severity of harvest control
39 measures than to availability of the non-limiting prey. Understanding the relative
40 magnitudes of such bottom-up processes, particularly in the presence of varied fishing
41 pressure can aid in developing ecosystem approaches to fisheries management that
42 account for such ecological interactions more explicitly.

43

44 **1. Introduction**

45 Bottom-up control in ecosystems is characterized by the regulation of higher-
46 trophic-level productivity and variability by processes acting on lower trophic levels.
47 Although other forms of control (top-down and wasp-waist) can be dominant in some
48 systems or under certain conditions (Hunt and Stabeno, 2002; Cury and Shannon, 2004;
49 Hunt and McKinnell, 2006), empirical evidence supports bottom-up structuring of
50 various marine ecosystems (Aebischer et al., 1990; Verheye, 2000; Chavez et al., 2003;
51 Frederiksen et al., 2006). Theoretically, a simple mechanism supporting such bottom-up
52 control can consist of four steps: 1) environmentally-mediated increases in prey
53 production and density, 2) enhanced foraging by predators, 3) improved growth, survival,
54 and fecundity of predators, and 4) greater recruitment to the following generation of the
55 predator population. The relationship between predator density and prey density that
56 would link the two ends of this mechanistic progression has been described in terrestrial
57 literature as a predator's reproductive numerical response (Solomon, 1949; Holling,
58 1959). For marine fishes, direct empirical support for such a mechanism is stronger for
59 steps 1-3 (e.g., McGowan et al., 1998; Ringuette et al., 2002; Castonguay et al., 2008),
60 but wanes through its progression to step 4 (e.g., Mcfarlane and Beamish, 1992;
61 Beaugrand et al., 2003). Thus, at broad scales, support for reproductive numerical
62 responses by fishes tends to be more correlative in nature (Aebischer et al., 1990; Ware
63 and Thomson, 2005; Frank et al., 2007), with the mechanistic components corroborated
64 empirically at smaller spatiotemporal scales or supported theoretically.

Two of the main difficulties in linking prey and predator densities at system-wide scales involve the high degree of interannual variability in predator-prey populations and the adaptive foraging behaviors of most fishes. Populations of fishes and other organisms commonly experience 10-fold variability in recruitment, but variations can be even more drastic (>100-fold) as recruitment and mortality are influenced by a complex suite of climatic, oceanographic, ecological, and anthropogenic factors (Rothschild, 1998; Hunt and Stabeno, 2002; Houde, 2009). Importantly, an aggregation of ameliorative conditions in some years can cause dramatic increases, or pulses, in production (Holland et al., 1987; Rothschild, 1998; Jung and Houde, 2004b). These pulses in production can be targeted and consumed heavily by predators, especially by relatively opportunistic fishes that can switch to these prey as they become more available (Ringuette et al., 2002; Castonguay et al., 2008). However, the ability of predators to exploit pulses in prey production is partially mediated by ontogenetic changes in diets and food preferences (Scharf et al., 2000). Years of abrupt failures in prey production or recruitment can also have important consequences for predator populations (Gjøsæter et al., 2009). Understanding a predator's growth and numerical responses to the large inherent variability in prey production can be an important component to characterizing the trophodynamic mechanisms controlling fisheries production.

The potential benefits of increased prey production to predators can interact with top-down fishing pressure and be influenced by spatiotemporal overlap of the interacting species. For exploited predator populations, fishery removals are a dominant source of mortality, and a reproductive numerical response could be dissipated by the harvest of any surplus predator production that results from prey pulses. Movement of predatory

88 populations also has the potential of obscuring any bottom-up effects, given that prey
89 production can be regionally confined. For example, many marine fishes have life
90 histories dependent on estuaries, in which prey production can be greater relative to
91 alternative offshore habitats (Beck et al., 2001; Able, 2005). Thus, the degree of
92 movement between estuarine and offshore regions could influence predator-prey overlap,
93 predatory growth, and the numerical response.

94 In this study, we evaluated the population-scale consequences of increased prey
95 availability on a predator stock using a mechanistic, multi-species simulation model,
96 parameterized for summer flounder, *Paralichthys dentatus*. The age-specific, spatial,
97 predator-prey model linked consumption, growth, and population dynamics. Summer
98 flounder was chosen as the model predator because its fishery and ecology (e.g.,
99 migration, ontogenetic diet shifts, life history) are representative of other exploited
100 marine groundfish, and because there is evidence that the species is responsive to pulses
101 in prey production. This species has supported a large fishery in the northwest Atlantic
102 Ocean, and overfishing led to significant declines of the stock, reaching record lows in
103 the late 1980s (Terceiro, 2002). After establishing a rebuilding plan and implementing
104 regulations, the stock recovered and was declared rebuilt in 2010 (Terceiro, 2011). Based
105 on research from the Chesapeake Bay (the largest estuarine nursery area serving the
106 coastal summer flounder population), summer flounder demonstrated strong episodic
107 increases in prey consumption likely driven by prey availability (Buchheister and Latour,
108 in press). These annual periods of increased consumption were also correlated with
109 larger weight-at-age for summer flounder (A. Buchheister, unpublished data).

Our simulation model provided a controlled virtual environment for examining questions regarding the potential population-scale response to pulses in prey production. We were specifically interested in examining the relative effects of three different prey groups that are consumed and targeted at varying rates through ontogeny, as is common in the diets of many fishes (Latour et al., 2008; Buchheister and Latour, 2015). Multiple modeling scenarios were used to address three major research questions: 1) How do pulses in productivity of different prey populations influence the growth, production, and reproductive numerical response of a migratory predator? 2) How do fishing rates and migration patterns interact with a population's ability to harness regionally-localized increases in prey production? 3) What influence would these prey pulses have on rebuilding timelines of an overfished predator population? Understanding the relative magnitudes of these bottom-up processes, particularly in the presence of varied fishing pressure can aid in developing ecosystem approaches to fisheries management that account for such ecological interactions more explicitly (Link, 2010a).

124

125 **2. Methods**

126 ***2.1 Base model formulation***

We developed a spatial, age-specific simulation model that consisted of linked population, growth, and consumption models. Within the population model, the key abundance changes modeled were decreases in abundance due to fishing and natural mortality, movement between regions, and additions through recruitment (Fig. 1). The model was parameterized to represent the summer flounder stock along the Northeast U.S. Atlantic coast, from North Carolina to Maine. We coded the model for two linked

133 spatial domains or ecosystems (region 1 – nearshore estuaries and bays; region 2 –
134 offshore continental shelf waters) to account for the strong migration of the species
135 between these habitats. Summer flounder were modeled with 8 age-classes from age-0 to
136 age-7+, following the convention of recent stock assessments (Terceiro, 2011). We
137 treated time discretely, using a seasonal (three-month) time-step to account for the highly
138 seasonal dynamics of summer flounder movement, spawning, and growth. Within each
139 time step, the order of processes proceeded with recruitment, mortality, consumption,
140 growth, and movement, with the census taken at the end of each season. Model
141 simulations were conducted for 55 years under various scenarios (see section 2.2)
142 following a 25-year burn-in period. All symbols for the simulation model are defined in
143 Table 1. Model equations are presented in Table 2 and referenced by Tx.y, with x
144 denoting the table number and y indicating the equation number within the table. All
145 model parameters are presented in Appendix Table A1.

146

147 2.1.1. *Population dynamics*

148 We modeled the summer flounder population abundance following initial
149 recruitment. Recruitment (i.e., with $a=0$ and $s=1$) followed Beverton-Holt stock
150 recruitment (SR) dynamics (eq. T2.1) and was dependent on: SR parameters presented by
151 Rothschild et al. (2012); the coast-wide annual spawning stock biomass during the
152 spawning season (eq. T2.8); the fraction of the total recruitment that occurs in each
153 region; a stochastic error term to generate lognormal deviates; and a survivorship
154 equation (eq. T2.9). Given the importance of estuaries as nursery areas for summer
155 flounder, we assumed that 90% of the recruitment occurred in region 1 (Packer et al.

1999). Survivorship was dictated by population declines generated with a constant, instantaneous natural rate ($M=0.25$) and age-specific annual fishing mortality rates based on age-dependent selectivities (eq. T2.10) following the stock assessment (Terceiro, 2011); due to fishing pressure throughout the year and a lack of adequate information, mortality rates were assumed to be constant across seasons and regions. Following initial recruitment, population abundances for each age and time step were calculated by tracking survivors and accounting for the net movement of fish between regions (eq. T2.2, T2.3, T2.6). Net movement (I) of fish was calculated based on proportions of individuals that migrate from each region to the neighboring region in each season (eq. T2.4, T2.5, T2.7; see also section 2.2.3). For the plus group, age- A predator abundance during $s=1$ ($P_{y,A,s=1,r}$) was calculated using the abundances of the surviving members of age- A fish plus age $a-1$ individuals that joined the group (eq. T2.3). To initiate the model, abundances by age in the first year were set to the stock assessment estimates for 1989 (Terceiro, 2011), divided evenly between regions and constant across seasons.

2.1.2. *Growth*

We used a gross conversion efficiency approach to model the changes in mean weight-at-age of summer flounder through time and space. Any changes in mean individual weight altered the spawning stock biomass of the population and subsequently recruitment. Prior to accounting for mixing between regions, weight-at-age ($w_{y,a,s,r}$) was defined as:

$$w_{y,a,s,r} = w_{y,a,s-1,r} + f_{s,r} K_{y,a,s,r} \sum_{j=1}^k C_{j,y,a,s,r} \quad (1)$$

178 The gross conversion efficiency ($K_{y,a,s,r}$), which is the proportion of prey mass that is
 179 converted to somatic mass, was modeled as a decreasing logistic function of weight to
 180 account for the physiological decline in growth rate and greater energy allocation to
 181 reproduction that occurs through ontogeny (T2.15; Brett, 1979). The consumption of
 182 each prey ($C_{j,y,a,s,r}$) was modeled with a Type-II functional response (see section 2.1.3).
 183 A temperature-dependent function ($f_{s,r}$) scaled the consumption of fish to account for the
 184 physiological changes in maximum consumption and growth attainable in different
 185 seasons (T2.16; Hanson et al., 1997). Parameters for $f_{s,r}$ (CTM, CTO, CQ; T2.16-T2.20)
 186 for summer flounder (a temperate species) were modified from a bioenergetics model of
 187 a subtropical congener, *Paralichthys lethostigma* (Burke and Rice, 2002). Seasonal mean
 188 temperatures for each region were obtained from monitoring data from the Chesapeake
 189 Bay Program and the Northeast Fisheries Science Center (Table A1). We set the initial
 190 weight of an age-0 individual in the first season (i.e., 3-month old) as a constant (w_0)
 191 derived from empirical data from the Chesapeake Bay (Table A1). The parameterization
 192 of the gross conversion efficiency is described below (see section 2.1.4). To account for
 193 mixing of fish from the two regions following their movement, the final seasonal weight-
 194 at-age within a region was calculated as an abundance-weighted mean of the individuals
 195 that ended in that location (as detailed in eq. T2.12), but for simplicity, equation 1
 196 describes the growth process prior to population mixing.

197

198 2.1.3. Consumption

199 We modeled three functional prey groups to represent the majority of general prey
 200 types consumed by summer flounder in the wild (Link et al., 2002; Staudinger, 2006;

201 Latour et al., 2008; Buchheister and Latour, 2011). Prey 1 represented small crustaceans
 202 such as mysids (e.g., *Neomysis americana*) and shrimps (e.g., *Crangon septemspinosa*),
 203 prey 2 represented small forage fishes (e.g., *Anchoa mitchilli*), and prey 3 represented
 204 larger fishes (e.g., *Leiostomus xanthurus*) and squid (e.g., *Doryteuthis pealeii*, *Illex*
 205 *illecebrosus*). Biomass of each prey ($N_{j,y,s,r}$) varied stochastically around a mean value
 206 based on random lognormal deviates ($e^{Y_{j,y,s,r}}$) that were year-, season-, and region-
 207 specific (eq. T2.25). The mean biomass for prey 2 ($\bar{N}_2$) was set at 30 kmt (Jung and
 208 Houde, 2004a), and biomasses for prey 1 and prey 3 biomasses were scaled (using
 209 parameter τ_j) to be an order of magnitude higher and lower than $\bar{N}_2$, respectively, based
 210 on their different trophic levels (Link, 2010b). A biomass multiplier (ψ) was used to
 211 simulate prey pulses (see section 2.2.1 for description).

212 Biomasses of prey species were forced in the model without predator feedbacks
 213 under the assumption that top down control of prey by the single modeled predator was
 214 negligible. This was done for several reasons. First, each general prey group is
 215 representative of multiple, generally shorter-lived species, and they are consumed by a
 216 diversity of predators in natural systems such that the influence of a single predator
 217 species on the dynamics of the general prey groups would be minimal. For example,
 218 based on an ecosystem model of Chesapeake Bay (Christensen et al., 2009), summer
 219 flounder (with a trophic level of 3.6) comprise only 1% of the biomass within trophic
 220 levels 3.25-3.75, and they account for <5% of the predation mortality on prey that are
 221 representative of prey groups 1 and 2 in our model. Second, many temperate marine
 222 ecosystems, like the one in which summer flounder reside, are characterized by generalist
 223 feeding patterns and weak interactions that hinder strong top-down control of prey

224 populations (Closs et al. 1999, Link 2002, Frank et al. 2007). Third, we were interested
225 in testing the effects of simulated prey pulses that represent short periods of excessive
226 prey production (see section 2.2.1 for description of prey pulses). These prey pulses are
227 controlled by density-independent environmental factors, and they can easily overwhelm
228 any top-down control by predators (e.g., Holland et al., 1987; Rothschild, 1998; Jung and
229 Houde, 2004b).

230 We modeled average, per capita consumption using a type-II multispecies
231 functional response model (eq. T2.21; Koen-Alonso, 2007). The functional response
232 model was dependent on prey biomasses, a shape parameter (h), maximum per capita
233 consumption ($C_{a,s}^{\max}$), and prey-specific attack rates ($\alpha_{j,a,s}$). We assumed $h=1$, which
234 corresponds with a hyperbolic type-II functional response (Koen-Alonso, 2007). We
235 estimated $C_{a,s}^{\max}$ as an allometric function of mean body weight (eq. T2.22) using values
236 for striped bass (Hartman and Brandt, 1995a) that reproduced size-based empirical trends
237 in maximum stomach fullness of wild summer flounder (A. Buchheister, unpublished
238 data). To account for observed ontogenetic transitions in dietary contributions of the
239 three prey (Buchheister and Latour, 2015; Buchheister and Latour, in press), we modeled
240 attack rates with an age-dependent logistic decline for prey 1 (eq. T2.23), a dome-shaped
241 double logistic curve for prey 2 (eq. T2.24), and a logistic increase for prey 3 (eq. T2.23).
242 The age-dependent, inflection-point parameters (η) for these attack rate functions were
243 assumed based on trends in empirical diet data (Table A1; Buchheister and Latour, in
244 press). Below, we describe and support the parameterization of the functional response
245 model.

246

247 2.1.4. Base model calibration

248 Parameterization of the base model was informed by fishery independent survey
249 data, stock assessment reports, and available literature (Table A1). Few suitable
250 empirical values existed for parameterizing the growth and consumption equations, so we
251 chose parameter values to closely match two empirical relationships: 1) mean weight-at-
252 age of summer flounder based on 4849 individuals captured over 10 years in a fishery-
253 independent trawl survey from Chesapeake Bay (Fig. 2C; Bonzek et al., 2011); and 2)
254 diet composition by age as informed by empirical stomach content data, reflecting
255 ontogenetic transitions in preferred prey (Fig. 2A; Buchheister and Latour, in press). We
256 used a two-stage approach to select suitable growth and functional response parameters.
257 First, we estimated the gross conversion efficiency parameters (KL , KR , KW) that
258 regulated growth by minimizing the mean square error of weight-at-age estimates
259 (relative to the empirical model; Fig. 2C). This was done while holding consumption
260 constant at 40% of C^{max} , which is a reasonable level for consumption in the wild
261 (Hartman and Brandt, 1995b; Stevens et al., 2006). Second, we estimated the functional
262 response parameters, λ and ρ (eq. T2.23-T2.24), that regulated the prey-specific attack
263 rates and the relative amounts of prey consumption. These parameters helped dictate
264 predatory growth (by affecting the total amount of food consumed) as well as dietary
265 composition. In the absence of empirical data on attack rates and prey biomasses, we
266 calibrated λ and ρ (for all prey simultaneously) to best approximate both the mean
267 weight-at-age and diet composition relationships by minimizing the sum of the mean
268 square errors to those two relationships. This estimation was done while holding prey
269 biomasses constant at their mean values (i.e., without stochasticity). In other words, the

parameters dictating the attack rates for each prey were chosen to best approximate the growth and dietary data, but are conditional on the assumed prey biomass and the other parameters in the model.

2.2. *Model scenarios*

2.2.1. *Prey scenarios*

With the simulation model, we explored a three-way factorial combination of scenarios involving different prey pulses, fishing pressure, and movement conditions (Table 3). The three prey scenarios involved introducing random pulses in prey production that elevated the standing stock biomass of each prey group above its long-term mean value (eq. T2.25). To induce pulses in prey production, prey biomass was modified using a year- and region-specific biomass multiplier, ψ . For the base model, this parameter was forced to be constant ($\psi=1$). For each prey scenario, five years ($n_{pulse}=5$) were randomly-selected within a 25-year “experimental” period (defined as years 26-50, following a 25-yr burn in period) during which ψ was assigned a random number between two and six for the nearshore region ($r=1$) only. This range for ψ was chosen because, on average, it generated a maximum increase of 10-fold for prey biomass levels across simulations (after accounting for the random stochastic variability, which alone generated 2-3 fold differences in N); a 10-fold variability in prey biomass and recruitment is not uncommon (Houde, 2009). The frequency of pulses was based on empirical diet data for summer flounder and other species that was indicative of annual pulses in consumption approximately 1-3 times in a 10-year period (Buchheister and Latour, in press). In summary, each prey oscillated randomly around its respective mean,

293 but for a given prey scenario, that prey would experience a 2-6 fold increase in biomass
294 (in addition to the stochastic variability) within the nearshore region during 5 random
295 years (Fig. 3).

296

297 2.2.2. *Fishing sub-scenarios*

298 We developed three sub-scenarios that examined the influence of fishing pressure
299 on the population's response to the simulated prey pulses (Table 3). These three sub-
300 scenarios represented different stages of annual fishing mortality rates experienced by the
301 northwest Atlantic summer flounder population. For sub-scenario H, fishing mortality
302 (F) was held constant and high ($F_{\max}=1.5$), representing the average F in the fishery from
303 1982 to 1996 (Terceiro, 2011). For sub-scenario L, F was held constant and low
304 ($F_{\text{MSY}}=0.31$), representing the sustainable level of F achieved after successful
305 management and regulation of the fishery. And for sub-scenario D, F declined linearly
306 through time from $F_{\max}$ to F_{MSY} over a period of 12 years (starting at year 26 of the
307 simulation), representing the approximate trajectory of F values observed in the summer
308 flounder fishery while fishing pressure was being reduced (Terceiro, 2011). For our
309 simulations, the target F value was set at $F_{\text{MSY}}=0.31$, the fishing mortality that achieved
310 maximum sustainable yield (MSY) in the base model under deterministic conditions (Fig.
311 A1). Spawning stock biomass for MSY (S_{MSY}) was defined as the equilibrium S when
312 F_{MSY} was maintained. Two additional fishing sub-scenarios were generated for
313 comparison with sub-scenario D, but only for assessing the time required to rebuild
314 depleted stocks. For sub-scenario D2, F was reduced twice as fast as sub-scenario D (i.e.,

315 a linear decline from $F_{\max}$ to F_{MSY} over 6 years), and for sub-scenario M, F mimicked a
316 moratorium (i.e., an immediate shift from $F_{\max}$ to $F=0$ at year 26 of the simulation).

317

318 2.2.3. *Movement sub-scenarios*

319 To evaluate the role of spatial connectivity in transferring the bottom-up pulses in
320 prey production to the predator population, two movement sub-scenarios were
321 constructed (Table 3). The migration sub-scenario relied on season-specific proportional
322 movements of fish between the two regions. These proportions were assumed based on
323 catch data that describes the summer flounder life history strategy of moving nearshore
324 during summer and offshore for winter (Table A1; Packer et al., 1999; Terceiro, 2002).
325 While there is a small amount of overwintering of age-0 fish in the nearshore area, the
326 majority of the population exhibits a similar migration between the two broadly defined
327 regions (Packer et al., 1999), so we treated movements as constant across ages. This
328 seasonal movement pattern was contrasted with a fully-mixed sub-scenario in which
329 recruitment to regions and migration between regions was held constant at 50%.

330

331 2.3. *Model evaluation*

332 2.3.1. *Output*

333 The output metrics of interest were classified at individual- and population-level
334 scales. Each simulation of a scenario was run with identical stochastic perturbations (in
335 recruitment and prey biomass) as the base model, and we evaluated the difference

336 between the two models. As an individual-scale response metric, we calculated the mean
 337 percent increase in weight-at-age (Δw) during the pulse years, defined as:

$$338 \quad \Delta w = 0.2 \sum_{y^*} \frac{w_{y^*,a,s=4,r=1}^{scen} - w_{y^*,a,4,1}^{base}}{w_{y^*,a,4,1}^{base}} \times 100 \quad (2)$$

339 where y^* are the years in which a prey pulse occurred, $w_{y^*,a,s=4,r=1}^{scen}$ is the weight-at-age of
 340 fish in years y^* in season 4 and region 1 for either a simulated scenario (*scen*) or for the
 341 base model (*base*), and the coefficient 0.2 represents the inverse of the number of years in
 342 which a pulse occurred ($1/n_{pulse}$). In this fashion, we isolated the change in mean
 343 individual body size that was solely due to the change in prey availability. As
 344 population-scale metrics, we calculated the mean percent increase in the spawning stock
 345 biomass (ΔS), the annual fishery yield (ΔY), and the following year's recruitment (ΔR)
 346 using equation 2, but substituting $S_{y^*,s}$, Y_{y^*} , and $\sum_r R_{y^*+1,r}$ for $w_{y^*,a,4,1}$ respectively.
 347 Annual fishery yield (Y_y) was calculated as the sum of all catches across seasons, regions,
 348 and ages, using Baranov's catch equation (eq. T2.11).

349 To assess the influence of the prey pulses on achieving management rebuilding
 350 goals, we calculated the percent decrease in the time needed to achieve S_{MSY} (Δt) as:

$$351 \quad \Delta t = \frac{t_{rebuild}^{base} - t_{rebuild}^{scen}}{t_{rebuild}^{base}} \times 100 \quad (3)$$

352 where $t_{rebuild}$ is the rebuilding time (yrs) needed for a depleted population to reach S_{MSY}
 353 following a reduction in F for either a simulated scenario (*scen*) or for the base model
 354 (*base*). For this metric, examined scenarios were restricted to combinations of the three
 355 prey pulse scenarios, the three non-constant F sub-scenarios (D, D2, and M), and the

356 migration sub-scenario. Larger Δt values indicate that S_{MSY} was attained more rapidly in
357 the scenario compared to the base model.

358 The stochastic simulation model was run 1000 times for each unique combination
359 of scenarios. The output metrics are presented as boxplots depicting the distribution of
360 values across the 1000 simulation runs. Cumulative frequency plots of $t_{rebuild}$ across the
361 1000 simulation runs were also used to quantify the probability of reaching S_{MSY} based on
362 the number of years following the reduction in F. We ran all models for 80 years, with
363 the first 25 years as a burn-in period. Prey pulses occurred randomly from years 26-50,
364 and the final 30 years allowed for the population to equilibrate.

365

366 2.3.2. *Sensitivity*

367 The sensitivity of the model output was investigated using two approaches. First,
368 we used a Monte-Carlo sensitivity approach. We ran 1000 simulations in which all
369 parameter values were simultaneously and randomly varied (uniformly within 20% of
370 their defaults) to examine the influence of parameter uncertainty and potential parameter
371 interactions on the model results and conclusions. Second, to evaluate the relative
372 sensitivity to each model parameter, we re-ran the simulation 100 times after increasing
373 or decreasing an individual parameter by 20%. This was done repeatedly for each
374 parameter, holding all of the other values at their default values. For the ψ values, the
375 default range of a 2-6 fold increase in production was modified to be either a 2-4 fold or a
376 4-6 fold increase in production. We calculated the mean difference of each output metric
377 (Δw , ΔS , ΔY , ΔR , Δt) from the default scenario models, restricting the models to the
378 decreasing fishing sub-scenario (D) and migration sub-scenarios.

379

380 **3. Results**

381 The calibrated base model reproduced the mean weight-at-age of wild summer
382 flounder and the general dietary trends with relatively high precision. Temporal
383 stochasticity in prey biomasses generated variability in the dietary composition of
384 simulated fish (± 10 -20%; Fig. 2A) as seen in normal conditions in the field; however,
385 simulated prey compositions deviated slightly from the generalized patterns for predators
386 less than age-2 due to the challenge of calibrating the functional response parameters to
387 match the expected diet composition across all ages. Seasonal consumption by predator
388 age did not attain the maximum value, but averaged 28-73% of the maximum
389 consumption, which are reasonable values based on bioenergetics studies for other fishes
390 (Fig. 2B; Hartman and Brandt, 1995b; Stevens et al., 2006). These patterns in
391 consumption-at-age translated into weight-at-age trajectories that corresponded strongly
392 with mean empirical values from the field (Fig. 2C), suggesting that the consumption and
393 growth models generated reasonable results.

394

395 **3.1. Scenario results**

396 Pulses in prey production were utilized by predators and increased their weight-
397 at-age to varying degrees (Fig. 4). Patterns in the percent increase in weight-at-age
398 followed trends in dietary composition (Fig. 2A); the weight of an age-class increased the
399 most when its most-consumed prey experienced a pulse in production. During pulse
400 years, pulses in prey 1 generated median increases in weight of 16-18% for age-0 and
401 age-1 fish and declined for older age classes (Fig. 4). Pulses in prey 2 caused a median

402 peak increase of 21% in weight of age-1 fish with a subsequent decline. Prey 3 pulses
403 generated a median peak of 13% at age-3 and slowly tapered off at older sizes. The
404 relatively large increases in weight-at-age generated by prey pulses were well within the
405 range of observed body sizes from wild fish suggesting that such changes in weight are
406 feasible in natural environments (Fig. 5). The model also reproduced the seasonality in
407 growth patterns that are observed for summer flounder and other fishes (Fig. 5; Powell,
408 1982). The fully-mixed sub-scenario generated nearly identical trends to the migration
409 sub-scenario presented, although the magnitudes of the increases were lower (by as much
410 as 8%). Fishing sub-scenarios had no effect on weight-at-age changes because there were
411 no density-dependent controls on individual growth.

412 The patterns in the three population-scale metrics (ΔS , ΔY , and ΔR) were similar
413 across the simulated scenarios, although the magnitudes varied (Fig. 6). Relative to the
414 base model, the simulated scenarios generated median increases in S , Y , and R as high as
415 19%, 11%, and 11% respectively. Generally, ΔS values were higher than ΔY or ΔR . In
416 comparing across the prey scenarios, pulses in prey 2 consistently yielded stronger
417 increases in ΔS , ΔY , and ΔR (with medians up to 13% higher) relative to pulses in prey 1
418 and 3, regardless of the fishing or movement sub-scenarios. However, an interaction
419 between the effect of prey pulses and fishing pressure was observed; prey 1 pulses
420 generated greater increases in S , Y , and R than prey 3 pulses in the high F sub-scenario,
421 yet the opposite was true for the low F sub-scenario. The two movement sub-scenarios
422 demonstrated that median increases in S for a given prey pulse were only slightly greater
423 (0.9-3.3%) for the migration sub-scenario relative to the fully-mixed scenario.

424 The influence of the different prey pulses on the recovery time of the overfished
425 stock was highly variable, yielding 0-63% reductions in $t_{rebuild}$ (Fig. 7). The median
426 declines in $t_{rebuild}$ for the prey 1 and prey 3 pulse scenarios were 0-1% and the declines
427 were modest for pulses in prey 2 (4%, or 1 year). However, reductions in $t_{rebuild}$ of 10%
428 were not uncommon across scenarios. The largest outliers occurred in simulations where
429 a prey pulse increased S sufficiently to achieve S_{MSY} prior to a random period of poor
430 recruitment that otherwise maintained the base model run below S_{MSY} for an extended
431 length of time (Fig. A2).

432 Expressing $t_{rebuild}$ values as cumulative probabilities demonstrated the relatively
433 modest declines in $t_{rebuild}$ that resulted from pulses in prey production compared to the
434 different implementations of fishing mortality controls (Fig. 8). For example, prey pulses
435 in fishing sub-scenario D increased the probability of achieving S_{MSY} within 14 years by
436 only ~3-6.5% relative to that sub-scenario's base run; in contrast, a more stringent
437 implementation of fishing controls (i.e., base run of sub-scenario D2) would increase the
438 probability of achieving S_{MSY} by 41% over the probability of success with the base run of
439 sub-scenario D. Under the moratorium fishing sub-scenario (M), prey pulses exhibited
440 no detectable effect on achieving the management target. Under moratorium there was a
441 50% probability of rebuilding the stock within 4-5 years, compared to 14 and 18 years for
442 the same probability benchmark under the D2 and D base scenarios, respectively.

443

444 **3.2. Sensitivity results**

445 Simulation outputs were not overly sensitive to the choice of parameter values.
446 Monte-Carlo sensitivity runs generated similar patterns in Δw , ΔS , ΔY , and ΔR to those

presented in Figures 4 and 6, although the variability across simulations increased (~2-fold increase in the interquartile spread), and the median responses tended to decrease slightly (Figs. A3 and A4). Based on perturbations of individual parameters (Fig. A5), ΔW , ΔS , and ΔY were most sensitive to prey biomass and consumption parameters (specifically ψ , $\bar{N}_2$, η_3 , and CTO), whereas ΔR was most sensitive to parameters of population dynamics (α_{SR} , β_{SR} , M), prey biomass time series (ψ , $\bar{N}_2$), and growth (KL , KR , KW , CTO). However, ΔW , ΔS , ΔY , and ΔR typically varied by no more than $\pm 3\%$ due to the parameter perturbations. The Δt estimates were most sensitive to growth (KL , KR , KW , CQ , CTO), population dynamics (α_{SR} , β_{SR} , κ_{SR} , M), and prey biomass ($\bar{N}_2$, σ_γ , n_{pulse}) parameters. Perturbations of these parameters for the pulse in prey 2 scenario resulted in median differences in Δt of -5% (Fig. A5); in other words, shifting these parameters by 20% yielded no median change in the time to rebuild when comparing a pulse in prey 2 scenario and the base model.

4. Discussion

In this study, we used a mechanistic predator-prey simulation model to evaluate the population-scale consequences of episodic increases of prey production that occur in the wild. The simulation model demonstrated the substantial bottom-up effects that prey pulses can have on the growth, production, and reproductive numerical response of a predator. Predator gains in growth and production were not equivalent across prey pulses with results suggesting that increases in production of small forage fishes, rather than in crustacean or large fish prey, may be more beneficial to predators like summer flounder. Fishing pressure (i.e., top-down control) mediated the strength of the predator's

470 numerical response to increased prey production by altering spawning stock biomass and
471 the resulting density-dependent recruitment. Prey pulses did not substantially alter the
472 rebuilding timelines for recovering populations, highlighting the stronger influences of
473 fishing and recruitment variability on stock rebuilding. Population responses to the
474 interactive effects of bottom up and top down effects are difficult to detect in natural
475 settings due to environmental variability and predator-prey dynamics, but simulation
476 modeling provides a valuable tool for exploring these ecological processes.

477 Patterns in the population-scale responses to prey pulses integrated the individual
478 growth response with population mortality losses and reproductive additions.
479 Physiologically, younger fish have a greater scope for growth facilitating larger
480 proportional increases in weight-at-age than older conspecifics (Brett and Groves, 1979);
481 however this did not necessarily correspond to greater increases in S , Y , and R . The
482 scaling of the weight-at-age responses to the population-level relied on integrating these
483 biomass gains demographically across ages, while partitioning the predatory production
484 gains to natural mortality, fishing, or spawning stock biomass accumulation. Although
485 some prey groups such as mysids and small crustaceans (prey 1) generated relatively
486 strong increases in weight-at-age, these gains were constrained to a more narrow age
487 range than the other prey, and a greater proportion of this production was lost through
488 natural mortality before fish could mature to contribute to increased S and R . Increased
489 production of small forage fishes (prey 2) translated into the largest increases in S , Y , and
490 R because young predators exhibited greater growth, the prey was consumed over a
491 broader range of ages, and many of these fish matured and spawned prior to becoming
492 vulnerable to fishing. Overall, this suggests that the magnitude of bottom-up effects on

493 predatory production reflects a balance between the predator's growth potential (with
494 greater scope at smaller sizes) and the total dietary contribution across age classes;
495 increased production is then routed to natural mortality losses, fishery removal, or S
496 accumulation based on the rates of mortality, fishing, and maturation.

497 Top-down pressure on the predator population, in the form of fishery removals,
498 affected the capacity of the population to respond to the resource-driven, bottom-up
499 forcing. Similar interactions between bottom-up and top-down forces are common in
500 natural ecosystems and demonstrate the dynamic nature of ecosystem structure and
501 control (Hunter and Price, 1992; Hunt and McKinnell, 2006). In our model, this
502 interaction was caused by the density-dependent processes underlying the SR function.
503 By maintaining S at lower levels, higher fishing rates produced stronger population
504 compensation whereby the recruits per spawner was larger (Rose et al., 2001), thus
505 facilitating greater increases in S and R within prey 1 and prey 2 pulse scenarios. In the
506 prey 3 pulse scenario with high F , the additional predatory production was shunted more
507 to the fishery restricting the accumulation of S , but R still increased (relative to the
508 decreasing and low fishing rate scenarios) due to compensation. Thus, top down fishing
509 pressure can influence a population's ability to capitalize on bottom-up forcing by
510 regulating the density-dependent production (i.e., compensation) expected at lower stock
511 sizes.

512 Recruitment is one of the most critical processes regulating population dynamics,
513 but it remains challenging to predict given the complex interactions among various
514 density-independent and density-dependent factors that govern recruitment strength
515 (Sissenwine, 1984; Houde, 2009). The reproductive numerical response in this

simulation model relied on the density-dependent nature of the SR function, but it was not overly sensitive to the parameterization of the SR function. Although summer flounder recruitment data can appear independent of S (Maunder, 2012), the empirical realization of an underlying density-dependent relationship is obscured by large natural variability in recruitment, in addition to sampling and estimation errors of those values. In our simulations, we could rely on broader theoretical and empirical support for compensatory mechanisms operating on fish populations (Rose et al., 2001), while also standardizing and accounting for uncertainty through the inclusion of the stochastic recruitment deviations. Summer flounder and other flatfishes have relatively high steepness values for SR relationships (Maunder, 2012; steepness=0.74 in this study) indicating that recruitment remains relatively high at low S compared to other commercial species (Myers et al., 1999; Rose et al., 2001). Therefore, other species with lower steepness could be expected to exhibit stronger proportional increases in R and S due to prey pulses, given similar conditions to our simulation.

From a fisheries management perspective, the numerical responses of predators to increases in prey production had relatively minor effects on rebuilding times relative to recruitment variability and fishing pressure. Recruitment stochasticity, which represented various climatic, oceanographic, and ecological processes known to influence recruitment (Houde, 2009), generated far greater variability in rebuilding time than prey pulses alone. The role of strong recruitment years can facilitate the recovery of overfished stocks (Richards and Rago, 1999; Hart and Rago, 2006), but in the wild any numerical responses of the form we have investigated would be embedded within a complex mosaic of environmental and biological controls on recruitment. However, our

539 simulations emphasized the predominant role that curbing top-down fishing pressure has
540 on the speed at which target stock sizes are attained (Safina et al., 2005; Rosenberg et al.,
541 2006). Given the greater accumulation of S and stronger reproductive numerical
542 responses of predators to pulses in prey 1 and 2 (at high F), conservation of prey for
543 younger age-classes of an overfished predatory stock could provide some benefits for
544 rebuilding the population. But, one important caveat is that our simulation assumed that
545 none of the prey resources were severely depleted or limiting. For example, if prey 3
546 represented a depleted forage fish population, then that trophic linkage could be a
547 bottleneck for predator nutrition, preventing suitable growth and stock recovery (e.g.,
548 Hartman and Margraf, 2003).

549 The movement patterns of the simulated population influenced the degree of
550 spatial-temporal overlap of predators with the spatially constrained pulses in prey
551 production. A fully mixed population was less able to capitalize on improved foraging
552 conditions in the nearshore environment. The availability of diverse and abundant prey
553 resources within estuarine and nearshore habitats is an important component selecting for
554 the estuarine-dependent life history strategies of summer flounder and many other coastal
555 fishes (Beck et al., 2001; Able, 2005). Although summer flounder are managed as a unit
556 stock in the northwest Atlantic, as many as three sub-populations have been proposed to
557 exist within the stock area (Terceiro, 2002). In cases of increased spatial structure among
558 subpopulations, we would anticipate any reproductive numerical responses of the
559 population to be similarly controlled by the extent of spatiotemporal overlap of predators
560 with areas of increased prey productivity but potentially modified by any spatial patterns
561 in fishing.

562 The level of complexity for the simulation model was chosen to simplify the
563 mechanistic processes governing consumption, growth, and population dynamics while
564 accounting for the major factors of influence and representing empirical data. For
565 example, our simple consumption and growth models accounted for the effects of
566 temperature, prey availability, predator size, and diet ontogeny, which rank as some of
567 the most dominant regulators of prey consumption and growth (Brett and Groves, 1979).
568 Any effects resulting from differences in prey quality were assumed to be minimal given
569 the similarity in energy densities (within 10%) among summer flounder and
570 representative species from the three prey groups (Hartman and Brandt, 1995b; A. Z.
571 Horodysky and R. W. Schloesser, unpublished data). For the multispecies functional
572 response, there was insufficient empirical data to adequately parameterize the model, as
573 is typically the case for predator-prey models at large spatial scales (Moustahfid et al.,
574 2010; Hunsicker et al., 2011). While the absolute values of the parameters used in the
575 functional response model may not be accurate for the wild population, the relative attack
576 rates and relative biomasses defined predator-prey dynamics that successfully represented
577 empirical patterns in weight-at-age and diet composition with reasonable levels of total
578 consumption relative to C^{max} .

579 Four model assumptions could potentially have a larger influence on the model
580 dynamics and our conclusions. First, we assumed that the predator-prey system was
581 adequately described using three prey groups. Marine food webs can be highly complex
582 and connected, characterized by a multitude of trophic linkages and high degree of
583 omnivory (Link, 2002). However, trophic complexity is reduced when prey are
584 aggregated into size or functional groups as we have done (French et al., 2013), and

585 omnivory and prey switching was incorporated at this coarse resolution of prey (with the
586 multi-species functional response). Second, although our assumption that predators have
587 negligible effects on prey dynamics is supported for our modeled species (see section
588 2.1.3), predator-prey feedbacks would be an important consideration for systems with
589 stronger interactions or evidence of top-down trophic cascades. Third, our model
590 formulation did not account for any indirect effects among the modeled groups (e.g.,
591 pulses affecting other prey groups and their predators), assuming that these effects would
592 be minimal and potentially delayed relative to the modeled direct effects. Fourth, we
593 assumed that natural mortality was constant as commonly employed in population
594 models and stock assessments (e.g., Terceiro, 2011). However, improved foraging and
595 growth can alter mortality rates and can be part of the mechanism regulating recruitment
596 strength and reproductive numerical responses (Cushing, 1990; Houde, 2009). These
597 foraging effects on survival appear most drastic and notable on early life history (i.e.,
598 larval and early juvenile) stages of fishes (Sissenwine, 1984; Caddy, 1991), therefore the
599 majority of this effect would occur prior to the initiation of our predator population at 3
600 months of age. Generally, there is limited empirical, quantitative information to
601 parameterize the ecological regulation of natural mortality across ages at the population-
602 scale (e.g., Caddy, 1991; Maunder and Wong, 2011), therefore we were unable to justify
603 the form and magnitude of any effects of prey pulses and improved growth on natural
604 mortality. Consequently, we consider our estimates to be conservative measures of the
605 effects that pulses in prey production have on a predator population, with regards to our
606 natural mortality assumption.

607 Age-specific predator-prey models like the one developed here provide a simple
608 framework for testing the effects of bottom-up and top-down influences on a predator
609 population. Given that ecosystem approaches to fisheries management ideally rely on a
610 blend of model types (Link, 2010a), this age-specific approach can complement more
611 complex ecosystem models. Ecosystem models can provide a broader assessment of
612 system-wide consequences (both direct and indirect) of changes in production or fishing,
613 but they do not typically provide high ontogenetic resolution within modeled species
614 groups. As shown in our study, the ontogenetically variable feeding habits of fishes have
615 bearing on the individual- and population-scale responses of predators to bottom-up
616 forcing, particularly for species with varying degrees of historical fishing pressure (Hunt
617 and McKinnell, 2006). In the simulations, depleted populations were the most sensitive
618 to episodic pulses in prey production, but detection of such effects would be easily
619 obscured in wild populations due to other factors influencing recruitment variability
620 which is particularly high at low stock sizes (Myers, 2001). While these bottom-up
621 effects of prey pulses can benefit rebuilding plans of overfished populations, their small
622 magnitude relative to changes in fishing mortality supports the primacy of regulating
623 fishing for stock recovery.

624

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822

823 **TABLE CAPTIONS**

824 Table 1. Description of symbols in Table 2 that were used for the simulation model.

825

826 Table 2. Equations for the summer flounder (*Paralichthys dentatus*) simulation model
827 consisting of population dynamics, growth, and consumption.

828

829 Table 3. Description of simulation scenario levels for prey pulses, fishing mortality, and
830 movement.

831 **FIGURE CAPTIONS**

832 **Fig. 1.** Diagram of predator-prey simulation model. Major mechanistic processes are
833 labeled (C – consumption, G – growth, R – recruitment, I – net immigration, F – fishing
834 mortality losses, M – natural mortality losses).

835

836 **Fig. 2.** Growth, consumption, and diet output from one stochastic 80-year run of the base
837 simulation model for summer flounder. A) Diet composition by age for each simulated
838 year (prey 1 – black; prey 2 – red; prey 3 – blue). The smooth, thick, overlaid lines
839 represent the generalized, empirical patterns in diet composition that were used for model
840 calibration. B) Per capita seasonal consumption for simulated cohorts (C , black lines)
841 relative to the maximum consumption (C^{max} , green line). C) Weight-at-age data for wild
842 summer flounder (gray points) with mean empirical growth curve (red line) and
843 simulated cohort growth curves (blue lines) overlaid.

844

845 **Fig. 3.** Prey biomass time-series (kmt) for a base model run (black line) and a prey pulse
846 scenario (red line) whereby base values are multiplied 2-6 fold for five randomly-selected
847 years between years 25 and 50 (dotted lines).

848

849 **Fig. 4.** Percent increase in weight-at-age (Δw) of simulated populations experiencing
850 pulses in prey production relative to the base model populations that experience no pulse.
851 At each age, boxplots are staggered for each of the prey pulse scenarios (prey 1 – gray;
852 prey 2 – red; prey 3 – blue). Boxplots show the distribution of mean values across 1000
853 stochastic simulation runs (colored bar – interquartile range, horizontal line – median,

854 notches – approximate 95% confidence interval for the median, whiskers – furthest value
855 from the quartile within 1.5x(interquartile range), individual points – outliers).

856

857 **Fig. 5.** Simulated growth trajectories for the single fastest-growing cohorts, from all
858 model runs, for each of the pulse scenarios (prey 1 – black; prey 2 – red; prey 3 – blue).
859 Mean growth of all base runs (dashed line) and empirical weight-at-age data (points) also
860 presented. Simulations used a migration sub-scenario with a constant, high fishing
861 mortality (fishing sub-scenario H).

862

863 **Fig. 6.** Population-scale output metrics of simulated summer flounder (*Paralichthys*
864 *dentatus*) populations. Percent increase in the A) spawning stock biomass (ΔS), B)
865 fishery yield (ΔY), and C) following year's recruitment (ΔR) for various scenarios were
866 calculated relative to base model runs. Scenarios were comprised of different
867 combinations of fishing mortality trends (high – H; decreasing – D; low – L), prey pulses
868 (prey 1 – gray; prey 2 – red; prey 3 – blue), and movement patterns (migration – Mig;
869 fully-mixed – Mix). See Figure 4 for boxplot description.

870

871 **Fig. 7.** Percent decrease in the time (Δt) needed for simulated depleted populations to
872 rebuild to target spawning stock biomass, relative to the base model. Scenarios were
873 comprised of different combinations of fishing mortality trends (decreasing – D; rapid
874 decrease – D2; and moratorium – M) and prey pulses (prey 1 – gray; prey 2 – red; prey 3
875 – blue). Results plotted for the migration sub-scenario only. See Figure 4 for boxplot
876 description.

877 **Fig. 8.** Cumulative probability of achieving the target spawning stock biomass (S_{MSY})
878 under different simulated pulse and fishing scenarios. Prey pulse scenario indicated by
879 solid line color (prey 1 – gray; prey 2 – red; prey 3 – blue) relative to its base model
880 (dashed line). Each group of curves reflects a different fishing mortality sub-scenario
881 (moratorium – M, rapid decrease – D2, decrease – D), with black triangles marking the
882 year in which the target F (F_{MSY}) was achieved for each F sub-scenario.

Symbol	Description	Units
Subscript indicators (range/level)		
<i>a</i>	Predator age (0-7+)	years
<i>A</i>	Maximum predator age; plus group (7+)	years
<i>j</i>	Prey type (crustaceans = 1, small fishes = 2, larger fishes = 3)	
<i>r</i>	Region (nearshore estuaries and bays = 1, offshore shelf = 2)	
<i>n</i>	Neighboring region (nearshore estuaries and bays = 1, offshore shelf = 2)	
<i>s</i>	Season (Jan-Mar, winter = 1; Apr-Jun, spring = 2; Jul-Sep, summer = 3; Oct-Dec, fall = 4)	
<i>s'</i>	Spawning season (fall)	
<i>y</i>	Year (1-80)	
<i>y*</i>	Year in which a pulse occurs (5 random years selected from y=26-50)	
Calculated values		
$P_{y,a,s,r}$	Predator abundance by year, age, season, and region	fish
$I_{y,a,s,r}$	Net immigration by year, age, season, and region	fish
$R_{y,r}$	Abundance of surviving recruits by year and region in season 1	fish
$S_{s'}$	Predator spawning biomass in the spawning season	kg
$L_{y,a,s}$	Fraction of fish that survive by year, age, and season	
$F_{y,a,s}$	Instantaneous fishing mortality rate by year, age, and season	year ⁻¹
$G_{y,a,s,r}$	Somatic growth by year, age, season, and region	kg
$w_{y,a,s,r}$	Average individual weight-at-age by year, season, and region	kg
$K_{y,a,s,r}$	Gross conversion efficiency by year, age, season, and region	
$C_{j,y,a,s,r}$	Per capita consumption by prey, year, age, season, and region	kg prey (kg pred) ⁻¹ s ⁻¹
$C_{a,s}^{\max}$	Maximum per capita consumption by age and season	kg prey (kg pred) ⁻¹ s ⁻¹
$\bar{w}_{a,s}$	Mean empirical weight-at-age by season	kg
$\alpha_{j,a,s}$	Functional response attack rate coefficient by prey, age, and season	(kg prey) ⁻¹
$N_{j,y,s,r}$	Prey <i>j</i> biomass year, season, and region	kg
$f_{s,r}$	Proportion of max consumption attainable by season and region	
V, X, Y, Z	Intermediate calculations for <i>f</i>	
Y_y	Biomass yield to the fishery by year	kg
Parameters		
$\phi_{s,n \rightarrow r}$	Proportion of predators migrating from region <i>n</i> into region <i>r</i> by age and season	
$\phi_{s,r \rightarrow n}$	Proportion of predators migrating from region <i>r</i> into region <i>n</i> by age and season	
F_y	Instantaneous fishing mortality rate by year	year ⁻¹
sel_a	Selectivity of fishery by age	
<i>M</i>	Instantaneous natural mortality rate	year ⁻¹
α_{SR}	Maximum recruitment-per-unit biomass for stock-recruitment relationship	10 ⁶ recruits (kmt) ⁻¹
	Threshold biomass above which the density-dependent effects dominate the density-independent effects.	
κ_{SR}		kmt
β_{SR}	Shape parameter for degree of density compensation ($\beta=1$ for Beverton Holt)	
θ_r	Fraction of total recruitment that recruits to region <i>r</i> .	
δ_y	Stochastic recruitment error term $\sim N(0, \sigma_\delta^2)$ by year	
$m_{a,s'}$	Proportion of fish that are mature by age during the spawning season	
w_0	Average individual weight of age-0 predator in first season	kg
<i>KL</i>	Maximum gross conversion efficiency	
<i>KR</i>	Rate parameter for change in gross conversion efficiency	g ⁻¹
<i>KW</i>	Weight at which <i>K</i> is 50% of <i>KL</i>	g
<i>h</i>	Shape parameter for functional response (Type II when <i>h</i> =1)	
λ_j	Scale parameter for maximum attack rate by prey	(kg prey) ⁻¹
ρ_j	Rate parameter for change in attack rate with age for prey <i>j</i>	years ⁻¹
η_j	Age at which attack rate is 50% of λ_j	years
η_{1j}, η_{2j}	Inflection points for ascending and descending limbs of double logistic equation	years
<i>CA</i>	Intercept for the allometric relationship between <i>C</i> and predator mass	
<i>CB</i>	Rate parameter for the allometric relationship between <i>C</i> and predator mass	
$\bar{N}$	Mean biomass for prey 2	kg
τ_j	Biomass of prey <i>j</i> relative to biomass of prey 2	
$\psi_{y,r}$	Prey biomass multiplier by year and region;	
$v_{j,y,s,r}$	stochastic error term $\sim N(0, \sigma_v^2)$ for prey <i>j</i> biomass by year, season, and region	
$T_{s,r}$	Mean bottom water temperature by season and region	C
<i>CTM</i>	Maximum water temperature above which consumption ceases	C
<i>CTO</i>	Optimal water temperature for maximum consumption	C
<i>CQ</i>	Rate parameter for temperature function	

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886 **Table 2.**

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Equation	Reference
Population submodel	
<i>Population dynamics ($s = 1$)</i>	
$P_{y,a=0,s=1,r} = R_{y,r} = \frac{\alpha_{SR} S_{y,s'}}{(1 + S_{y,s'} / \kappa_{SR})^{\beta_{SR}}} \theta_r e^{\delta_y} L_{y,a,s}$	T2.1
$P_{y,a,s=1,r} = (P_{y-1,a-1,4,r} + I_{y,a,s,r}) L_{y,a,s}$	T2.2
$P_{y,A,s=1,r} = (P_{y-1,A-1,4,r} + P_{y-1,A,4,r} + I_{y,A,1,r}) L_{y,a,s}$	T2.3
$I_{y,a,s=1,r} = \varphi_{s,n \rightarrow r} P_{y-1,a-1,4,n} - \varphi_{s,r \rightarrow n} P_{y-1,a-1,4,r}$	T2.4
$I_{y,A,s=1,r} = \varphi_{s,n \rightarrow r} (P_{y-1,A-1,4,n} + P_{y-1,A,4,n}) - \varphi_{s,r \rightarrow n} (P_{y-1,A-1,4,r} + P_{y-1,A,4,r})$	T2.5
<i>Population dynamics ($s > 1$)</i>	
$P_{y,a,s,r} = (P_{y,a,s-1,r} + I_{y,a,s,r}) L_{y,a,s}$	T2.6
$I_{y,a,s,r} = \varphi_{s,n \rightarrow r} P_{y,a,s-1,n} - \varphi_{s,r \rightarrow n} P_{y,a,s-1,r}$	T2.7
<i>Supporting equations</i>	
$S_{y,s'} = \sum_{r=1}^2 \sum_{a=0}^A P_{y,a,s',r} w_{y,a,s',r} m_{a,s'}$	T2.8
$L_{y,a,s} = e^{-0.25(M+F_{y,a})}$	T2.9
$F_{y,a} = F_y \cdot sel_a$	T2.10
$Y_y = \sum_{s=1}^4 \sum_{r=1}^2 \sum_{a=0}^A \frac{F_{y,a}}{M + F_{y,a}} (1 - L_{y,a,s}) P_{y,a,s,r} w_{y,a,s,r}$	T2.11
Growth submodel	
<i>Growth</i>	
$w_{y,a,s,r} = \frac{1}{P_{y,s,r,a}} \left(\frac{P_{y,a,s-1,r} L_{y,a} (1 - \varphi_{s,r \rightarrow n}) (w_{y,a,s-1,r} + G_{y,a,s,r}) +}{P_{y,a,s-1,n} L_{y,a} \varphi_{s,n \rightarrow r} (w_{y,a,s-1,n} + G_{y,a,s,n})} \right)$	T2.12
$G_{y,a,s,r} = f_{s,r} K_{y,a,s,r} \sum_{j=1}^k C_{j,y,a,s,r}$	T2.13
$w_{a=0,s=1,r} = w_0$	T2.14
$K_{y,a,s,r} = \frac{KL}{(1 + e^{-KR(1000w_{y,a,s,r} - KW)})}$	T2.15
<i>Temperature dependence</i>	
$f_{s,r} = V^X e^{(X(1-V))}$	T2.16
$V = (CTM - T_{s,r}) / (CTM - CTO)$	T2.17

914	$X = \frac{Z^2(1 + \sqrt{(1 + 40/Y)})^2}{400}$	T2.18
915	$Y = \ln(CQ) \cdot (CTM - CTO + 2)$	T2.19
916	$Z = \ln(CQ) \cdot (CTM - CTO)$	T2.20
917	Consumption submodel	
918	<i>Functional response</i>	
919	$C_{j,y,a,s,r} = \frac{C_{a,s}^{\max} \alpha_{j,a,s} N_{j,y,s,r}^h}{C_{a,s}^{\max} + \sum_{j=1}^k \alpha_{j,a,s} N_{j,y,s,r}^h}$	T2.21
920	$C_{a,s}^{\max} = 91 \cdot \bar{w}_{a,s-1} \cdot CA(\bar{w}_{a,s-1})^{CB}$	T2.22
921	$\alpha_{j,a,s} = \frac{\lambda_j}{(1 + e^{-\rho_j(a_s - \eta_j)})}$	T2.23
922	$\alpha_{j=2,a,s} = \lambda_j \left(\frac{1}{(1 + e^{-\rho_j(a_s - \eta_{1j})})} \right) \left(1 - \frac{1}{(1 + e^{-\rho_j(a_s - \eta_{2j})})} \right)$	T2.24
923	<i>Prey biomass</i>	
924	$N_{j,y,s,r} = \bar{N}_2 \tau_j \psi_{y,r} e^{\gamma_{j,y,s,r}}$	T2.25
925	<hr/>	

926 Table 3.

Scenarios	Description
<i>Pulse Scenario</i>	
Prey 1	5 annual increases in biomass (2-6 fold) of prey group 1, representing small crustaceans (e.g. mysids, shrimps)
Prey 2	5 annual increases in biomass (2-6 fold) of prey group 2, representing small forage fishes (e.g. anchovies)
Prey 3	5 annual increases in biomass (2-6 fold) of prey group 3, representing larger fishes & cephalopods (e.g. sciaenids, squids)
<i>Fishing Sub-scenarios</i>	
H	Constant, high fishing mortality ($F_{\max}$)
L	Constant, low fishing mortality for maximum sustainable yield (F_{MSY})
D	Linear decrease in fishing mortality from $F_{\max}$ to F_{MSY} over 12 years
D2*	Linear decrease in fishing mortality from $F_{\max}$ to F_{MSY} over 6 years
M*	Immediate, knife-edge decrease in fishing mortality from $F_{\max}$ to zero
<i>Movement Sub-scenarios</i>	
Mig	Seasonal migrations between offshore and nearshore habitats
Mix	Spatially mixed population with equal distribution and movement between offshore and nearshore habitats

*These fishing sub-scenarios only used as contrasts to the D sub-scenario for estimating time to recovery.

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Fig. 1.

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934 **Fig. 2. [color figure]**

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936 **Fig. 3. [color figure]**
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940 **Fig. 4.** [color figure]

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Fig. 5. [color figure]

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 946 **Fig. 6. [color figure]**

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952 **Fig. 8. [color figure]**

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956 **APPENDIX TABLE CAPTIONS**

957 Appendix Table A1. Parameter values for the base simulation model. See Tables 1 and 2
958 for symbol definitions and model equations.

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962 APPENDIX FIGURE CAPTIONS

963 Appendix Fig. A1. Sustainable fishery yield (kmt) at varying levels of instantaneous
964 fishing mortality (F). Results were generated from the simulation model with all
965 stochasticity removed. Maximum sustainable yield (MSY) was achieved at $F_{MSY}=0.31$.

966

967 Appendix Fig. A2. Recovery of spawning stock biomass (S) for a simulated population
968 under the decreasing fishing mortality sub-scenario. This outlier simulation run yielded a
969 large difference in the time to reach S_{MSY} (horizontal dashed line) between a pulse
970 scenario (black line) and the base model (red line). Vertical dotted lines denote the start
971 and end of the period in which prey pulses could occur.

972

973 Appendix Fig. A3. Monte-Carlo sensitivity results for population-scale output metrics of
974 simulated summer flounder (*Paralichthys dentatus*) populations. Percent increase in the
975 A) spawning stock biomass (ΔS), B) fishery yield (ΔY), and C) following year's
976 recruitment (ΔR) for various scenarios were calculated relative to base model runs.

977 Scenarios were comprised of different combinations of fishing mortality trends (high – H;
978 decreasing – D; low – L), prey pulses (prey 1 – gray; prey 2 – red; prey 3 – blue), and
979 movement patterns (migration – Mig; fully-mixed – Mix), with model parameters
980 randomly selected within $\pm 20\%$ of default values. See Figure 4 for boxplot description.

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982 Appendix Fig. A4. Monte-Carlo sensitivity results for the difference in rebuilding times
983 (Δt) relative to the base model. Models were run by randomly selecting all parameters

984 within $\pm 20\%$ of default values. Scenarios were comprised of different combinations of
985 fishing mortality trends (decreasing – D; rapid decrease – D2; and moratorium – M) and
986 prey pulses (prey 1 – gray; prey 2 – red; prey 3 – blue). Results were plotted for the
987 migration sub-scenario only. See Figure 4 for boxplot description.

988

989 Appendix Fig. A5. Sensitivity of model outputs to perturbations of individual model
990 parameters. Each parameter was shifted $\pm 20\%$ (see legend) while holding all other
991 parameters at default values. Mean or median differences in weight-at-age (Δw),
992 spawning stock biomass (ΔS), fishery yield (ΔY), recruitment (ΔR), and rebuilding time
993 (Δt) are presented relative to the standard simulation scenario runs (zero line). Standard
994 simulation scenario runs included pulses in prey 1 (P1), prey 2 (P2), and prey 3 (P3),
995 using the migration and decreasing fishing mortality sub-scenarios. Parameters are
996 grouped based on the process they most directly influence (consumption, growth, prey
997 biomass, or population dynamics). Weight-at-age plot is for age-1 fish which was
998 representative of other age-classes. See Table 1 for parameter definitions. Positive
999 values indicate a stronger effect of a pulse relative to the default simulation.

1000

1001 **Appendix Table A1.**

Symbol	Parameter Value	Sources
$\phi_{s,n \rightarrow r}$	$\phi_{s,1 \rightarrow 2}=0.0, 0.0, 0.4, 0.9$	Packer et al. 1999; Terceiro 2002
$\phi_{s,r \rightarrow n}$	$\phi_{s,2 \rightarrow 1}=0.3, 0.95, 0.0, 0.0$	Packer et al. 1999; Terceiro 2002
F_y	see F scenarios	Terceiro 2011
sel_a	$sel_a=0.0, 0.1, 0.5, 1, 1, 1, 1, 1$	Terceiro 2011
M	0.25	Terceiro 2011
α_{SR}	3.4	Rothschild et al. 2012
κ_{SR}	27	Rothschild et al. 2012
β_{SR}	1	Rothschild et al. 2012
θ_r	$\theta_1=0.9, \theta_2=0.1$	assumed
δ_y	$\sigma_\delta=0.4$	Terceiro 2011
$m_{a,s'}$	$m_{a=0-3+}=0.38, 0.72, 0.90, 1.0$	Terceiro 2011
w_0	0.051	A. Buchheister unpublished
KL	0.5	optimized
KR	-0.0014	optimized
KW	-600	optimized
h	1	assumed, corresponds with a Type-II functional response
λ_j	$\lambda_1=e^{-19.5}, \lambda_2=e^{-16.3}, \lambda_3=e^{-13.5}$	optimized
ρ_j	$\rho_1=-1.1, \rho_2=0.46, \rho_3=1.9$	optimized
η_j	$\eta_1=2, \eta_3=3.5$	assumed, based on survey diet data (ChesMMA, NEAMAP)
η_{1j}, η_{2j}	1, 4	assumed, based on survey diet data (ChesMMA, NEAMAP)
CA	0.3	modified from Hartman and Brandt 1995
CB	-0.2	modified from Hartman and Brandt 1995
$\bar{N}$	3×10^{10}	Jung and Houde 2003
τ_j	$\tau_1=10, \tau_3=0.1$	assumed, based on Link 2010b
$\psi_{y,r}$	$\psi_{y^*,1}=U(2,6)$; otherwise $\psi=1$	assumed
σ_v	$\sigma_v=0.4$	assumed
	$T_{s,1}=4.4, 13.6, 24.4, 14.8$;	
$T_{s,r}$	$T_{s,2}=7.6, 10.8, 13.5, 15.2$	Chesapeake Bay Program and NEFSC databases
CTM	35	Modified from Burke and Rice 2002
CTO	22	Modified from Burke and Rice 2002
CQ	2.5	Modified from Burke and Rice 2002

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1006 **Appendix Figure A1.**

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1010 **Appendix Figure A2.**

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Appendix Figure A3. [color figure]

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Appendix Figure A5. [color figure]