

Multispecies functional responses reveal reduced predation at high prey densities and varied responses among and within trophic groups

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Abstract

Understanding predator–prey interactions is critical for marine fisheries and ecosystem management as they shape community structure, regulate prey populations and present energy demands critical for community sustainability. We examined multispecies functional responses of 17 fishes (48 predator-size combinations) spanning piscivores, planktivores and benthivores for the northeast US continental shelf. Similar to previous work, linear relationships between predation and prey density (Holling type I response) were not supported, since model estimates of handling time were greater than zero for the prey considered. Instead, a clear majority of the predators sampled were Holling type III feeders (sigmoidal; prey switching or learning). For piscivores, nearly all responses were Holling type III with the exception of one being Holling type II (hyperbolic; satiation). Planktivores and benthivores exhibited a combination of type IV (feeding confusion at high prey density) and Holling type III responses. The relationships were predator- and prey-dependent, which is counter to assumptions that are often made of trophic groups. Decreased predation at high prey densities (type IV response) present among planktivores and benthivores suggests an overestimation of predation can occur if ignored. This contrasts with fish and squid prey which primarily invoked a Holling type III response. Functional responses are key to modelling trophic interactions for multispecies and ecosystem models. By refining these inputs in a multispecies context with empirical data, we can advance our understanding of whole-shelf ecology and improve decision-making tools for resource management.

KEYWORDS

Bayesian inference, continental shelf, feeding guilds, functional feeding response, Northwest Atlantic, trophic interactions

1 | INTRODUCTION

Predatory functional responses for single and multiple prey have been quantified for many organisms and environments such as

fishes (Buckel & Stoner, 2000; Moustahfid et al., 2010; Rindorf & Gislason, 2005), birds (Bijleveld et al., 2016; Buren, Koen-Alonso, & Montevechi, 2012; Smout et al., 2013), terrestrial and marine mammals (Hobbs, Gross, Shipley, Spalinger, & Wunder, 2003; Smout

& Lindstrøm, 2007; Suryawanshi et al., 2017), and even mites (Okuyama, 2012). In the marine environment, quantifying piscivory by fishes, birds and mammals has received particular interest with an aim to understand forage fish predation and make multispecies or ecosystem models operational for fisheries management (Fulton, Smith, & Johnson, 2003; Steele, Aydin, Gifford, & Hofmann, 2013; Yodzis, 1994). Within these modelling frameworks, an understanding of community ecology is possible at the scale of a continental shelf (Link, Fulton, & Gamble, 2010), but predator–prey interactions need not be limited to piscivory nor assumed to have similar predatory functional responses. Other major trophic groups such as planktivores and benthivores are often ignored or assumed less critical due to a lack of empirical data or due to specific management objectives (e.g. managing commercial piscivores and their prey).

Predator–prey interactions sit at the core of all ecological sciences and have a long history of monitoring, modelling and theory due to their complexity (e.g. Layman et al., 2015; May, Beddington, Clark, Holt, & Laws, 1979; Montoya, Pimm, & Solé, 2006; Pimm, 1982). One major concern is the relationship between prey density and predation rate (e.g. functional feeding response). Does a predator choose prey randomly or exhibit switching, preferentially feeding upon prey in highest abundance and effectively stabilizing prey population numbers (i.e. no prey is heavily reduced or allowed to become overly abundant; Murdoch, 1969)? Receiving less interest, particularly in the marine environment, is how prey density at the upper end of its range influences predation (e.g. predator confusion or prey toxicity; Gentleman, Leising, Frost, Strom, & Murray, 2003; Koen-Alonso, 2007). Fundamentally, variation in prey abundance can influence predatory responses (i.e. adaptive foraging; Abrams, 1992; Beckerman, Petchey, & Morin, 2010; Gremillet et al., 2004) and predation functions to regulate prey populations (Bax, 1998; Link & Garrison, 2002). Quantifying functional responses is a key component of the description of predator and prey dynamics. Relating consumption and prey availability has received attention, particularly for fisheries management objectives with marine piscivores (e.g. Essington & Hansson, 2004; Moustahfid et al., 2010), but also for marine planktivores (e.g. Brachvogel, Meskendahl, Herrmann, & Temming, 2013; Houde & Schekter, 1980) and benthivores (Alexander, Dick, & O'Connor, 2013). Despite comprehensive reviews of functional response studies (e.g. Jeschke, Kopp, & Tollrian, 2004), no studies have quantified multispecies functional responses among and within suites of piscivores, planktivores and benthivores including long time series of in situ fish diets and respective fish and invertebrate prey densities.

In global marine environments, specialist feeding has been linked to areas of high prey biodiversity and generalist feeding to areas of low prey biodiversity (Hayden, Palomares, Smith, & Poelen, 2019). Predators and their feeding strategies directly affect community structure and function (Dayton, 1971; Paine, 1980), and their feeding habits influence energy flows within ecological communities (Smout et al., 2013). Accounting for species interactions is particularly important for marine communities and their management from an ecosystem perspective, since ignoring interactions can

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underestimate removals of prey species and overestimate potential system yield (May et al., 1979; Smith, Link, Cadrin, & Palka, 2015; Tam et al., 2017). In a community of opportunistic generalist feeders, single-prey functional responses are less appropriate compared to multispecies functional responses which account for generalists regularly adapting their diet, resulting in weaker interaction strengths within food webs (Link, 2002; McCann, Hastings, & Huxel, 1998; Smout, Rindorf, Hammond, Harwood, & Matthiopoulos, 2014). The classic single-species responses promoted by Holling (1959b) type I linear, type II hyperbolic and type III sigmoidal (e.g. Kroetz & Powers, 2015; Moustahfid et al., 2010) and their expansions to consider multiple prey are well documented (e.g. Morozov & Petrovskii, 2013; Smout et al., 2010; Smout et al., 2013). Additionally, a type IV functional response allowing for reduced predation with higher prey density, albeit less often considered, includes predator confusion, prey toxicity and stomach capacity constraints as potential mechanisms (e.g. Abrams, 1989; Gentleman et al., 2003; Koen-Alonso, 2007). Thus, the dynamics of opportunistic generalist feeding can be retained by multispecies predatory response modelling and the benefits over the single-species approach have been shown with contrasting outcomes (Smout et al., 2010).

The objectives of this study were to determine the multispecies predatory responses for 17 fishes (48 predator-size combinations) and 14 prey of the northwest Atlantic. The predators comprised three trophic groups: piscivores, planktivores and benthivores. With a Bayesian approach accounting for multiple sources of error, three multispecies functional response models were tested, their fits to

the data were compared, and response patterns among and within trophic groups and predator–size categories were examined.

2 | METHODS

2.1 | Data

The multispecies functional responses of 17 piscivores, planktivores and benthivores were examined with data from the northeast US continental shelf: Mid-Atlantic Bight, Southern New England, Georges Bank, Gulf of Maine and Scotian Shelf (>290,000 km²; Figure 1). Annual means of per capita consumption (g) and prey density (number of fish per nm², number of zooplankton per 100 m³ and number of benthos per L) for each spring and fall season were the base for all functional response models. As detailed below and where applicable, prey densities were estimated from stratified random samples across the US continental shelf, which is standard input into prey stock assessments (e.g. NEFSC, 2018) and is representative of the density of prey available to the predator in a given region.

Diet information and prey density were sampled with dedicated bottom trawl, plankton monitoring and benthic macroinvertebrate surveys of the National Marine Fisheries Service (NMFS) and Northeast Fisheries Science Center (NEFSC; Azarovitz, 1981; Kane, 2007; Theroux & Wigley, 1998). Shelf-wide fish diet

sampling in concert with fish monitoring to estimate trends in abundance began in 1973 and is currently available through 2016. This has primarily occurred in the spring (March through May) and fall (September through November) across the time series. Details of the NEFSC fish diet monitoring programme are provided in Link and Almeida (2000) and Smith and Link (2010). In brief, the prey contents of 17 fish predators consistently sampled throughout the time series were examined microscopically and quantified by mass (0.01 g; prior to 1981) or examined macroscopically and quantified volumetrically (0.1 cm³; since 1981) as part of the NEFSC standardized bottom trawl survey. A volume-to-mass conversion of 1.1:1 was applied based on linear regression ($r^2 = .906$, $p < .0001$) by Link and Almeida (2000). The fish predators (Table 1) were placed into three trophic groups (piscivore, planktivore and benthivore) by size category. This was based on the majority of prey eaten by per cent of diet by mass (prey grouped as benthic invertebrates, fishes, planktonic invertebrates, squids and other; unidentifiable animal remains were excluded; Table S1), and used hierarchical cluster analysis, Euclidean distance and the “complete” agglomeration method respective of predator size. Diet dissimilarity was expressed as a per cent of the maximum Euclidean distance. The delineation of three trophic groups was supported by a bootstrap randomization approach similar to Jaksic and Medel (1990) whereby with 90% confidence, the identified groups did not occur by chance. A frequency distribution of 148,500 simulated diet

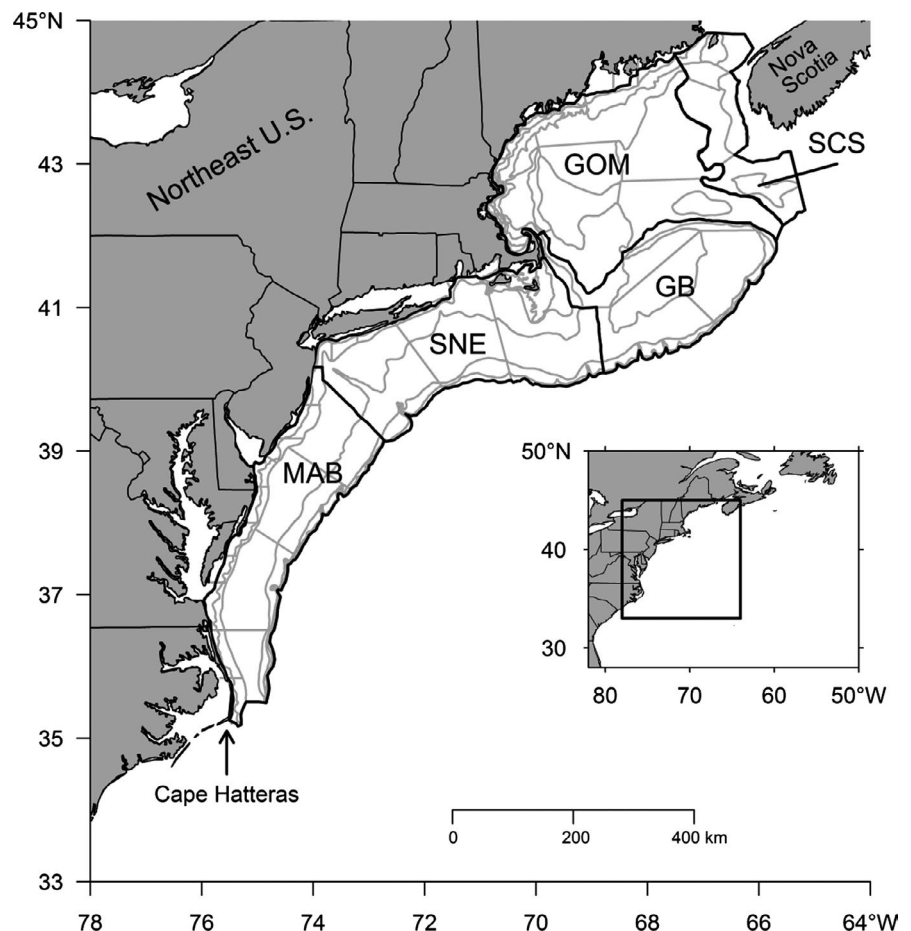


FIGURE 1 Map of northeast U.S. continental shelf. Grey lines denote sampling strata. Regions labelled as SCS, Scotian shelf; GOM, Gulf of Maine; GB, Georges Bank; SNE, Southern New England and MAB, Mid-Atlantic Bight. Nova Scotia and Cape Hatteras, North Carolina labelled for reference.

TABLE 1 List of fish predators, size categories and their trophic groups.

Predator	Species name	Size (cm)	Trophic group
Atlantic cod	<i>Gadus morhua</i> , Gadidae	S (≤ 20)	Benthivore
		M (21–50)	Benthivore
		L (51–80)	Piscivore
		XL (≥ 80)	Piscivore
Atlantic herring	<i>Clupea harengus</i> , Clupeidae	XS (≤ 10)	Planktivore
		S (11–20)	Planktivore
		M (21–30)	Planktivore
		L (> 80)	Planktivore
Atlantic mackerel	<i>Scomber scombrus</i> , Scombridae	S (11–20)	Planktivore
		M (21–35)	Planktivore
		L (> 35)	Planktivore
Haddock	<i>Melanogrammus aeglefinus</i> , Gadidae	S (≤ 20)	Benthivore
		M (21–50)	Benthivore
		L (51–80)	Benthivore
		XL (> 80)	Piscivore
Goosefish	<i>Lophius americanus</i> , Lophiidae	S (≤ 30)	Piscivore
		M (31–60)	Piscivore
		L (61–90)	Piscivore
		XL (> 90)	Piscivore
Little skate	<i>Leucoraja erinacea</i> , Rajidae	S (≤ 30)	Benthivore
		M (31–60)	Benthivore
Longhorn sculpin	<i>Myoxocephalus octodecemspinosus</i> , Cottidae	S (≤ 25)	Benthivore
		M (26–50)	Benthivore
Ocean pout	<i>Zoarces americanus</i> , Zoarcidae	S (≤ 30)	Benthivore
		M (31–60)	Benthivore
		L (> 60)	Benthivore
Pollock	<i>Pollachius virens</i> , Gadidae	S (≤ 20)	Benthivore
		M (21–50)	Planktivore
		L (51–80)	Planktivore
		XL (> 80)	Piscivore
Red hake	<i>Urophycis chuss</i> , Gadidae	S (≤ 20)	Benthivore
		M (21–40)	Benthivore
		L (> 40)	Piscivore
Silver hake	<i>Merluccius bilinearis</i> , Merlucciidae	S (≤ 20)	Planktivore
		M (21–40)	Piscivore
		L (> 40)	Piscivore
Spiny dogfish	<i>Squalus acanthias</i> , Squalidae	S (≤ 36)	Planktivore
		M (36–80)	Planktivore
		L (> 80)	Piscivore
White hake	<i>Urophycis tenuis</i> , Gadidae	S (≤ 20)	Benthivore
		M (21–40)	Planktivore
		L (> 40)	Piscivore
Winter flounder	<i>Pseudopleuronectes americanus</i> , Pleuronectidae	S (≤ 20)	Benthivore

(Continues)

TABLE 1 (Continued)

Predator	Species name	Size (cm)	Trophic group
		M (21–40)	Benthivore
		L (41–70)	Benthivore
Winter skate	<i>Leucoraja ocellata</i> , Rajidae	S (\leq 30)	Benthivore
		M (31–60)	Benthivore
		L (61–80)	Benthivore
		XL (>80)	Piscivore
Witch flounder	<i>Glyptocephalus cynoglossus</i> , Pleuronectidae	S (\leq 20)	Benthivore
		M (21–40)	Benthivore
		L (41–70)	Benthivore
Yellowtail flounder	<i>Limanda ferruginea</i> , Pleuronectidae	S (\leq 20)	Benthivore
		M (21–40)	Benthivore
		L (41–70)	Benthivore

dissimilarities was produced by randomizing the predator–prey matrix of per cent diet composition by mass (Table S1) 100 times while retaining zeros and reproducing matrices of diet dissimilarity (55×55) among predator–size categories. Groups were considered distinct when they clustered above the dissimilarity level which included 90% (133,650) of the simulated values.

Annual mean prey densities of fishes and squid were estimated by weighting the number of individuals caught in the swept area of the tow (0.01 nm^2) by the area (nm^2) of the stratum where they were collected during the standardized fall and spring NEFSC bottom trawl surveys (NEFC, 1988). The stratified random sampling design of the NEFSC bottom trawl survey allows for random samples taken from standardized tows (verified by net performance metrics; Politis, Galbraith, Kostovick, & Brown, 2014) to be expanded to the area of the strata. This is routinely used in fisheries research and stock assessments to produce an unbiased estimate of density (e.g. Cochran, 1977). These prey included Atlantic herring (*Clupea harengus*, Clupeidae), Atlantic mackerel (*Scomber scombrus*, Scombridae), butterflyfish (*Peprilus triacanthus*, Stromateidae), loligo squid (*Loligo* spp., Loliginidae), sand lance (*Ammodytes* spp., Ammodytidae) and silver hake (*Merluccius bilinearis*, Merlucciidae) and represent common prey of varying importance across the piscivore size categories (Smith & Link, 2010; Table 1, Table S1). Their annual densities spanned 1973 through 2016 for the fall and spring separately.

Zooplankton were sampled seasonally with a 61 cm bongo frame fitted with a 333- μm mesh net towed obliquely to a maximum depth of 200 or 5 m above the bottom. Distributed uniformly within each region of the continental shelf, 30–60 sampling stations were selected randomly either approximately 8–35 km apart or by depth strata as part of the NEFSC bottom trawl survey (Figure 1). A mechanical flowmeter at the centre of the bongo frame measured the volume of water towed. Specimens were preserved in 5% formalin and later identified by the Polish Plankton Sorting and Identification Center in Szczecin, Poland, with density expressed as abundance per 100 m^3 . Mean annual amounts of zooplankton per fall and spring

season spanned 1977 through 2016, and were grouped into four broad categories commonly observed in zooplankton and fish diet samples: Copepoda, Euphausiidae, Hyperiididae and Mysida (Smith & Link, 2010; Table 1, Table S1).

Benthic macroinvertebrates of the northeast US continental shelf were sampled from 1956 to 1965 with a Smith-McIntyre bottom sampler or Campbell grab sampler. Sampling stations were selected non-randomly by grid with at least one sample per 20-min area squared. Samples were washed through a 1-mm mesh screen, and remaining material was preserved in 5% formalin for laboratory processing. The abundance of benthos was standardized by the volume of sediment sampled by each benthic sampler and presented as abundance per litre. Although this benthic sampling pre-dates the other sampling in this study, this is the only shelf-wide standardized benthic survey that has occurred on the northeast US continental shelf. The five regions of the shelf were not sampled annually; thus, it was assumed benthos abundance was time invariant. We felt this assumption was reasonable at this regional scale for two reasons: (a) the use of fish stomachs as benthic samplers of marine environments is well documented (e.g. Fahrig, Lilly, & Miller, 1993; Frid & Hall, 1999; Lilly & Parsons, 1991) with minimal evidence of variability over time for this continental shelf (Link, 2004); and (b) the diet variability for several benthivores of this region was shown to be influenced by predator size, geographic region and season, and not influenced by time (e.g. 5-year blocks; Byron & Link, 2010). Mean fall and spring amounts of benthos by region of the continental shelf (year excluded) were available and included the adequately sampled taxa and common prey: Amphipoda, Bivalvia, Echinodermata and Isopoda (Smith & Link, 2010; Table 1, Table S1).

Per capita consumption was estimated with the evacuation rate methods of Eggers (1977) and Elliot and Persson (1978). Daily per capita consumption (C_{daily} ; g) by season was modelled as:

$$C_{\text{daily}} = 24 \times E_{\text{season}} \times D_{\text{season}} \quad (1)$$

where 24 is the number of hours in a day, E is the seasonal evacuation rate, and D is the seasonal mean amount of prey eaten either by year (piscivores and planktivores) or geographic region (benthivores; Figure 1). The seasonal mean amount of prey per stomach was weighted by the number of a predator collected per 1 cm length bin and weighted by the total number of a predator caught per station to account for cluster sampling of diet data within the stratified random sampling design of the NEFSC bottom trawl survey (similar to Latour, Gartland, Bonzek, & Johnson, 2008; Link & Almeida, 2000). Season-years and season-geographic regions with <20 stomachs per predator were excluded from analyses based on cumulative trophic diversity curves (Belleggia et al., 2008; Koen Alonso, Crespo, García, & Pedraza, 2002). The seasonal evacuation rate was modelled as:

$$E_{\text{season}} = \alpha e^{\beta T_{\text{season}}} \quad (2)$$

where α and β are evacuation rate parameters and T is the seasonal bottom temperature. In this study, α is prey-specific when available (mainly for fishes and squid; Temming & Herrmann, 2003) or assumed to be 0.004 (Durbin, Durbin, Langton, & Bowman, 1983). For all zooplankton prey, α was assumed to be similar to euphausiids (0.01; Temming & Herrmann, 2003). For all prey, parameter β was set to 0.115 (Durbin et al., 1983). T was collected during the NEFSC bottom trawl survey each season and year, and was estimated as the stratified mean temperature for a given season associated with the presence of the predator.

Seasonal per capita consumption was estimated by scaling the daily rate (C_{daily}) to each season by multiplying by 91.25 (days in a quarter-year):

$$C_{\text{season}} = C_{\text{daily}} \times 91.25 \quad (3)$$

We assumed a uniform consumption rate per season since sampling was continuous throughout each eight- to 10-week sampling season and included the variation in consumption that would be expected each season annually. The time series of seasonal per capita consumption varied by fish predator but included most years from 1973 through 2016 (piscivores and planktivores). Seasonal per capita consumption for benthivores was by geographic region.

2.2 | Analysis

Functional feeding responses were modelled for 48 out of 55 possible predator-size combinations spanning the three trophic groups. Seven predator-size categories were excluded due to limited sampling by season-year or season-geographic region (e.g. extra-large and small size categories; <4 data points). Fish per capita consumption was related to prey density by implementing three hierarchical Bayesian models of multispecies functional responses. One advantage of a multispecies approach is the inclusion of other prey of varying importance when predicting a functional response with notable contrasts to single-prey approaches (Smout et al., 2010). Given that

these data were non-negative and continuous, we adopted gamma distributions for the response and explanatory terms, and inverse gamma distributions for the error terms. Vague prior distributions with shape and rate equal to 0.001 were gamma distributed. The joint posterior distributions of the parameters were directly approximated by MCMC. We applied three multispecies functional response models equivalent to Holling types II and III, and a modified type IV response (Gentleman et al., 2003; Holling, 1959a, 1959b, 1965; Smout et al., 2013). To allow for all functional response types considered, we fit a multispecies form of the single-species equation to model per capita consumption (C_i) by a single predator of prey i and j :

$$C_i = \frac{a_i X_i^n}{1 + \sum_{j=1}^k a_j h_j X_j^m} \quad (4)$$

where all notation is prey-specific with k being the number of prey taxa, a is the attack rate, h is handling time, and X is prey density. The parameters n and m determine the type of a predator's functional response and were fixed values. Typically, these parameters are allowed to be equal and constitute the classic Holling type II (n and $m = 1$) and Holling type III (n and $m = 2$) responses, but we also included a type IV response (allowing for decreased predation at high prey densities; $n = 1$ and $m = 2$). Other response types are possible (e.g. Abrams, 1982); however to limit the scope of this study, the response types common to fisheries were prioritized. Type IV responses have been previously documented, discussed, and have various forms (see Gentleman et al., 2003; Koen-Alonso, 2007). We applied this type IV form for its similarity to the two other functional response types used, and consequently, Equation 4 can easily be modified to account for the types II-IV responses as well as collapse to a linear model when $h_j = 0$ and $n = 1$ or 0 for all prey. The parameters n and m were fixed rather than using a more generalized form (Baudrot, Perasso, Fritsch, Giraudoux, & Raoul, 2016; Smout et al., 2010) to focus on the functional response forms that are conventional to fisheries and marine ecosystem models, and minimize ambiguity with response selection (e.g. Moustahfid et al., 2010; Rindorf & Gislason, 2005; Zhou & Smith, 2017). Despite varying activity times of prey, Equation 4 is reasonable since sampling occurred 24 hr a day during the spring and fall seasons, the predators included are generalists with numerous prey options available, and season and year or geographic region were isolated in our analyses.

MCMC was applied with GIBBS updates in R with the rjags and coda packages (version 3.3.0; R Core Team, 2016) and JAGS software (Plummer, 2017). Plots of each estimated parameter relative to the number of iterations suggested 500,000–1,000,000 iterations were necessary for convergence. Chain convergence for each parameter value was monitored with a combination of trace plots and the potential scale reduction factor indicating low variance within and among chains (see Gelman, Carlin, Stern, Dunson, & Rubin, 2013; Hobbs & Hooten, 2015). These iterations were preceded by a burn-in phase of 100,000 draws which did not contribute to the posterior distribution. The Bayesian network used for modelling multispecies

functional responses is provided in Figure 2 with variables a , h , X and C equivalent to those in Equation 4 and included μ_i (process model or true unobserved per capita consumption), and process (σ_p^2) and sampling (σ_s^2) errors.

The full conditional equation used to specify how values were sampled by MCMC for each unobserved quantity ($\mu_i, a_i, a_j, h_j, \sigma_p^2, \sigma_s^2$) is shown in Equation 5 with N equal to the number of observations available per predator-size category. The deterministic model (Equation 4) is denoted by $g()$ with model arguments inside the parentheses.

$$\begin{aligned}
 & [\mu_i, a_i, a_j, h_j, \sigma_p^2, \sigma_s^2 | C_i] \propto \prod_{\text{obs}=1}^N \text{gamma} \left(C_i \mid \frac{\mu_i^2}{\sigma_s^2}, \frac{\mu_i}{\sigma_s^2} \right) \\
 & \times \text{gamma} \left(\mu_i \mid \frac{g(X_i, X_j, a_i, a_j, h_j, n, m)^2}{\sigma_p^2}, \frac{g(X_i, X_j, a_i, a_j, h_j, n, m)}{\sigma_p^2} \right) \quad (5) \\
 & \times \text{gamma} (a_i | 0.001, 0.001) \text{gamma} (a_j | 0.001, 0.001) \\
 & \quad \times \text{gamma} (h_j | 0.001, 0.001) \\
 & \times \text{inverse gamma} (\sigma_p^2 | 0.001, 0.001) \text{inverse gamma} (\sigma_s^2 | 0.001, 0.001)
 \end{aligned}$$

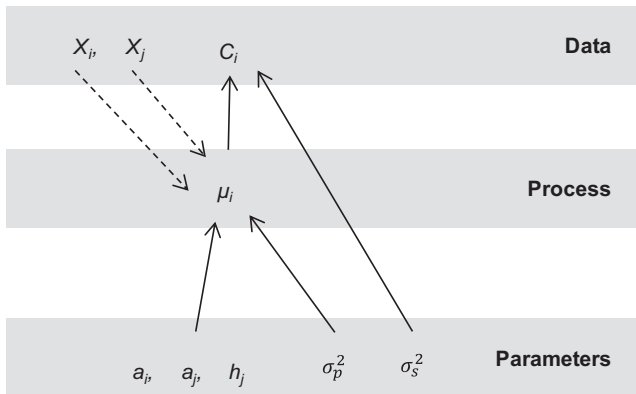


FIGURE 2 Bayesian network or directed acyclic graph describing the full model (Equation 5). Dashed lines show deterministic relationships, and solid lines show stochastic relationships. The data: X_i and X_j are prey-specific densities, and C_i is the per capita consumption for the initial prey of interest. The process: μ_i is the true unobserved per capita consumption. Parameters a_i and a_j are prey-specific attack rates, and h_j is the prey-specific handling time. The sigma parameters represent process (σ_p^2) and sampling (σ_s^2) error.

Multimodel inference has many applications in the life sciences, particularly with the use of maximum likelihood methods for parameter estimation (e.g. Anderson, 2008; Burnham & Anderson, 2002). There are multiple options for model selection regarding Bayesian methods (Hobbs & Hooten, 2015). We chose posterior predictive loss (PPL) as it is appropriate for many classes of hierarchical models and depends directly on the posterior predictive distribution instead of likelihood and posterior mean of a parameter or even a count of parameters (Hobbs & Hooten, 2015). With PPL, and similar to other selection criteria, lower values indicate model support. Additionally, goodness of fit was assessed with posterior predictive checks by computing the proportion of times the coefficient of variation (CV) of simulated data from the model exceeded the CV of the observed data. As suggested by Hobbs and Hooten (2015), evidence of extreme proportions indicating poor fit (i.e. <0.1 or >0.9) was not found.

3 | RESULTS

Holling type III was the predominant functional response for the 48 predator-size categories considered with the lowest PPL values per

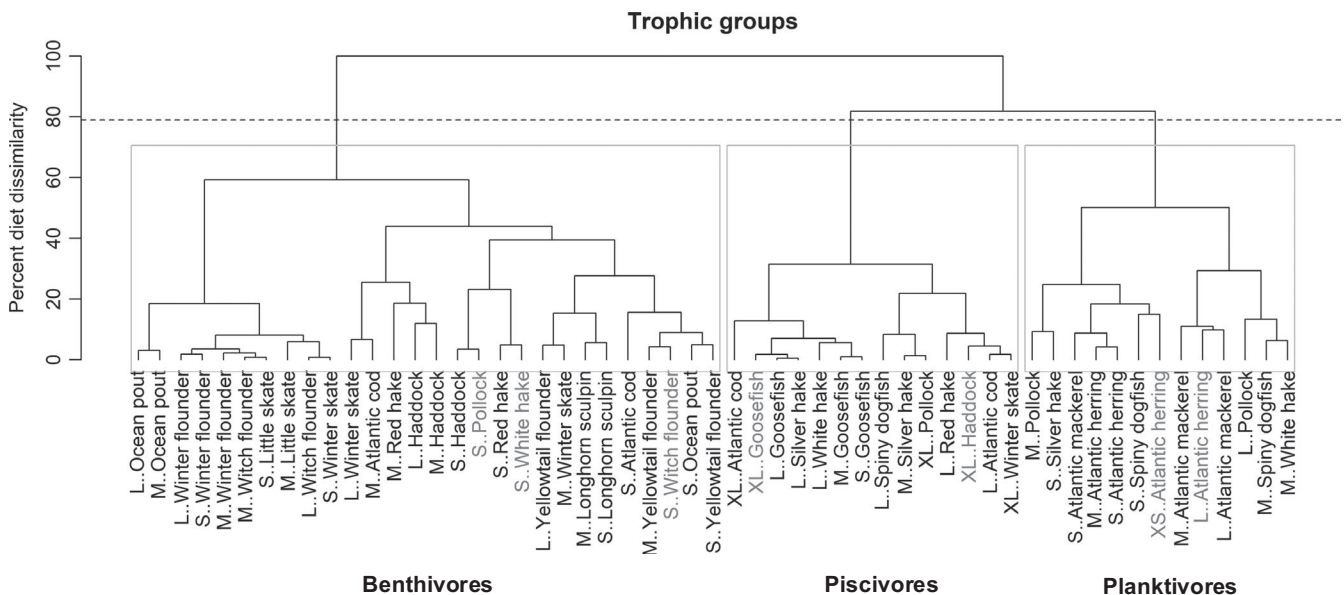


FIGURE 3 Dendrogram of fish predator-size categories and their trophic groups: benthivores, piscivores and planktivores from hierarchical cluster analysis. Size categories defined as XS: extra small, S: small, M: medium, L: large and XL: extra large. The dashed line denotes significant per cent dissimilarity with probability = 0.9. Grey predator-size categories indicate insufficient data across time or geographic regions.

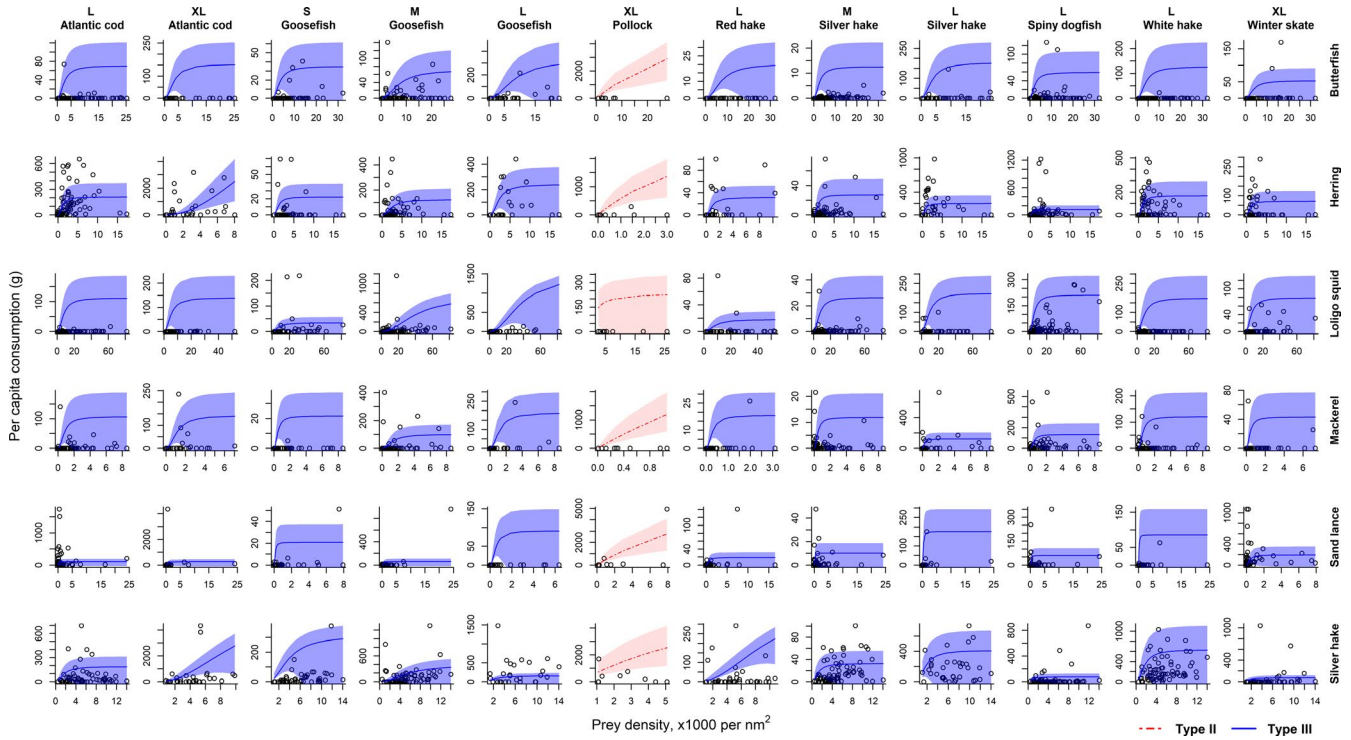


FIGURE 4 Piscivore multispecies functional responses for 12 predator-size categories (columns) and six prey (rows). The letters “S,” “M,” “L” and “XL” denote size class. Holling type III response was the best-fit model for all predators (solid blue) except XL Pollock (Holling type II; dot-dashed red). Shading denotes 95% confidence interval. Figure appears in colour in the online version. [Colour figure can be viewed at wileyonlinelibrary.com]

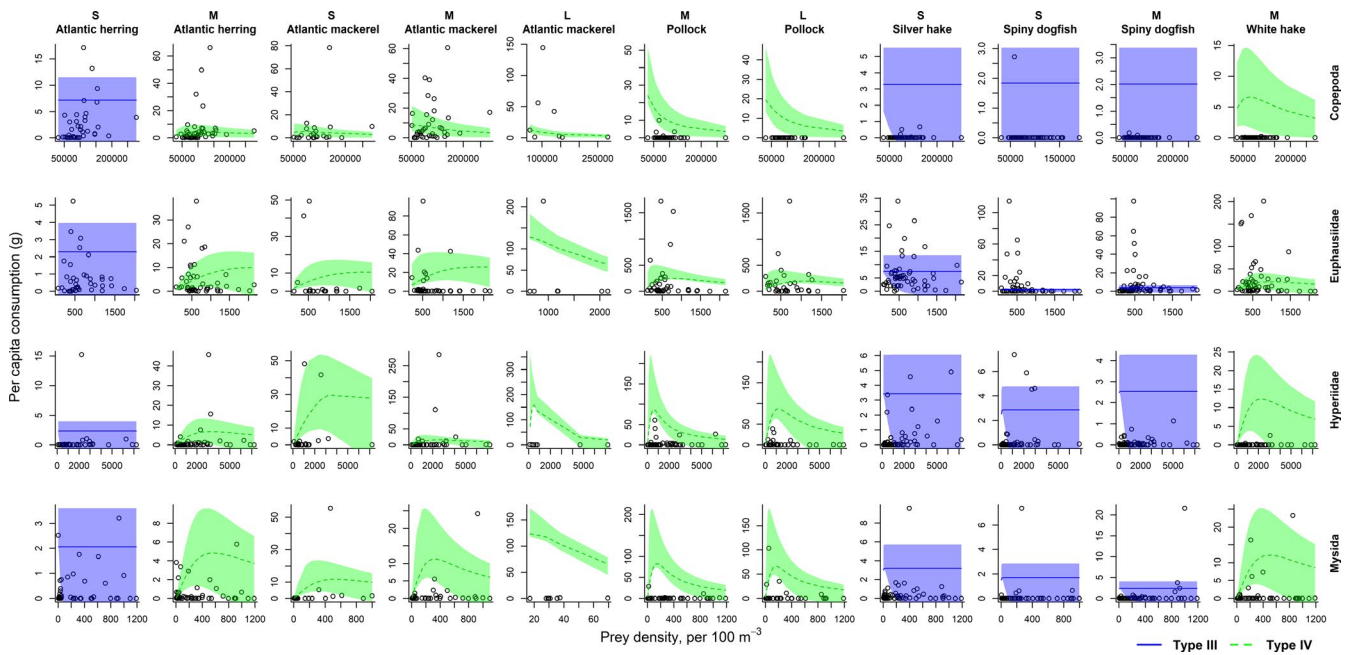


FIGURE 5 Planktivore multispecies functional responses for 11 predator-size categories (columns) and four prey (rows). The letters “S,” “M” and “L” denote size class. Holling type III (solid blue) and type IV (dashed green) responses were the best-fit models for all predators. Shading denotes 95% confidence interval. Figure appears in colour in the online version. [Colour figure can be viewed at wileyonlinelibrary.com]

predator and size (Figures 4–6; Table S2). For the three response types tested, each was present, including the type IV response with decreased predation at high prey densities. However, the Holling

type II response was only detected for one piscivore (extra-large pollock; Figure 4), and linear relationships between prey density and per capita consumption by predator-size category were not

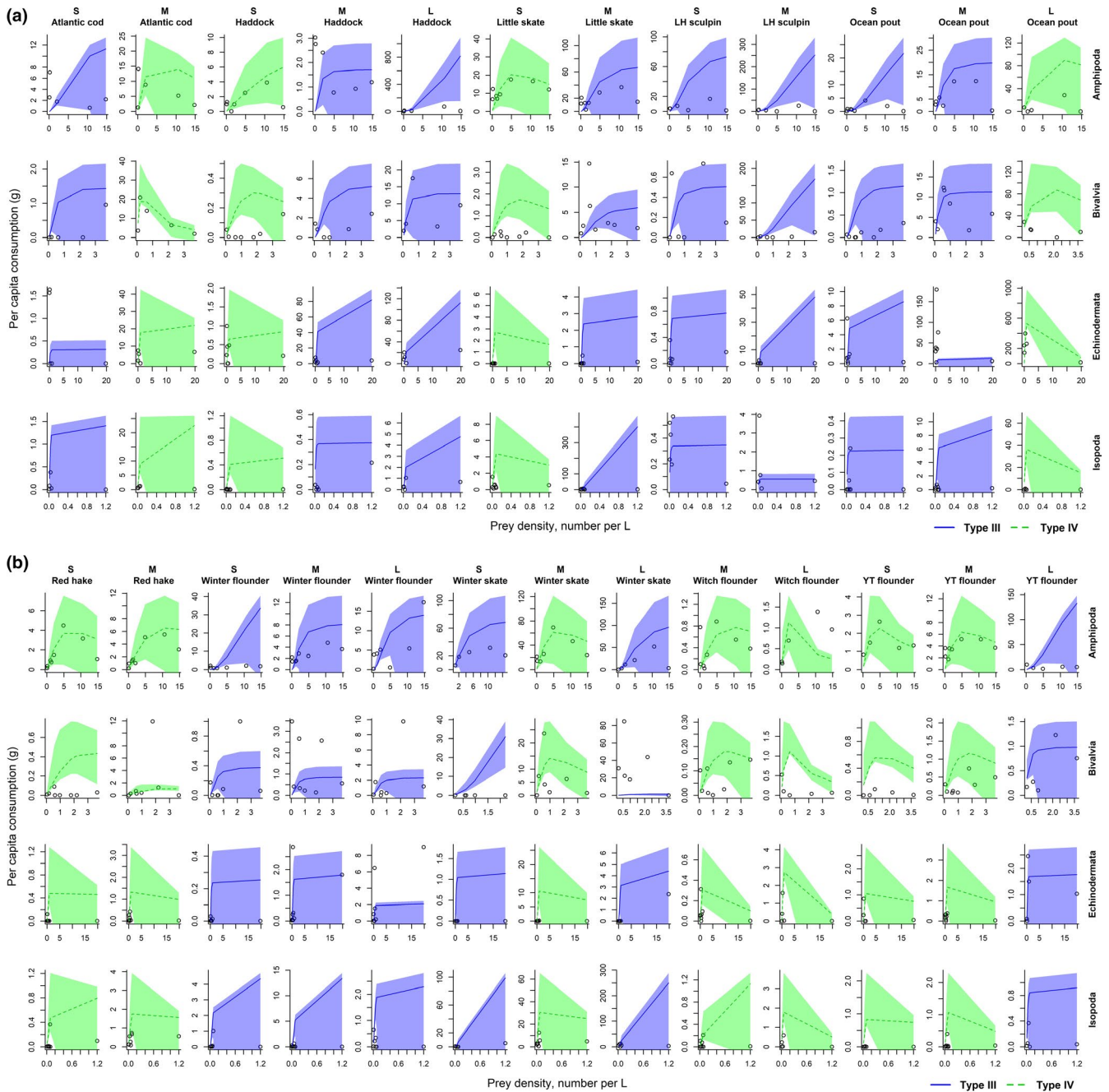


FIGURE 6 Benthivore multispecies functional responses for 25 predator-size categories (columns) and four prey (rows). The letters “S,” “M” and “L” denote size class. Holling type III (solid blue) and type IV (dashed green) responses were the best-fit models for all predators. Shading denotes 95% confidence interval. Figure appears in colour in the online version. [Colour figure can be viewed at wileyonlinelibrary.com]

suggested based on model estimates of parameter values ($h > 0$; Table S3). Across the trophic groups, responses were predator- and prey-dependent with small, densely aggregated prey (zooplankton [1,000 s–100,000 s of individuals per 100 m³] and benthic invertebrates [10 s of individuals/L] eliciting a type IV response for some planktivores and benthivores. Larger, less aggregated prey such as fishes and squid (10,000 s of individuals per nm²) primarily expressed a Holling type III response for the piscivores tested. Given our multispecies approach, prey within each trophic group varied in importance per predator-size category; thus, model fit was largely

driven by the predominant prey with rarer prey contributing less information. Parameter values of the best-fit functional response models for all predator–prey combinations are in Table S3.

3.1 | Trophic groups

Placement of fish predator-size categories into trophic groups was defined by per cent diet dissimilarity and correspond to values that were >78.1 (90 percentile) and were statistically more dissimilar than

those expected by random chance. This included 12 piscivores, 11 planktivores and 25 benthivores (Table 1; Figure 3). Of these members, extra-large haddock and extra-large goosfish (piscivores), extra-small and large Atlantic herring (planktivore), and small pollock, small white hake, and small witch flounder (benthivores) were excluded given their low amount of sampling over time or geographic region. Partitioning the predators and their size categories allowed the examination of functional response patterns within and among trophic groups as well as among the 48 predator-size categories.

3.2 | Piscivores

The piscivores included the largest size categories for cod, goosfish, pollock, red hake, silver hake, spiny dogfish, white hake and winter skate with most predators following a Holling type III multispecies functional response with the exception of extra-large pollock (Holling type II; Figure 4). This implies the primary mode of feeding for these predators includes an element of prey switching or learning (e.g. Murdoch, 1969) with a sigmoidal relationship between prey density and per capita consumption. The Holling type III responses had the best fit based on PPL with the type IV model having the poorest fit most often among predators (Table S2). Since all but one of these piscivores on the northeast U.S. continental shelf shared a Holling type III response, it is reasonable that this response can be generalized across other piscivorous fishes within this region and throughout a broader geographic range.

The inclusion of predator-size categories permitted the examination of functional responses over each predator's life history which was indicative of the various feeding groups occupied by these predators. For these piscivores, their smaller size categories generally were less piscivorous and had diets with predominantly benthic or planktonic invertebrates and minimal squid. These smaller predators had a type IV or Holling type III functional response. When fish and squid became a major part of the diet at larger sizes, the responses became or remained Holling type III.

3.3 | Planktivores

The planktivores included all size categories for Atlantic herring and Atlantic mackerel, and the smaller sized pollock, silver hake, spiny dogfish and white hake. Predators demonstrated type IV (primary) and Holling type III multispecies functional responses considering a subset of prey from the zooplankton community (Figure 5). Here, most best-fit models included decreased predation at high prey densities, and this is in contrast to Holling type II and Holling type III responses which are asymptotic at the maximum feeding rate. When encountered, small, dense aggregations of planktonic invertebrate prey (1,000 s–100,000 s individuals per 100 m³) may disorient or confuse many of these planktivores, reducing their feeding on zooplankton. For all but one planktivore (small spiny dogfish), the poorest fitting model was Holling type II (Table S2).

3.4 | Benthivores

The smaller size categories of Atlantic cod, red hake and winter skate, and all sizes of haddock, little skate, longhorn sculpin, ocean pout, winter flounder, witch flounder and yellowtail flounder comprised the benthivores. They were a mix of Holling type III and type IV feeders when examining multispecies functional responses (Figure 6). The poorest fitting model was frequently Holling type II (Table S2). Although functional responses were variable among benthivores, a majority of the predators that were type IV feeders (Atlantic cod, haddock, little skate, red hake, winter skate and yellowtail flounder) ate predominantly small benthic invertebrates as small or medium sizes, but larger individuals of these species were mostly Holling type III piscivores (Figures 4 and 6; Table S2). Similarly, the Holling type III benthivores (longhorn sculpin and winter flounder) remained as type III feeders for all sizes. Ocean pout was an exception to this pattern, being a type III feeder at small and medium sizes, but switching to a type IV response when large. We suspect the identified diet of nearly 100% benthic invertebrates and 0% fish of these larger-sized individuals may play a role where a preference for small invertebrate prey may force a type IV response. Interestingly, of the predator-size categories examined with 0% fish in the diet, all (large ocean pout and large witch flounder) ate a high percentage of benthic invertebrates and were type IV feeders.

4 | DISCUSSION

With three multispecies functional response models, we examined the predator-prey relationships of three major trophic groups of the NW Atlantic. Our results support previous conclusions of functional responses for NW Atlantic piscivores (Moustahfid et al., 2010), which implied Holling type III responses for predators of demersal fishes, Holling type II responses for pelagic fishes and very few linear relationships (Holling type I). For piscivores, our results advocated almost entirely for Holling type III responses when using a multispecies approach to define functional responses. Handling time (*h*), albeit lowest for planktivorous prey (Table S3), was greater than zero for many prey for each predator-size category, suggesting non-linear responses were favoured by these trophic groups. These lower handling times for planktonic (filter-fed) prey were not surprising as linear feeding responses occur with various filter-feeding invertebrates (Jeschke et al., 2004).

Examining multispecies functional responses of opportunistic generalist predators requires large amounts of diet and prey density data, particularly when considering variability across multiple trophic groups, and for large prey fields it is thought to be impossible (Gentleman et al., 2003). Here, considering the long time series of ecosystem data available for the NE US continental shelf, our approach had some caveats and limitations. In contrast to single-species measures of predatory responses, targeting specific predator-prey interactions of interest for multispecies and

ecosystem modelling (e.g. Moustahfid et al., 2010), our methods were applied similarly with the crux that the complete prey field did not have adequate sampling, and not one sampler (e.g. trawl or plankton net, or grab) could achieve this objective. Most notably, the absence of annual benthic macroinvertebrate surveys for this NW Atlantic region was the greatest limitation. Therefore, we targeted recurring prey that were important in the diets as well as for the ecosystem such as forage fishes and major zooplankton and benthic taxa, and our results demonstrate major predatory response patterns within and among trophic groups of this region. We also note that for some of the predator-size categories, the prey considered here represented important as well as rare items (particularly for the planktivores and some benthivores) which could be an artefact of sampling or simply rare predation events. Either way, by including prey of varying importance, model fit was largely driven by prey with recurring presence in the diet. It would be worthwhile to further examine the predator-size categories which have overlap between trophic groups to address varying levels of prey importance. Future work would also benefit from including other functional response forms and their multi-species equivalents in this context as well as exploring within-season variability of the consumption parameters considered here (e.g. evacuation rate). Lastly, corrections for prey catchability by the samplers herein (i.e. trawl, plankton and benthos) were not included as these values were not available for all of the fauna considered. As a scalar, accounting for catchability could improve absolute estimates of prey density, but this would have minimal effect on the functional response.

4.1 | A prevalent response?

The prevalence of a Holling type III response for piscivores (all predator-size categories except extra-large pollock) and across all trophic groups (29 of 48 predator-size categories) suggests behaviour such as prey switching occurs as these predators learn which prey are in higher abundance, functionally stabilizing prey populations (Murdoch, 1969). In the context of multi- and single-species predatory responses, the type III response was also common for other studies examining terrestrial, freshwater and marine environments (Sarnelle & Wilson, 2008; Smout et al., 2010, 2014). Thus, our results support the use of a Holling type III over the Holling type II response for many fishes of this region. When considering only Holling types II and III responses for the 48 predator-size combinations studied here, the better-fit response model was indeed the Holling type III for 47 predators (Table S2). Prey populations are not static for multiple reasons such as predation, harvesting and other drivers of environmental change (e.g. climate). By choosing a Holling type II instead of Holling type III response, multispecies and ecosystem models could overestimate predation relative to fishing mortality when not accounting for the likelihood of prey switching with changes in prey abundance.

4.2 | Generalists

Generalist feeding and the selection of numerous prey types are widespread among many fishes of the NW Atlantic regardless of trophic group (Garrison & Link, 2000; Smith & Link, 2010). This feeding trait is believed to be the product of specific drivers or a combination thereof, most notably, biodiversity of prey field (Hayden et al., 2019) and may even be due to community homogenization through anthropogenic pressures (Iacarella et al., 2018). Similarly, prey switching has also been observed in response to human influences such as harvesting (Link & Garrison, 2002; Smith, Collie, & Lengyel, 2013) and invasive species (Smith, Collie, & Lengyel, 2014). Again, our results support the argument that generalist feeders tend to diminish variability in prey populations by removing prey which are most abundant (Murdoch, Avery, & Smyth, 1975; Murdoch & Oaten, 1975).

Interestingly, functional responses and predation rates will vary as organisms can switch their response types throughout different life stages. In terms of environmental influence, drivers of functional responses or predation rates include habitat complexity (Alexander et al., 2013; Savino & Stein, 1989), light intensity (Townsend & Risebrow, 1982) and temperature (Taylor & Collie, 2003). With temperature, the potential for increased predation (Holling type II vs. Holling type III) of juvenile winter flounder (*Pseudopleuronectes americanus*, Pleuronectidae) at low densities was revealed with increased temperature, suggesting greater challenges for recovering fish stocks in the wake of ocean warming (Taylor & Collie, 2003). The results of this study indicated 10 predators with such non-stationary functional responses: Atlantic cod, Atlantic herring, haddock, little skate, ocean pout, pollock, red hake, white hake, winter skate and yellowtail flounder. These predators exhibited a type IV response when in a small or medium size category (mainly planktivorous or benthivorous), but a Holling type III response was shown for large or extra-large individuals (mainly piscivorous). With increased size, a period of switching or seeking larger prey fishes and squids promoted a Holling type III response; thus, these predators feed until satiation with their consumption reaching an asymptote at the maximum feeding rate. There were exceptions to this for species that remained within their trophic group even with increased size: Atlantic herring and Atlantic mackerel (true planktivores) and ocean pout and witch flounder (true benthivores) remained type IV feeders even at their largest size categories examined. Pollock exhibited a Holling type II response for its largest size category when switching to a diet with high fish consumption. Interestingly, goosefish (true piscivore) remained a Holling type III feeder for all of its size categories with fish being at least 90% of their diet by size.

4.3 | Decreased predation

The type IV functional response, as shown here, does play a role in the feeding relationships of fishes of the NW Atlantic. Previously documented and having multiple forms, the type IV response allows for decreased predation at high prey density; a product of predator

confusion, prey toxicity, physical deterrents, or nutrient limitations (Gentleman et al., 2003; Heuermann, van Langevelde, van Wieren, & Prins, 2011; Koen-Alonso, 2007; Mezzalana et al., 2017). We chose to include it as it is not often considered in the marine environment, and if ignored, one could overestimate predation rates particularly when prey are in high abundance. Reported here, a recurring pattern of fishes feeding on small, densely aggregated invertebrate prey (zooplankton and benthic macroinvertebrates) exhibited the type IV response with a deceleration in feeding as prey reached their maximum observed densities. We suggest the denser aggregations of planktonic and benthic invertebrate prey being smaller in size and higher in density relative to fish and squid prey can cause confusion which limits predation for smaller size categories. Additionally, our results suggest that this response is more important for the NW Atlantic than previously perceived, particularly for planktivores and benthivores.

4.4 | Trophic group responses

Multispecies functional responses can vary within and among trophic groups of marine fishes as shown here. To our knowledge, studies have considered the variability of functional responses among species within a specific trophic group (e.g. piscivores; Moustahfid et al., 2010), but none have examined multiple species comprising several trophic groups such as piscivores, planktivores and benthivores. Within trophic groups, predatory responses do vary by fish species and size category with a mechanism being prey type (e.g. pelagic vs. demersal forage fishes; Moustahfid et al., 2010). This has important implications for multispecies and ecosystem modelling as proposed data requirements have often included predators categorized as trophic groups of similar function rather than by species and size category (e.g. Link et al., 2010; Steele et al., 2013; Steele & Ruzicka, 2011). Although challenging to implement functional responses specific to each predator-prey interaction, the “lumping” approach could result in inaccurate predation rates with over- or underestimation of predation relative to prey density. In particular, ignoring a type IV response would overestimate predation that may not otherwise be occurring. And within multispecies stock assessment models, this could lead to overestimation of mortality and affect related parameters such as recruitment (Hollowed, Ianelli, & Livingston, 2000; Tsou & Collie, 2001; Tyrrell, Link, Moustahfid, & Smith, 2007). Aside from retaining the generalist nature of predation, a benefit of providing multispecies functional responses is a predator-specific rather than prey-specific response by considering a larger prey field. Fortunately in the NW Atlantic, all but one of the piscivores examined on the NE US continental shelf displayed a Holling type III multispecies functional response. Although we advise caution with lumping predators by trophic group and applying a single functional response per group, for the piscivores examined, this approach has less risk given the consistent results shown here. Similarly for the planktivores and benthivores preferring small

invertebrate fauna, they displayed a type IV response, but this was mainly limited to smaller size categories or predators preferring these prey throughout their life histories. Interestingly, the variability of predatory responses among trophic groups was driven by predator-size category and prey type. For schooling fish and squid prey regardless of life history (pelagic or demersal), the piscivores, which were mostly demersal groundfishes of large size categories, were primarily Holling type III feeders. These results demonstrate high variability in functional responses among trophic groups of the NW Atlantic.

In a multispecies modelling context, the predatory responses examined here offer an expanded view of predation relative to prey density considering many prey and predator-size categories across several trophic groups of the NE US continental shelf. The recurring pattern of observing Holling type III feeding responses, presence of type IV responses and changes in feeding response with predator size herein will improve the accuracy of fisheries models for management of important forage fishes and the predators that naturally remove them (Essington et al., 2015; Pikitch et al., 2014; Warzybok et al., 2018). Following the charge to improve our understanding of whole-shelf ecology (Link et al., 2010), these results provide insight into predation on and by commercial resources that feed throughout the water column including fishes, zooplankton and benthic prey types. With refined predation components such as functional responses for multispecies and ecosystem models, a fuller understanding of shelf ecology will contribute to improved advice for Ecosystem-Based Fisheries Management.

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DATA AVAILABILITY STATEMENT

Data are available from the US Federal Government InPort (Information Portal) repository for the Northeast Fisheries Science Center (<https://inport.nmfs.noaa.gov/inport/hierarchy/1368>).

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REFERENCES

- Abrams, P. A. (1982). Functional-responses of optimal foragers. *American Naturalist*, 120(3), 382–390.
- Abrams, P. A. (1989). Decreasing functional responses as a result of adaptive consumer behavior. *Evolutionary Ecology*, 3, 95–114. <https://doi.org/10.1007/BF02270915>
- Abrams, P. A. (1992). Adaptive foraging by predators as a cause of predator-prey cycles. *Evolutionary Ecology*, 6, 56–72. <https://doi.org/10.1007/BF02285334>

- Alexander, M. E., Dick, J. T. A., & O'Connor, N. E. (2013). Trait-mediated indirect interactions in a marine intertidal system as quantified by functional responses. *Oikos*, 122, 1521–1532. <https://doi.org/10.1111/j.1600-0706.2013.00472.x>
- Anderson, D. R. (2008). *Model Based Inference in the life sciences: A primer on evidence*. New York: Springer.
- Azarovitz, T. R. (1981). A brief historical review of the Woods Hole laboratory trawl survey time series. In W. G. Doubleday, & D. Rivard (Eds.), *Bottom trawl surveys* (vol. 58, pp. 62–67). Ottawa, Canada: Canadian Special Publication of Fisheries and Aquatic Sciences.
- Baudrot, V., Perasso, A., Fritsch, C., Giraudoux, P., & Raoul, F. (2016). The adaptation of generalist predators' diet in a multi-prey context: Insights from new functional responses. *Ecology*, 97, 1832–1841. <https://doi.org/10.1890/15-0427.1>
- Bax, N. J. (1998). The significance and prediction of predation in marine fisheries. *ICES Journal of Marine Science*, 55, 997–1030. <https://doi.org/10.1006/jmsc.1998.0350>
- Beckerman, A., Petchey, O. L., & Morin, P. J. (2010). Adaptive foragers and community ecology: Linking individuals to communities and ecosystems. *Functional Ecology*, 24, 1–6. <https://doi.org/10.1111/j.1365-2435.2435.2009.01673.x>
- Belleggia, M., Mabrugaña, E., Figueroa, D. E., Scenna, L. B., Barbini, S. A., & Díaz de Astarloa, J. M. (2008). Food habits of the broad nose skate, *Bathyraja brachyurops* (Chondrichthyes, Rajidae), in the south-west Atlantic. *Scientia Marina*, 72, 701–710.
- Bijlvelde, A. I., MacCurdy, R. B., Chan, Y., Penning, E., Gabrielson, R. M., Cluderay, J., ... Piersma, T. (2016). Understanding spatial distributions: Negative density-dependence in prey causes predators to trade-off prey quantity with quality. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20151557. <https://doi.org/10.1098/rspb.2015.1557>
- Brachvogel, R., Meskendahl, L., Herrmann, J.-P., & Temming, A. (2013). Functional responses of juvenile herring and sprat in relation to different prey types. *Marine Biology*, 160, 465–478. <https://doi.org/10.1007/s00227-012-2104-5>
- Buckel, J. A., & Stoner, A. W. (2000). Functional response and switching behavior of young-of-the-year piscivorous bluefish. *Journal of Experimental Marine Biology and Ecology*, 245, 25–41. [https://doi.org/10.1016/S0022-0981\(99\)00155-0](https://doi.org/10.1016/S0022-0981(99)00155-0)
- Buren, A. D., Koen-Alonso, M., & Montevechi, W. A. (2012). Linking predator diet and prey availability: Common murre and capelin in the Northwest Atlantic. *Marine Ecology Progress Series*, 445, 25–35. <https://doi.org/10.3354/meps09465>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference* (2nd ed.). New York: Springer-Verlag.
- Byron, C. J., & Link, J. S. (2010). Stability in the feeding ecology of four demersal fish predators in the US Northeast shelf large marine ecosystem. *Marine Ecology Progress Series*, 406, 239–250. <https://doi.org/10.3354/meps08570>
- Cochran, W. G. (1977). *Sampling techniques* (3rd ed.). New York: John Wiley & Sons.
- Dayton, P. K. (1971). Competition, disturbance, and community organization: The provision and subsequent utilization of space in rocky intertidal community. *Ecological Monographs*, 41, 351–389.
- Durbin, E. G., Durbin, A. G., Langton, R. W., & Bowman, R. E. (1983). Stomach contents of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus morhua*, and estimation of their daily rations. *Fishery Bulletin*, 81, 437–454.
- Eggers, D. M. (1977). Factors in interpreting data obtain by diel sampling of fish stomachs. *Journal of the Fisheries Research Board of Canada*, 34, 290–294.
- Elliot, J. M., & Persson, L. (1978). The estimation of daily rates of food consumption for fish. *Journal of Animal Ecology*, 47, 977–991. <https://doi.org/10.2307/3682>
- Essington, T. E., & Hansson, S. (2004). Predator-dependent functional responses and interaction strengths in a natural food web. *Canadian Journal of Fisheries and Aquatic Sciences*, 61, 2215–2226. <https://doi.org/10.1139/F04-146>
- Essington, T. E., Moriarty, P. E., Froehlich, H. E., Hodgson, E. E., Koehn, L. E., Oken, K. L., ... Stawitz, C. C. (2015). Fishing amplifies forage fish population collapses. *Proceedings of the National Academy of Sciences*, 112, 6648–6652. <https://doi.org/10.1073/pnas.1422020112>
- Fahrig, L., Lilly, G. R., & Miller, D. S. (1993). Predator stomachs as sampling tools for prey distribution: Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 50, 1541–1547.
- Frid, C. L. J., & Hall, S. J. (1999). Inferring changes in North Sea benthos from fish stomach analysis. *Marine Ecology Progress Series*, 184, 183–188. <https://doi.org/10.3354/meps184183>
- Fulton, E. A., Smith, A. D. M., & Johnson, C. R. (2003). Mortality and predation in ecosystem models: Is it important how these are expressed? *Ecological Modelling*, 169, 157–178. [https://doi.org/10.1016/S0304-3800\(03\)00268-0](https://doi.org/10.1016/S0304-3800(03)00268-0)
- Garrison, L. P., & Link, J. S. (2000). Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. *Marine Ecology Progress Series*, 202, 231–240. <https://doi.org/10.3354/meps202231>
- Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., & Rubin, D. (2013). *Bayesian data analysis*. Boca Raton, Florida: CRC Press, Chapman and Hall/CRC.
- Gentleman, W., Leising, A., Frost, B., Strom, S., & Murray, J. (2003). Functional responses for zooplankton feeding on multiple sources: A review of assumptions and biological dynamics. *Deep-Sea Research Part II*, 50, 2847–2875.
- Gremillet, D., Kuntz, G., Delbart, F., Mellet, M., Kato, A., Robin, J.-P., ... Le Maho, Y. (2004). Linking the foraging performance of a marine predator to local prey abundance. *Functional Ecology*, 18, 793–801. <https://doi.org/10.1111/j.0269-8463.2004.00914.x>
- Hayden, B., Palomares, D., Smith, B. E., & Poelen, J. (2019). A global assessment of the biological and environmental drivers of trophic traits in marine fishes. *Scientific Reports*, 9, 11415. <https://doi.org/10.1038/s41598-019-47618-2>
- Heuermann, N., van Langevelde, F., van Wieren, S. E., & Prins, H. H. T. (2011). Increased searching and handling effort in tall swards lead to a Type IV functional response in small grazing herbivores. *Oecologia*, 166, 659–669. <https://doi.org/10.1007/s00442-010-1894-8>
- Hobbs, N. T., Gross, J. E., Shipley, L. A., Spalinger, D. E., & Wunder, B. A. (2003). Herbivore functional response in heterogeneous environments: A contest among models. *Ecology*, 84, 666–681. [https://doi.org/10.1890/0012-9658\(2003\)084\[0666:HFRIHE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0666:HFRIHE]2.0.CO;2)
- Hobbs, N. T., & Hooten, M. B. (2015). *Bayesian models: A statistical primer for ecologists*. Princeton, NJ: Princeton University Press.
- Holling, C. S. (1959a). Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, 91, 385–398. <https://doi.org/10.4039/Ent91385-7>
- Holling, C. S. (1959b). The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist*, 91, 293–320. <https://doi.org/10.4039/Ent91293-5>
- Holling, C. S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada*, 45, 3–60. <https://doi.org/10.4039/entm9745fv>
- Hollowed, A. B., Ianelli, J. N., & Livingston, P. A. (2000). Including predation mortality in stock assessments: A case study for Gulf of Alaska walleye pollock. *ICES Journal of Marine Science*, 57, 279–293. <https://doi.org/10.1006/jmsc.1999.063>

- Houde, E. D., & Schekter, R. C. (1980). Feeding by marine fish larvae: Developmental and functional responses. *Environmental Biology of Fishes*, 5, 315–334. <https://doi.org/10.1007/BF00005186>
- Iacarella, J. C., Adamczyk, E., Bowen, D., Chalifour, L., Eger, A., Heath, W., ... Baum, J. K. (2018). Anthropogenic disturbance homogenizes seagrass fish communities. *Global Change Biology*, 24, 1904–1918. <https://doi.org/10.1111/gcb.14090>
- Jaksić, F. M., & Medel, R. G. (1990). Objective recognition of guilds: Testing for statistically significant species clusters. *Oecologia*, 82, 87–92. <https://doi.org/10.1007/BF00318537>
- Jeschke, J. M., Kopp, M., & Tollrian, R. (2004). Consumer-food systems: Why type I functional responses are exclusive to filter feeders. *Biological Reviews*, 79, 337–349. <https://doi.org/10.1017/S1464793103006286>
- Kane, J. (2007). Zooplankton abundance trends on Georges Bank, 1977–2004. *ICES Journal of Marine Science*, 64, 909–919. <https://doi.org/10.1093/icesjms/fsm066>
- Koen Alonso, M., Crespo, E. A., García, N. A., & Pedraza, S. N. (2002). Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina. *Environmental Biology of Fishes*, 63, 193–202.
- Koen-Alonso, M. (2007). A process-oriented approach to the multispecies functional response. In N. Rooney, K. S. McCann, & D. G. L. Noakes (Eds.), *From energetics to ecosystems: The dynamics and structure of ecological systems* (pp. 1–36). Dordrecht, the Netherlands: Springer.
- Kroetz, A. M., & Powers, S. P. (2015). Eating between the lines: Functional feeding response of bonnetheads (*Sphyrna tiburo*). *Environmental Biology of Fishes*, 98, 655–661. <https://doi.org/10.1007/s10641-014-0302-3>
- Latour, R. J., Gartland, J., Bonzek, C. F., & Johnson, R. A. (2008). The trophic dynamics of summer flounder (*Paralichthys dentatus*) in Chesapeake Bay. *Fishery Bulletin*, 106, 47–57.
- Layman, C. A., Giery, S. T., Buhler, S., Rossi, R., Penland, T., Henson, M. N., ... Archer, S. K. (2015). A primer on the history of food web ecology: Fundamental contributions of fourteen researchers. *Food Webs*, 4, 14–24. <https://doi.org/10.1016/j.foooweb.2015.07.001>
- Lilly, G. R., & Parsons, D. G. (1991). *Distributional patterns of the northern shrimp (Pandalus borealis) in the Northwest Atlantic as inferred from stomach contents of cod (Gadus morhua)*. International Council for Exploration of the Sea CM 1991/K:41.
- Link, J. (2002). Does food web theory work for marine ecosystems? *Marine Ecology Progress Series*, 230, 1–9. <https://doi.org/10.3354/meps230001>
- Link, J. S. (2004). Using fish stomachs as samplers of the benthos: Integrating long-term and broad scales. *Marine Ecology Progress Series*, 269, 265–275. <https://doi.org/10.3354/meps269265>
- Link, J. S., & Almeida, F. P. (2000). *An overview and history of the Food Web Dynamics Program of the Northeast Fisheries Science Center, Woods Hole, Massachusetts*. U.S. Department of Commerce NOAA Tech. Memo., NMFS-NE-159, 60 pp.
- Link, J. S., Fulton, E. A., & Gamble, R. J. (2010). The northeast US application of ATLANTIS: A full system model exploring marine ecosystem dynamics in a living marine resource management context. *Progress in Oceanography*, 87, 214–234. <https://doi.org/10.1016/j.pocean.2010.09.020>
- Link, J. S., & Garrison, L. P. (2002). Changes in piscivory associated with fishing induced changes to the finfish community on Georges Bank. *Fisheries Research*, 55, 71–86. [https://doi.org/10.1016/S0165-7836\(01\)00300-9](https://doi.org/10.1016/S0165-7836(01)00300-9)
- May, R. M., Beddington, J. R., Clark, C. W., Holt, S. J., & Laws, R. M. (1979). Management of multispecies fisheries. *Science*, 205, 267–277. <https://doi.org/10.1126/science.205.4403.267>
- McCann, K., Hastings, A., & Huxel, G. R. (1998). Weak trophic interactions and the balance of nature. *Nature*, 395, 794–798. <https://doi.org/10.1038/27427>
- Mezzalana, J. C., Bonnet, O. J. F., Carvalho, P. C. D. F., Fonseca, L., Bremm, C., Mezzalana, C. C., & Laca, E. A. (2017). Mechanisms and implications of a type IV functional response for short-term intake rate of dry matter in large mammalian herbivores. *Journal of Animal Ecology*, 86, 1159–1168. <https://doi.org/10.1111/1365-2656.12698>
- Montoya, J. M., Pimm, S. L., & Solé, R. V. (2006). Ecological networks and their fragility. *Nature*, 442, 259–264. <https://doi.org/10.1038/nature04927>
- Morozov, A., & Petrovskii, S. (2013). Feeding on multiple sources: Towards a universal parameterization of the functional response of a generalist predator allowing for switching. *PLoS One*, 8, e74586. <https://doi.org/10.1371/journal.pone.0074586>
- Moustahfid, H., Tyrrell, M. C., Link, J. S., Nye, J. A., Smith, B. E., & Gamble, R. J. (2010). Functional feeding responses of piscivorous fishes from the northeast US continental shelf. *Oecologia*, 163, 1059–1067. <https://doi.org/10.1007/s00442-010-1596-2>
- Murdoch, W. W. (1969). Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecological Monographs*, 39, 335–354. <https://doi.org/10.2307/1942352>
- Murdoch, W. W., Avery, S., & Smyth, M. E. B. (1975). Switching in predatory fish. *Ecology*, 56, 1094–1105. <https://doi.org/10.2307/1936149>
- Murdoch, W. W., & Oaten, A. (1975). Predation and population stability. *Advances in Ecological Research*, 9, 1–125.
- NEFC (Northeast Fisheries Center) (1988). *An evaluation of the bottom trawl survey program of the Northeast Fisheries Center*. U.S. Department of Commerce NOAA Technical Memorandum, NMFS-F/NEC-52, 83 pp.
- NEFSC (Northeast Fisheries Science Center) (2018). *65th Northeast Regional Stock Assessment Workshop (65th SAW) Assessment Report*. U.S. Department of Commerce Northeast Fisheries Science Center Reference Document: 18–11, 659 p.
- Okuyama, T. (2012). Flexible components of functional responses. *Journal of Animal Ecology*, 81, 185–189. <https://doi.org/10.1111/j.1365-2656.2011.01876.x>
- Paine, R. T. (1980). Food webs: Linkage, interaction strength and community infrastructure. *Journal of Animal Ecology*, 49, 666–685. <https://doi.org/10.2307/4220>
- Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., ... Munch, S. B. (2014). The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries*, 15, 43–64. <https://doi.org/10.1111/faf.12004>
- Pimm, S. L. (1982). *Food webs*. New York: Chapman and Hall.
- Plummer, M. (2017). *JAGS Version 4.3.0 user manual*. Retrieved from http://people.stat.sc.edu/hansont/stat740/jags_user_manual.pdf
- Politis, P. J., Galbraith, J. K., Kostovick, P., & Brown, R. W. (2014). *Northeast Fisheries Science Center bottom trawl survey protocols for the NOAA Ship Henry B. Bigelow*. US Department of Commerce, Northeast Fisheries Science Center Reference Document, 14–06, 138 p.
- R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rindorf, A., & Gislason, H. (2005). Functional and aggregative response of North Sea whiting. *Journal of Experimental Marine Biology and Ecology*, 324, 1–19. <https://doi.org/10.1016/j.jembe.2005.04.013>
- Sarnelle, O., & Wilson, A. E. (2008). Type III functional response in *Daphnia*. *Ecology*, 89, 1723–1732.
- Savino, J. F., & Stein, R. A. (1989). Behavioural interactions between fish predators and their prey: Effects of plant density. *Animal Behaviour*, 37, 311–321. [https://doi.org/10.1016/0003-3472\(89\)90120-6](https://doi.org/10.1016/0003-3472(89)90120-6)
- Smith, B. E., Collie, J. S., & Lengyel, N. L. (2013). Effects of chronic bottom fishing on the benthic epifauna and diets of demersal fishes on northern Georges Bank. *Marine Ecology Progress Series*, 472, 199–217. <https://doi.org/10.3354/meps10031>
- Smith, B. E., Collie, J. S., & Lengyel, N. L. (2014). Fish trophic engineering: Ecological effects of the invasive ascidian *Didemnum vexillum*

- (Georges Bank, northwestern Atlantic). *Journal of Experimental Marine Biology and Ecology*, 461, 489–498. <https://doi.org/10.1016/j.jembe.2014.09.009>
- Smith, B. E., & Link, J. S. (2010). *The trophic dynamics of 50 finfish and 2 squid species on the northeast US continental shelf*. U.S. Department of Commerce NOAA Technical Memorandum, NMFS-NE-216, 640 pp.
- Smith, L. A., Link, J. S., Cadrin, S. X., & Palka, D. L. (2015). Consumption by marine mammals on the Northeast U.S. continental shelf. *Ecological Applications*, 25, 373–389. <https://doi.org/10.1890/13-1656.1.sm>
- Smout, S., Asseburg, C., Matthiopoulos, J., Fernández, C., Redpath, S., Thirgood, S., & Harwood, J. (2010). The functional response of a generalist predator. *PLoS One*, 5, e10761. <https://doi.org/10.1371/journal.pone.0010761>
- Smout, S., & Lindstrøm, U. (2007). Multispecies functional response of the minke whale *Balaenoptera acutorostrata* based on small-scale foraging studies. *Marine Ecology Progress Series*, 341, 277–291. <https://doi.org/10.3354/meps341277>
- Smout, S., Rindorf, A., Hammond, P. S., Harwood, J., & Matthiopoulos, J. (2014). Modelling prey consumption and switching by UK grey seals. *ICES Journal of Marine Science*, 71, 81–89. <https://doi.org/10.1093/icesjms/fst109>
- Smout, S., Rindorf, A., Wanless, S., Daunt, F., Harris, M. P., & Matthiopoulos, J. (2013). Seabirds maintain offspring provisioning rate despite fluctuations in prey abundance: A multi-species functional response for guillemots in the North Sea. *Journal of Applied Ecology*, 50, 1071–1079. <https://doi.org/10.1111/1365-2664.12095>
- Steele, J. H., Aydin, K., Gifford, D. J., & Hofmann, E. E. (2013). Construction kits or virtual worlds; Management applications of E2E models. *Journal of Marine Systems*, 109–110, 103–108. <https://doi.org/10.1016/j.jmarsys.2011.10.016>
- Steele, J. H., & Ruzicka, J. J. (2011). Constructing end-to-end models using ECOPATH data. *Journal of Marine Systems*, 87, 227–238. <https://doi.org/10.1016/j.jmarsys.2011.04.005>
- Suryawanshi, K. R., Redpath, S. M., Bhatnagar, Y. V., Ramakrishnan, U., Chaturvedi, V., Smout, S. C., & Mishra, C. (2017). Impact of wild prey availability on livestock predation by snow leopards. *Royal Society Open Science*, 4, 170026. <https://doi.org/10.1098/rsos.170026>
- Tam, J. C., Link, J. S., Rossberg, A. G., Rogers, S. I., Levin, P. S., Rochet, M.-J., ... Rindorf, A. (2017). Towards ecosystem-based management: Identifying operational food-web indicators for marine ecosystems. *ICES Journal of Marine Science*, 74, 2040–2052. <https://doi.org/10.1093/icesjms/fsw230>
- Taylor, D. L., & Collie, J. S. (2003). Effect of temperature on the functional response and foraging behavior of the sand shrimp *Crangon septemspinosa* preying on juvenile winter flounder *Pseudopleuronectes americanus*. *Marine Ecology Progress Series*, 263, 217–234. <https://doi.org/10.3354/meps263217>
- Temming, A., & Herrmann, J.-P. (2003). Gastric evacuation in cod: Prey-specific evacuation rates for use in North Sea, Baltic Sea and Barents Sea multi-species models. *Fisheries Research*, 63, 21–41. [https://doi.org/10.1016/S0165-7836\(03\)00041-9](https://doi.org/10.1016/S0165-7836(03)00041-9)
- Theroux, R. B., & Wigley, R. L. (1998). *Quantitative composition and distribution of the microbenthic invertebrate fauna of the continental shelf ecosystems of the northeastern United States*. U.S. Department of Commerce, NOAA Technical Report, NMFS, 140, 240 pp.
- Townsend, C. R., & Risebrow, A. J. (1982). The influence of light level on the functional response of a zooplanktonivorous fish. *Oecologia*, 53, 293–295. <https://doi.org/10.1007/BF00389002>
- Tsou, T. S., & Collie, J. S. (2001). Predation-mediated recruitment in the Georges Bank fish community. *ICES Journal of Marine Science*, 58, 994–1001. <https://doi.org/10.1006/jmsc.2001.108>
- Tyrrell, M. C., Link, J. S., Moustahfid, H., & Smith, B. E. (2007). The dynamic role of pollock (*Pollachius virens*) as a predator in the Northeast US Continental Shelf Ecosystem: A multi-decadal perspective. *Journal of Northwest Atlantic Fisheries Science*, 38, 53–65. <https://doi.org/10.2960/J.v38.m605>
- Warzybok, P., Santora, J. A., Ainley, D. G., Bradley, R. W., Field, J. C., Capitolo, P. J., ... Jahncke, J. (2018). Prey switching and consumption by seabirds in the central California Current upwelling ecosystem: Implications for forage fish management. *Journal of Marine Systems*, 185, 25–39. <https://doi.org/10.1016/j.jmarsys.2018.04.009>
- Yodzis, P. (1994). Predator-prey theory and management of multi-species fisheries. *Ecological Applications*, 4, 51–58. <https://doi.org/10.2307/1942114>
- Zhou, S., & Smith, A. D. (2017). Effect of fishing intensity and selectivity on trophic structure and fishery production. *Marine Ecology Progress Series*, 585, 185–198. <https://doi.org/10.3354/meps12402>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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