

RESEARCH ARTICLE

Accounting for a nonlinear functional response when estimating prey dynamics using predator diet data

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Abstract

1. Forage fish species are key in the transfer of energy from lower to upper trophic levels in marine ecosystems. Therefore, understanding their population dynamics, including population levels, is crucial for understanding productivity and the regulation of marine food webs. However, many forage fishes are poorly sampled by bottom trawl surveys, leading to poor estimates of their abundance. These estimates can be improved by using predator stomachs contents as an additional sampling strategy; however, nonlinear relationships between prey abundance and predator consumption (i.e. the functional response) may bias stomachs data as well.
2. Using predator stomachs contents and bottom trawl survey data, this study aimed to minimize this bias by developing a model to estimate prey dynamics and account for the predator functional response. This model was tested using a series of simulations and applied to a case study of northern sand lance *Ammodytes dubius* on the Grand Bank, Newfoundland, Canada.
3. The simulations revealed that when predators consumed prey following a nonlinear functional response, our model outperformed a classical model (the model adopted by most studies) that assumed a linear functional response. In the case study, we estimated the relative abundance of sand lance from 1995 to 2018, which exhibited oscillatory dynamics with a period of approximately 7 years.
4. Our results demonstrate that our model is capable of more accurately estimating the abundance of data-limited prey populations, which contributes to a better understanding of food web dynamics.

KEYWORDS

food web, forage fish, Grand Bank, integrated model, population dynamics, sand lance

1 | INTRODUCTION

In marine ecosystems, intermediate trophic-level species (i.e. forage fishes) play a key role in regulating the energy flow from primary and secondary producers to top predators (Pikitch et al., 2014),

and understanding their population dynamics is crucial for food web studies and ecosystem-based fisheries management (Link et al., 2020; Tam et al., 2017). However, reliably estimating the abundance of forage fishes is challenging; these species are often data limited because they are not directly targeted and/or poorly

sampled by fisheries, and while they often spend time in pelagic habitats, regular research surveys typically focus on demersal species and use bottom trawls as the sampling gear (O'Driscoll et al., 2002; Stockwell et al., 2006).

The estimation of forage fish abundance can be improved by employing multiple sampling strategies that provide alternative perspectives (Jech & McQuinn, 2016; Yule et al., 2007). For example, predator stomachs contents are increasingly used as an additional data source to estimate prey abundance (Deroba, 2018; Mills et al., 2007), especially for species that lack targeted and effective surveys (e.g. Staudinger et al., 2020). Since predators are often the main targets of research surveys and commercial harvests, they tend to be better sampled and their stomachs contents can be indicative of prey abundance/biomass (Dwyer et al., 2010; Link, 2004; Ng et al., 2021). For instance, trends in the frequency of occurrence of capelin and sand lance in fish predator stomachs contents in the Gulf of Alaska matched abundance estimates from research surveys and seabird diet data (Piatt et al., 2018). Similar analyses have been conducted using a variety of methods (e.g. GLMs, generalized additive models) that have tended to assume that the frequency and/or amount (e.g. number, weight) of prey in stomachs is linearly correlated with the abundance of that prey (Buchheister & Latour, 2015; Roseneau & Byrd, 1997; but see Mills et al., 2007).

Nonlinear relationships between consumption and prey abundance can affect the estimates of abundance based on stomachs content data. The relationship between prey abundance and consumption rate is known as the functional response (Koen-Alonso, 2007). Single-species functional responses are often described following Holling (1959): linear with an asymptote (type I), decelerating (type II) or sigmoidal (type III), but evidence from studies of marine fishes indicates that type II and III functional responses are the most common forms (Moustahfid et al., 2010; Uiterwaal et al., 2018). Given these observations, and considering that many estimates of abundance from stomachs contents still rely on linear assumptions, a research gap exists for methods that account for more realistic functional response forms when using stomachs contents to estimate trends in prey abundance.

To address this gap, we developed the NonLinear Functional response Prey dynamics Model (NLFPM). This model estimates prey dynamics by combining survey and predator stomachs content data, and accounting for the predator functional response. The functional response is modelled by treating average survey catch as a relative index of prey population abundance to compare to the probability of consumption of prey from stomachs content data. These two sources of data are combined to provide an improved index of prey abundance. This method was tested using simulations and was then applied to a case study for northern sand lance *Ammodytes dubius* on the Grand Bank, Newfoundland, Canada. The case study used bottom trawl survey data and stomachs content data from two groundfish predator species (Atlantic cod *Gadus morhua* and American plaice *Hippoglossoides platessoides*). These two predator species were specifically chosen because they are commonly caught and sampled by the trawl survey and stomachs content

sampling programs on the Grand Bank, and because both species have been observed to regularly consume northern sand lance on the Grand Bank (e.g. Gonzalez et al., 2006; Koen-Alonso, 2018).

Northern sand lance is a forage fish that substantially contributes to the diet of several commercially important species on the Grand Bank off Newfoundland in Northwest Atlantic Fisheries Organization (NAFO) divisions 3LNO (Koen-Alonso, 2018). Despite their importance in this ecosystem, sand lance has received little research attention. For example, our understanding of their population dynamics and ecology on the Grand Bank has been limited to potentially inaccurate abundance and biomass estimates from bottom trawl surveys (Lilly & Simpson, 2000; Nogueira et al., 2015; Winters, 1983). The inaccuracy of the survey estimates is driven by sand lance's limited catchability in bottom trawl surveys due to their narrow, anguilliform morphology and alternating pelagic and burrowing behaviours (Staudinger et al., 2020). Therefore, alternative methods are required to more accurately estimate sand lance abundance and population dynamics.

2 | MATERIALS AND METHODS

2.1 | NonLinear Functional response Prey dynamics Model (NLFPM)

We developed a model to estimate a relative index of abundance for a prey species and account for a type II/III functional response. The model uses comparable trawl and stomachs content data, where data are reduced to the presence/absence of prey (i.e. their most basic form of information). Although categorizing data as presence/absence removes information on abundance/biomass per tow for trawl surveys and gravimetric (i.e. weight) estimates for stomachs contents, doing so removes the need to determine how comparable individual stomachs content weights are to abundance/biomass of fish in a tow. The model has process and observation components, where process components specify the underlying dynamics of the unobserved response variable (i.e. prey population abundance) while the observation components link the observed data (i.e. survey catch and predator stomachs contents) to the unobserved response (Aeberhard et al., 2018).

The latent variable of interest is the total abundance of a prey population (N_y) over time (y). Whole populations are, however, rarely available to a survey, especially for forage species. Therefore, a relative index of average population abundance (n_y) is used as the response variable. The process component of the model estimates n_y as a random effect that follows a Gaussian random walk likelihood function,

$$n_y \sim N(n_{y-1}, \sigma^2). \quad (1)$$

There are two observation components to the model: (a) fitting the trawl data and (b) fitting the stomachs content data. The first component involves modelling the probability of encountering at least one prey in a random trawl tow (pt) in a given year (y),

$$pt_y = 1 - \exp(-n_y), \quad (2)$$

such that $pt_y \rightarrow 1$ as $n_y \rightarrow \infty$ (Thorson, 2017). Although the spatial distribution of prey is likely not homogeneous (e.g. prey distribution may depend on habitat availability), we assume that prey are distributed homogeneously throughout the sampling area here as a first step. Since trawl data are reduced to binomial (presence/absence) data, pt_y is then directly estimated using a Bernoulli distribution,

$$\text{trawl}_i \sim \text{Bernoulli}(pt_y), \quad (3)$$

where trawl_i is a single presence/absence observation of prey in the i th trawl tow. This transformation and estimation process matches the first step in delta/hurdle models (specifically a Poisson-link delta model; Thorson, 2017) that are commonly used to standardize catch-per-unit-effort fisheries data (Maunder & Punt, 2004; Zuur et al., 2009). If the prey is homogeneously distributed and trawl catches are Poisson distributed, then the probability of catching at least one of the prey is given by Equation (2), which is the motivation for this equation. Assuming an exponential relationship between relative abundance and encounter probability is reasonable because encounter probability has been found to scale with abundance for many taxa (e.g. Gaston et al., 2000; McCarthy et al., 2013). Furthermore, nonlinear relationships between encounter probability and abundance can occur as a result of species biology/ecology and data collection methodology (Harley et al., 2001; Maunder et al., 2006; Walsh, 1996).

The second observation component of the model involves fitting the stomachs content data. These data are indirect samples of presence/absence that are dependent on direct sampling by predators via consumption. Being indirect, the probability of encountering prey in stomachs content data may be dependent on the functional response of the predator. One flexible parameterization that can account for type II and III functional response shapes is the general form described by Real (1979),

$$r = \frac{k(d^\beta)}{\chi^\beta + d^\beta}, \quad (4)$$

where r represents the rate of consumption of prey, d is the density of prey, k represents the upper asymptote of the curve, χ is a shape parameter and β describes the form of the curve ($\beta = 1$: type II, $\beta > 1$: type III). This representation assumes a single species functional response, where the consumption rate only depends on prey density and it is not affected by other changes in the prey field. Furthermore, if both sides of Equation (4) are divided by k , the consumption rate can be expressed as a fraction of its maximum, and the probability of encountering a prey in a random stomachs could be used as a proxy for the r/k fraction. We use this approximation to represent the connection between stomachs and trawl information,

$$ps_y = \frac{(pt_y^\beta)}{\chi^\beta + pt_y^\beta}, \quad (5)$$

where the probability of encountering a prey in a random predator's stomachs in a given year (ps_y) is a proxy for the (r/k) ratio, and the probability of encountering a prey in a random trawl tow in a given year (pt_y ; Equation 2) represents a proxy for the local prey density (d). This proxy is more valid at lower prey densities (e.g. when the relationship between pt_y and n_y is more linear; see Section 2.2.2 and S.I. Section 1). This approach effectively bounds the functional response between (0,1), but preserves the ability of producing a wide variety of shapes consistent with type II and III formulations. Finally, ps_y is estimated using a Bernoulli distribution function,

$$\text{stomach}_i \sim \text{Bernoulli}(ps_y), \quad (6)$$

where stomach_i is a single presence/absence observation of prey in a predator stomachs.

We used the Template Model Builder (TMB, Kristensen et al., 2016) package in R (R Core Team, 2018) to evaluate the negative logarithms of the marginal likelihoods (nll) of these models and the data, and to evaluate the nll gradients. Further, we used the R function `nllmin()` to find the maximum likelihood estimates. Model convergence was evaluated by ensuring that the nll gradient for all parameters was $<10^{-4}$ and that the Hessian matrix was positive definite at the maximum likelihood estimates.

2.2 | Simulation

2.2.1 | Overview of simulation structure

To identify whether our model could reliably account for nonlinear functional responses and estimate prey abundance, we implemented simulations that involved four types of models: operating, observation, estimation and evaluation (Figure 1). The operating models simulated random time series for both predator and prey species and simulated the consumption of prey by predator following a functional response. The observation models simulated bottom trawl sampling of prey and stomachs content sampling of predators. The estimation models included the NLFPM, a model that used trawl and stomachs contents data and assumes a linear functional response (Linear Functional response Prey dynamics Model [LFPM]), and a model that only used trawl data. Finally, the evaluation models compared the mean squared error (MSE) and bias between the estimated and true prey population dynamics as well as the precision of estimates between the NLFPM and the trawl data-only model. Each aspect of the simulation is described in detail in the subsequent subsections.

2.2.2 | Operating models

Simulations were run with time series of 25 years, where both the size of predator and prey populations varied following a Gaussian random walk with an initial mean of 10,000 and variability of 200,

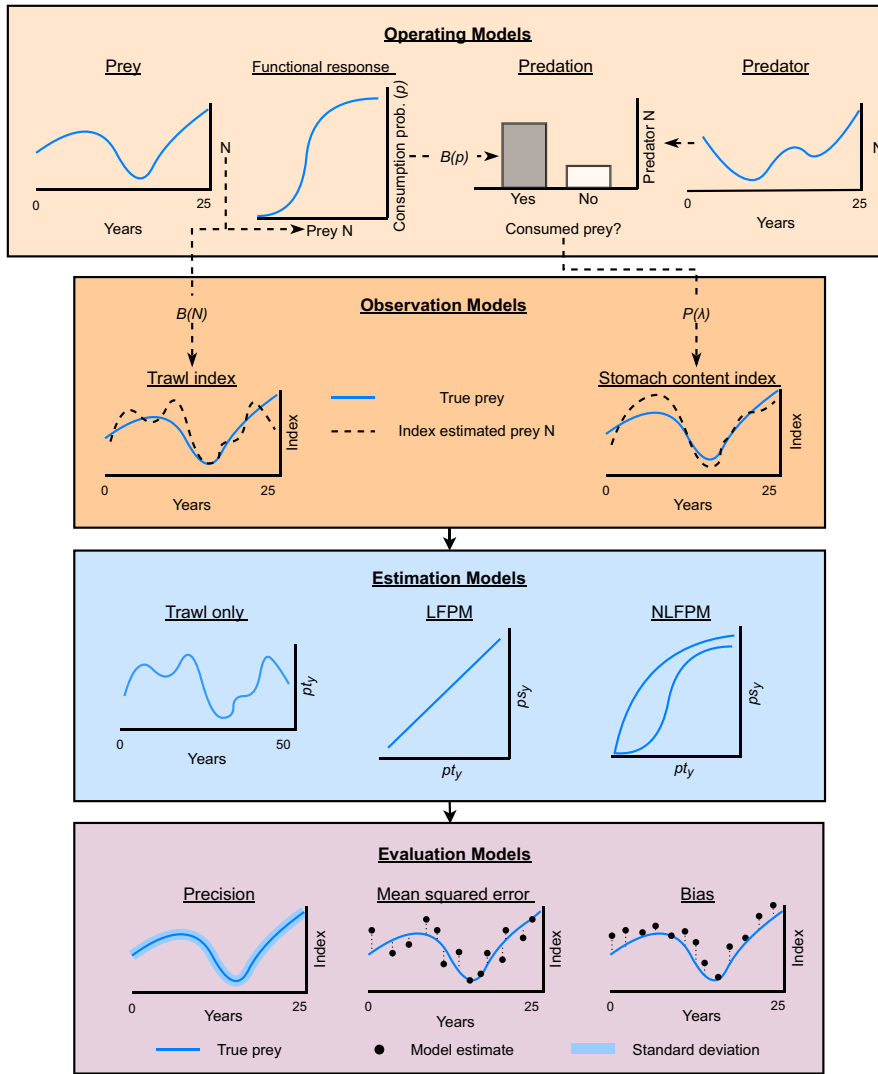


FIGURE 1 Overview diagram for the simulation. The Operating Models panel portrays prey and predator abundance over time (Equations 7 and 8), the functional response (Equation 4) and the number of predators that have consumed prey (Equation 10). The Observation Models panel portrays comparisons between the true dynamics and a trawl index estimated based on the random draws from a binomial distribution and a stomachs content index estimated from a Poisson distribution. The Estimation Models panel portrays functional response curves from the LFPM and NLFP as well as an estimate of prey dynamics from a model with only trawl data. The Evaluation Models panel portrays the calculations of precision, mean squared error and bias between the Estimation Models and the true prey dynamics

$$N_1 \sim N(10,000, 200), \quad (7)$$

$$N_y = N_{y-1} + \sim N(0, 200). \quad (8)$$

For simplicity, we allowed the size of the populations to vary independently. All uses of prey abundance in the simulations relied on inputting abundance into Equation 2. However, since the prey abundance specified in Equations 7 and 8 is large, estimated p_{ty} from Equation 2 would always be equal to 1 if abundance was not scaled. To account for this, we scaled prey abundance by normalization using the standard score equation,

$$N_{y, \text{normalized}} = \frac{N_y - \bar{N}_y}{\sigma_{N_y}}, \quad (9)$$

and then logit transformed the normalized abundance to bound the values between (0,1) before using them in Equation 2. In addition to requiring scaled abundance, we bounded abundance between (0,1) to maintain abundances that would not approach the asymptote of the exponential relationship (values >1) where large changes in

abundance may only yield small changes in the probability of encounter. Abundance values are still estimable but become less accurate as they approach the asymptote (see S.I. Section 1).

Our simulation allowed predation to follow a specified type II or III functional response (Equation 4). Prey density in the functional response equation was based on inputting scaled prey abundance into Equation 2. Every predator in the population sampled the prey field using a random draw from a binomial distribution where p in that distribution represented the probability of consumption that was calculated using the functional response (Equation 5).

2.2.3 | Observation models

Both prey and predator populations were sampled using simulated trawl surveys. We used 200 random trawl samples per year. The trawl samples of the prey population were taken using a binomial distribution, where the probability of encountering prey increased with average population abundance and was based on inputting scaled prey abundance into Equation 2. The trawl survey for the predator population represented the stomachs sampling configuration used

on the Grand Bank, where <20 fish per species have their stomachs sampled per trawl sample, and less than half of the trawl samples (75) examine predator stomachs (Koen-Alonso, 2018). This process involved samples being derived from a Poisson distribution with mean λ that was proportional to predator population size following,

$$\lambda = \alpha + \frac{N - \min(N)}{(\max(N) - \min(N))} (\omega - \alpha), \quad (10)$$

where α describes the minimum scaled value (here 10), ω describes the maximum scaled value (here 20) and N is the number of predators in the population. By representing the process in this way, the number of predators sampled varies randomly based on the size of the predator population and a minimum of 10 and maximum of 20 predators are sampled on each tow (see S.I. Section 4 for analyses on the effects of stomachs sample size). Every predator captured had its stomachs sampled and stomachs samples always correctly identified whether the predator had consumed prey or not.

2.2.4 | Estimation models

For each simulation, we compared estimates from the NLFPM to the LFPM and a model with only trawl data. The LFPM was identical to the NLFPM except for how stomachs content data were treated in the process model. Rather than assuming that these data followed a general functional response (Equation 5), they were assumed to be relative indices of abundance like the trawl data in the NLFPM (Equation 2). The trawl data model was formulated in the same way as the LFPM and NLFPM for the trawl data component (i.e. Equations 1–3) and had all stomachs content components (i.e. Equations 5 and 6) removed. By comparing these estimation models, we were able to determine whether our method would provide improved estimates of prey abundance.

2.2.5 | Evaluation models

We ran 1,000 simulations for operating models with predators using type II and type III functional response forms, where the shape parameters for the type II form were $\chi = 0.3$, $\beta = 1$ and $\chi = 0.3$, $\beta = 3$ for the type III form (Figure 2). The ability of the models to recover true estimates of changes in the prey population size was evaluated by comparing the MSE and mean difference (i.e. bias) between model estimates of n_y and the true values for relative (normalized and logit transformed) population size that were used in the simulation (Section 2.2.2). To determine whether adding predation data would improve model precision, we also compared model estimates of standard deviation in each year for n_y between the NLFPM and the model with only trawl data. We then tested whether the model representing the true dynamics (i.e. the NLFPM) would be identified using Akaike's information criterion (AIC) when compared to the LFPM. Finally, we compared NLFPM estimates of the functional

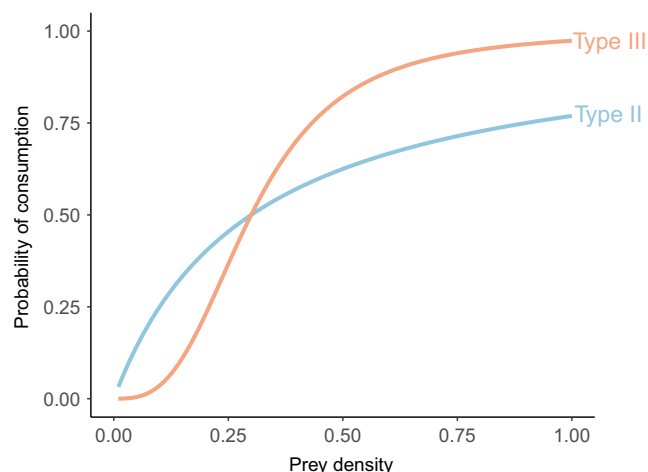


FIGURE 2 The different functional response shapes used in the simulation

response shape parameters and the median shape of the estimated functional response to the true values.

2.3 | Case study

2.3.1 | Data

We used catch-per-unit-effort data from annual stratified-random bottom trawl surveys, conducted in the spring (April–June) by the Canadian Department of Fisheries and Oceans (DFO), on the Grand Bank, Newfoundland, Canada in NAFO divisions 3LNO from 1995 to 2018. Due to the model assumption that prey are distributed homogeneously, we removed samples from locations where sand lance were never caught since adding samples from locations that do not match the distribution of prey could bias our estimates of abundance (S.I. Section 2).

We used two types of stomachs content data, 'called' and full, collected during the bottom trawl surveys for two predators, Atlantic cod *Gadus morhua* and American plaice *Hippoglossoides platessoides*. Called stomachs data records the presence/absence of prey species, where the top two prey species that are present in a stomachs are recorded to estimate the frequency of consumption of dominant prey. Atlantic cod called stomachs data were collected every year from 1995 to 2018, while American plaice called stomachs data were not collected in 2006 or 2016–2018. Full stomachs content data (gravimetric stomachs analyses) recorded the mass of each prey item in a predator's stomachs. However, these data generally had smaller sample sizes and were only available for a limited number of years (Atlantic cod: 1995–1997 and 2013–2018, American plaice: 2013–2018). We only examined stomachs content data for Atlantic cod and American plaice >25 cm in length (see S.I. Section 3 for rationale) because both predators undergo ontogenetic diet shifts.

To allow comparability between data types, all data were converted to presence/absence. This reduced some of the information that was available from trawls (numbers and weight) and full

stomachs content data (weight). However, it has been acknowledged that the Campelen surveys were not designed to capture forage species, and while they can provide useful presence/absence information, their ability to provide reliable quantitative estimates is more limited (DFO, 2012; O'Driscoll et al., 2002).

We ran separate models for each predator species. These models used both called and full stomachs content data to estimate a shared functional response. However, the models estimated separate probabilities of encounter for the different types of stomachs content data since the data represented different observation processes and therefore may have unique temporal trends. In addition to running models for each predator species separately, we ran one model that included both types of stomachs content data from both predator species. This model estimated separate encounter probabilities for each type of stomachs contents and for each predator species (six total encounter probabilities, one pt_y for each species and one ps_y for each stomachs content data source for each species), but all data contributed to a single, fully integrated relative index of abundance.

3 | RESULTS

3.1 | Simulation

The simulation indicated that the NLFPM estimated relative prey abundance trends that were close to the true relative prey abundance trends (i.e. MSE close to 0) regardless of the true form of the functional response (Figure 3). The NLFPM had a median MSE that was approximately 39 and 499 times lower than the LFPM and 2.1 and 4.9 times lower than the model with only trawl data when the true dynamics were type II and III respectively. Estimates from the NLFPM were less biased than estimates from the LFPM but slightly more biased than the trawl data-only model (Figure 4). The NLFPM median bias was 2.1 and 3.2 times higher than the model with only trawl data but was 44 and 62 times lower than the LFPM when the true dynamics were type II and III respectively. These results indicate that the NLFPM is capable of accounting for type II and III functional responses to provide more precise estimates of the actual changes in prey abundance, although using stomachs contents data

can slightly bias abundance estimates when compared to a model with only trawl data. Furthermore, these improved estimates from the LFPM are observable in model AIC score, where the median decreases in AIC for the NLFPM in comparison to the LFPM were 536 and 1,337 for operating models with type II and III functional responses respectively (Figure 5).

The NLFPM estimated functional response shape parameter values that were close to, but sometimes less than, the true shape parameter values (Figure 6). When type II dynamics were the true form of the functional response, the median estimate of χ was approximately equal to the true value and β was underestimated by 0.05. When type III dynamics were the true form of the functional response, the median estimate of χ was approximately equal to the true value and β was underestimated by 0.150. Despite the underestimates of β , the median functional response shapes were not much different from the true shapes, indicating that these small deviations from the truth will not have a large effect on prey abundance estimates (S.I. Fig. 4.4).

When compared to a model with only trawl data, the NLFPM always had smaller annual standard deviation estimates for the prey abundance index for both operating models (Figure 7). These results indicate that adding diet information can improve the precision of abundance index estimates.

3.2 | Case study

Estimated relative prey density (Equation 2) and probability of consumption (Equation 5) indicated that both American plaice and Atlantic cod have exhibited type III functional responses (i.e. $\beta > 1$; Figure 8, Table 1) and the NLFPM had smaller AIC scores compared to the LFPM (Table 2). American plaice were estimated to have a relatively shallow type III functional response curve compared to Atlantic cod, and American plaice had a lower probability of consuming sand lance (maximum probability 0.27) compared to Atlantic cod (maximum probability 0.36). Furthermore, the range of estimated prey density was small (~0.3–0.55) indicating that any changes in sand lance abundance were relatively small (see S.I. Section 4 for analyses on the effects of a narrow range of prey density). All data

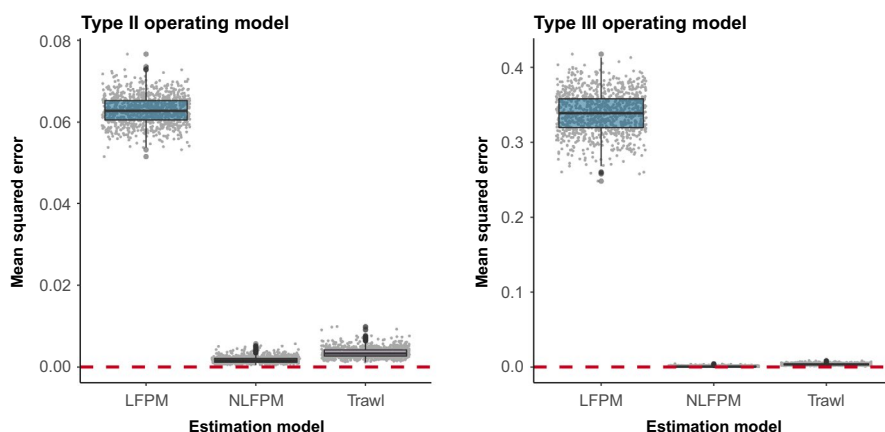


FIGURE 3 Mean squared error (MSE) between estimated relative index of prey abundance and the scaled true prey abundance from all simulations. Grey points represent the MSE from each simulation and the dashed red line represents zero. The grey points were jittered on the x-axis to improve visualization

FIGURE 4 Bias between estimated relative index of prey abundance and the scaled true prey abundance from all simulations

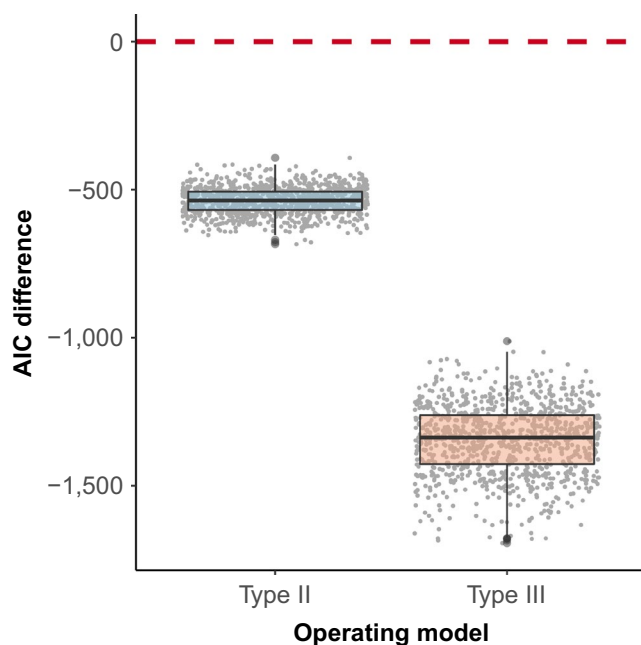
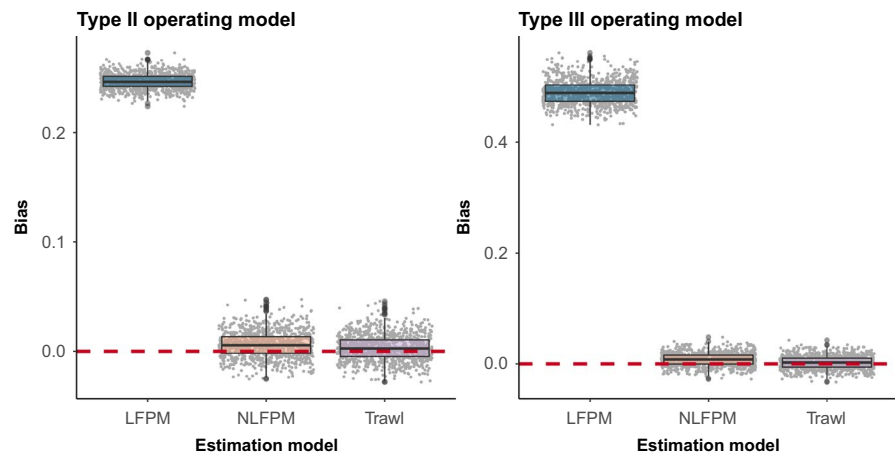


FIGURE 5 Difference in AIC between the NLFPM and LFPM for both operating models. Negative values indicate that the LFPM had a larger AIC than the NLFPM

were below the midpoint of the estimated functional responses indicating that any increases in prey abundance should yield relatively large increases in the probability of consumption. Finally, when American plaice and Atlantic cod were used in the same model, their functional response shape parameters differed slightly from when they were modelled separately. Both curves became flatter, with larger values for χ and smaller values for β (Figure 8).

All three models estimated trends indicating that sand lance abundance has fluctuated since 1995, with approximately three peaks and four valleys estimated at a period of around 7 years (Figure 9). Each of these time series varied slightly, with Atlantic cod having a less pronounced peak in the middle of the time series (2005–2010), and the American plaice and both species models having a lower initial peak (1997–1998). Finally, when American plaice

and Atlantic cod data were combined, the trend was similar to what had been observed when those species were modelled separately.

4 | DISCUSSION

This study aims to develop a model that can estimate prey dynamics by integrating survey and stomachs content data, while accounting for predator functional responses. The efficacy of the NLFPM was justified by simulations and we then applied the NLFPM to a case study for northern sand lance on the Grand Bank. When predators exhibited nonlinear functional responses in the simulations, the NLFPM outperformed the LFPM in all assessed metrics. The NLFPM also outperformed a model with only trawl data in MSE and standard deviation but produced estimates that were slightly biased in comparison. Furthermore, the NLFPM was capable of estimating functional response shape parameter values that closely corresponded with the true values. In the case study, the model estimated sand lance dynamics using bottom trawl survey and two types of predator stomachs content data from two predators. Results indicated that both predators consume sand lance following a type III functional response. Furthermore, we identified coherent patterns between all data sources, indicating that sand lance abundance followed an oscillating pattern over time from 1995 to 2018. Here, we discuss the advantages of our model, its assumptions, future directions and the implications of estimated dynamics of sand lance in the case study.

4.1 | Model advantages

We developed a model that estimates and accounts for nonlinear predator functional responses when combining predator diet data with survey trawl data to estimate prey dynamics. Estimating and accounting for the predator functional response improves the biological realism of the processes that influence predator consumption since predators are unlikely to consume prey at rates that are linearly proportional to prey population size (Holling, 1959; Koen-Alonso, 2007). Furthermore, as shown in our simulations, if predator

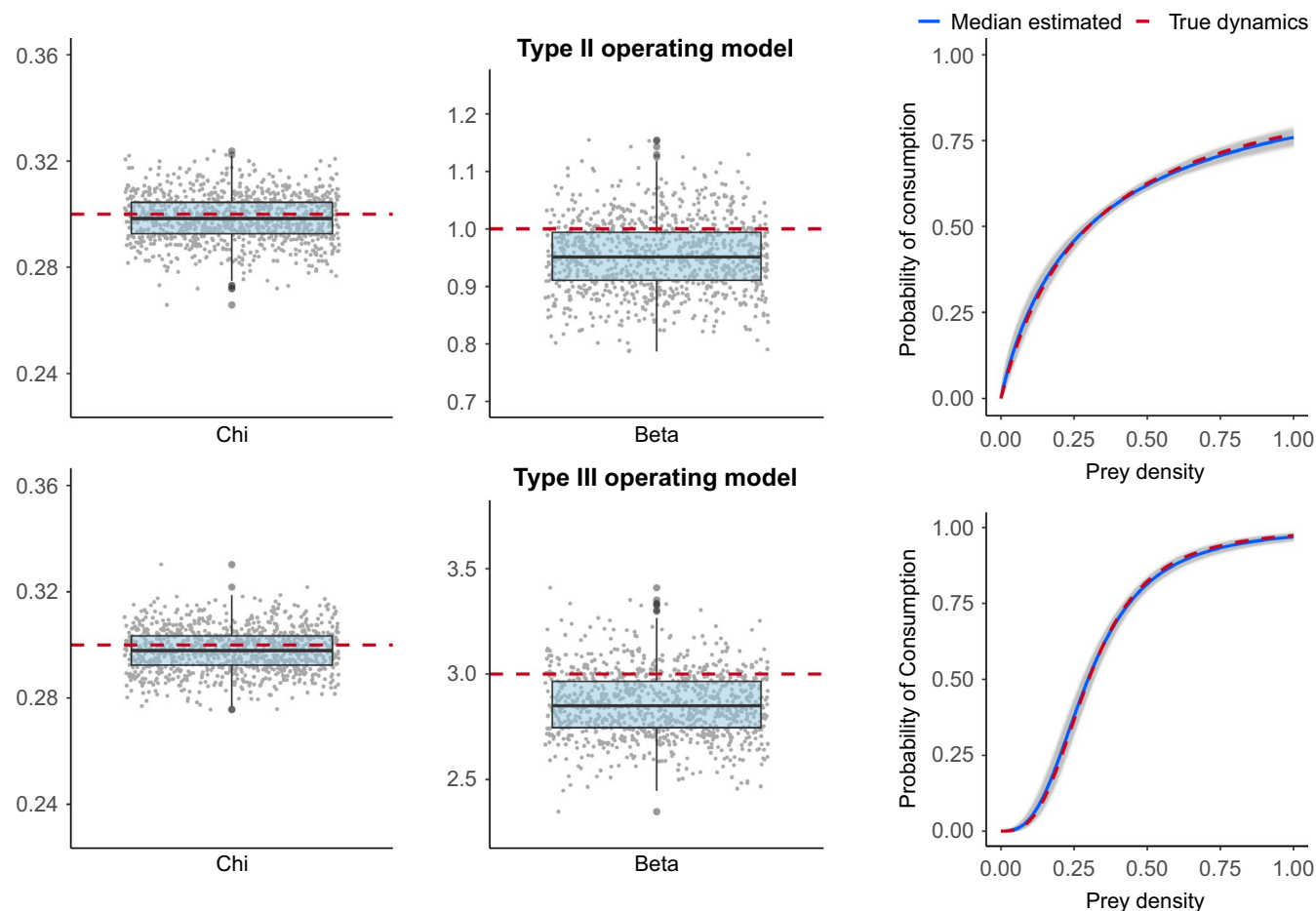


FIGURE 6 Estimates for the shape parameter values in the functional response from the simulation. The dashed red line indicates the true parameter value for each shape. The panels on the far right represent the true shape of the functional response (dashed red lines), the shapes given by all estimated shape parameter values (grey lines) and the median shape parameter values from all estimates (dark blue lines)

diet data are assumed to be linearly proportional to prey population size, when predators consume prey following a nonlinear functional response, estimates of prey dynamics can be biased. Apart from minor increases in bias, simulation results also indicate that precision is improved when predator diet data are used in concert with trawl data to inform changes in prey dynamics. Our NLFPM was capable of substantially reducing this bias and improving the precision, thus providing an improved index for the modelled prey species when including stomachs content data.

Another advantage of the NLFPM is that it can integrate multiple data sources to estimate prey dynamics. Integrating data sources into a combined index using a joint likelihood is preferred over comparing separate indices because it reduces the loss of information and better accounts for uncertainty than non-integrated analyses (Link, 1999; Maunder & Punt, 2013). To our knowledge, the model developed here is the first to integrate fisheries survey data with predator stomachs content data to estimate prey dynamics, therefore avoiding two-step procedures that have been used previously (e.g. Mills et al., 2007; Richardson et al., 2014). Additionally, by combining multiple sources of data with different sampling approaches, the NLFPM increases the sampling resolution in time and space. By

increasing sample sizes with stomachs content data, our prey abundance index had improved MSE and precision when compared to a model with only trawl data. However, including stomachs content data led to slightly more biased estimates when compared to a trawl data-only model, likely in response to slight misspecifications in shape parameter estimates. Integrated models occasionally weight the influence of data on the joint likelihood to account for conflicting signals (Maunder & Piner, 2017). We did not observe conflicting data signals in our case study, but data weighting may be a future research direction for improving the NLFPM. Overall, combining data sources can result in estimates that are more representative of the true dynamics than any index would have been on their own (Gibson-Reinemer et al., 2017; Yule et al., 2007).

The final major advantage of the NLFPM is that it is flexible enough to account for a variety of saturating and sigmoidal functional response shapes. Oftentimes, permitting shape flexibility requires models to estimate numerous shape parameters which can be challenging and uncertainty around those parameter estimates can result in cumulative errors that reduce model accuracy (Fulton et al., 2003; Ludwig & Walters, 1981, 1985). Here, we reduced the number of estimated shape parameters in the functional response

by modifying the general form (Equation 4), to express the consumption rate as a fraction of its maximum (Equation 5). By expressing the consumption rate in this way, our formulation consistently achieved

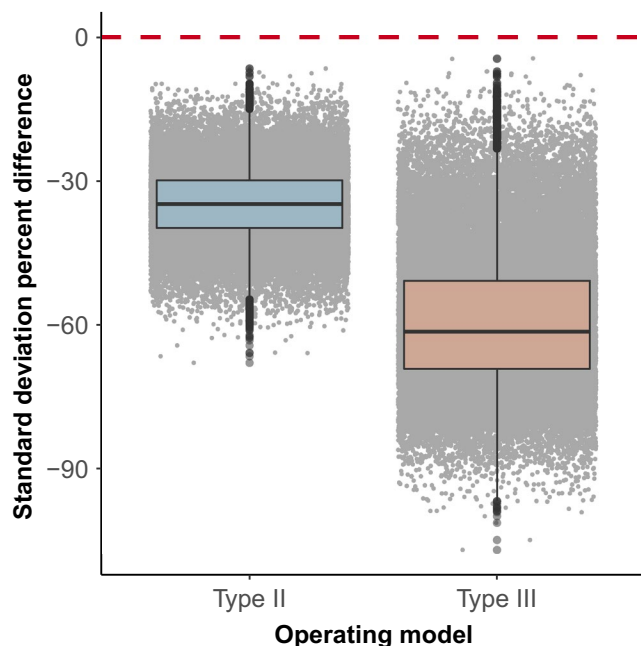
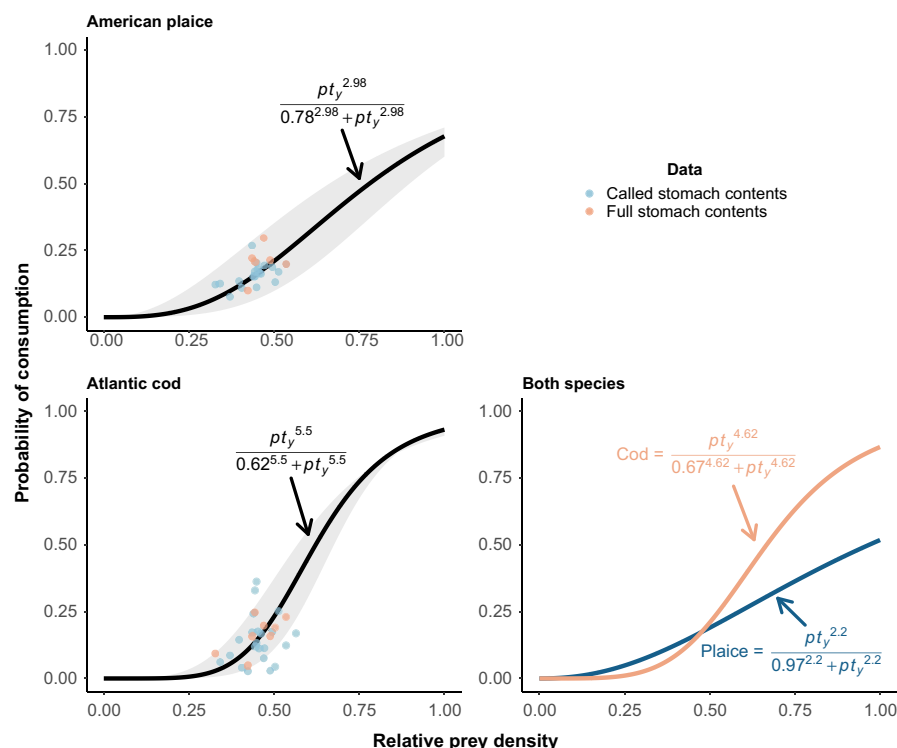


FIGURE 7 Per cent difference in annual standard deviation estimates for the prey abundance index between the NLFPM and a model with no stomachs content data for both operating models. Per cent difference was based on the mean of the standard deviation estimates from the model with no stomachs content data. Negative values indicate a smaller standard deviation for a particular year in the NLFPM

FIGURE 8 Estimated functional responses (lines) and 95% confidence interval (shaded grey polygon) for both predator species when modelled separately and together



convergence and yielded more accurate, less biased shape parameter estimates and functional response curves that were close to the simulated truth. As a result, our formulation should provide a relatively robust platform for estimating functional responses that will minimize problems with convergence and error aggregation. However, it is worth noting that model convergence and estimate accuracy will depend on the quality and quantity of data used when fitting the model (see S.I. Section 4).

4.2 | Model assumptions and future directions

The NLFPM relies on several assumptions that may need to be addressed by future studies to permit more general applications. One of the main assumptions is that presence/absence in trawl surveys can act as an unbiased indicator of prey abundance. Presence/absence of pelagic fishes in bottom trawl surveys can be a more appropriate measure of abundance than the number or weight of fish caught in that survey due to their behaviour and size/body form (O'Driscoll et al., 2002). Furthermore, the indices of abundance based on presence/absence from survey trawls have been used previously for several species (Overholtz & Friedland, 2002) including northern sand lance (Frank et al., 2013). However, by assuming that there is a direct relationship between the probability of encountering prey in trawl and diet samples, we also assumed that prey distribution and predation are equal through space and time which may not be correct. Variability in prey distribution across space and time may be accounted for by using habitat covariates (e.g. bottom type, temperature) in a similar way to how covariates are added to delta models (Zuur et al., 2009) or by adding spatio-temporal error structures (Ng

Species	Parameter	Estimate	95% C.I.
American plaice	χ	0.78	[0.66, 0.90]
	β	2.98	[2.17, 3.79]
Atlantic cod	χ	0.62	[0.57, 0.68]
	β	5.50	[4.06, 6.94]
American plaice and Atlantic cod	χ_{plaice}	0.97	[0.77, 1.16]
	β_{plaice}	2.20	[1.61, 2.79]
	χ_{cod}	0.67	[0.60, 0.73]
	β_{cod}	4.62	[3.44, 5.80]

TABLE 1 Functional response shape parameter estimates and associated 95% confidence intervals

Species	LFPM AIC	NLFPM AIC	Δ AIC	NLL
American plaice	30,507	28,440	2,068	14,217
Atlantic cod	20,289	18,339	1,950	9,166
American plaice and Atlantic cod	40,853	38,374	2,479	19,183

TABLE 2 Model outputs for all three models run. Δ represents difference and NLL represents the negative log-likelihood (NLL) from the NLFPM

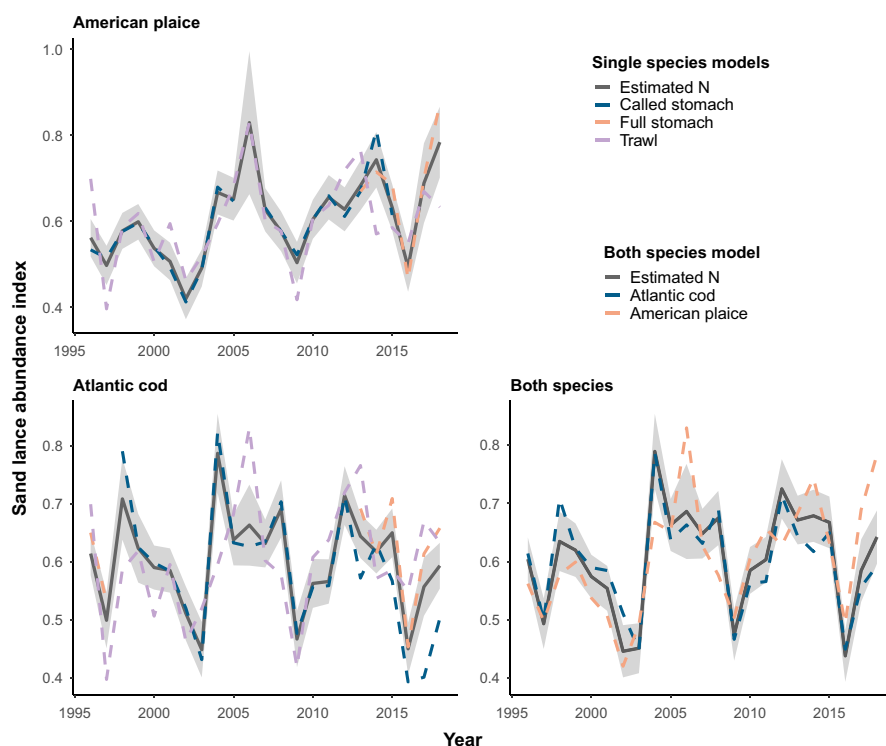


FIGURE 9 Estimated sand lance relative abundance index and 95% confidence interval (shaded grey polygon) from models that used each predator's data separately and one that modelled American plaice and Atlantic cod data together

et al., 2021). Similarly, incorporating covariates to account for variability in gut evacuation rates (e.g. predator body size) may improve estimates of prey detection in stomachs contents (Hyslop, 1980). As such, we advocate future research to examine the validity of extending the NLFPM to include covariates and spatio-temporal error.

The NLFPM is based on a prey-dependent, single prey species functional response formulation. The number of predators in a population can affect consumption rates (i.e. predator-dependent functional response) through interference or facilitation behaviours (Skalski & Gilliam, 2001; Yodzis, 1994). These formulations tend

to be acknowledged as more biologically realistic than the prey-dependent functional response formulation that we have used (Arditi & Ginzburg, 2012; Delong & Vasseur, 2011). Additionally, we used a single species functional response formulation. Most marine predators are generalists that consume a variety of prey species and their consumption rates may be more realistically modelled using multi-species formulations that account for the behaviours associated with this type of predation (Koen-Alonso, 2007; Yodzis, 1994). One important consideration for generalist predators is that changes in their diet composition will match relative changes in the availability

among prey rather than absolute changes, which may lead to observations of increases in a diet despite the abundance of that prey declining. However, estimating predator-dependent and multi-species functional responses requires additional data sources and the estimation of more parameters. The increased complexity of predator-dependent and multi-species formulations may be valuable, and even necessary in some systems, and are important future research directions for extending the NLFPM. Despite the advantages of more complex models, the current formulation of the NLFPM is an important step to account for a basic predation process that has yet to be accounted for, and the low data demand enables the NLFPM to be potentially widely applicable to data-limited situations.

4.3 | Case study

The two predators examined in our case study were estimated to consume northern sand lance following a type III functional response. Type III functional responses are sigmoidal and have a variety of proposed mechanisms including predator learning to capture prey as density increases and predators switching prey types in the presence of alternative prey species (Koen-Alonso, 2007). However, the functional responses estimated here may not reflect the true functional responses of the predators at the behavioural scale due to this approach representing a population-level functional response. As a result, using these estimates to examine behavioural-scale mechanisms should be approached with caution. Nonetheless, our estimates may provide information on the aggregate behaviours of predator fish populations. We estimated that Atlantic cod consumed more sand lance than American plaice and were more sensitive to changes in sand lance population size. It is possible that the importance of sand lance in these predator's diets may have implications for their population productivity as has been observed for Atlantic cod productivity on the Newfoundland shelf (NAFO div. 2J3KL) and its link with capelin *Mallotus villosus* availability (Buren et al., 2014).

The oscillatory pattern in sand lance abundance could be driven by both abiotic and biotic factors. For example, environmental indicators (e.g. sea surface temperature), chlorophyll and zooplankton biomass have all had oscillatory dynamics in the last 20 years (Colbourne et al., 2018; NAFO, 2019) which may have driven some of the variability in sand lance population dynamics. In fact, the oscillatory pattern observed here for sand lance loosely matches the patterns that have been estimated for 2J3KL capelin (Lewis et al., 2019), indicating that capelin and sand lance may be affected by similar environmental drivers. Additionally, dynamics of sand lance may further affect species at upper trophic levels. For example, juvenile Atlantic cod natural mortality among several Newfoundland stocks (NAFO divs. 2J3KL, 3NO and 3Ps) have been estimated to fluctuate over a similar period to what was observed for sand lance here (Zhang et al., 2020), suggesting that sand lance may affect predator population dynamics. Although examining the drivers and effects of variability in sand lance abundance is beyond the scope of this study, given their role as an intermediate trophic-level species on

the Grand Bank, such examinations are an important future research direction. Overall, our understanding of sand lance species throughout the Northwest Atlantic is limited despite their important functional role in food webs (Staudinger et al., 2020). Our analysis of sand lance here may allow their inclusion in food web, ecosystem or stock assessment models to better understand their population dynamics and role in the Grand Bank ecosystem.

Ecosystem-based management requires understanding interactions among species in an ecosystem. To model species interactions, we need information on species dynamics which may not be available for all species in a community from abundance/biomass samples in bottom trawl surveys (Link, 2004; Sydeman et al., 2017). Therefore, the index from the NLFPM may bolster our understanding of poorly sampled species dynamics and thus serve as a stepping stone towards including those species in ecosystem models. This approach may be particularly useful because predator diets are relatively easily measured, are responsive to changes in the environment and can enhance the information that is collected during research surveys (Dwyer et al., 2010; Mills et al., 2007). Additionally, multi-species and ecosystem models rely on information about interactions between species, including the functional response, yet the parameterization of these models is often uninformed due to a lack of empirical research (Hunsicker et al., 2011). Our model may be able to help inform the parameterization of the functional response in such models and potentially improve the accuracy of model estimates.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

M.D.R. and F.Z. designed the research; M.D.R. developed the model and ran the analysis; and M.D.R., M.K.-A., P.M.R., N.C. and F.Z. wrote the paper.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/2041-210X.13795>.

DATA AVAILABILITY STATEMENT

The code used to create the simulation data and to run all analyses presented in this paper can be accessed online (Robertson, 2021a). The data analysed during the case study are available from Fisheries

and Oceans Canada at The Northwest Atlantic Fisheries Centre but restrictions apply to the availability of these data, which were used due to collaboration with Fisheries and Oceans Canada scientists, and are not publicly available. Data are however available from the authors associated with Fisheries and Oceans Canada and with permission of Fisheries and Oceans Canada. The NLFPM model code has been developed into an R package, 'TASTYFISH', to allow future use and it can be found online (Robertson, 2021b). Finally, the northern sand lance abundance index can be found as a csv file within the TASTYFISH package.

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