

Predator stomach contents can provide accurate indices of prey biomass

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Diet-based annual biomass indices can potentially use predator stomach contents to provide information about prey biomass and may be particularly useful for species that are otherwise poorly sampled, including ecologically important forage fishes. However, diet-based biomass indices may be sensitive to underlying ecological dynamics between predators and prey, such as predator functional responses and changes in overlap in space and time. To evaluate these factors, we fit spatio-temporal models to stomach contents of five Atlantic herring (*Clupea harengus*) predators and survey catch data for predators and Atlantic herring. We identified drivers of variation in stomach contents, evaluated spatial patterns in stomach content data, and produced predator-specific indices of seasonal Atlantic herring biomass. After controlling for spatio-temporal processes and predator length, diet-based indices of biomass shared similar decadal trends but varied substantially between predators and seasons on shorter time scales. Diet-based indices reflected prey biomass more than prey availability, but weak correlations indicated that not all biological processes were controlled for. Results provide potential guidance for developing diet-based biomass indices and contribute to a body of evidence demonstrating the utility of predator diet data to provide information about relative prey biomass.

Keywords: biomass index, diet data, food habits, herring, predator–prey dynamics, spatial overlap, spatio-temporal model, stomach

Introduction

Annual indices of biomass are important components of stock assessments that are used to determine stock status, estimate productivity, and inform fisheries management policy (Hilborn and Walters, 1992). Ideally, indices are based on fishery-independent survey data, but these data may not be available for all systems or species due to costs or difficulty of sampling target species. In

such cases, indices can be derived by standardizing opportunistic data sources, such as fishery catch per unit fishing effort data (Maunder and Punt, 2004; Grüss *et al.*, 2019). Another potential data source for developing biomass indices is predator diet data. In some marine regions, such as the Northwest Atlantic (Smith and Link, 2010), Alaska (Livingston *et al.*, 2017), and the Barents Sea (Holt *et al.*, 2019; Eriksen *et al.*, 2020), there is

extensive information about predator feeding habits. For data-rich systems, a diet-based biomass index can corroborate or contradict trends observed from traditional assessment methods, while for data-limited fisheries, a diet-based biomass index may be the only source of information available.

Previous analyses point to the potential use of predator stomach contents to inform prey abundance. Early work employed predator diets to identify rare species (Templeman, 1970), and to sample predator size classes that were not easily collected using traditional gears (Gotshall, 1969). More recently, predator stomach contents have been used to estimate the local distribution of prey species (Fahrig *et al.*, 1993; Link, 2004; Eriksen *et al.*, 2018), provide information about prey recruitment (Scopel *et al.*, 2018), assess fluctuations in prey abundance resulting from changes in ecosystem function (Hanson and Chouinard, 2002; Smith *et al.*, 2016), and identify changes in community composition as a result of fishing (Frid and Hall, 1999; Smith *et al.*, 2013). Many of these studies also found strong correlations between the amount of prey in predator stomachs and independent measures of prey abundance, such as from stock assessments or scientific surveys (Deroba, 2018). In addition to strategic management guidance, predator diet data have been used to provide abundance-index information for tactical fisheries management. For example, the overfishing limit and allowable biological catch for Bering Sea octopus are set using estimates of consumption by Bering Sea Pacific cod (Ormseth *et al.*, 2018).

For an index of abundance to be useful, it should reflect changes in the underlying abundance or biomass of the target species by changing in constant proportion to the population of interest (Thorson *et al.*, 2015). When proportionality is not preserved over time, the index can provide misleading information about changes in abundance (Maunder and Punt, 2004; Bishop, 2006). This proportion may change due to changes in the target species' availability (e.g. schooling, migration), how the data are collected (e.g. gear type, vessel size), or both (Bishop, 2006; Cordue, 2007). Traditional approaches to index standardization use models to account for changes in target species availability, including the effects of habitat and the distribution of sampling in space and time (Campbell, 2004; Thorson and Ward, 2013; Cao *et al.*, 2017), as well as changes in sampling effort over time (Maunder and Punt, 2004). Similarly, potential indices of prey abundance may show correlation with true population abundance, a hyper-stable relationship (i.e. the indices of prey abundance remain elevated while true population abundance decreases; Rose and Kulk, 1999), or no relationship (Figure 1). An index standardization method for diet data should account for processes that alter the proportionality assumption, including spatio-temporal and biological aspects of predation.

If predators are opportunistic, which is the case for many marine piscivores (Bax, 1998), then their feeding habits might provide information about prey abundance (e.g. Einoder, 2009; Eriksen *et al.*, 2018). Predator stomachs would be most informative if they are non-selective and prey-dependent (i.e. eat prey in proportion to their density; Abrams and Ginzburg, 2000). However, predator feeding could be density-dependent (i.e. saturating functional relationship), or be ratio-dependent, where prey consumption depends on both predator density and prey density (Abrams and Ginzburg, 2000; Abrams, 2015). Abundance of alternative prey resources could also erroneously drive changes in predator diets, independent of changes in target prey abundance (Murdoch, 1969; Fortin *et al.*, 2015; Smith and Smith, 2020). These well-known theoretical

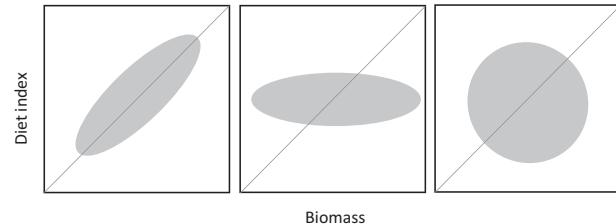


Figure 1. Potential relationships (shading) between a diet-based index of prey biomass and true underlying prey abundance, illustrating accurate reflection of relative abundance (left panel), hyper-stable index of abundance due to Type II functional response or predator tracking of prey (centre panel), or absence of relationship between index and prey abundance (right panel).

properties of predator-prey systems could be one obstacle for using diet data to estimate indices of prey abundance.

Standardizing predator diet data presents unique challenges because predator diets are the result of complex interactions between two or more species that occur over unknown spatial and temporal scales (Taylor, 1984; Bax, 1998). When using predator stomach contents to generate biomass indices, one needs to consider how prey availability and predator dietary preferences change over space and time. Prey availability is likely primarily driven by spatio-temporal distributional overlap between predators and prey, including alternative prey resources (Sih, 2005; Koen-Alonso, 2006; Winemiller, 2007), which can vary among years and seasons. Similarly, because predator ranges may not fully overlap with prey ranges within a year, and because predator and prey distributions are dynamic, one needs to account for the variation in spatial scopes across years (Campbell, 2004). Predator dietary preferences are also likely to differ by predator species and size (Cohen *et al.*, 1993; Mittelbach and Persson, 1998), due to factors such as feeding specialization, gape size, and energetic requirements (Juanes *et al.*, 2008).

In this study, we explore how spatio-temporal processes and predator characteristics affect an index of prey biomass developed from predator stomach contents, using an extensive time series available for the Atlantic herring (*Clupea harengus*) population of the Northwest Atlantic. We sought to answer two main questions: (i) to what extent do fine-scale spatio-temporal processes (e.g. prey availability, predator distribution) govern annual biomass indices that are based on predator stomach contents; and (ii) to what extent do predator characteristics (e.g. species and length) affect annual indices based on predator stomach contents. Finally, given these potential sources of variation, we evaluated whether predator diet data contained sufficient information to estimate useful standardized indices of prey abundance.

Methods

Atlantic herring are a schooling, pelagic species that undergoes complex north-south and inshore-offshore migrations for feeding, spawning, and overwintering (Sinclair and Iles, 1985; Reid *et al.*, 1999; Jech and Stroman, 2012). In the Gulf of Maine-Georges Bank region of the Northwest Atlantic, Atlantic herring predominantly spawn in fall before migrating southwest to overwinter as far as south of Cape Cod. During the summer, they return to the Gulf of Maine to feed before aggregating on spawning grounds. Although Atlantic herring exhibit spawning site fidelity, they are assessed as a single stock complex by the National Oceanic and Atmospheric Administration (NOAA) Northeast

Fisheries Science Center (NEFSC). The Northwest Atlantic herring complex has undergone major changes in abundance. After the stock collapsed in 1977 due to overfishing by foreign fleets, rebuilding began to occur in the mid-1980s, and biomass exceeded pre-collapse levels by the mid-1990s (Overholtz and Friedland, 2002). Atlantic herring are assessed using an age-structured population model, incorporating catch data from two gear types and abundance data from four surveys. Previous assessments used age-varying natural mortality (Deroba, 2015) but emergence of retrospective patterns (Mohn, 1999) motivated use of a constant natural mortality rate in the most recent assessment (NEFSC, 2018).

We analysed spatio-temporal patterns in seasonal predation on Atlantic herring by Atlantic cod (*Gadus morhua*), goosefish (*Lophius americanus*), spiny dogfish (*Squalus acanthias*), white hake (*Urophycis tenuis*), and silver hake (*Merluccius bilinearis*). These predators were chosen because they contained the largest amounts of herring (in total mass, g) of all sampled predators when summed across years (87.9% of sampled Atlantic herring mass). These demersal species are opportunistic, generalist predators (Chang et al., 1999; McMillan and Morse, 1999; Morse et al., 1999; Steimle et al., 1999; Lough, 2004) and overlap spatially and vertically in the water column with Atlantic herring during portions of the year and day (Jech and Sullivan, 2014).

We fit spatio-temporal models to mass of herring in predator stomachs obtained during spring and fall bottom trawl surveys to obtain standardized diet-based biomass indices of Atlantic herring. Additionally, we fit spatio-temporal models to biomass/tow data of Atlantic herring and predators from trawl surveys to calculate a spatially explicit measure of overlap between predators and prey, which we employed to evaluate the relationship between predator-prey overlap and diet-based indices of annual Atlantic herring abundance.

Data

Biannual bottom trawl surveys have been conducted by the NEFSC in the western North Atlantic since the 1960s, along with supplementary surveys conducted to aid in stock assessments in this ecosystem (Supplementary Appendix Table S1; NEFSC, 2011). Survey data were divided into two seasons, spring (14 January to 31 May, mean 26 March) and fall (28 June to 5 December, mean 7 October). Although sampling occurred during winter and summer, these tows represented a small proportion of the data set (e.g. <8% of fall tows were conducted prior to September), and were grouped with spring and fall, respectively, to maximize sample sizes. Stomach contents were collected, analysed, and catalogued in the NEFSC food habits database. This suite of surveys provides direct information about the abundance and biomass of Atlantic herring captured in trawls in addition to information about predation on Atlantic herring from predator stomach contents.

Briefly, stomachs were randomly examined per predator length bins (1 per 10 cm: Atlantic cod, white hake, and silver hake; or 1 per 20 cm: goosefish and spiny dogfish) as part of a random depth-stratified survey design for station selection (Azarovitz, 1981; NEFC, 1988). Prey were examined microscopically and quantified by mass (0.01 g; prior to 1981) or examined macroscopically and quantified volumetrically (0.1 cm³; since 1981). A volume to mass conversion of 1.1:1 was applied based on linear regression ($r^2 = 0.906$, $p < 0.0001$) by Link and Almeida (2000). Additional details

about sampling procedures are documented elsewhere (Link and Almeida, 2000; Smith and Link, 2010).

The data used to produce diet-based biomass indices were collected from 1973 to 2015, and included mass of Atlantic herring in predator stomachs (g), predator species, predator length (cm), and predator size category (small, medium, or large; based on percent of maximum body length, L_∞), location of each tow (latitude and longitude), and season of sampling (spring or fall). For mass of Atlantic herring in predator stomachs, samples that were identified as *Clupeidae* were combined with *C. harengus* because Atlantic herring are the predominant clupeid in the study system, and so samples identified as *Clupeidae* were also likely Atlantic herring (Deroba, 2018, p. 201).

For spatio-temporal models fit to predator stomach content data, we calculated average mass of Atlantic herring consumed for each predator species per tow. Sampling practices have changed over time and stomach contents were collected primarily based on length-stratified sampling (Link and Almeida, 2000). Furthermore, stomach samples from predators in the same tow may not be independent (Millar and Anderson, 2004; Moriarty et al., 2017; Binion-Rock et al., 2018). We chose to account for these dependencies by treating the tow-level average as the unit of observation when there were multiple stomachs per predator species in a tow (68% of tows contained multiple stomachs per predator species; on average there were four stomach samples per species per tow). Predator-specific covariates (e.g. length) were calculated as averages across predators with multiple stomach samples per tow; observed values were used if only one predator was present in the tow. In some year-season-predator combinations, fewer than two observations of Atlantic herring were recorded in predator stomach. No diet-based index was estimated for these year-season combinations to improve model convergence rates.

The data used to calculate a spatially explicit measure of overlap between Atlantic herring and predators were also collected from 1973 to 2015 and included biomasses of Atlantic herring and predators (kg), vessel used for the survey, location of each tow, and biomass per tow of individual species.

Spatio-temporal model structure

We fit two types of spatio-temporal models, the first to predator stomach content data and the second to trawl survey catches using the framework developed by Thorson and Barnett (2017), which allows for simultaneous estimation of unmeasured (latent) spatial and spatio-temporal variation in dependent variables.

Spatio-temporal models of tow-averaged predator stomach content data were fit independently for each species-season combination. First, discrete locations (i.e. knots) were defined from data to approximate the continuous spatial extent of the model, thereby reducing the computation time (Shelton et al., 2014). Specifically, 100 knots were distributed using a *k*-means clustering algorithm applied to the locations of data. The *k*-means clustering algorithm spatially distributes knots with a density proportional to sampling intensity (Shelton et al., 2014; Thorson et al., 2015). The definition of knots allowed aggregation of predator stomach observations from over 6000 unique survey locations to 100 knot locations that were consistent across years for each predator-season combination. After knots were defined, their location was held fixed when the parameters of the spatio-temporal models were estimated. Knot locations differed between predators and

seasons because not all predator species stomach contents were sampled in every survey tow.

The spatio-temporal model structure was a Poisson-link delta model (Thorson, 2018), which estimates the expected mass of Atlantic herring per predator stomach $b(i)$ (in g; where i indexes each tow in the dataset) as the product of two linear predictors: the number of Atlantic herring per predator stomach $n(i)$, and the average mass of Atlantic herring in a predator stomach $w(i)$ (in g per number). There are two primary benefits to modelling mass as a function of two unobserved, derived quantities (i.e. unmeasured n and w). First, as shown below, the relationship between n and w induces correlation between the two components of the model, which is not present in a traditional delta model, where probability of encounter is assumed to be independent of biomass, given an encounter. Second, both predictors use the same log-link function, which simplifies interpretation of covariate effects. The expected mass of Atlantic herring per predator stomach $b(i)$ can also be expressed as a product of the expected probability of encounter of Atlantic herring in a predator stomach $p(i)$, and the expected mass of Atlantic herring per predator stomach given encounter $r(i)$ (in g):

$$E[b(i)] = n(i)w(i) = p(i)r(i). \quad (1)$$

The Poisson-link delta model assumes that the spatial distribution of individuals in the neighbourhood of sampling is random, such that the probability of encountering at least one Atlantic herring in a predator stomach follows a Poisson distribution with intensity equal to the expected number of Atlantic herring per predator stomach (Thorson, 2018; Grüss and Thorson, 2019):

$$p(i) = 1 - \exp[-n(i)]. \quad (2)$$

Then, given the equivalencies shown in Equation (1), it is possible to calculate the mass of Atlantic herring per predator stomach given encounter as:

$$r(i) = \frac{n(i)}{p(i)} w(i) \quad (3)$$

Finally, given the above, the probability of Atlantic herring mass data is calculated as:

$$\Pr[b(i) = B] = \begin{cases} 1 - p(i), & B = 0 \\ p(i) \times g[B|r(i), \sigma_b^2], & B > 0 \end{cases}, \quad (4)$$

where B is the observed mass of Atlantic herring consumed; and $g[B|r(i), \sigma_b^2]$ is a Gamma probability density function with mean equal to $r(i)$ and dispersion parameter equal to σ_b^2 .

Both linear predictors, $n(i)$ and $w(i)$, are potentially modelled as functions of temporal variation, spatial variation, and spatio-temporal variation effects, as well as predator-specific covariates (e.g. predator size). The fully saturated version of the first linear predictor is:

$$\log[n(i)] = \beta_n(t_i) + \sum_{k=1}^{n_k} \lambda_n(k)Q(i, k) + \omega_n(s_i) + \varepsilon_n(s_i, t_i), \quad (5)$$

where $\beta_n(t_i)$ is the intercept for year t_i ; $\lambda_n(k)Q(i, k)$ is the log-linear effect of covariate k on the number of Atlantic herring per predator stomach (see below for more details); s_i is the location

associated with tow i ; t_i is the year associated with tow i ; and $\omega_n(s_i)$ and $\varepsilon_n(s_i, t_i)$ represent, respectively, spatial and spatio-temporal variation in the number of Atlantic herring per predator stomach (see below).

To evaluate whether predator characteristics affect annual diet-based indices of abundance, we included predator traits into the model as $Q(i, k)$, which is a matrix of n_k measured covariates that explain variation in predation, and $\lambda_n(k)$ is the vector of estimated fixed effects of the predator traits. We considered four potential predator covariate sets for $Q(i, k)$: no covariate effects, length (continuous), length and length squared, or size category (as indicator variables; see Data section above). This results in a log-linear (power-function) effect of each predator trait on prey biomass in stomachs. Analogous to “catchability covariates”, standardized predator traits are set to mean values when predicting the diet-based annual biomass index (see diet-based biomass index below; Thorson, 2019).

The second linear predictor had the same structure as the first linear predictor and included the same predator covariates:

$$\log[w(i)] = \beta_w(t_i) + \sum_{k=1}^{n_k} \lambda_w(k)Q(i, k) + \omega_w(s_i) + \varepsilon_w(s_i, t_i), \quad (6)$$

where the parameters on the right side of Equation (6) have the same meaning and characteristics as the parameters on the right side of Equation (5), except that they apply to the predicted mass per Atlantic herring in a predator stomach.

To evaluate fine-scale processes that may affect predator stomach contents, we evaluated spatial and spatio-temporal random effects. The spatial variation terms in Equations (5) and (6) represent unmeasured (latent) spatial variation in the linear predictors that is stable over time, while the spatio-temporal variation terms represent unmeasured (latent) spatial variation in the linear predictors that changes between years. Although these effects could reflect a variety of drivers, such as habitat (e.g. depth), oceanographic processes (e.g. temperature), or biological processes (e.g. prey distribution), we chose to model aggregated latent processes to understand patterns and trends in spatial effects, rather than to attribute variation to specific sources. These terms can be modelled as random effects follow a multivariate normal distribution:

$$\omega_n \sim \text{MVN}\left(0, \sigma_{n_o}^2 \mathbf{R}_n\right)$$

$$\omega_w \sim \text{MVN}\left(0, \sigma_{w_o}^2 \mathbf{R}_w\right)$$

$$\varepsilon_n(t) \sim \text{MVN}\left(0, \sigma_{n_e}^2 \mathbf{R}_n\right)$$

$$\varepsilon_w(t) \sim \text{MVN}\left(0, \sigma_{w_e}^2 \mathbf{R}_w\right), \quad (7)$$

where \mathbf{R}_n and \mathbf{R}_w are the correlations among locations as a function of decorrelation distance κ_n and κ_w , respectively; $\sigma_{n_o}^2$ and $\sigma_{w_o}^2$ are the estimated pointwise variances of the spatial variation in the number of Atlantic herring per predator stomach and the

average mass of Atlantic herring in a predator stomach, respectively; and $\sigma_{n_e}^2$ and $\sigma_{w_e}^2$ are the estimated pointwise variances of the spatio-temporal variation in the number of Atlantic herring per predator stomach and the average mass of Atlantic herring in a predator stomach, respectively. The spatial correlation matrices \mathbf{R}_n and \mathbf{R}_w are defined by Matérn correlation functions (Thorson, 2019; Table 2, eq. 2.7) that allow for geometric anisotropy (i.e. correlations are directionally dependent) or geometric isotropy (i.e. correlations are the same in all directions).

Spatio-temporal models of trawl survey catch data were also fit independently for each species-season combination to understand how seasonal and inter-annual variability in predator-prey overlap might affect a diet-based biomass index. We developed a second type of spatio-temporal model to estimate indices of overlap between Atlantic herring and predators for each year. Spatio-temporal models similar to those described above were fit to biomass catch data for Atlantic herring, Atlantic cod, goosefish, spiny dogfish, white hake, and silver hake. These additional spatio-temporal models predicted biomasses in kilogram, instead of mass of herring in predator stomachs in gram. The same model structure was used as for diet data, except that predator-trait covariates were replaced by the identity of vessel used for the survey, because vessels employed for NEFSC bottom trawl surveys changed over the study period (Miller et al., 2010; Politis, 2020). Vessel catchability covariates were not used in diet-based index models because predator stomachs were considered the unit of inference and differences in catchability were accounted for by the length covariates.

Model fitting and selection

Spatio-temporal models were fit using R package “VAST” (Vector Autoregressive Spatio-Temporal) version 3.2.2, which is described in Thorson and Barnett (2017) and Thorson (2019), and is available at <https://github.com/James-Thorson-NOAA/VAST>. All models were fit using a spatial mesh with 50 km grid resolution. Convergence was verified by examining parameter gradients and ensuring that none were $>10^{-4}$. We also verified that observed herring mass (in predator stomachs) data conformed to the given distribution by comparing the empirical distribution to simulated distributions using a Q-Q plot and density histogram (Zuur et al., 2009).

We used a three-phase model selection process similar to the one described in Zuur et al. using restricted maximum likelihood (REML) to provide unbiased estimates of variance terms and maximum likelihood (ML) to estimate (2009), which was necessitated by the use of Akaike’s Information Criterion (AIC) for model selection for a model with both fixed covariate and random effects. For all models, we first evaluated whether the inclusion of spatial and spatio-temporal random effects was supported by fitting models using REML and four spatio-temporal random effect structures: (i) no spatio-temporal random effects; (ii) spatial random effect in the first predictor only (e.g. for the number of Atlantic herring per predator stomach); (iii) spatial and temporal random effects in the first predictor only; and (iv) spatio-temporal random effects in both linear predictors. Additionally, we evaluated all models with and without anisotropy. We selected the lowest marginal AIC values (Thorson, 2019; Grüss et al., 2020b). If models were within two AIC values, we chose the simpler model (i.e. model with fewer random effects, without anisotropy, or both; Burnham and Anderson, 2004). REML was used during model selection of random effects because this method

provides unbiased estimates of variance terms. Using the random effect structure selected in the first phase, we then determined whether the data supported the inclusion of covariates for predator effects by fitting models using maximum likelihood (ML) and comparing AIC values. We chose the most parsimonious covariate structure for each predator based on the lowest AIC values, or the simpler model if $\Delta\text{AIC} < 2$ (Burnham and Anderson, 2004). ML was used during selection of fixed effects because comparisons using AIC are not valid for models fit with REML that have different fixed effects. Once the top model was identified, we re-fit the models using REML to obtain parameter estimates and model predictions. We used bilinear interpolation between knots to obtain model predictions between knot locations (see Grüss et al., 2020a for details).

The same model selection procedure was used for models of survey catch data, omitting the covariate selection. The most parsimonious models as determined by AIC were used to model biomass per tow of each predator and Atlantic herring.

Diet-based biomass index

For each predator-season combination, we estimated an annual index of abundance by predicting values of the random effects for each knot location in each year, which encompassed the NEFSC bottom trawl survey area. Each knot location was associated with an average surface area of 2740 km². Predicted values of random effects were used in the linear predictors, n and w , and covariate values were set to zero (i.e. the mean value observed for centred covariates) giving:

$$\hat{b}_{s,t} = \hat{n}_{s,t} \hat{w}_{s,t}, \quad (8)$$

where $\hat{b}_{s,t}$ is the predicted biomass per stomach of Atlantic herring (g/stomach) for each knot location s in year t . Predicted biomass across space was used to calculate a diet-based biomass index for Atlantic herring:

$$\hat{I}_t = \sum_{s=1}^m a_s \hat{b}_{s,t}, \quad (9)$$

where \hat{I}_t is the estimated index value in year t , m is the number of knots (i.e. 100), and a_s is the area associated with knot location s .

Estimated spawning stock biomass from stock assessment models (NEFSC, 2018) was compared to our diet-based annual indices of Atlantic herring biomass. To allow for this comparison, both metrics were mean-centred and standardized to have a standard deviation of 1 across years (Grüss and Thorson 2019; Grüss et al., 2019).

Predator-prey overlap index

Overlap between each predator and Atlantic herring was calculated using range overlap, which measures the proportion of Atlantic herring range where predators co-occur (Carroll et al., 2019). Range overlap is defined as:

$$\hat{O}_t = \frac{\sum_{s=1}^m \hat{u}_{s,t} \hat{v}_{s,t}}{\sum_{s=1}^m \hat{v}_{s,t}}, \quad (10)$$

where $O_t \in [0, 1]$ is range overlap in year t ; s is a location; m is the total number of locations (i.e. 100); \hat{u} is the estimated

probability of predator presence at location s in year t (i.e. $\hat{p}_{s,t}$, Eq. 2); and \hat{v} is the estimated probability of prey presence at location s in year t . The product $\hat{u}_{s,t}\hat{v}_{s,t}$ represents the probability that predator and prey both occur at location s in year t , and since locations are associated with equal areas, this sum is proportional to the expected area where predator and prey co-occur. Range overlap therefore provides insight into how much of the prey population was available to the predator population.

Diet-based biomass indices and predator–prey overlap indices were compared to estimated Atlantic herring spawning stock biomass from the most recent stock assessment (NEFSC, 2018). Although we selected spawning stock biomass to use as a benchmark, other stock assessment estimates of Atlantic herring biomass show similar temporal patterns (Supplementary Appendix Figure S1). To evaluate how well each index correlated with Atlantic herring spawning stock biomass, we created correlation plots and calculated Pearson's correlation coefficient to help interpret qualitative comparisons (Aldrich, 1995).

Results

Diet-based biomass index

Predator stomach contents were structured in space and time, as evidenced by model selection that supported inclusion of spatio-temporal random effects in the first linear predictor, n the number of Atlantic herring per predator stomach (Supplementary Appendix Table S2). Of the 80 models fit to diet data, nine models had singular Hessian matrices, indicating that some parameter combinations were not identifiable. Only white hake diets during spring were found to be described by a non-spatial model. However, frequency of Atlantic herring in white hake stomachs was very low in spring (Supplementary Appendix Table S1). Diagnostic plots of model fits were satisfactory, except for white hake diets in spring, which indicated lack of fit due to sparse observations. For all other predators, model selection indicated

support for latent spatial patterns in diet data and that these patterns change among years (Supplementary Appendix Table S3).

Spatial patterns in diet data also differed between predators and seasons (Figure 2). During fall, diet patterns appeared more similar among predators, with higher occurrence of Atlantic herring in diets concentrated near Atlantic herring spawning grounds on Georges Bank. During spring, spatial patterns in predator diets tended to be less similar among predators, with a more southerly distribution overall. For white hake in spring, data sparsity prevented estimation of more than 4 years of diet data.

Predator length was an important predictor for predator stomach contents. Model selection statistics indicated that for most predators, length and length-squared terms were included in the top models (Supplementary Appendix Table S4), which generally created a convex relationship between predator length and amount of Atlantic herring found in predator stomachs (Figure 3). For spring goosefish, spring silver hake, and spring white hake, only predator length was included in top models. As predator lengths increased, the amount in weight and number of Atlantic herring tended to increase. These patterns were consistent between seasons.

Although data early in the time series were sparse, diet-based biomass indices showed evidence that Atlantic herring biomass was lower from the 1970s until the early 1990s, with higher biomass later in the time series (Figure 4, Supplementary Appendix Figure S2). These multi-decadal patterns were generally reflected across predators and consistently between seasons. However, indices were more different on shorter timescales. For example, Atlantic cod and spiny dogfish in fall exhibited peaks in biomass around 1995 and 2005. In contrast, goosefish, silver hake, and spiny dogfish in spring exhibited peaks in Atlantic herring biomass around 2000 and 2010. Additionally, most of the indices included individual years with very high, yet imprecisely estimated index estimates (Supplementary Appendix Figure S3).

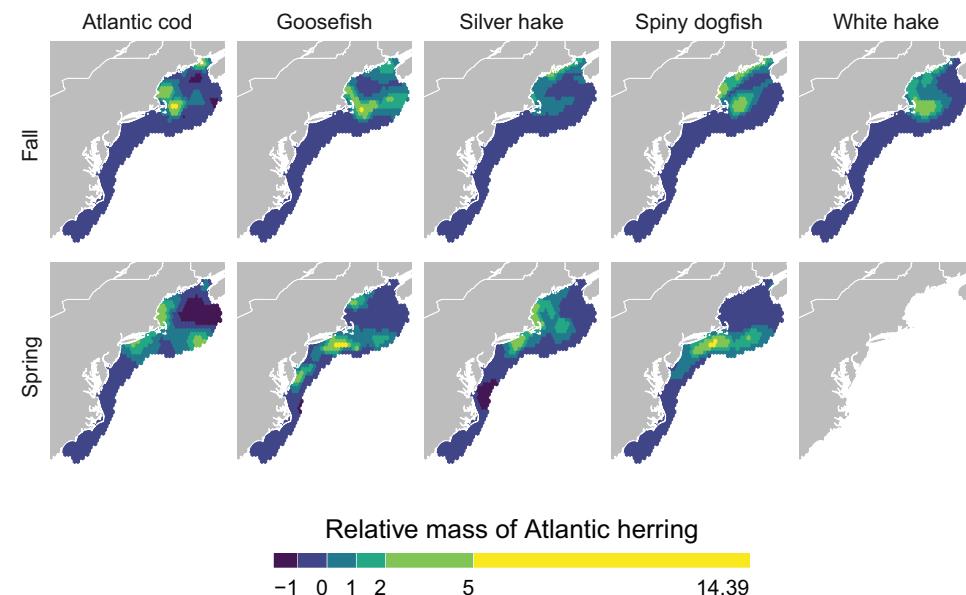


Figure 2. Annually averaged biomass $\hat{b}_{s,t}$ of Atlantic herring in predator stomachs (g/stomach) after controlling for predator length and standardizing (mean zero and standard deviation of one) across predator–season combinations. Warmer colours indicate regions where predators had, on average, higher masses of Atlantic herring per stomach, as predicted by spatio-temporal standardization models. No spatial estimates were generated for white hake in spring due to sparse data.

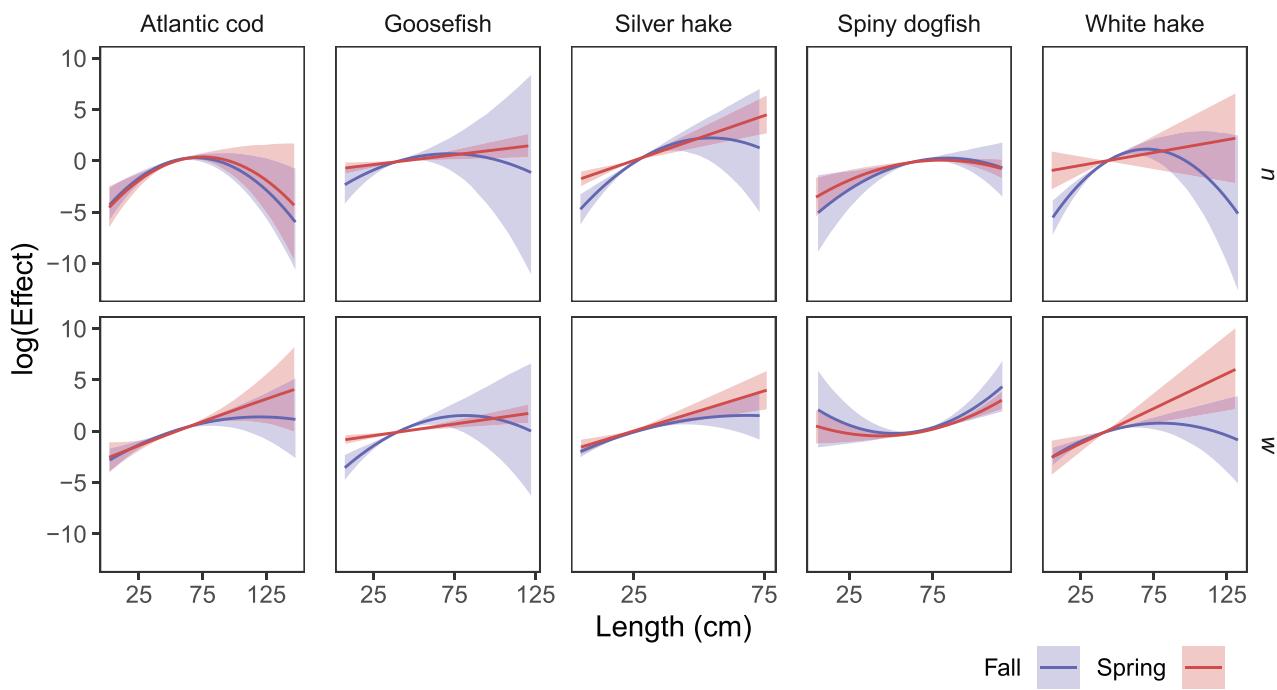


Figure 3. Relationship between predator length (cm) on the log effect of the first linear predictor (n , top row) and second linear predictor (w , bottom row) of spatio-temporal models of mean Atlantic herring mass in predator stomachs. Shaded regions indicate 95% prediction intervals. Estimates are plotted for fall (blue lines) and spring (red lines) for each predator. Rug plots (black lines, bottom of each panel) depict the number of predators observed of each length.

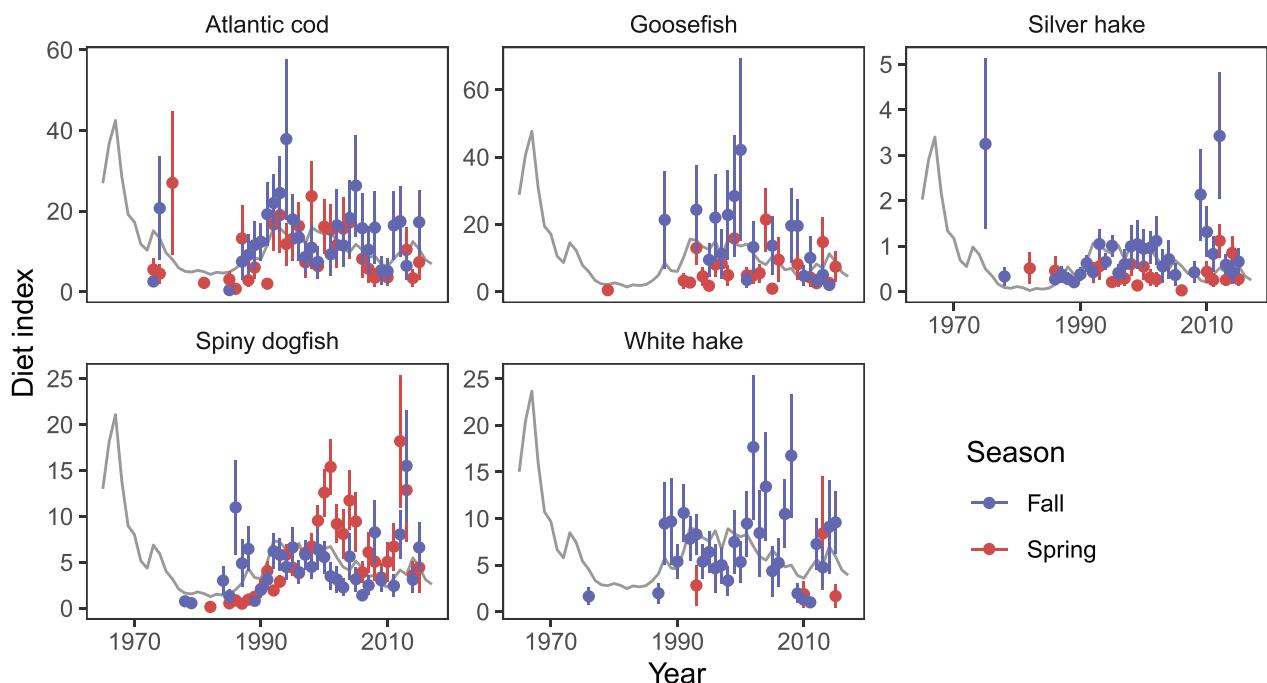


Figure 4. Diet-based annual biomass index estimated with spatio-temporal models from Atlantic herring mass in predator stomachs and controlling for predator length. Models were fit to predator diet data separately for each season. Estimated mean values are shown \pm one standard error. Grey line indicates estimated Atlantic herring spawning stock biomass from stock assessment, scaled the mean and standard deviation of the diet index in each panel.

Annual diet-based biomass indices did not correlate strongly with assessment-estimated Atlantic herring spawning stock biomass (Figure 5). Indices based on Atlantic cod diets had the highest correlation with Atlantic herring stock assessment estimates, followed those based on fall goosefish and spring spiny dogfish diets. Stomach contents from silver hake in both seasons and spiny dogfish and white hake in fall did not correlate to assessment-generated Atlantic herring spawning stock biomass, despite similarities between broad-scale temporal trends. Inter-

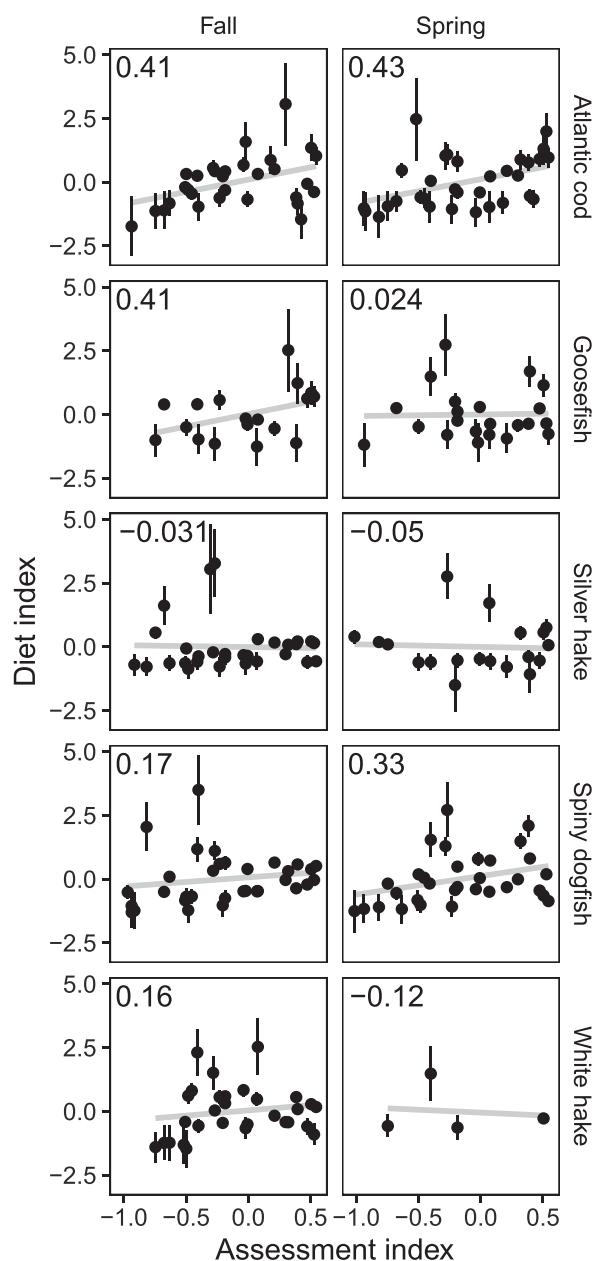


Figure 5. Diet-based biomass index estimated using spatio-temporal models accounting for predator length plotted against Atlantic herring spawning stock biomass estimated from stock assessment. Indices are standardized across years (mean zero and standard deviation one), error bars represent ± 1 C.V. (SE of estimate), and grey lines indicate a fitted linear regression. Pearson correlation's coefficient is shown in upper left corner of each panel.

annual fluctuations and several years of very high index values could have reduced this apparent correlation.

Predator–prey overlap index

Predator and prey distributions were strongly structured in space and time, as evidenced by model selection favouring inclusion of spatio-temporal random effects for all species and seasons (Supplementary Appendix Table S5). All models of trawl data converged, and diagnostic plots indicated satisfactory fits (Supplementary Appendix Table S6). During fall, areas of high overlap with Atlantic herring tended to be fairly consistently located between predators, concentrated around Atlantic herring spawning areas near Georges Bank (Figure 6). During spring, areas of high overlap were distributed further south and varied more between predators. Annual overlap indices calculated from these distributions indicated that overlap tended to be highest during fall, particularly for silver hake and white hake (Figure 7). Although some predators, such as spiny dogfish and goosefish had high inter-annual variability in overlap with Atlantic herring, no consistent directional trends were apparent. Goosefish in both seasons, silver hake in spring, and to lesser extent white hake in spring exhibited increases in range overlap from 2008 to 2009, when there was a survey vessel change. The change in bottom trawl survey vessel led to a change in catchability, which due to the design of the survey, confounds the change in catchability with potential changes in abundance (NEFSC, 2018). Because the range overlap metric is sensitive to abundance (Carroll *et al.*, 2019), this appears to have created an erroneous increase in the overlap index for these species from 2008 to 2009 (Supplementary Appendix Figure S1). In contrast, true changes in abundance may have driven the consistent decrease in range overlap between Atlantic cod and Atlantic herring, which declined from nearly 75% in the early 1970s to close to 30% by 2015. Over this period, Atlantic cod biomass decreased, leading to a decrease in the area occupied, and subsequently lowering range overlap with Atlantic herring.

Annual diet-based prey indices did not correlate consistently to predator–prey overlap indices, indicating limits to the extent that spatio-temporal modelling can standardize diet indices (Figure 8). For example, spiny dogfish and silver hake had relatively strong, positive correlations between range overlap and diet indices, while goosefish and white hake had low or negative correlation between overlap and diet indices. Atlantic cod had negative correlations between overlap and diet indices, perhaps reflecting the inverse trends in abundance for Atlantic herring and Atlantic cod. Overall, predators that had the highest range overlap with Atlantic herring corresponded to diet indices that had stronger correlations with the assessment index, except for Atlantic cod.

Discussion

Predator stomach contents can be useful for developing diet-based indices of prey biomass, but they are also affected by complex interactions between predators, prey, and the environment. Focusing on Atlantic herring as a case-study species, we found that dynamic spatial processes were important for governing predator–prey interactions in the Northwest Atlantic. Predator species characteristics and body size were also important drivers of the amount of Atlantic herring found in predator stomachs. After controlling for spatio-temporal processes and predator traits, we found that diet-based indices of biomass

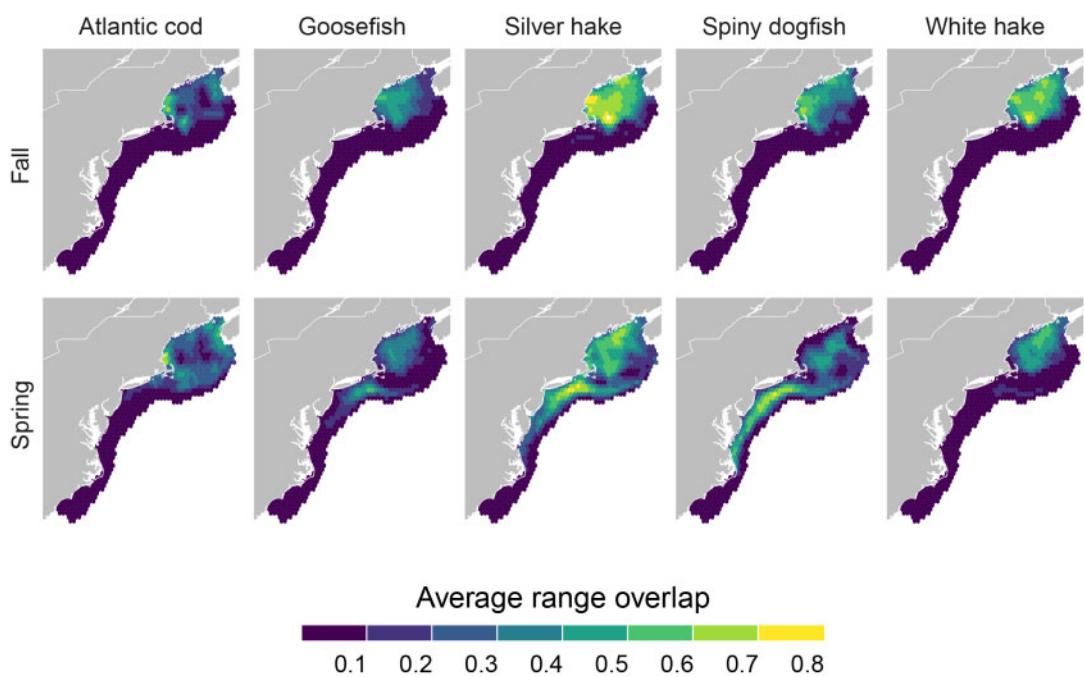


Figure 6. Annually averaged spatially explicit range overlap \hat{O}_t between Atlantic herring and five predators as estimated from spatio-temporal index standardization models fit to bottom trawl survey biomass data for two seasons for all predator–season combinations. Warmer colours indicate regions where each predator tended to overlap more with Atlantic herring.

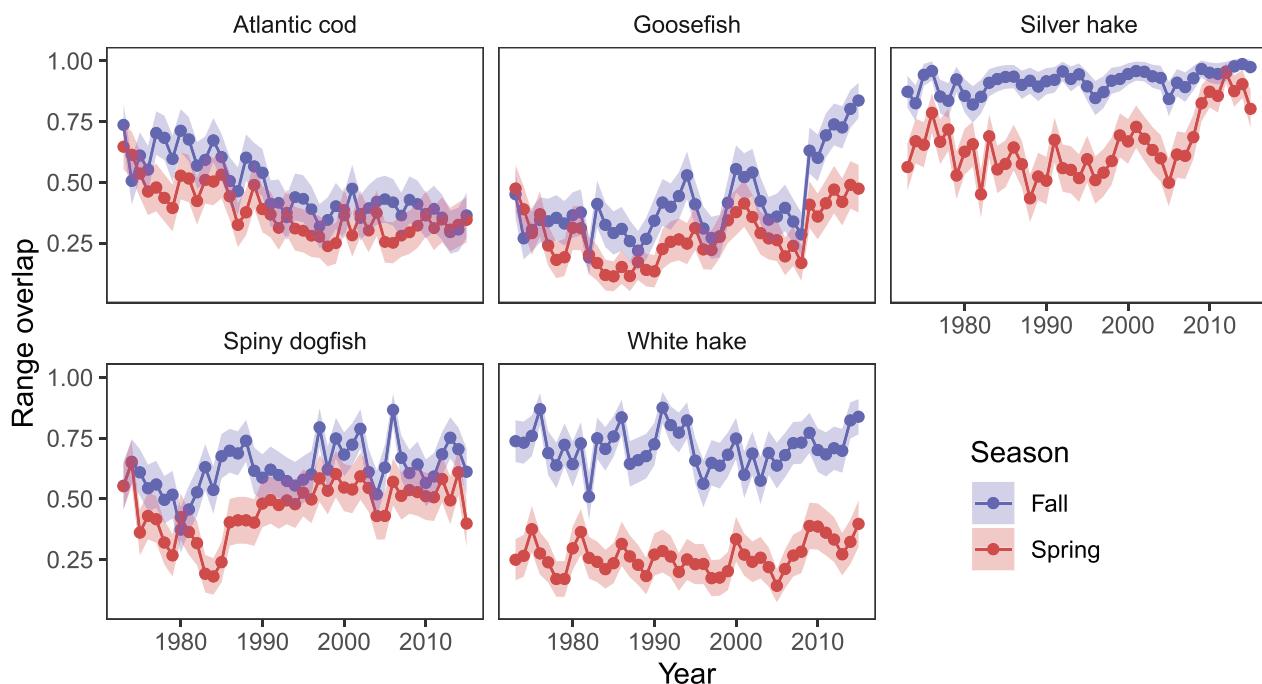


Figure 7. Annual index of predator–prey overlap $O_t \in [0, 1]$ between Atlantic herring and predators as estimated from spatio-temporal models fit to bottom trawl survey biomass data for two seasons (spring, and fall). Predator and prey biomasses were predicted at nearly continuous locations across the sampling region and the proportion of the prey range encompassed by the predator distribution was calculated for each season in each year.

shared similar decadal trends but varied substantially among predators and seasons on shorter time scales. Comparisons between diet-based indices and stock assessment indices assume that stock assessments accurately represent trends in Atlantic

herring biomass. Additionally, for some predators, diet indices may correlate more strongly to other metrics, such as age-1 recruitment, which we did not evaluate. Atlantic cod stomachs provided a reasonable index in both spring and fall, while

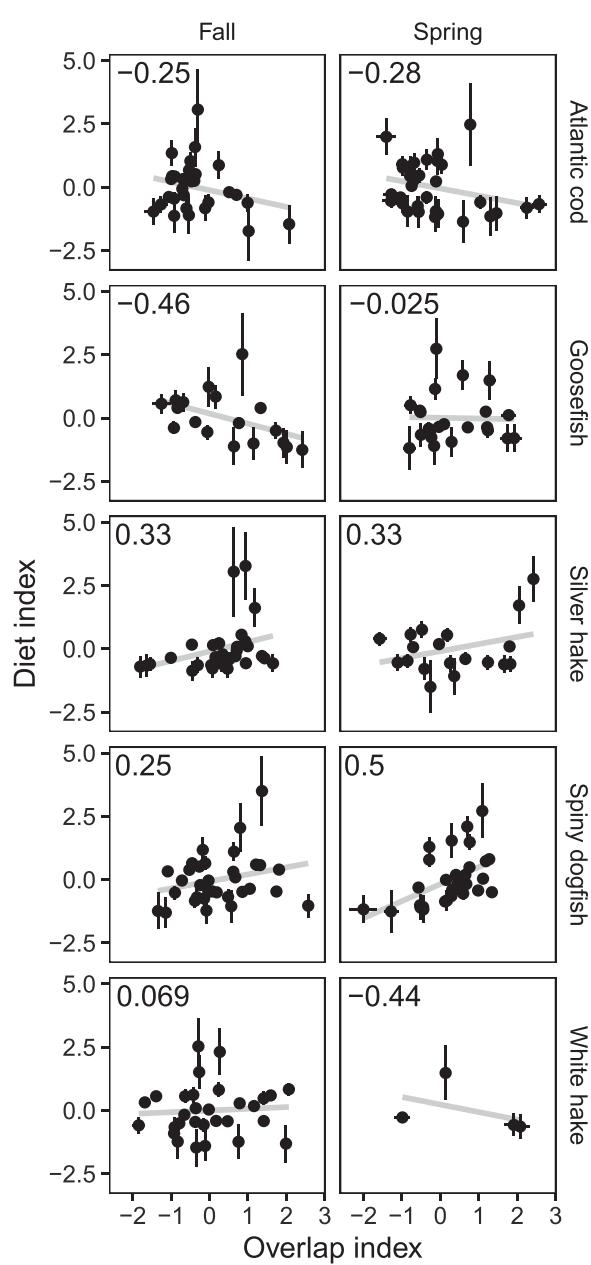


Figure 8. Diet-based biomass index estimated using spatio-temporal models accounting for predator length plotted against overlap index estimated using spatio-temporal models. Indices are standardized across years (mean zero and standard deviation one), error bars represent ± 1 C.V. (SE of estimate), and grey lines indicate a fitted linear regression. Pearson correlation coefficient is shown in upper left corner of each panel.

goosefish provided a good index in the fall and spiny dogfish provided a good index in spring.

Diet-based indices consistently captured decadal patterns in Atlantic herring biomass, reflecting low biomass through the 1970s, increasing biomass in the mid-1980s, and higher biomass by the mid-1990s to 2000s (Overholtz and Friedland, 2002). However, there is still uncertainty about the true Atlantic herring biomass over time, including more recent declines. For example, Richardson *et al.* (2010) developed a larval index for Atlantic

herring that was strongly correlated with stock assessment estimated SSB from 1971 to 2003, but not 2004. As with differences between our diet-based index and the stock assessment index, it is unclear whether these types of discrepancies are due to population changes that are not captured by the stock assessment model, or with the formulation of alternative indices. Given uncertainty in these estimates of Atlantic herring biomass, diet-based indices adequately captured broad temporal trends, and could provide additional information about Atlantic herring population biomass. In systems lacking surveys, diet-based indices could be useful by identifying broad trends in biomass. For example, seabird diet data may be available in systems lacking fishery-based or scientific-survey data (Einoder, 2009), or may augment shorter time-series data, as in the use of penguin diets to inform Antarctic krill biomass (Bost *et al.*, 1994; Brierley *et al.*, 1997). One limitation of our diet-based biomass indices is that, compared to stock assessment output, they exhibit much higher inter-annual variation. This “spikiness” can obscure relationships as measured by correlation coefficients, and may increase overall estimation error when used in stock assessments (Bulgakova *et al.*, 2001; Francis, 2017).

Differences among diet-based indices provide insight about how to approach estimation of prey biomass from predator stomach contents. Given differences between predators and seasons, one comprehensive approach to constructing diet-based biomass indices would be to combine data across predators and seasons in a unified statistical framework, in the hopes of more robustly extracting shared temporal patterns. This idea has been explored previously, for example in population viability analysis, where multiple surveys are combined to account for changes in survey methods over time and to extract a shared underlying population trend (Conn, 2010; Ward *et al.*, 2010; Tolimieri *et al.*, 2017). Similarly, techniques such as dynamic factor analysis could be used to combine diet indices estimated separately to identify shared trends (e.g. Zuur *et al.*, 2003a, b). Where available, jointly modelling predator biomass and stomach contents (i.e. estimate “predator expanded stomach contents”; Grüss *et al.*, 2020b) could provide similar improvement in biomass index estimation by buffering noisy observations in stomach contents through an estimation of the spatial autocorrelation terms from both diet and predator biomass data.

More targeted approaches to developing diet indices could alternatively use our findings to focus sampling on one or two predators or during specific seasons when predator diets are thought to more closely track prey biomass. Seasonal changes in predator-prey interactions are known to occur in the Northwest Atlantic (Garrison, 2000). For example, diet indices from fall stomach samples tended to better reflect prey biomass, as also shown in the present study. In the Northwest Atlantic, fall is generally when Atlantic herring aggregate to spawn (Jech and Sullivan, 2014), which may result in higher and more consistent spatial overlap through time, despite changes in predator or prey abundance. In cases such as spawning, core spatial distributions may be conserved and, therefore, produce more reliable areas for predator-prey interactions over time (Sinclair and Iles, 1985; Rose and Kulk, 1999; Fisher and Frank, 2004), thus producing more reliable diet data (Richardson *et al.*, 2014). Additionally, predator ecology may *a priori* guide our selection of candidate predators. For example, Atlantic cod are generalist piscivores, whose diets are known to shift with changing prey assemblages (Link and Garrison, 2002; Link *et al.*, 2009). Despite changes in

Atlantic cod biomass that appeared to reduce range overlap with Atlantic herring, Atlantic cod diets still correlated strongly to Atlantic herring abundance, indicating that core areas of overlap may be preserved, even as abundance declines.

A related implication is that changes in overlap over time, particularly if those changes are systematic, could affect the utility of diet-based biomass indices unless those changes can be controlled for. However, range overlap may not capture overlap dynamics in way that is relevant to determining utility of a diet index. In particular, although Atlantic cod had the strongest temporal patterns in range overlap with Atlantic herring, Atlantic cod diets appeared to provide useful indices of prey biomass. This contradiction demonstrates the challenge of measuring and understanding predator-prey interactions through a single metric, since decline in Atlantic cod abundance appears to have been the main driver of declining range overlap.

We observed changes in overlap between predators and Atlantic herring that could be due to changes in environmental conditions, predator biomass, timing of surveys, or a combination of factors (Jech and Stroman, 2012; Selden *et al.*, 2018). Diet-based biomass indices did not correlate with overlap between predators and prey, indicating that we successfully accounted for differences in overlap, despite evidence of systematic changes in overlap over time (e.g. for spiny dogfish). However, overlap may also be important at finer grains than we were able to measure. The NEFSC bottom trawl surveys are designed to capture broad, regional patterns (Azarovitz, 1981), but finer-scale spatial processes could also drive diet patterns. Additionally, fish distributions are structured by environmental factors such as temperature (Murawski and Finn, 1988; Fortin *et al.*, 2015) and currents (Walsh *et al.*, 2015). This is a particularly important area for future research because spatial distributions of fish populations in the Northwest Atlantic have changed rapidly and are likely to continue change in the future (Selden *et al.*, 2018).

Predation by marine fishes is size-mediated (Werner and Gilliam, 1984; Mittelbach and Persson, 1998). One benefit of our approach to modelling diets was that we allowed data to inform what predator sizes were important, rather than arbitrarily binning or removing data. We found support for maximal selection of Atlantic herring by intermediate predator lengths, similar to previous modelling that used splines to relate predator length to Atlantic herring in diets (Deroba, 2018). Although predator length was an important driver of stomach contents, we did not examine the length distribution of predators in space. Ontogenetic shifts in spatial distribution are common among fishes and lead to variation in predator length across space (Scharf *et al.*, 2009; Grüss *et al.*, 2017). Given the relationship between diets and predator length, accounting for spatial predator length distribution during index estimation, rather than evaluating for an average-length predator, could improve accuracy of the index.

This study builds on a body of evidence demonstrating the utility of predator diet data to provide information about prey species, and in particular, relative biomass (Fahrig *et al.*, 1993; Link, 2004; Rohan and Buckley, 2017; Scopel *et al.*, 2018). Although diets reflect complex interactions between predators, prey, and their environment, spatio-temporal modelling approaches can help account for these drivers. When used alongside stock assessment models, diet-based indices can provide additional insight into model performance (Gaichas *et al.*, 2010;

Deroba, 2015). In the absence of stock assessments, diet-based biomass indices can provide useful guidance for managers about species lacking traditional surveys due to resource limitations or logistical constraints (Staudinger, 2006).

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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Data availability

The data underlying this article 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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