Original Article

Sources of variation in stomach contents of predators of Atlantic herring in the Northwest Atlantic during 1973–2014

Jonathan J. Deroba*

NOAA Fisheries, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, USA

Corresponding author: tel: +1 508 495 2310; fax: +1 508 495 2393; e-mail: jonathan.deroba@noaa.gov.

Spatial and temporal variation in stomach-contents data is often unquantified or combined in such a way (e.g. averaged among years) that true signal in diets may be lost. Using a delta approach, this paper fits generalized additive mixed models (GAMMs) to the amount of Atlantic herring (*Clupea harengus*) identified in predator stomachs using only data from stomachs in which herring occurred, and to the probability that a stomach contained herring. Both the amount of herring in stomachs and the probability of a stomach containing herring varied seasonally, spatially, and among years. Of the random effects in each GAMM, the effect of predator species had the largest variance. An index of herring abundance derived from the stomach-contents data was generally consistent with recent herring stock assessments. The temporal and spatial variation in the stomach-contents data suggested that the effect of averaging or combining stomach-contents data among years, seasons, or areas may lead to falsely precise or biased estimates from multispecies assessments or in estimates of consumption, and may restrain the relevance of static foodweb models.

Keywords: food habits, foodweb, GAMM, generalized additive mixed model, gut, herring, multispecies, stomach

Introduction

Fish diet and subsequent stomach-contents (gut) data vary temporally and spatially (Reum and Essington, 2008; Nunn *et al.*, 2012), and the utility of stomach data has been argued to be subject to a range of unquantifiable errors and biases (Baker *et al.*, 2014). For example, stomach data represent a short time-span of prey selection that may not represent seasonal or even daily predator preference (Reum and Essington, 2008; Baker *et al.*, 2014). Furthermore, as a result of partial digestion, prey items in stomach contents are difficult to distinguish to species, and prey size is difficult to measure or estimate.

Stomach-contents data, however, have a range of uses, including multispecies stock assessment models, foodweb models, and estimating total annual consumption of prey species (Overholtz *et al.*, 2008; Tyrrell *et al.*, 2008; Gaichas *et al.*, 2011; Curti *et al.*, 2013). The treatment of stomach-contents data to serve those purposes has different consequences. Multispecies virtual population analyses (MSVPA) and multispecies statistical catch-at-age (MSCAA) models attempt to capture some temporal (usually annual) variation among species interactions, but concerns about relatively high measurement error have forced analysts into combining or averaging stomach contents among seasons, years, and across broad geographic regions (Gislason and Helgason, 1985; Livingston and Jurado-Molina, 2000; Lewy and Vinther, 2004; Tyrrell *et al.*, 2008; Kinzey and Punt, 2009; Curti *et al.*, 2013). Combining or averaging stomach samples among space and time may result in artificially reducing true variation in the data, as opposed to just measurement error, and may induce bias if systematic differences among space or time are ignored. Subsequent estimates from multispecies assessments may then be falsely precise or biased. MSCAA models are also sensitive to the model-fitting weight given to stomach-contents data relative to other data sources (Curti *et al.*, 2013; Van Kirk *et al.*, 2015). Thus, not accounting for true variation in the data may result in false confidence in the data and biased model estimates.

Static foodweb models provide insight into ecosystem function for a snapshot of time and have used stomach-contents data from relatively few years to represent longer time-frames, sometimes over broad geographic areas (Harvey et al., 2003; Gaichas et al., 2010). Systematic and significant variation among space and time in stomach contents that is not accounted for in the modelling will consequently affect where and for how long these models remain relevant for management. Dynamic foodweb models also provide insight into ecosystem function and attempt to inform the degree of temporal variation in the processes (Gaichas et al., 2011). Consequently, not accounting for variation in stomach-contents data among space and time may produce falsely precise or biased estimates, as in multispecies assessments.

Stomach contents of fish predators have also been used to estimate total annual consumption of a prey fish, with the intent of using the consumption estimates to allow for estimation of natural mortality in single-species stock assessments of the prey (Overholtz and Link, 2007; Overholtz et al., 2008; Moustahfid et al., 2009). Not accounting for non-random spatial or seasonal variation in the stomach-contents data would likely result in biased estimates of consumption for a given year and, subsequently, biased estimates of natural mortality and other stock assessment quantities. Similarly, averaging stomach contents among years in these contexts would dampen true variation and may result in inaccurate estimates of annual natural mortality. Issues with the treatment of stomach-contents data in the estimation of consumption are further compounded if the measurement and estimation uncertainty that stems from the predator stock assessments is ignored when deriving consumption estimates (Brooks and Deroba, 2015).

Understanding sources of variation in stomach-contents data can also inform possible consequences of climate change and the strength of predator–prey relationships. For example, water temperatures in the Northwest Atlantic have increased over years, and the strength of those changes varied by season (Thomas et al., 2017). Fish species in the region are expected to exhibit a range of responses to these temperature changes (Hare et al., 2016). Coupled with an understanding of temporal and spatial variation in stomach contents, the effects of species distribution shifts in response to climate change on predator–prey interactions might be better anticipated. Similarly, understanding how stomach contents vary among predator species can reveal the relative importance of predators in their ability to affect prey mortality rates. Thus, the effects of changes in predator abundance on prey mortality rates can be anticipated and possibly incorporated into management.

Stomach contents can also be seen as biological samples of available prey, which permits predator diet data to be used to create indices of prey abundance (Link, 2004; Mills et al., 2007; Buchheister and Latour, 2016). Frequency of occurrence was used as an index of benthic prey abundance in the Northeast United States (Link, 2004). Likewise, proportion of juvenile rockfish (Sebastes spp.) in the diet of seabirds and number of rockfish in chinook salmon (Oncorhynchus tshawytscha) stomachs were combined to create an index of rockfish abundance in the California Current System (Mills et al., 2007). Such indices are useful as points of comparison with more commonly used indices of abundance, such as trawls, and with stock assessment estimates of abundance (Mills et al., 2007).

Atlantic herring (C. harengus) (hereafter herring) in the Northwest Atlantic are preyed upon by fish, seabirds, and marine mammals and can account for 20–50% of the diet of these predators (Overholtz and Link, 2007; Smith and Link, 2010; Curti et al., 2013). Atlantic herring have also been the focal species in several multispecies modelling efforts that utilized stomach-contents data (Read and Brownstein, 2003; Overholtz and Link, 2007; Tyrrell et al., 2008). Thus, an increased understanding of the stomach contents of herring predators in the Northwest Atlantic would be especially relevant and impactful. Bottom-trawl surveys used in herring stock assessments are also relatively imprecise, and changes in trawl gear and vessel have caused temporal changes in catchability that increased assessment uncertainty (Miller et al., 2010; NEFSC, 2012; Miller, 2013; Jech and Sullivan, 2014). So, having an index of abundance based on predator stomach contents would be useful in the stock assessment process. The first objective of this manuscript was to evaluate sources of variation in the amount and occurrence of herring in the stomachs of piscivorous predators in the Northwest Atlantic during 1973–2014. This objective was addressed by fitting separate generalized additive mixed models (GAMMs) to: (i) the amount of herring observed in predator stomachs using only those stomachs in which herring were identified, and (ii) a model of the probability of a stomach containing herring using data from all sampled stomachs. This method is analogous to the delta approach that has been used to standardize catch-per-effort data and has been previously applied in fish diet studies (Stefánsson and Pálsson, 1997; Maunder and Punt, 2004; Buchheister and Latour, 2016). The second objective was to develop an index of herring abundance by treating the stomach contents as catch-per-effort observations, and combining the results of the GAMMs as in the delta approach.

Methods
Data
Stomach-contents data were collected on National Marine Fisheries Service Northeast Fisheries Science Center spring and fall bottom-trawl surveys. Details about the methods for sampling stomach contents can be found in Link and Almeida (2000) and Smith and Link (2010). Details about bottom-trawl survey design can be found in Grosslein (1969), Azarovitz (1981), and Miller et al. (2010). A brief overview was provided here. Bottom-trawl survey sampling stations between Nova Scotia, Canada and Cape Hatteras, NC were selected using a stratified random design, with strata defined by depth and latitude. A total of 350–400 stations were sampled each year and season, which resulted in sampling being approximately proportional to stratum area. A minimum of two stations were sampled per stratum. Catch was sorted by species and weighed, individuals were measured for length, and a subset of species was sampled for food habits. Quantitative stomach contents have been sampled since 1973. Total stomach contents and individual prey mass were measured to the nearest 0.01 g. Prey was identified to the lowest possible taxonomic group. For this analysis, unidentified clupeid remains were combined with explicit herring observations to define the amount and occurrence of herring in a stomach (explicit herring observations accounted for 66% of the herring weight observed among all stomachs). Atlantic herring are the dominant clupeid prey in the region, and most of the unidentified clupeid remains are also likely Atlantic herring (Smith and Link, 2010; NEFSC, 2012). Analyses were restricted to those predators that had at least ten stomach observations that contained herring and at least

0.1% of all stomachs sampled among all years contained herring. Restricting the analyses to these 15 predators was similar to what has been done in recent herring stock assessments (NEFSC, 2012), but was also intended to help avoid model convergence problems that might occur by including predators with relatively low sample sizes.

GAMM for amount of herring in stomachs with positive herring occurrence

In GAMMs for the amount of herring in stomachs, the natural log of the weight (g) of herring in the stomach was always the dependent variable. All models were fit using package gamm4 in the R statistical software (version R-3.3.3; Wood and Scheipl, 2014; R Core Team, 2017). Fixed effects included factors for (i) geographic area (Georges Bank, Gulf of Maine, Mid-Atlantic Bight, Southern New England, and Scotian Shelf; Figure 1; a), (ii) season (spring or fall; s), or (iii) the product factor of area and season (α_{as}; the product factor was never included in a model with either of the individual effects to avoid collinearity; see below). Area was considered a fixed effect because samples covered the entire range of the Atlantic herring stock and represented the entire spatial domain of interest. Season was considered a fixed effect because spring and fall do not represent subsamples from a larger population of interest, which would justify a random effect, but systematically chosen sampling times. Treating season as random would also require estimating a variance for a distribution using two observations (i.e. spring and fall), which would be inestimable or poorly determined at best. Smooths in the form of thin plate regression splines (Wood, 2003) were applied to predator length [$f(l_i)$] and the amount of herring catch in the tow from which a stomach was sampled [$f(c_i)$]. Random intercepts were included for year [$b_y \sim N(0, \sigma_b^2)$], predator species [$m_r \sim N(0, \sigma_m^2)$], and all two- and three-way interactions of year, predator, area, and season. Models with the four-way interaction did not converge. Random intercepts were assumed to be normally distributed with mean zero and variance estimated by the model. Random effects of year, predator species, and interaction of year and predator species each nested within the fixed effects of area and/or season were also evaluated, where the random effects were assumed distributed as multivariate normal, with each row of the variance/covariance matrix corresponding to a level of the given fixed effect (e.g. a random effect nested within area would have a separate variance estimated for each level of area; Bates *et al.*, 2015). Year was considered a random effect because variance among years was of interest and the ability to make inference about years outside those sampled was desired. Similarly, the bottom-trawl surveys are not efficient samplers of all herring predators [e.g. striped bass (*Morone saxatilis*), blue shark (*Prionace glauca*), and bluefish (*Pomatomus saltatrix*)], but the ability to draw inference about predators that were poorly or not sampled was of interest, as was the variance among predators (see Results). The fully saturated model, excluding all of the random interactions for brevity, was

$$\ln(h_i) = \mu + \alpha_{as} + f(l_i) + f(c_i) + b_y + m_r + q_{y|a} + o_{y|s} + k_{r|a} + z_{r|s} + \varepsilon_i,$$

(1)

where h was the observed weight of herring in stomach i, μ was the overall model intercept, $q_{y|a}$ was the random year effect nested
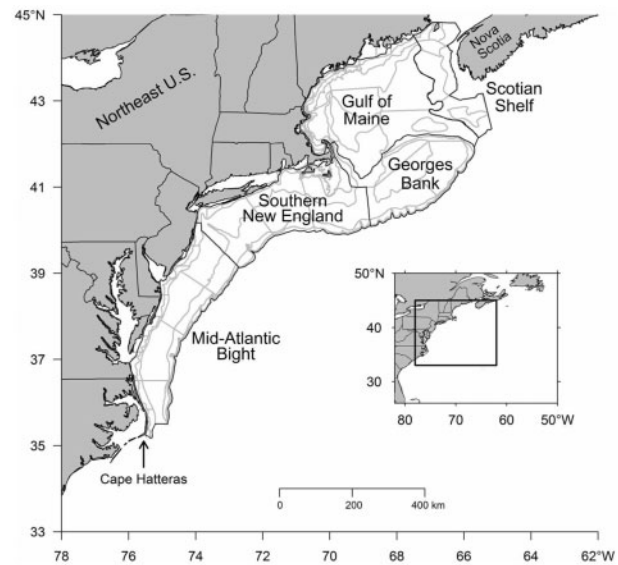

Figure 1. Map of the geographic areas.

within area and $\sim MVN(0, \sigma_q^2)$, $o_{y|s}$ was the random year effect nested within season and $\sim MVN(0, \sigma_o^2)$, $k_{r|a}$ was the random effect of predator species nested within area and $\sim MVN(0, \sigma_k^2)$, $z_{r|s}$ was the random effect of predator species nested within season and $\sim MVN(0, \sigma_z^2)$, and ε was residual error $\sim N(0, \sigma_\varepsilon^2)$. A random effect for tow that would account for the correlation among stomachs sampled from the same tow was considered, but ~75% of tows only had one stomach that contained herring, which made estimation of a tow effect impractical.

Model selection was conducted using Akaike's Information Criterion (AIC; Burnham and Anderson, 2002) and a two-step procedure. In step 1, the random effects were evaluated while retaining all the fixed effects and smooths in the model (Ngo and Brand, 1997; Deroba and Bence, 2009), and with model fitting done using restricted maximum likelihood (REML). REML was used in step 1 because it is superior to maximum likelihood (ML) for estimating random effects (McCulloch and Searle, 2001). Random effects were evaluated before fixed effects so that the final model had the simplest error structure possible (i.e. retaining a fixed effect that explained a similar source of variation was preferred to including a random effect). The full factorial combination of random effects was evaluated. In step 2, the fixed effects were evaluated while using the set of random effects that had the lowest AIC in step 1, and with model fitting done with ML instead of REML. Models in step 2 were fit using ML instead of REML because comparisons with AIC based on fits using REML are not valid for models with different fixed effects (Deroba and Bence, 2009). The full factorial combination of fixed effects and smooths was evaluated. The product factor of area and season was never included in a model with either of the individual effects to avoid collinearity. Smooths were evaluated with the fixed effects because smooths in gamm4 are parameterized to be composed of a fixed effect and a random effect with eight levels (Wood, 2006; Wood and Scheipl, 2014). The variance estimate for the random effect portion dictates the degree of smoothness. In this way, the GAMM reduces to a generalized linear mixed model and no longer requires the use of penalized likelihood or the somewhat subjective determination of a basis dimension and

effective number of parameters, as is typically required in a generalized additive model (Hastie and Tibshirani, 1990). The fixed effects and smooths from the model with the lowest AIC were retained in the final model, along with the set of random effects that had the lowest AIC in step 1.

Results were reported for the final model fit using REML. Results for the fixed effects, smooths, and random effects in the final model were reported by exponentiating the sum of the model intercept and each coefficient:

$$\hat{h}_j = e^{\mu+j}, \qquad (2)$$

where j was a generic representation of any coefficient from a fixed effect, smooth, or random effect. The method puts results in more intuitive units of grams of herring in stomachs $\hat{h}$ associated with the given coefficient. The method also isolates the results for a given effect while ignoring the other effects retained in the final model.

GAMM for probability of a positive herring occurrence in a stomach

The probability (p) of a positive herring occurrence was modelled as binomial using a GAMM with a logit link function. Initially, model selection was attempted using the same approach as for GAMMs of the amount of herring in stomachs, but nearly all models did not converge. Models in the binomial family, especially using data with many zeros, are known to have convergence issues (Collett, 2003; Wood, 2006; Buchheister and Latour, 2016). Instead, GAMMs were fit using the mgcv package in the R statistical software (Wood, 2004; R Core Team, 2017). The GAMMs fit in mgcv used penalized likelihood for model fitting; therefore, the more parsimonious parameterization of gamm4, especially as it pertains to the smooths and random effects, was lost. Changing the modelling approach to improve model convergence was preferred over further reducing the dataset to predators that have more frequent positive occurrences of herring in their stomachs because continued restriction of the dataset would reduce generality and comparability of the predator species that have been considered of interest for stock assessment (NEFSC, 2012).

The fixed effects, smooths, and random intercepts that were considered were the same as in the GAMMs for the amount of herring in stomachs. Package mgcv does not, however, have the capability to nest random effects within other factors; therefore, those types of random effects were not evaluated. Treating year as a random effect (alone or as an interaction) resulted in non-convergence or a variance parameter on the bound of 0.0. Consequently, year was evaluated as a fixed effect because temporal trends in the probability of herring occurrence in stomachs was still of interest. Smooths for predator length and the amount of herring catch in the tow were still applied using thin plate regression splines (Wood, 2003). The fully saturated model, again excluding the random interactions for brevity, was

$$\ln\left(\frac{p_i}{(1-p_i)}\right) = \mu + \beta_y + \alpha_{as} + f(l_i) + f(c_i) + m_r; \qquad (3)$$

where β_y was the fixed effect of year, and all other symbols were defined as above. The variance terms of random effects were estimated, and the coefficients for each level of the random effects were estimated using an identity penalty matrix (i.e. a ridge penalty; Wood, 2008). The identity penalty is equivalent to assuming that the coefficients are independent and identically distributed as normal. Unlike fits using REML or ML, where the coefficients associated with each level of the random effects are integrated out of the likelihood and do not contribute to the number of parameters, the coefficients for random effects using penalized ML contributed to the effective number of parameters (Wood, 2008). The two-step model-selection procedure used for GAMMs for the amount of herring in stomachs, where random effects were evaluated using REML before fixed effects were evaluated using ML, was not needed here because the superiority of REML for random effects was lost by estimating the coefficients of the random effects using penalized ML. So, all models were fit using penalized ML in a full factorial design with model selection done using AIC. Results for the fixed effects, smooths, and random effects in the final model were reported by summing the model intercept and each coefficient, and then converting this logit scale value into a probability $\hat{p}$:

$$\hat{p}_j = \frac{e^{\mu+j}}{(1+e^{\mu+j})}. \qquad (4)$$

Developing an index of herring abundance

An annual index of herring abundance I_y was developed using the year effect coefficients from the GAMM for the amount of herring in stomachs b_y, and the probability of a stomach containing a herring β_y:

$$\hat{h}_y = e^{\mu+b_y};$$

$$\hat{p}_y = \frac{e^{\mu+\beta_y}}{(1+e^{\mu+\beta_y})}; \qquad (5)$$

$$I_y = \hat{h}_y \times \hat{p}_y.$$

Measures of uncertainty (e.g. confidence intervals) were not provided for the index of abundance because methods for combining uncertainty measures from the multistage sampling of the stomachs within the bottom-trawl survey and those from the separate GAMMs have not been developed. The trend among years in the index of abundance was qualitatively compared to the time-series of estimated total herring biomass from the 2015 stock assessment (Deroba, 2015).

Results
GAMM for amount of herring in stomachs with positive herring occurrence

The model with the set of random effects that had the lowest AIC and was, therefore, considered "best" was 2.26 units better than the second-best model, and all other models had <0.01% probability of being the best (Table 1). Similarly, the model with the best set of fixed effects had an AIC that was 3.99 units better than the second-best model, and all other models had <0.01% probability of being the best (Table 1). The overall best model, for

Table 1. Fit and model selection criteria for the five best models based on AIC from each of the GAMMs.

No. of parameters	Log likelihood	AIC	AIC-best AIC	Model likelihood	Model probability	Model covariates
Random effects for GAMM for the amount of herring in stomachs						
19	−3 514.60	7 067.19	0.00	1.00	0.76	$\alpha_{as} + f(l_i) + f(c_i) + b_y + m_r + d_{y,as} + g_{y,r,as}$
18	−3 516.72	7 069.45	2.26	0.32	0.24	$\alpha_{as} + f(l_i) + f(c_i) + m_r + d_{y,as} + g_{y,r,as}$
72	−3 470.07	7 084.13	16.94	0.00	0.00	$\alpha_{as} + f(l_i) + f(c_i) + m_r + q_{y|a} + o_{y|s} + g_{y,r,as}$
73	−3 470.08	7 086.16	18.97	0.00	0.00	$\alpha_{as} + f(l_i) + f(c_i) + b_y + m_r + q_{y|a} + o_{y|s} + g_{y,r,as}$
34	−3 509.21	7 086.42	19.23	0.00	0.00	$\alpha_{as} + f(l_i) + f(c_i) + m_r + q_{y|a} + v_{y,r|s}$
Fixed effects for GAMM for the amount of herring in stomachs						
17	−3 502.36	7 038.73	0.00	1.00	0.88	$\alpha_{as} + f(l_i) + b_y + m_r + d_{y,as} + g_{y,r,as}$
19	−3 502.36	7 042.72	3.99	0.14	0.12	$\alpha_{as} + f(l_i) + f(c_i) + b_y + m_r + d_{y,as} + g_{y,r,as}$
8	−3 518.87	7 053.74	15.02	0.00	0.00	$f(l_i) + b_y + m_r + d_{y,as} + g_{y,r,as}$
9	−3 518.35	7 054.70	15.97	0.00	0.00	$\tau_s + f(l_i) + b_y + m_r + d_{y,as} + g_{y,r,as}$
12	−3 516.03	7 056.07	17.34	0.00	0.00	$\theta_a + f(l_i) + b_y + m_r + d_{y,as} + g_{y,r,as}$
GAMM for the probability that a stomach contains herring						
132.75	−10 806.38	21 878.26	0.00	1.00	0.32	$\beta_y + \alpha_{as} + f(l_i) + f(c_i) + m_r + n_{r,a,s}$
136.61	−10 804.18	21 881.58	3.31	0.19	0.06	$\beta_y + \tau_s + f(l_i) + f(c_i) + m_r + n_{r,a,s}$
138.31	−10 802.56	21 881.74	3.48	0.18	0.06	$\beta_y + \theta_a + f(l_i) + f(c_i) + m_r + n_{r,a,s}$
138.66	−10 802.34	21 881.98	3.72	0.16	0.05	$\beta_y + f(l_i) + f(c_i) + m_r + n_{r,a,s}$
138.66	−10 802.34	21 881.98	3.72	0.16	0.05	$\beta_y + f(l_i) + f(c_i) + n_{r,a,s}$

Fixed effect product factor of area and season α_{as}, smooth of predator length $f(l_i)$, smooth of herring in catch $f(c_i)$, random year effect b_y, random predator species effect m_r, random interaction of year and product factor of area and season $d_{y,as}$, random interaction of year, predator species, and product factor of area and season $g_{y,r,as}$, random effect of year nested within area $q_{y|a}$, random effect of year nested within season $o_{y|s}$, random interaction of year and predator species nested within season $v_{y,r|s}$, fixed effect of season τ_s, fixed effect of area θ_a, fixed effect of year β_y, and random interaction of predator species, area, and season $n_{r,a,s}$.

which results were reported, included a fixed effect for the product factor of area and season, a smooth for predator length, and random intercepts for year, predator species, the interaction of year and the product factor of area and season $d_{y,as}$, and the interaction of year, predator species, and the product factor of area and season $g_{y,r,as}$:

$$\ln(h_i) = \mu + \alpha_{as} + f(l_i) + b_y + m_r + d_{y,as} + g_{y,r,as} + \varepsilon_i. \quad (6)$$

More northerly areas (Georges Bank and Gulf of Maine) tended to have higher amounts of herring in stomachs in fall than in spring, with the exception of the Scotian Shelf, which was similar between seasons, while the opposite was true for the more southerly areas (Mid-Atlantic Bight and Southern New England; Figure 2a). The amount of herring in stomachs generally increased with predator length (Figure 3a). Of the random effects, predator species had the highest variance estimate, year had the lowest, and the interactions were intermediate (Figure 4a). The random coefficients for the year effect generally did not have a consistent trend among years (Figure 5a). Flatfish (Pleuronectiformes) and skates (Rajidae) tended to have less herring in their stomachs than did other predators (Figure 6a).

GAMM for probability of a positive herring occurrence in a stomach

The best model had an AIC that was 3.31 units better than the second-best model, and all models other than the best had ≤6% probability of being the best (Table 1). The overall best model, for which results were reported, included fixed effects for year and the product factor of area and season, smooths for predator length and the amount of herring catch in the tow from which a stomach was sampled, and random effects for predator species,

and the interaction of predator species and the product factor of area and season $n_{r,as}$:

$$\ln\left(\frac{p_i}{(1-p_i)}\right) = \mu + \beta_y + \alpha_{as} + f(l_i) + f(c_i) + m_r + n_{r,as}. \quad (7)$$

The probability of a stomach containing a herring generally increased from the 1970s to the late 1990s and has varied without trend since (Figure 5b). Similar to the amount of herring in stomachs, more northerly areas (Georges Bank and Gulf of Maine) had higher probabilities in fall than in spring, and the Scotian Shelf was similar between seasons (Figure 2b). In Southern New England, probabilities were higher in spring than in fall, but the opposite was true for the Mid-Atlantic Bight (Figure 2b). The probability of a stomach containing herring was dome shaped with predator length, with the probability increasing to a peak at ∼90 cm and declining thereafter, although uncertainty was relatively high at larger sizes (Figure 3b). The probability of a stomach containing herring increased with the amount of herring catch in a tow from 0.0 to ∼50 kg, and varied without trend at larger catches where changes in probability were also more likely due to low sample size than true effects (Figure 7). As with the amount of herring in stomachs, the random effect for predator species had the largest variance of the random effects, with standard deviation being nearly double that of the effect for the interaction of predator species and the product factor of area and season (Figure 4b). Also, similar to results for the amount of herring in stomachs, the probability of a stomach containing a herring was generally lower for flatfish and skates than for other species (Figure 6b). While sea raven (*Hemitripterus americanus*) had a below-average probability of a stomach containing a herring, it had the largest weight of herring observed in those stomachs that did have herring (Figure 6a and b).
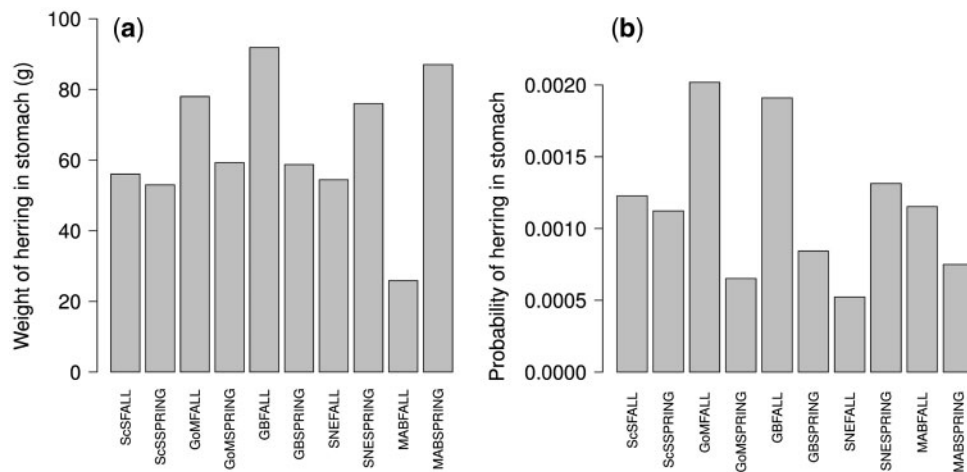
Figure 2. Results for the product factor of area and season from a GAMM for the amount of herring in stomachs (a) and the probability of a stomach containing herring (b). The area and season combinations were: Georges Bank in fall (GBFALL), Georges Bank in spring (GBSPRING), Gulf of Maine in fall (GoMFALL), Gulf of Maine in spring (GoMSPRING), Mid-Atlantic Bight in fall (MABFALL), Mid-Atlantic Bight in spring (MABSPRING), Scotian Shelf in fall (ScSFALL), Scotian Shelf in spring (ScSSPRING), Southern New England in fall (SNEFALL), and Southern New England in spring (SNESPRING).
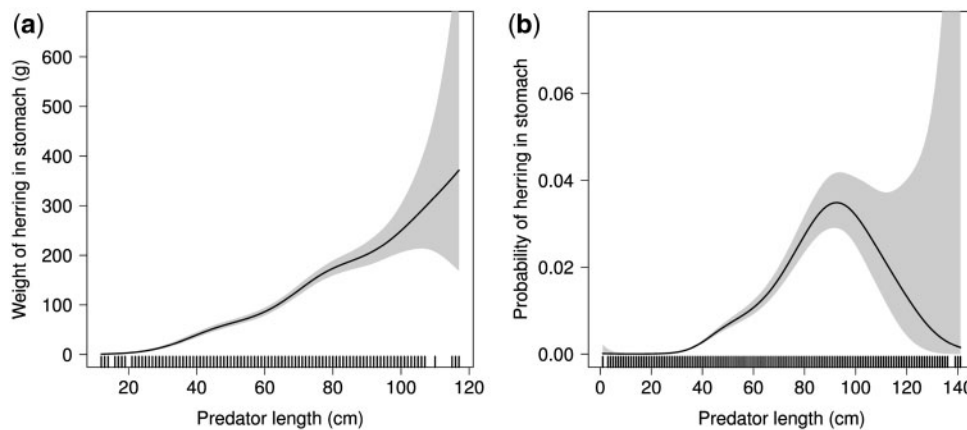
Figure 3. Results for smooths of predator length from a GAMM for the amount of herring in stomachs (a) and the probability of a stomach containing herring (b). The grey-shaded areas are 95% confidence intervals, and the vertical bars along the *x*-axis are a "rug plot" that indexes the distribution of data at each predator length.

Developing an index of herring abundance

The index of abundance generally increased from the 1970s to a peak in 2000, decreased for 3 years, and varied without trend through the end of the time-series (Figure 8). The index of abundance generally matched the trend among years in estimated total herring biomass (Figure 8).

Discussion

Stomach-contents data vary temporally and spatially for a variety of reasons, such as ontogeny, habitat variability, prey diversity, and temperature (Nunn *et al.*, 2012), and knowledge of this variation can improve the use of stomach-contents data in multispecies assessments, foodweb models, and predator consumption estimates. Reum and Essington (2008) defined predator guilds in Puget Sound, WA using stomach-contents data and found that one-third of predators switched guilds among fall, winter, and summer seasons. Although in a different context, the results of

this study are consistent with Reum and Essington (2008). More specifically, the product factor of area and season was included in the final models for the amount of herring in stomachs and the probability of a stomach containing a herring. Stomach-contents data are often not available from all seasons, however, so samples from one season have been assumed to reflect conditions in other seasons in order to define annual diet compositions or consumption. Stomach-contents data that varied in availability by quarter of the year (i.e. a proxy for season) were used to construct a MSVPA in the eastern Bering Sea, with the implicit assumption that in some cases samples from a single quarter represented annual diets (Livingston and Jurado-Molina, 2000). If diet varies among seasons, as in this study, however, the observations from one season would be a biased representation of the annual stomach contents and result in biased estimates from the MSVPA. Using similar datasets as in this study, annual predator consumption of Atlantic mackerel (*Scomber scombrus*) and herring were
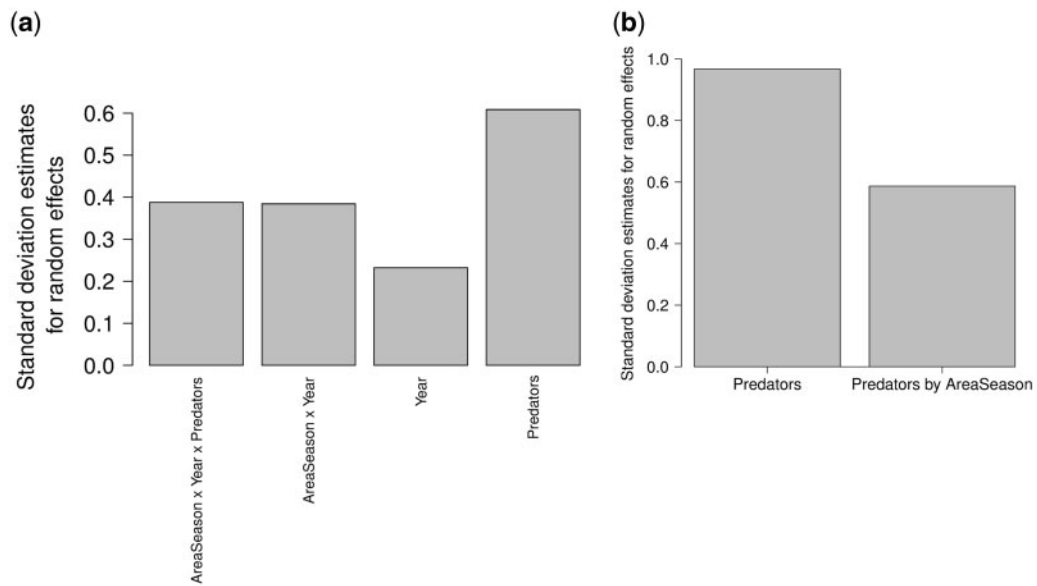
Figure 4. Standard deviation estimates for the random effects from a GAMM for the amount of herring in stomachs (a) and the probability of a stomach containing herring (b).
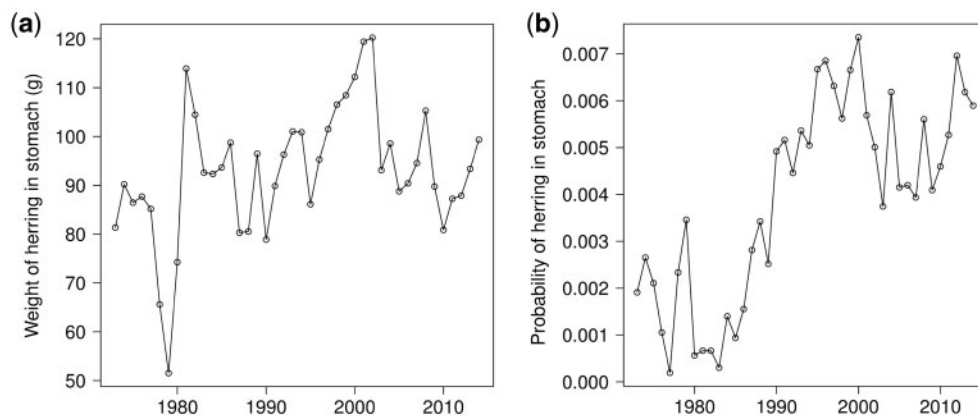
Figure 5. Results for the random effect of year from a GAMM for the amount of herring in stomachs (a) and the probability of a stomach containing herring (b).
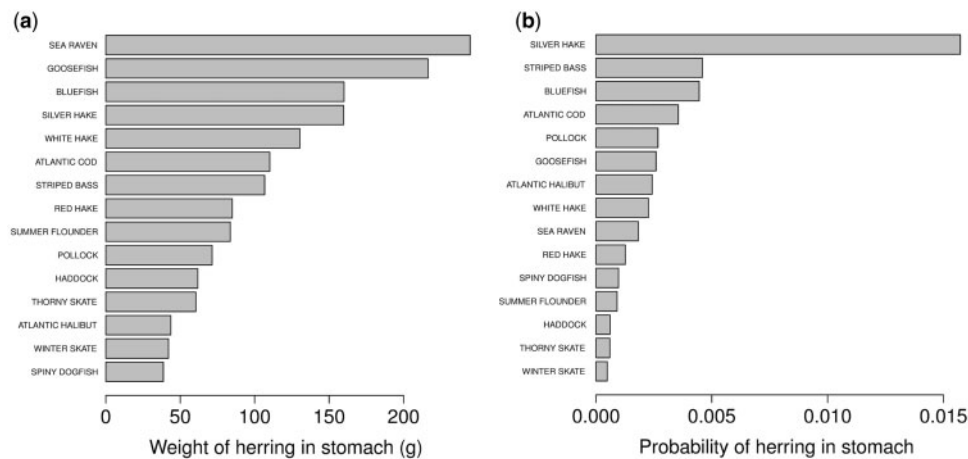
Figure 6. Results for the random effect of predator species from a GAMM for the amount of herring in stomachs (a) and the probability of a stomach containing herring (b).
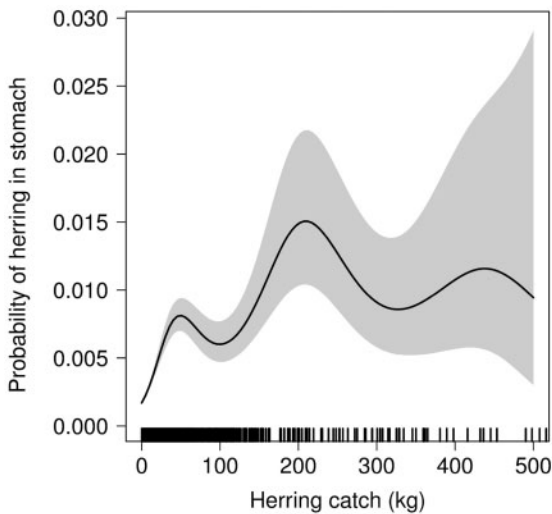
Figure 7. Results for a smooth of the amount of herring caught in a tow from a GAMM for the probability of a stomach containing herring. The grey-shaded areas are 95% confidence intervals, and the vertical bars along the x-axis are a "rug plot" that indexes the distribution of data at each amount of herring catch.
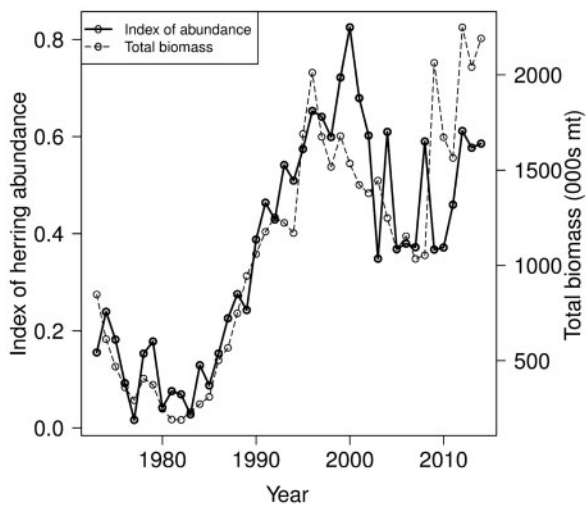

Figure 8. An index of Atlantic herring abundance derived from GAMMs of stomach-contents data (solid line) and time-series estimates of total herring biomass from a stock assessment (dashed line; Deroba, 2015).

estimated by assuming stomach contents from the fall also represented the winter, and spring observations also represented the summer (Overholtz and Link, 2007; Overholtz et al., 2008; Moustahfid et al., 2009). While only variation between the spring and fall seasons were evaluated in the GAMMs here, the differences suggest that the stomach contents of herring predators during summer and winter may also systematically differ. If so, then the annual consumption estimates will be biased to some degree because accounting for only the two seasons is insufficient to represent annual habits, and consumption estimates calculated in this manner have been shown to be sensitive to diet composition (Overholtz and Link, 2007). Stomach-contents samples from the summer season in 2 years were used to construct a static foodweb

model representative of the early 1990s in the Gulf of Alaska (Gaichas et al., 2010). Such methods produce a model indicative of that single season, which may restrict utility for management decisions needed in other seasons or on an annual basis. These results suggest a need for broader seasonal sampling of stomach contents.

As with seasons, stomach-contents samples have also been combined across broad geographic regions, or samples from a limited spatial range have been assumed to represent a broader range, but knowledge of how stomach contents vary spatially can be used to evaluate these assumptions and make model improvements. An MSVPA for the Northeast US continental shelf combined stomach contents across the entire shelf and assumed 100% spatial overlap between predators and prey (Tyrrell et al., 2008). Similarly, annual predator consumption of Atlantic mackerel and herring were estimated by combining stomach contents across the entire Northwest Atlantic, and these consumption estimates were used to estimate natural mortality of Atlantic mackerel and herring (Overholtz and Link, 2007; Overholtz et al., 2008; Moustahfid et al., 2009). Both the amount of herring in stomachs and the probability of a stomach containing herring varied spatially in this study, which also focused on a similar study area (i.e. Northwest Atlantic). Results from the GAMMs could be used to inform how stomach-contents data should be combined in a spatially stratified way, which would improve measures of uncertainty in the stomach contents and consumption estimates. Improved measures of uncertainty could inform sensitivity analysis for the MSVPA and be used in weighting consumption estimates in subsequent statistical model fitting (e.g. statistical catch-at-age models). Some of the spatial variation in stomach contents is also likely driven by variation in overlap of herring and their predators; not acknowledging this variation might induce positive bias in the strength and scale of the predator–prey interactions from an MSVPA (Tyrrell et al., 2008) or positively bias estimates of consumption (Overholtz and Link, 2007; Overholtz et al., 2008; Moustahfid et al., 2009). Further studies on movement of predators and prey would be required to inform a more accurate specification of overlap.

Stomach-contents data have also been combined among years to reduce noise caused by measurement error (Van Kirk et al., 2010; Curti et al., 2013), but results of this study suggest that some of the variation among years is likely true process variation. In a MSCAA of Georges Bank (Curti et al., 2013) and in estimating consumption of Atlantic mackerel in the Northwest Atlantic (Moustahfid et al., 2009), stomach contents were averaged over 5-year periods. The amount of variation among years (i.e. including random interactions with year) in both GAMMs in this study suggests that such averaging would likely miss true variation in herring predator diets, which may also be true for other prey items like mackerel. Averaging stomach contents among years and missing true signals in the data could induce bias of scale in a MSCAA and in estimating consumption by falsely increasing or decreasing the strength of interactions in some years. Similarly, such averaging could induce bias in trends by assigning observations to years that do not reflect conditions in those years. A trade-off is likely to exist between averaging enough years to reduce the effect of measurement error, but not averaging so many as to induce bias. In a static foodweb model of the Gulf of Alaska, 2 years of stomach-contents data were used to reflect conditions in the early 1990s (Gaichas et al., 2010), while stomach contents from single years for some predators were used to reflect

conditions during 1974–2000 in a foodweb model of the Baltic Sea (Harvey *et al.*, 2003). The degree of variation in stomach-contents data among years will dictate how long such models will remain indicative of the system, but such an evaluation (e.g. the GAMMs in this study) will require sampling stomach contents more consistently among years. Similarly, a dynamic foodweb model was applied in the Gulf of Alaska, but did not use stomach-contents data (Gaichas *et al.*, 2011). Fits of the foodweb model to input biomass and catch time-series were generally poor, and this may have been due to not permitting enough variation in diets among years, which was supported by existing stomach-contents data from the Gulf of Alaska, but not used in model fitting (Gaichas *et al.*, 2011). Gaichas *et al.* (2011) encouraged the expansion of the foodweb model to include stomach-contents data in fitting, which would also serve the purpose of reducing the number of plausible hypotheses related to predator and prey vulnerabilities, although foodweb models have been shown to be less sensitive to uncertainty in diet composition data than other inputs (e.g. input biomass; Essington, 2007).

Results of GAMMs like those in this study could serve as the basis for an operating model that simulates predator–prey interactions and the collection of diet data with measurement error. The estimates from the GAMMs could define how the predator–prey interactions (i.e. amount and probability of prey occurring in a stomach) vary spatially and temporally, and the degree of measurement error in the simulated diet data could be consistent with the residual and random-effect variance estimates. The simulated diet data could then be combined across space, seasons, or years to evaluate the consequences of such data aggregations in subsequent multispecies modelling. This approach has been used extensively to evaluate the performance of single-species stock assessments (Deroba *et al.*, 2015) and for some multispecies applications (Essington, 2007). Using the results of the GAMMs has the advantage of conditioning the operating model on actual data, as opposed to using uninformative uniform distributions to represent the uncertainty in diet composition, as has been done previously (Overholtz and Link, 2007). Conditioning operating models on fits to real data has been identified as a best practice for simulation tests of this sort (Deroba *et al.*, 2015).

Results of models such as GAMs that explore variation in stomach-contents data could also be used to more efficiently allocate sampling effort. Stefánsson and Pálsson (1997) used a delta approach and GAM models to analyse the spatial variation in Icelandic cod (*Gadus morhua*) stomach contents. The spatial variance of the stomach contents was suggested for use to allocate stomach sampling effort so that resources were not wasted trying to collect many stomachs from locations where prey were scarce and observations imprecise. The only species of interest in Stefánsson and Pálsson (1997), however, was Icelandic cod, whereas the surveys used to collect stomach-contents data in this study were designed for multispecies sampling. If the information lost by focusing sampling efforts on the stomachs of herring predators is considered acceptable, however, then this study could serve as a starting point to consider revisions to the spatial and temporal distribution of stomach sampling in the Northwest Atlantic because results inform how the amounts and probabilities of herring encounters vary among seasons and areas. However, follow-up studies directed at measuring the intraregion/season variance of stomach contents would still be needed.

Results for the product factor of area and season in the GAMMs were generally consistent with knowledge about the migration patterns of Atlantic herring. Gulf of Maine and Georges Bank herring spawn in September–October and then migrate south for the winter months before returning to feed in the Gulf of Maine and Georges Bank areas in summer (Reid *et al.*, 1999). Herring on the Scotian Shelf, however, spawn approximately at the same time, but migrate north along the east coast of Nova Scotia in winter, returning south in summer (Reid *et al.*, 1999). These migration patterns are likely why the amount of herring and probability of herring were generally higher in predator stomachs in the Gulf of Maine and Georges Bank in fall than in spring, while the opposite was true for the Mid-Atlantic Bight and Southern New England, and results for the Scotian Shelf were less variable between seasons.

Water temperatures in the Northwest Atlantic have increased over years in some seasons and areas, and these changes may have implications for predator–prey interactions and subsequent diet (Thomas *et al.*, 2017). Thomas *et al.* (2017) found that the strongest increases in sea surface temperature occurred in the Scotian Shelf and Gulf of Maine, while the Mid-Atlantic Bight had weaker increasing trends. The trends were also strongest in late summer (July–September), while winter temperature trends were relatively constant or weak. Predators of herring, and herring themselves, are expected to have a range of responses to these temperature changes, including distribution shifts and changes in mortality and growth, with responses varying by functional group (Hare *et al.*, 2016). Consequently, the role of herring as prey is likely to change among years, areas, and predators, and the results of the GAMMs support this conclusion. Year and the product factor of area and season were included in the final models of both GAMMs. Furthermore, the inclusion of random effects for the interaction of year and the product factor of area and season, and the interaction of year, predator species, and the product factor of area and season in the final GAMM for the amount of herring in stomachs suggests that significant temporal and spatial variation has already occurred and that the effects differ by predator. Continued monitoring and quantification of variation in predator diet would be beneficial and could be used to anticipate foodweb shifts as a result of climate change.

The variance of the random effect for predator species was the largest of the random effects in both GAMMs, which suggests that a main source of variation is features of the predators themselves. Flatfish and skates were consistently below average in both GAMMs. One explanation may be that predators with subterminal or inferior mouths are less efficient predators of herring than species with terminal mouths, which seems logical given that herring is generally a pelagic species. Gape size may also offer an explanation. In the Northwest Atlantic, Scharf *et al.* (2000) found that relatively large-gaped predators like goosefish (*Lophius americanus*) consumed larger prey than relatively small-gaped predators like spiny dogfish (*Squalus acanthias*), which fed more on invertebrates than fish. Results of this study are consistent with the conclusions of Scharf *et al.* (2000), as the coefficients for the random effect of predator identified relatively large-gaped predators (e.g. goosefish) as containing more herring with greater probability than relatively smaller-gaped predators (e.g. spiny dogfish). The importance of predator effects in the GAMMs also implies that changes in the abundance of different predators will have different consequences for Atlantic herring. For example, given spatial and temporal overlap, changes in the abundance of consistently above-average predators will have a greater effect on the amount of herring consumed than changes in consistently below-average predators.

The GAMM for the probability of a stomach containing a herring included smooths for predator length and the amount of herring catch in the tow. The smooth for predator length was dome shaped, which implies that predators' preference for herring as prey is also dome shaped. One explanation may be that the range of prey available to a predator increases as the predator grows and their gape width increases, which expands the prey field to fish that generally grow longer than herring (Scharf *et al.*, 2000). Predator length was also included in GAMM models examining variation in diet data in Chesapeake Bay, United States, but the shape of the relationship varied by predator and prey (Buchheister and Latour, 2016). An expanding prey field that increased with body size and gape width was also suggested as an explanation for some of the results in that study. Alternatively, digestion rates may differ among predator sizes such that prey identification is more difficult in stomachs from larger predators. Examining the diversity of prey in relationship to predator length or controlled experiments in prey identification would help disentangle these possibilities, and this might be done using the same stomach-contents data used in this study. The smooth for the amount of herring catch in a tow could be used to develop a threshold that indicates a level of herring biomass, as indexed by survey catches, below which the availability of herring to predators is reduced. The probability of a predator stomach containing a herring increased in tows with herring catches from 0 to ~50 kg, and the number of observations in this range were relatively high such that the effect was likely real, compared to some of the variation above ~50 kg where the number of observations were relatively few. The changes in the probability between 0 and ~50 kg may be indicative of the availability of herring to predators when herring biomass varies in this range. Consequently, mean herring survey catches of $\sim 50\,\mathrm{kg\ tow^{-1}}$ might serve as a threshold below which the availability of herring to predators is reduced. The consequences of reduced availability of herring, and possible management responses, should be the focus of future research.

The index of herring abundance developed from the stomach contents was generally consistent with recent Atlantic herring stock assessment estimates of total biomass (Figure 8; NEFSC, 2012; Deroba, 2015). Stomach contents are relatively time consuming to collect, however, so their use for the sole purpose as an index of abundance may be relatively inefficient when compared to directed surveys, unless a species of interest is not well sampled in surveys (Link, 2004). Nonetheless, treating predators as a survey platform can provide a useful point of comparison for stock assessments and other survey indices. A measure of precision has not been developed for the index of abundance derived from the stomach-contents data in this study. Such measures of precision are necessary, however, to evaluate the index for trends among years and for weighting this index relative to others. Given that the stomach contents were collected during standardized bottom-trawl surveys that also provide indices of abundance, the measures of precision from the bottom-trawl survey indices could serve as a lower bound for the indices derived from stomach contents.

Accounting for the correlation in stomach contents sampled from the same tow was not possible in this analysis, but since ~75% of tows only had one predator stomach that contained herring, the results and conclusions were likely robust. Stefánsson and Pálsson (1997) reported significant within-tow correlation in stomach-contents samples of Icelandic cod, but also discussed the difficulty in accounting for such correlation, including in the GAM models used in their analysis. Buchheister and Latour (2016) included a random effect for tow in delta-GAMMs of predator diets in Chesapeake Bay, United States and advocated for the continued use of random effects as a way to account for correlation among observations. Given the relative sparseness of stomach-contents datasets, accounting for such correlation may significantly increase measures of precision in models of predator–prey relationships (e.g. GAMM models as in this study), and software to include random effects has expanded (e.g. package gamm4), which makes the suggestions of Buchheister and Latour (2016) increasingly feasible.

Acknowledgements

References

Azarovitz, T. R. 1981. A brief historical review of the Woods Hole Laboratory trawl survey time series. *In* Bottom Trawl Surveys, pp. 62–67. Ed. by W.G. Doubleday and D. Rivard. Canadian Special Publication of Fisheries and Aquatic Sciences 58. Government of Canada, Fisheries and Oceans, Hull, Quebec. 273 pp.

Baker, R., Buckland, A., and Sheaves, M. 2014. Fish gut content analysis: robust measures of diet composition. Fish and Fisheries, 15: 170–177.

Bates, D., Mächler, M., Bolker, B. M., and Walker, S. C. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67: 1–48.

Brooks, E. N., and Deroba, J. J. 2015. When "data" are not data: the pitfalls of post hoc analyses that use stock assessment model output. Canadian Journal of Fisheries and Aquatic Sciences, 72: 634–641.

Buchheister, A., and Latour, R. J. 2016. Dynamic trophic linkages in a large estuarine system – support for supply-driven dietary changes using delta generalized additive mixed models. Canadian Journal of Fisheries and Aquatic Sciences, 73: 5–17.

Burnham, K. P., and Anderson, D. R. 2002. Model Selection and Multimodel Inference: A Practical Information Theoretic Approach, 2nd edn. Springer-Verlag, New York. 488 pp.

Collett, D. 2003. Modeling Binary Data, 2nd edn. Chapman & Hall/CRC, Boca Raton, FL. 408 pp.

Curti, K. L., Collie, J. S., Legault, C. M., and Link, J. S. 2013. Evaluating the performance of a multispecies statistical catch-at-age model. Canadian Journal of Fisheries and Aquatic Sciences, 70: 470–484.

Deroba, J. J. 2015. Atlantic herring operational assessment report 2015. Northeast Fisheries Science Center Reference Document 15-16. 30 pp.

Deroba, J. J., and Bence, J. R. 2009. Developing model-based indices of lake whitefish abundance using commercial fishery catch and effort data in Lakes Huron, Michigan, and Superior. North American Journal of Fisheries Management, 29: 50–63.

Deroba, J. J., Butterworth, D. S., Methot, Jr, R. D., De Oliveira, J. A. A., Fernandez, C., Nielsen, A., Cadrin, S. X., et al. 2015. Simulation testing the robustness of stock assessment models to error: some results from the ICES strategic initiative on stock assessment methods. ICES Journal of Marine Science, 72: 19–30.

Essington, T. E. 2007. Evaluating the sensitivity of a trophic mass-balance model (Ecopath) to imprecise data input. Canadian Journal of Fisheries and Aquatic Sciences, 64: 628–637.

Gaichas, S. K., Aydin, K. Y., and Francis, R. C. 2010. Using food web model results to inform stock assessment estimates of mortality and production for ecosystem-based fisheries management. Canadian Journal of Fisheries and Aquatic Sciences, 67: 1490–1506.

Gaichas, S. K., Aydin, K. Y., and Francis, R. C. 2011. What drives dynamics in the Gulf of Alaska? Integrating hypotheses of species, fishing, and climate relationships using ecosystem modeling. Canadian Journal of Fisheries and Aquatic Sciences, 68: 1553–1578.

Gislason, H., and Helgason, T. 1985. Species interaction in assessment of fish stocks with special application to the North Sea. Dana, 5: 1–44.

Grosslein, M. D. 1969. Groundfish survey methods. Bureau of Commercial Fisheries, Woods Hole, MA Laboratory Reference Document 69-02. 34 pp.

Hare, J. A., Morrison, W. E., Nelson, M. W., Stachura, M. M., Teeters, E. J., Griffis, R. B., Alexander, M. A., et al. 2016. A vulnerability assessment of fish and invertebrates to climate change on the northeast US continental shelf. PLoS One, 11: e0146756.

Harvey, C. J., Cox, S. P., Essington, T. E., Hansson, S., and Kitchell, J. F. 2003. An ecosystem model of food web and fisheries interactions in the Baltic Sea. ICES Journal of Marine Science, 60: 939–950.

Hastie, T. J., and Tibshirani, R. J. 1990. Generalized Additive Models. Chapman & Hall, New York. 352 pp.

Jech, J. M., and Sullivan, P. J. 2014. Distribution of Atlantic herring in the Gulf of Maine from 1998 to 2012. Fisheries Research, 156: 26–33.

Kinzey, D., and Punt, A. E. 2009. Multispecies and single-species model of fish population dynamics: comparing parameter estimates. Natural Resource Modeling, 22: 67–104.

Lewy, P., and Vinther, M. 2004. A stochastic age-length structured multispecies model applied to North Sea stocks. ICES Document CM 2004/FF: 20. 33 pp.

Link, J. S. 2004. Using fish stomachs as samplers of the benthos: integrating long-term and broad scales. Marine Ecology Progress Series, 269: 265–275.

Link, J. S., and Almeida, F. P. 2000. An overview and history of the food web dynamics program of the Northeast Fisheries Science Center, Woods Hole, MA. NOAA Technical Memorandum NMFS-NE-159. 60 pp.

Livingston, P. A., and Jurado-Molina, J. 2000. A multispecies virtual population analysis of the eastern Bering Sea. ICES Journal of Marine Science, 57: 294–299.

Maunder, M. N., and Punt, A. E. 2004. Standardizing catch and effort data: a review of recent approaches. Fisheries Research, 70: 141–159.

McCulloch, C. E., and Searle, S. R. 2001. Generalized, Linear, and Mixed Models. Wiley, New York. 325 pp.

Miller, T. J. 2013. A comparison of hierarchical models for relative catch efficiency based on paired-gear data for US Northwest Atlantic fish stocks. Canadian Journal of Fisheries and Aquatic Sciences, 70: 1306–1316.

Miller, T. J., Das, C., Politis, P. J., Miller, A. S., Lucey, S. M., Legault, C. M., Brown, R. W., et al. 2010. Estimation of Albatross IV to Henry B. Bigelow calibration factors. Northeast Fisheries Science Center Reference Document 10-05. 233 pp.

Mills, K. L., Laidig, T., Ralston, S., and Sydeman, W. J. 2007. Diets of top predators indicate pelagic juvenile rockfish abundance in the California Current System. Fisheries Oceanography, 16: 273–283.

Moustahfid, H., Link, J. S., Overholtz, W. J., and Tyrrell, M. C. 2009. The advantage of explicitly incorporating predation mortality into age-structured stock assessment models: an application for Atlantic mackerel. ICES Journal of Marine Science, 66: 445–454.

NEFSC (Northeast Fisheries Science Center). 2012. 54th Northeast Regional Stock Assessment Workshop (54th SAW) Assessment Report. Northeast Fisheries Science Center Reference Document 12-18. 600 pp.

Ngo, L., and Brand, R. 1997. Model selection in linear mixed effects models using SAS proc mixed. Proceedings of the 22nd Annual SAS Users Group International Conference, San Diego, CA, March 16–19, 1997: 1335–1340.

Nunn, A. D., Tewson, L. H., and Cowx, I. G. 2012. The foraging ecology of larval and juvenile fishes. Reviews in Fish Biology and Fisheries, 22: 377–408.

Overholtz, W. J., and Link, J. S. 2007. Consumption impacts by marine mammals, fish, and seabirds on the Gulf of Maine-Georges Bank Atlantic herring complex during the years 1977–2002. ICES Journal of Marine Science, 64: 83–96.

Overholtz, W. J., Jacobson, L. D., and Link, J. S. 2008. An ecosystem approach for assessment advice and biological reference points for the Gulf of Maine-Georges Bank Atlantic herring complex. North American Journal of Fisheries Management, 28: 247–257.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ (last accessed 6 March 2017).

Read, A. J., and Brownstein, C. R. 2003. Considering other consumers: fisheries, predators, and Atlantic herring in the Gulf of Maine. Conservation Ecology, 7: 2.

Reid, R. N., Cargnelli, L. M., Griesbach, S. J., Packer, D. B., Johnson, D. L., Zettin, C. A., Morse, W. W., et al. 1999. Essential fish habitat source document: Atlantic herring, *Clupea harengus*, life history and habitat characteristics. NOAA Technical Memorandum NMFS-NE-126. 48 pp.

Reum, J. C. P., and Essington, T. E. 2008. Seasonal variation in guild structure of the Puget Sound demersal fish community. Estuaries and Coasts, 31: 790–801.

Scharf, F. S., Juanes, F., and Rountree, R. A. 2000. Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Marine Ecology Progress Series, 208: 229–248.

Smith, B. E., and Link, J. S. 2010. The trophic dynamics of 50 finfish and 2 squid species on the northeast US continental shelf. NOAA Technical Memorandum NMFS-NE-216. 640 pp.

Stefánsson, G., and Pálsson, Ó. K. 1997. Statistical evaluation and modelling of the stomach contents of Icelandic cod. Canadian Journal of Fisheries and Aquatic Sciences, 54: 169–181.

Thomas, A. C., Pershing, A. J., Friedland, K. D., Nye, J. A., Mills, K. E., Alexander, M. A., Record, N. R., et al. 2017. Seasonal trends and phenology shifts in sea surface temperature on the North American northeastern continental shelf. Elementa Science of Anthropocene, 5: 48.

Tyrrell, M. C., Link, J. L., Moustahfid, H., and Overholtz, W. J. 2008. Evaluating the effect of predation mortality on forage species population dynamics in the Northeast US continental shelf ecosystem using multispecies virtual population analysis. ICES Journal of Marine Science, 65: 1689–1700.

Van Kirk, K. F., Quinn, T. J., and Collie, J. S. 2010. A multispecies age-structured assessment model for the Gulf of Alaska. Canadian Journal of Fisheries and Aquatic Sciences, 67: 1135–1148.

Van Kirk, K. F., Quinn, II, T. J., Collie, J. S., and A'mar, Z. T. 2015. Assessing uncertainty in a multispecies age-structured assessment framework: the effects of data limitations and model assumptions. Natural Resource Modeling, 28: 184–205.

Wood, S. 2003. Thin plate regression splines. Journal of the Royal Statistical Society B, 65: 95–114.

Wood, S. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. Journal of the American Statistical Association, 99: 673–686.

Wood, S. 2006. Generalized Additive Models: An Introduction with R. Chapman & Hall/CRC Press, Boca Raton, FL. 410 pp.

Wood, S. 2008. Fast stable direct fitting and smoothness selection for generalized additive models. Journal of the Royal Statistical Society B, 70: 495–518.

Wood, S., and Scheipl, F. 2014. gamm4: Generalized additive mixed models using mgcv and lme4. R package version 0.2-3. https://CRAN.R-project.org/package=gamm4 (last accessed 23 August 2016).

Handling editor: Emory Anderson