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Seabird diets as bioindicators of Atlantic herring recruitment and stock size: a new tool for ecosystem-based fisheries management

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Abstract

Ecosystem-based fishery management requires understanding of relationships between exploited fish and their predators, such as seabirds. We used exploratory regression analyses to model relationships between Atlantic herring (*Clupea harengus*) in the diet of seabird chicks at nine nesting colonies in the Gulf of Maine, and four types of fishery- and survey-derived herring data. We found several strong relationships, which suggests spatial structuring in herring stocks and likely patterns of herring movements before they recruit into the fishery. Some types of herring data seldom used in stock assessments – notably acoustic surveys, fixed-gear landings, and weight-at-age – correlated as strongly with seabird data as more commonly used series, such as mobile-gear landings and modeled spawning stock biomass. Seabird chick diets collected at specific locations thus offer a promising means to assess the size, distribution, and abundance of juvenile herring across a broad area prior to recruitment, which is a major source of uncertainty in fisheries. Common terns showed the most potential as a bioindicator, correlating well and showing consistent spatial patterns with 11 of 13 fishery data series.

35 Introduction

36 Fisheries managers world-wide are increasingly expected to oversee harvested stocks with due regard to
37 their interactions with other species in the ecosystem (Stephenson 2012). Successful application of this
38 approach, often referred to as ecosystem-based fishery management or EBFM, is widely recognised as
39 essential to the maintenance of healthy marine ecosystems and the communities they support
40 (Christensen et al. 1996; Dickey-Collas et al. 2013; Skern-Mauritzen et al. 2016).

41 A fundamental feature of EBFM is understanding the multiple interactions among constituent species
42 (Travis et al. 2014), including (but not limited to) harvested species and their prey. Fishery harvest is
43 treated as a key ecosystem service to be sustained, yet many other predators rely on the same prey
44 species, and sustaining their populations is an equally valid ecosystem service (Diamond 2012; Fogarty
45 2014). The idea that the needs of natural predators 'deserve' consideration alongside those of fisheries
46 is increasingly becoming accepted (Travis et al. 2014) and incorporated into both global biodiversity
47 goals (Convention on Biodiversity no date) and national fishery-management policies (Stephenson 2012;
48 Skern-Mauritzen et al. 2016).

49 Seabirds are among the most widespread and best-studied predators of marine fish, and they are
50 affected by large-scale changes in abundance of prey stocks especially as a result of over-fishing (Duffy
51 1983; Cury et al. 2011; Cook et al. 2014). Seabirds may also reflect other changes in the marine
52 environment including contamination and oceanographic and climatic change, leading to well-
53 established use of 'seabirds as environmental indicators' or SEI (Cairns 1987; Diamond and Devlin 2003;
54 Einoder et al. 2009). Most of the SEI literature examines various behavioral responses – such as time
55 budgets (Jodice et al. 2006) or reproductive success (Monaghan et al. 1989; Wanless et al. 2005) – to
56 changing food availability, but Parsons et al. (2008) pointed out that seabird chick diet data offer "the
57 most immediate signal of availability," which are not widely available because they are time-consuming

to collect. We take advantage of our long time-series of seabird chick diet data to conduct exploratory analyses using data routinely collected to manage one widely-harvested forage fish, Atlantic herring *Clupea harengus*, which has been prominent in the diet of seabirds and many other top predators (see below).

Forage fish are the target of many fisheries throughout the world (Pikitch et al. 2012). They are generally small or medium-sized, pelagic, schooling species, often with high fat content (Harris and Hislop 1978; Hislop et al. 1991; Wanless et al. 2005), characterised ecologically by their position mid-way in the food chain between phytoplankton and larger predators; in such marine systems the energy required by higher trophic levels is channeled through the forage fish (Pikitch et al. 2012). In such 'wasp-waist' systems (Bakun et al. 2009) the forage fish play a 'keystone' role (i.e. a species that exerts influences out of proportion to its abundance, *sensu* Paine 1995; Johnson et al. 2017), supporting a variety of top predators including larger fish, marine mammals, and marine birds; if these forage fish are the target of a fishery, it is critically important to avoid over-fishing because of all the predators that rely on the same prey as the fishery (Cury et al. 2011). If such forage fish show high caloric density (i.e., are high in fat content) they are particularly likely to be targeted by optimal foragers and function as keystone prey.

In systems where seabirds feed on forage fish which are also the target of a fishery, there is enhanced potential both for negative impacts of the fishery on the birds and for the birds to respond quickly to changes in the fish stock; much of the SEI literature refers to such systems. Among many examples are: sandeels (or sandlance) *Ammodytes* spp. in the North Sea (Monaghan et al. 1989; Frederiksen et al. 2008; Cook et al. 2014) and Gulf of Alaska (Jodice et al. 2006; Suryan et al. 2006); capelin *Mallotus villosus* around Newfoundland and Labrador (Montevecchi and Myers 1996; Regehr and Montevecchi 1997), the Barents Sea (Barrett and Furness 1990) and Gulf of Alaska (Jodice et al. 2006); anchovy and sardines in the Benguela Current (Crawford et al. 2008; Green et al. 2015), the Humboldt Current (Duffy 1983) and California Current (Mills et al. 2007; Sydeman et al. 2009; Thompson et al. 2012); and Atlantic

herring *Clupea harengus* in Iceland, Norway (Anker-Nilssen 1987), and the Gulf of Maine (Diamond and Devlin 2003; Breton and Diamond 2014).

Atlantic herring in the Gulf of Maine play a widely recognised keystone role (Kenney et al. 1997; Bakun et al. 2009; Diamond 2012) as a forage fish. Predators with a predominantly herring diet include bluefin tuna (*Thunnus thynnus*), themselves the object of an important fishery (Golet et al. 2007; 2015), humpback *Megaptera novaeangliae* and fin whales *Balaenoptera physalus*, other cetaceans and seals (Kenney 1997), and several species of long-distance migratory seabirds as well as those breeding locally (Diamond 2012). However, different predators consume different sizes (and therefore age classes) of the herring stock. Juvenile herring hatched in fall are referred to as "0-group" until 1 January when they become 1-group (or 1-yr-olds). Herring reach sexual maturity at 3-4 years but can enter the fishery at age 2 (Stephenson et al. 1993; Fig. 1). Herring in the Gulf of Maine spawn mostly in late summer or fall, so those eaten by seabirds breeding the following summer are most often 1 yr old, though the larger auks (razorbill *Alca torda* and common murre *Uria aalge*) also take 2-yr-old fish. Seabirds sample herring younger than 2 yrs old, offering the possibility that data on their diets could predict recruitment, and aid in stock assessment and EBFM.

Our focus in this paper is on assessing possible relationships between the herring content in the diet of seabird chicks and various measures of herring abundance, with a view to identifying possible predictors of future herring stock size. We assume that seabirds take preferred prey (in this case, 1-yr-old herring) in relation to the abundance of that prey; thus, a high proportion of herring in the diet reflects an abundance of herring within the foraging range of the colony. Specifically, we assess relationships between sets of herring data commonly used in stock assessments in both Canadian and American parts of the Gulf of Maine, and several measures of diets of breeding seabirds and their chicks. From this assessment, we examine the potential of diet data from seabird species and colonies as indicators of value to future EBFM. We include diet data from multiple species at widely-separated colonies, allowing

us to address both the different spatial and temporal scales at which seabirds and fisheries operate, and the varied foraging behaviours of different species of seabird (Greenstreet et al. 2000; Becker and Chapdelaine 2003). Our analyses are driven by two broad hypotheses: 1) the diets of seabirds indicate the strength of a herring cohort at age 1, which predicts future stock size (seabird diets predict fishery), and 2) data on breeding herring from fisheries predict future productivity, and the prevalence of herring in future seabird diets (fishery predicts seabird diets). To reflect these hypotheses, and the temporal disjuncture between the age-1 cohorts targeted by seabirds and the older ages targeted by various parts of the fishery, we perform an exploratory analysis examining relationships between fishery and seabird data at lags ranging from -3 (fishery predicts seabirds 3 years later) to +5 (seabirds predict fishery 5 years later). We identify the strongest seabird-fishery relationships, rank herring data for their relevance to herring predators, and identify seabird colonies and species as potentially useful indicators of the herring stock.

Methods

Seabird study area and diet data collection

Seabird diet data were collected from nine colonies in the Gulf of Maine and Bay of Fundy region, where long-term seabird monitoring programs have been conducted since the early 1970s (Fig. 2). Seven Maine colonies (Stratton Island, Outer Green Island, Jenny Island, Pond Island National Wildlife Refuge (NWR), Eastern Egg Rock, Matinicus Rock, and Seal Island NWR) are managed by National Audubon Society's Seabird Restoration Program (SRP), one is managed by the U.S. Fish and Wildlife Service (USFWS; Petit Manan Island, Maine), and one (Machias Seal Island, New Brunswick, "MSI") is managed by the Canadian Wildlife Service and monitored by the University of New Brunswick (UNB). Protocols to collect diet data were similar across islands. The animal care committee at UNB reviewed annual

procedures performed at MSI, and all SRP and USFWS data collection was in accordance with federal banding permits. We consider four colonies as “western” (Stratton Island, Outer Green Island, Jenny Island, and Pond Island NWR), three colonies as “central” (Eastern Egg Rock, Matinicus Rock, and Seal Island NWR), and two as “eastern” (Petit Manan Island, MSI).

We included diet data from four species – two surface-feeding tern species (common tern *Sterna hirundo* and Arctic tern *S. paradisaea*) and two diving alcid species (Atlantic puffin *Fratercula arctica* and razorbill *Alca torda*). Common terns breed on all nine colonies, and we used data from Arctic terns on four (Matinicus Rock, Seal Island, Petit Manan Island, and MSI), Atlantic puffins on four (Eastern Egg Rock, Matinicus Rock, Seal Island, and MSI), and razorbills on two (Matinicus Rock and MSI). The latter three species tended to nest in colonies in the central and eastern parts of the Gulf of Maine, representing the southern limit of their North American ranges.

Feeding watches were performed throughout the chick-rearing period of each study species on each island, from multiple observation blinds erected in each colony. Observers used binoculars to identify common prey species at each colony, estimating prey length relative to the adult’s bill length. For each feeding, observers recorded the nest number, prey recipient, number of prey, prey length, and prey species. Further details on seabird diet observations are included in Supplementary Data S1.

A full summary of the time series for all species at all colonies is included in Table S1. Time series at SRP colonies begin in 1991 or 1992 for Arctic terns, 2002 or 2003 for common terns, and 2005 for alcids. Time series at Petit Manan Island begin in 2000 for Arctic terns and 2002 for common terns. At MSI, data begin in 1990 for Arctic terns and 1995 for common terns and alcids. The tern colony at MSI collapsed in 2006 (Diamond 2009; Gaston et al. 2009), so no tern feeding observations could be performed from 2006-2013. The diet study for Arctic terns resumed in 2014 with the restoration of the

colony (Scopel and Diamond 2017), and diet estimates for common terns were derived from video observations in 2016.

Seabird diet data treatment

Seabird diet data treatment follows that performed in Scopel and Diamond (*in press*). All raw feeding data were converted into annual estimates of wet weight. For each species at each colony, taxa that made up at least 1% of the diet by number were retained for conversion into weight (Table S2). If possible, length-weight conversion formulae were developed from prey samples collected opportunistically by UNB at MSI as part of their annual protocol (available at <http://www.unb.ca/research/alar/msi-seabirds/protocol-methods.html>); prey samples were measured for total length to the nearest 0.1 mm, and wet weight to the nearest 0.1 g. For prey taxa with too few samples to develop conversions ($n = 8$), we used values from the literature (Table S3). Once all prey conversions were developed, we applied the conversion formulae to our annual diet data for each colony-species pair (e.g., common tern-Jenny Island, Atlantic puffin-Seal Island), to derive estimates of wet weight for each prey taxon and for each year. Sums of weight for each prey taxon were tallied and summarized for each year.

For this study, we calculated four representations of herring in the seabird diet: two rates (herring mass per feeding, herring mass per observed chick-hour (i.e., the total number of hours each chick was observed at a nest (tern) or plot-hour (alcid))), proportion of herring in the diet, and average mass of individual herring. A summary of these representations of seabird diet, including sample sizes, can be found in Tables S4-S12 in supplemental material. Strength of herring cohort by colony-species pair is included in Table 1.

174 *Herring stock data sources*

175 Herring in the Gulf of Maine and Bay of Fundy region are managed by an American and a Canadian
176 fishery, respectively; although both countries manage their quotas and stocks independently, they do
177 share data, and issue status reports jointly through the Transboundary Resource Assessment Committee
178 (TRAC). The Canadian fishery manages the Bay of Fundy and Scotian Shelf herring as the 4WX herring
179 stock complex, requiring the separation of Bay of Fundy herring (4X) from reported totals in the 4VWX
180 reports. The American fishery identifies the Gulf of Maine and Georges Bank as separate spawning
181 components (5Y and 5Z, respectively), but both are modeled as part of the same stock complex (NEFSC
182 2012).

183 Owing to the diversity of data that can represent a fish stock, we considered a variety of potential
184 herring data types for this analysis. We selected four broad categories that represent different aspects
185 of the herring fishery: fishery-independent acoustic surveys of spawning stock biomass, landings,
186 weights-at-age, and output from stock assessment models. Although landings are relatively simple to
187 measure and data are abundant, they do represent targeted and technologically-assisted sampling of
188 fish that does not necessarily represent the behaviour of small piscivores, such as seabirds. We
189 therefore included data from acoustic surveys to obtain a fishery-independent estimate of spawning
190 stock biomass. The Canadian fishery has reported declining average weights-at-age since the 1970s
191 (Department of Fisheries and Oceans (DFO) 2015), so we included Canadian weight data to reflect this
192 potentially important property of the stock. Finally, we included two types of output from stock
193 assessment models. Age-1 recruitment was estimated by both the American and Canadian stock
194 assessments via forward-cast (Age Structured Assessment Program with a Beverton-Holt stock-
195 recruitment relationship) and back-cast (Virtual Population Assessment, no longer used officially) age-
196 structured models, respectively; these serve as the best available data to estimate the abundance of 1-
197 yr-old herring in the fishery, which can be compared directly with seabird diets. Finally, we included

198 estimates of spawning stock biomass from the American stock assessment model, for comparison with
199 landings and acoustic surveys.

200 Landings data were obtained from stock assessment reports. We included mobile-gear landings
201 (primarily purse-seine and mid-water trawl) from the American fishery (Deroba 2015), mobile-gear
202 landings from New Brunswick (Stephenson et al. 1998; Singh et al. 2016), combined landings (American
203 mobile-gear landings and all fixed-gear landings, Deroba 2015), and fixed-gear landings from
204 southwestern New Brunswick (Deroba 2015). Most fixed-gear landings in the region are caught in weirs
205 in southwestern New Brunswick.

206 Acoustic data were obtained for the Canadian and American stocks; Canadian data were obtained from
207 stock assessment reports (DFO 2015), and American data were obtained directly from M. Jech at the
208 NEFSC, following the format published in the American stock assessment report (NEFSC 2012). Canadian
209 surveys sampled herring at Trinity Ledge, German Bank, and Scots Bay, Nova Scotia; American surveys
210 sampled herring at Georges Bank (Fig. 2). Acoustic survey data in both regions begin in 1999, and
211 continue through 2012 in the USA and 2014 in Canada.

212 Weight-at-age data were obtained directly from M. Power at DFO. We selected three types of weight
213 data – weight-at-age estimates for age-1 fish (the youngest available, the same age that most of the
214 seabirds would consume), fish aged 3-5 years (which represent the majority of the spawning stock), and
215 fish aged 3+ years. The majority of spawners in the stock are 3-5 years old, but the entire spawning
216 component can reach age 10+. We compared the importance of just young spawners (3-5 yrs) and the
217 entire spawning stock; although younger spawners are more abundant, older and larger fish may
218 contribute more to future recruitment owing to greater fecundity (Wootton 1998; Hsieh et al. 2006).
219 DFO also identified a significant decline in the average growth of herring between ages 2 and 3 in recent

years (M. Power, DFO, St. Andrews, New Brunswick, personal communication, 2016), which we included as a fourth data type in our weight category as “growth increment”.

Finally, we included spawning stock biomass estimates from the American model (Deroba 2015), and estimates of the number of age-1 herring as predicted by the American (NEFSC 2012) and Canadian (obtained directly from R. Singh, DFO) models.

Complete herring data used in this analysis, including years of available data, are included in table S13-S14 in supplemental material. Strength of herring cohorts, as measured by the American stock assessment model, are included in Table 1.

Data analysis – Exploratory assessment of lags

Herring sampled by seabirds and by the fishery are rarely of the same age class; most seabirds consume 1- or 2-year old herring, but the herring fishery targets 2+ (fixed gear) and 3+ year old (mobile gear, acoustic surveys) fish (Fig. 1). This age discrepancy offers the potential to predict future stock data from the younger age classes consumed by seabirds. In order to investigate potentially useful predictive lags, we identified significant lags using the cross-correlation function (`ccf()`, package “stats”) in R (version 3.1.2, R Core Team 2014). We examined all lags between -3 to +5 for each seabird-colony and fishery data pair; positive lags indicate that seabird diets predict fishery data, and vice versa for negative lags. Any lag that was deemed significant by the cross-correlation function (>0.4 , R Core Team 2014) was retained for further analysis. We identified three classes of lags: (1) no lag or lags of +1 years, “no” or “short lags”, (2) lags of +2 to +5 years, “long lags”, and (3) lags of -1 to -3 years, “negative lags.”

We used 19 colony-species pairs of seabird diet data (e.g., common tern on Martinicus Rock, Atlantic puffin at Eastern Egg Rock), each with four representations of seabird-derived herring (e.g., herring

weight per feeding), and correlated them to 13 variables derived from the herring fishery (e.g., fixed-gear landings). For average mass of individual herring (seabird), we correlated these to the four fishery-derived weight variables only.

Data analysis – Validation of significant correlations

Following the exploratory assessment of lags, we examined all significant seabird-fishery correlations in greater detail. All analyses were performed in R. All data were normalized (mean of 0, standard deviation ± 1). We used univariate lagged regression to predict fishery-derived estimates of herring from seabird-derived estimates of herring. Owing to the direct comparison of two herring measures, we tested only simple linear relationships; we assumed that differences in cohort size would persist linearly throughout the time series.

Since seabirds can consume 1- or 2-year-old herring, we tested the possibility of temporal autocorrelation by including an autoregressive (AR) correlation structure within our models (Zuur et al. 2009). We prepared two sets of models for each significant lag, one with and one without an AR1 correlation structure. We used generalized least squares regression (GLS, `gls()`, package “nlme”, Pinheiro et al. 2016) and compared each model pair using AICc (package “AICcmodavg”, Mazerolle 2015); for each model, the structure with the lowest AICc was selected.

Models were built with fishery data as the response variable and seabird data as the predictor. Series of models were produced for each fishery variable and ranked using AICc. Any models that ranked lower than a model using only year as a predictor (i.e., the “null” model) were considered uninformative and removed from further consideration.

After fitting GLS models, we checked models for meaningful effect sizes and explained variation, using regression slopes and McFadden's pseudo- R^2 (McFadden 1974), respectively. Models that scored lower than 0.5 in either category were considered uninformative and removed from further consideration. In some cases, a single seabird-fishery lag was represented multiple times with different rate and proportional data; if one model was ranked more than 3 $\Delta AICc$ units higher than another model within the same seabird-fishery lag (e.g., Seal Island puffins-acoustic +3), we removed it from consideration. All instances with lags within 3 $\Delta AICc$ units were kept.

For all remaining models, leave-one-out cross-validation (Efron and Tibshirani 1993) was performed to assess the model's predictive ability and stability of slope. Models where slopes dropped below 0.25 were considered uninformative and removed from further consideration. Once cross-validation was performed, we reduced the model set to a single instance of each seabird-fishery pair, if possible, based on prediction error (CV), pseudo- R^2 , slope, and potential outlier years. Multiple lags for one seabird-fishery pair were retained if they were well supported. Models with greater pseudo- R^2 , greater slopes, and lower prediction error were considered stronger.

Relevance rankings

GLS models were separated into potential quantitatively and qualitatively useful lags; CVs of <0.5 were considered suitable for quantitative prediction, but those >0.5 were considered useful to represent general qualitative trends only. CVs <0.2 were considered the strongest predictive models, and these were considered potentially reliable bioindicators.

Using the cross-validated GLS models, fishery data were ranked based on their potential relevance to future EBFM. Ranking criteria for each fishery data type included the number of seabird species, seabird colonies, and geographical subregions (western, central, or eastern) that were represented by cross-

validated models, the number of models that passed cross-validation, and the number of models with CVs <0.2. Model sets that were representative of a larger spatial area, highly correlated with more species, and had strong predictive value were considered the most relevant to future study.

Post hoc analyses

Following our initial analyses, we performed a *post hoc* comparison between our seabird variables and American weight-at-age data (NEFSC 2012). We found a marked reduction in weight-at-age after age 3 in both Canadian and U.S. data (Fig. 3) which encouraged us to include both datasets, using the same age categories (age 1, 3-5, and 3+) as the Canadian weight data. The American time series included data through 2011.

We also examined the importance of time series length within our longest seabird time series. We divided four time series (MSI Atlantic puffins and razorbills, Martinicus Rock and Seal Island NWR Arctic terns) into two subsets – an “early” time series including years 2005 and earlier (to emulate the length of the MSI tern series), and a “late” time series including years 2002 and later (to emulate the length of the SRP common tern series). We examined cross-correlations between these subsets and compared them with cross-correlations of the full time series, in order to determine if changes in the seabird-fishery relationship over time weakened the strength of the observed correlations in these data. This division coincides with the timing of a regime shift between 2000 and 2004 (Smith et al. 2012) with potential consequences for nutrient status and the plankton community (Townsend et al. 2010) which can be expected to affect responses in species higher in the food-web such as forage fish and their predators.

Results

Assessment of lags and validation of models

We performed 6,555 seabird-fishery cross-correlation comparisons, identifying 472 seabird-fishery data pairs with significant lags during the first stage of the analysis; 71 included an autoregressive correlation structure. We performed cross-validation on 347 GLS models, retaining 70 (Table S15). Of these, 19 had CVs >0.5, 38 had CVs between 0.2 and 0.5, and 13 had CVs <0.2. Models with CVs <0.2 we consider to be the highest quality (Table 2), and are examined in full detail below. Models with CVs between 0.2 and 0.5 had quantitative value but showed higher prediction error, and those with CVs >0.5 were considered qualitatively useful only; general trends from these two lower ranked categories are also discussed below.

Top ranked models – CV <0.2

A complete list of the 13 top-ranked models, including their CVs, pseudo- R^2 , and slopes, can be found in Table 2. Depictions of these models can also be found in Figs. 4 and S1-S2 in supplemental material. Eight of 13 fishery data types and 10 of 19 seabird-colony pairs were involved in this model set, including all four seabird species, and six of nine seabird colonies, encompassing all three geographic subregions. Acoustic surveys, landings, and model output were equally represented in this model set, but only one model included weight data. Common tern models were the most abundant, featured nine times, and six colonies of common terns were represented in this model set. Eight models had long lags, four models had short or no lag, and just one model had a negative lag.

Trends in lower-ranked models – $0.2 < CV < 0.5$ and $CV > 0.5$

Twelve of 13 fishery data types were represented in these models; only mobile-gear landings from New Brunswick were absent from cross-validated models. Several fishery data types featured prominently in these lower ranked models, including estimated recruitment from the Canadian fishery, Canadian weight-at-age data for all three age categories, modeled spawning stock biomass, and mobile-gear landings from the American fishery.

All nine seabird colonies were included in these models, although only 16 of 19 seabird-colony pairs were represented. Razorbills from MSI, and Arctic terns from Matinicus Rock and Seal Island NWR were not part of any of the cross-validated models; no strong relationships could be found between fishery data and any of these seabirds. Of the remaining seabird-colony pairs, common terns were part of 25 models, puffins in 17, Arctic terns in 9, and razorbills in 6.

Negative lags featured in 17 models, particularly those including weight, fixed- or mobile-gear landings data. Long lags were in 12 models, including acoustic surveys, mobile-gear landings, spawning stock biomass, and weight data. The remaining 28 models included short or no lag, and incorporated 11 different fishery variables.

By fishery data type – all models

Acoustic surveys from the Bay of Fundy showed long lags with western common tern and central alcid data, and short or no lags with terns at MSI and razorbills at Matinicus Rock. Acoustic surveys from Georges Bank linked exclusively to terns at MSI (Fig. 4), at long and short or no lags.

Fixed-gear landings had a consistent lag of -2 for four of six cross-validated models; three seabird species from MSI, both tern species from Petit Manan Island, and common terns from Matinicus Rock showed links to fixed-gear landings, which primarily occur in waters near MSI (Fig. S1). American

mobile-gear landings correlated with data from seven seabird-colony pairs, spread across western and central colonies, but neither eastern nor Arctic tern data were included in these models. Lags for mobile-gear models included three long lags, two short lags, and two negative lags. American mobile-gear landings had the second-highest number of significant correlations in early model-testing, but many models failed cross-validation owing to high-leverage points in 2006 and 2009.

Modeled spawning stock biomass was the most prolific fishery type in the full cross-validated model set, including 10 seabird-colony pairs at eight colonies, yet many models failed cross-validation owing to high leverage from the 2014 data point. Five models included long lags, and the remaining models had short or no lags. Recruitment data from the USA were most strongly linked to common tern and puffin data from two central colonies, but overall were much more spatially limited; all models had no lag. This indicates that recruits, as defined by the American stock assessment, are of the same age as the fish consumed by seabirds. Conversely, recruits from the Canadian stock assessment were represented primarily by +1-yr lags, indicating that recruits, as defined by the Canadian stock assessment, are one year younger than the fish consumed by seabirds. Canadian recruitment models involved common terns, puffins, and razorbills from five central or western colonies. Although Canadian recruitment data were more widespread in their links with seabird data relative to American recruitment data, American models on average had lower prediction error; no Canadian recruitment models were included in the top-ranked model set. Common terns and puffins at Seal Island NWR were the only seabird-colony pairs to correlate with both sets of recruitment data.

Canadian weight data were included in 23 total models, but only one ranked highly and lags were inconsistent, especially in the weight-at-age 1 category. Similarly to the Canadian recruitment data, weight-at-age 1 models involved common tern, puffin, and razorbill data from central and western colonies, incorporating five colonies. The lags featured in the weight-at-age 1 data, however, were quite variable, including seven negative lags and four long lags. Weight-at-age 3-5 data and growth increment

were included in seven models, representing alcids from central colonies and terns at Petit Manan Island. Weight-at-age 3+ data were linked with terns at MSI only.

By seabird species and colony – all models

Common terns were represented strongly; all nine colonies had models that passed cross-validation, and eight colonies were included in models with CVs <0.5. Common tern models also involved 11 of 13 fishery data series, showing high concordance with a variety of fishery data types. The strongest models for common terns included both acoustic surveys, all three types of landings, and American recruitment and spawning stock biomass estimates. Common tern data also formed the strongest models, as ranked by CV and by pseudo- R^2 .

Arctic tern data at MSI were linked with all four types of fishery data, including five variables, most often by +1 lags. MSI Arctic tern data correlated most frequently and most strongly with acoustic survey data, especially in Georges Bank. At Petit Manan Island, Arctic tern data were linked to just three variables, representing either weight or landings data, and relationships were weaker than the MSI models. Arctic tern data from central colonies did not correlate strongly with anything.

Atlantic puffins at all four colonies had models with CVs <0.5, including nine fishery variables, yet only one model was included in the top ranked set, featuring weight-at-age data. Puffins at Seal Island NWR and Matinicus Rock were the best represented in these models, showing strong relationships with weight, landings, and model data. All central colonies had models including Canadian recruitment estimates, American mobile-gear landings, and Canadian weight-at-age data. Puffins at MSI were linked only to fixed-gear landings.

Razorbills at Martinicus Rock were linked to six fishery variables, including all four types of fishery data. Only one model was included in the top-ranked set, incorporating estimates of spawning stock biomass. Razorbill models were similar to puffin models from central colonies, also including Canadian recruitment estimates, mobile-gear landings, and weight-at-age data. Razorbills at MSI showed no relationship with any fishery data.

Relevance rankings

Rankings are listed in Table 3. Of the 13 fishery data series, two have high relevance to future ecosystem-based fisheries management, four have moderate relevance, six have low or limited relevance, and one has poor relevance.

Post hoc analyses

Six American weight-at-age models passed cross-validation; five involved ages 3-5, and one included ages 3+. Two models had CVs between 0.2 and 0.5, and the rest were >0.5. Three models were consistent between the American and Canadian datasets; a comparison can be found in Table S16. American weight-at-age models were considered of low relevance to future EBFM. We compared the four truncated seabird time series with 13 fishery data types, for a total of 52 comparisons. In 25 cases, one subset had a significant lag while the other subset had none; in 12 cases, both subsets had significant lags, but the lag lengths were two or more years apart between subsets. Acoustic biomass models had significant correlations prior to 2005 only, and model-derived recruitment had stronger correlations in 2002 and later. Weights and landings had cases where early and late lags were the only ones with significant correlations, depending on the variable.

419

420 **Discussion**

421 We found encouraging support for the idea that measures of 1-yr-old herring in the diet of seabird
422 chicks on colonies throughout the Gulf of Maine can provide important insight into the otherwise
423 poorly-known process of herring recruitment. Selected measures both predict recruitment to the
424 spawning stock, and illuminate spatial and temporal patterns in the first two years of herring life. We
425 focus our discussion on the strongest models (Table 2), with reference, where appropriate, to models
426 with CV between 0.2 and 0.5.

427

428 *Seabirds as herring indicators*

429 Our results show strong potential applications of seabird data to predict herring recruitment. We
430 identified 13 seabird-fishery relationships that show great promise in predicting the herring stock. The
431 lack of an independent recruitment index makes it impossible to predict future catch until herring reach
432 age 2, when they can be captured by fixed gear. Bottom trawls catch few juveniles unless cohorts are
433 strong (NEFSC 2012), and recruitment has been weak since 2005, aside from the strong 2009 age-1
434 cohort, and potentially the 2012 cohort (Libby and Yuen 2013; Deroba 2015). Seabird diet data may
435 thus fill an important knowledge gap in herring stock assessment, and inform managers about the
436 behavior of young herring at shorter time scales between assessments.

437 Seabird diets generally tracked both strong and weak age-1 cohorts as identified in stock assessments
438 (Table 1); all three of the cohorts >30,000 tons (1995, 2009, and 2012), and two of the four <10,000 tons
439 (2000, 2001, 2005, 2007), were reflected in chick diet at one or more colonies. These data suggest that
440 seabirds are better at corroborating good cohorts, according to the fishery, rather than weak ones; our

441 data suggest that cohorts are not equally strong across the entire region, and some of the discrepancies
442 between the fishery and the seabirds may be related to spatial scales of the respective datasets (see
443 below). Fishery data did a poor job of predicting weak cohorts according to seabird data; 2004, 2010,
444 and 2011 were poor herring years for most seabirds, yet these years are unremarkable according to the
445 American stock assessment model. The fishery may be worse at detecting weak cohorts because
446 technological aids allow catches even when availability may be low; five of 19 seabird-colony pairs
447 delivered no herring to chicks in 2005, and zero abundance is unlikely to be replicated in the fishery.

448 Information on diet of herring predators is frequently listed as a priority for future herring research (e.g.,
449 Libby and Yuen 2013), and we present multiple measures of seabird diets located throughout the Gulf of
450 Maine as a contribution to this requirement for EBFM. We caution, however, that herring predator data
451 should not be used to simply corroborate findings from previous stock assessments. One of our most
452 striking findings was that some of the strongest correlations (five of our top-ranked 13 models) were
453 between seabird diet data and fishery data not usually incorporated into stock assessments, such as
454 acoustic surveys and weights-at-age. Acoustic surveys are no longer performed on Georges Bank (M.
455 Jech, NEFSC, Woods Hole, MA, personal communication, 2016), and were excluded from the 2012 stock
456 assessment because they disagreed with bottom-trawl and fishery monitoring data (NEFSC 2012), yet
457 we found a strong relationship between patterns of this acoustic survey and tern diet at MSI, which
458 showed a marked decline after 2000 that has not otherwise been explained.

459 Furthermore, weight-at-age data, although considered stable by TRAC and NEFSC, actually show steep
460 declines after 1980, as also reported by DFO (Fig. 3). Although these data may not match conclusions
461 from landings or bottom-trawl surveys, we encourage fisheries scientists to consider the biological
462 relevance of these data sources, especially as they support trends observed in diet of herring predators.

463 Seabirds are often overlooked in studies of herring predators because the relative proportion of the
464 herring stock that they consume is much less than that of groundfish or marine mammals (NEFSC 2012),

but herring can be integral to seabird reproductive success and survival (Massias and Becker 1990; Durant et al. 2003; Breton and Diamond 2014), emphasizing the need for EBFM in this ecosystem. Correlations between mobile-gear landings and data of common terns, puffins, and razorbills suggest that these seabirds select herring preferentially, further supporting the need for cautious herring management.

Spatial relationships among seabird colonies

We observed unexpected spatial patterns among seabird colonies. The easternmost colony, MSI, frequently had relationships with spawning components and fishery-derived data not shown by other seabird colonies. Western colonies often had similar lags among colonies, sometimes shared with central colonies, but never with MSI. Western common tern data sometimes showed similar patterns with central common terns, but more often showed patterns similar to central alcids, suggesting that different species may target herring differently.

There were also distinct spatial differences among western, central, and eastern colonies with regard to the abundance of herring in their seabird diets. Three of the four easternmost colonies (Matinicus Rock, Seal Island NWR, and MSI) tended to have low proportions of herring in the seabird diet, especially after 2000. Petit Manan Island, while part of this eastern group, is located close inshore and tended to have more abundant herring in the diet in the mid-2000s, but herring sharply declined in seabird diets after 2009. In contrast, chick diets in western colonies and the nearshore Eastern Egg Rock in the central Gulf of Maine showed increases in herring in recent years. Strong cohorts also tended to be spatially restricted (Table 1); strong cohorts in 2009, 2012, and 2014 were generally found in either the eastern or western half of the Gulf of Maine, and were poor to average on the other half. These broad differences support the idea that spawning components are distinct and self-sustaining (Berkeley et al.

2004; Overholtz et al. 2004), and also suggest that juvenile herring in the eastern Gulf of Maine are now less abundant than those in the west. Links between seabirds at MSI and Georges Bank acoustic data suggest that recruitment from this spawning component may be reduced from previous years, especially after 2000. The strong relationship between the Canadian spawning component and the western seabird data corroborates descriptions in Tupper et al. (1998) that young herring occupy discrete areas, where environmental conditions may differ considerably (Fig. 5; see below). Applying a single estimate of spawning stock biomass and recruitment to all herring in the stock may put the weaker stock components at risk of overfishing (Tupper et al. 1998). The Gulf of Maine has an east-west oceanographic profile (Jordaan et al. 2010; Friedland et al. 2015), with more favourable conditions for growth in the west (Tupper et al. 1998), suggesting that productivity of young herring in the east may be reduced.

Although separate quotas are allocated to different parts of the American side of the fishery (Libby and Yuen 2013), the general outlook for the most recent American stock survey was optimistic (Deroba 2015), and did not mention weak recruitment in the east. Our results suggest that more rigorous estimates for smaller regions within the Gulf of Maine would be beneficial for herring management. Although American models represent a much larger proportion of the stock relative to Canadian models, American estimates of recruitment correlated with fewer seabird colonies. A potential issue with the American model is that it combines a spatially broad dataset into a single estimate of recruitment, ignoring natural oceanographic differences between Georges Bank and the eastern and western Gulf of Maine. Even within management units, the stock is divided into the northern (Gulf of Maine, 5Y) and southern (Georges Bank, 5Z) halves of the region, and does not reflect the differences in seabird diet that we have observed in an east-west pattern. Strong spatial patterns in our seabird-herring relationships imply similar patterns in distribution and numbers of juvenile herring, arguing for consideration of more spatially explicit assessments of Gulf of Maine herring.

512

513 *Connectivity between spawning components and juvenile habitat*

514 Managers have identified the connectivity between different spawning components of herring as a
515 major source of uncertainty (Tupper et al. 1998; Overholtz et al. 2004). Our results show clear spatial
516 patterns of juvenile herring movement, and may help to resolve some of this uncertainty. Acoustic
517 surveys by DFO track spawning components in southwestern Nova Scotia, and show that larvae either
518 remain in this vicinity, or advect into the Bay of Fundy (Stephenson et al. 2015). However, we observed
519 a consistent relationship between western and central seabird diets and the Bay of Fundy acoustic
520 surveys, all with +3 lag. This pattern of movement is suggestive of movements of larvae from New
521 Brunswick and eastern Maine (Tupper et al. 1998). Herring can first spawn at age 3, so this lag could
522 represent the movement of juvenile herring to these breeding grounds, and potentially indicate natal
523 fidelity. A link between Canadian spawning grounds and western seabird colonies was further
524 supported by the Canadian recruitment and weight-at-age 1 data (Fig. 5). These datasets also showed
525 strong ties to these western and central seabird colonies, supporting the idea that a considerable
526 portion of these Canadian spawning components produce juveniles that spend their first summers in the
527 western and central Gulf of Maine. Curiously, although data from MSI, which is closest to the Bay of
528 Fundy, had significant lags with the acoustic data, they were exclusively short lags of +1 year or no lag.
529 This suggests that the juveniles around the central and western seabird colonies returned to the Bay of
530 Fundy only just before spawning, and may have experienced similar environmental conditions to those
531 experienced by juveniles consumed by seabirds at MSI. These data may represent broad spatial
532 movements of multiple age classes of these spawning components, revealed without the need for direct
533 assessment through tagging studies.

We observed a second unexpected spatial pattern between the Georges Bank acoustic survey and the tern diets at MSI; our post hoc analysis revealed that alcids at MSI showed a similar pattern, but only prior to 2005. These relationships were among the strongest in the model set. MSI terns often consumed >80% herring by mass in their diet in the 1990s, peaking in 1997, but herring declined in chick diets after 2000. This decline predicts the decline in biomass observed in acoustic surveys on Georges Bank in 2001, which remained at much lower levels thereafter. Although the biomass decline at Georges Bank is considered odd in the American stock assessment report (NEFSC 2012), it is one of the few datasets that matches the magnitude of decline in herring observed at this colony. Georges Bank juveniles are generally expected to remain on Georges Bank or travel “inshore” (Boyar et al. 1973; Anthony and Waring 1980; Reid et al. 1999; Overholtz et al. 2004), rather than spending time in the Bay of Fundy around MSI, and such behaviour has been suggested by others (Iles 1971; Anthony and Waring 1980 in Tupper et al. 1998). The absence of acoustic data after 2012 and the collapse of the MSI tern colony in 2006 make future links between these datasets currently impossible, but the tern colony has now been restored (Scopel and Diamond 2017) and this link could be explored further if acoustic sampling were resumed.

Models including the longest seabird time series usually had weaker relationships than shorter time series. Our post hoc analysis revealed that many longer seabird time series – three of which did not produce significant cross-validated models – had significant correlations for only part of series, or had differing lags between different subsets of years. One potential explanation is that there were fundamental bottom-up changes in the ecosystem following the regime shift of 2000-2004 (Townsend et al. 2010; Smith et al. 2012) that altered the relationship between herring and their seabird predators. Another explanation is that if the connectivity between juvenile habitat and spawning components changes, or if the relative production from spawning components changes through time, the seabird-fishery relationships would also change, and thus become weaker when viewed at longer temporal

scales. The strong spatial pattern observed between the Bay of Fundy herring stock and western-central seabird colonies is consistent across colonies and corroborates larval movement observed in other studies (Tupper et al. 1998), leading us to believe that these relationships are real. Since the connectivity of these spawning components is poorly understood, linkages between seabirds and herring should continue to be monitored to ascertain potential changes in spatial relationships.

Diets of local seabird populations offer a means to sample and assess the size and abundance of juvenile herring from different spawning components. Herring from these colonies could also be obtained directly from the birds, generating samples to explore spatial dynamics with other techniques (DNA, otoliths, stable isotopes, etc.). A more sophisticated analysis of these spatially dispersed seabird colonies may allow better development of indices to predict the movement of young herring and the contribution of different spawning components to different parts of the Gulf of Maine.

Interpretation of lags

We observed three types of lags in our data – short (0 or +1 years), long (+2 to +5 years), and negative lags (-1 to -2 years). We offer an interpretation of these three lags.

Long lags represent the fate of a herring cohort as it moves from potential prey to seabirds in its first or second years, into and through the fishery. These lags were found especially in models including acoustic surveys, mobile-gear landings, modeled spawning stock biomass, and weights-at-age. These data types typically represent older age classes of fish, supporting our interpretation. These lags are most useful in predicting future stock size or productivity.

Short lags are more difficult to interpret, especially when fishery data represent older age classes, such as landings and acoustic surveys; there is no obvious reason why 1-yr-old herring should be prominent in

seabird diet in the same year that fishery catches of older cohorts are high. While some short lags could represent cohort size (e.g., modeled age-1 recruitment), we suggest that most reflect local environmental conditions, such as temperature, which affect all age classes equally. Good or poor growth conditions experienced by juvenile herring near seabird colonies may also reflect the environmental conditions experienced by adults at the same time, depending upon coincidence in spatial distribution of young and adult herring.

Negative lags were observed in fixed-gear landings and weight-at-age models. In these cases, the fishery predicts the bird diets, and potentially age-1 recruitment. Although weight-at-age could serve as a representation of condition and potential fecundity in herring adults (Berkeley et al. 2004), fixed-gear landings are harder to interpret. Fixed-gear landings capture 2-yr-old fish primarily, which could indicate that the abundance of fish captured by this passive gear indicates the size or condition of the incoming cohort to the spawning population, and subsequent reproductive potential. These relationships may be useful in developing an index of recruitment, although they are likely more complicated than the simple linear relationships that we tested.

Please see Supplementary Data S2 for a discussion of data limitations.

Relevance of stock data to EBFM

The most recent American stock assessment report (Deroba 2015) suggested that spawning stock biomass in the near future should be high, based on the modeled spawning stock biomass in 2014 being the highest ever recorded. However, 2014 modeled spawning stock biomass frequently appeared as an outlier in our cross-validation process, and American models have a severe retrospective pattern that tends to overestimate spawning stock biomass and underestimate fishing mortality (NEFSC 2012), by as much as 56% (TRAC 2009). While the high spawning stock biomass in 2014 likely reflects the strong

2009 cohort, more recent cohorts have been much weaker, especially in the east. This assessment report also suggested that the 2012 cohort was of equivalent magnitude to the 2009 cohort – the largest ever recorded in the region – and that the herring stock was consequently in strong shape. Seabird diet data from the eastern and central Gulf of Maine do not support the optimism expressed in this assessment; 22 of 33 diet variables were of 2x or greater magnitude in 2009 vs. 2012, 13 of which were 5x or greater; only two showed a 2x or greater magnitude of 2012 over 2009. Only diets of western common terns favoured the 2012 cohort over 2009, with 8 of the 12 variables being higher in 2012 (4 > 2x).

Weight-at-age has been considered “stable” (TRAC 2009), but American and Canadian weight data both show a decline since the 1980s, the latter correlating well with seabird diet data. Declining weights-at-age imply a larger number of herring per unit of biomass, where smaller individuals have lower fecundity and survival (Pauly 1980; Berkeley et al. 2004), leading to a negative feedback loop where spawning stock biomass continues to decline. Overholtz et al. (2004) observed that mean weights-at-age in the American stock components had declined significantly after 1980, representing a 20% decrease in biomass for fish at age 6 – of similar timing and magnitude to Canadian data – yet most recent assessments by TRAC and NEFSC have not identified this long-term decline in weight-at-age as an area of concern. The variable lag patterns observed between seabird data and Canadian weights-at-age suggest that these relationships are not resolved well by this analysis, but inclusion of positive and negative lags suggest that both adults and juveniles are affected by this decline in weight-at-age.

The fixed-gear fishery – which is restricted to the eastern Gulf of Maine – has had poor landings for the past decade, and showed negative lags with seabirds at three of the easternmost colonies. These trends reflect declining herring in the east, and represent economic and social needs of part of the fishing community that has been overlooked. Our result is a reversal of the finding in Amey (1998), who examined the predictive value of MSI Arctic terns to the weir fishery in New Brunswick. Amey's study

was carried out 1990-97 when herring dominated MSI Arctic tern diet and weir catches nearby were high; different relationships can be expected when herring availability falls below the threshold when predators switch to alternative prey, as seems to have occurred since 2000 (see above). Herring data from mobile-gear landings and modeled spawning stock biomass typically correlated with central Gulf of Maine alcids and western common terns; these relationships were much weaker for central terns and eastern seabirds, suggesting that they are also getting overlooked in stock assessment. Eastern and central terns generally had stronger relationships with acoustic surveys or fixed-gear landings data, suggesting that these measures better represent herring availability to terns, and may be underutilized in stock assessment. Arctic terns in central colonies were particularly underrepresented, leading to the question of which data would represent these birds' needs.

Importance of ecological variables

Sea-surface temperatures in the Gulf of Maine have been increasing more rapidly than in most of the world's oceans since 2004, exceeding historic values since 2012 (Pershing et al. 2015); further, regime shifts in the late 1980s and late 1990s have changed zooplankton communities significantly (Hare and Kane 2012). This argues that ecosystem-based management in the Gulf of Maine must take ecosystem changes into account, yet environmental data are not currently included in the stock assessment model (NEFSC 2012). Using temperature as an example, Bell et al. (2015) warned that changes in temperature can have effects as great as those of fishing, and Pershing et al. (2015) found a strong effect of temperature on the survival and growth of Atlantic cod (*Gadus morhua*) in the Gulf of Maine, leading to an overestimate of cod biomass, perpetual overfishing, and a delay in stock recovery. Herring are susceptible to changes in temperature at all life stages (Tupper et al. 1998; Rijnsdorp et al. 2009; Corten 2013); increasing temperatures are especially dangerous for young fish, raising metabolic rate without

increased food to support their greater energetic needs, resulting in greater mortality and thus depressed recruitment (Brander 2007; Rijnsdorp et al. 2009). Recruitment has been shown to be sensitive to temperature in several herring stocks in the northeast Atlantic (Cardinale et al. 2009; Ottersen et al. 2013; Payne et al. 2013). Increasing temperatures can also lead to trophic mismatch, as well as changes in behaviour, mortality rate, timing of maturity, growth rate, and generation time (Stevenson and Scott 2005; Hsieh et al. 2006; Rijnsdorp et al. 2009). No ecological approach to fishery management can legitimately exclude environmental variables, especially when, like temperature, they are known to strongly influence fish biology; we strongly recommend the inclusion of at least temperature data in future assessment models in order to account for rapid environmental changes in this ecosystem.

Overall we found strong relationships between seabird diet and a variety of sources of herring data; the most striking patterns were clear spatial differences in those relationships among colonies, which reflect spatial structuring in herring stocks and likely patterns of movements of herring in the years before they recruit into the stock and the fishery. Some types of herring data which are not routinely used in stock assessments— notably acoustic surveys and weight-at-age data – provided relationships as convincing as those with the more commonly used data types (mobile-gear landings, modeled spawning stock biomass). This suggests that these sources provide important insight into the process of recruitment, which is widely acknowledged to be poorly understood. We urge more focused incorporation of such data, and data on seabird diets, as well as environmental variables such as temperature, if herring management is to move closer to a truly ecological approach. The dependence of seabirds on pre-recruit life stages of herring, and the widespread and long-term collection of seabird diet data at all major seabird colonies, offers a unique opportunity for significant progress toward the goal of a broader-based approach to herring management.

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References

Amey, K. 1998. Seabirds as indicators of changes in availability and commercial weir landings of herring. M.Sc. thesis, Department of Biology, University of New Brunswick, Fredericton, NB.

Anker-Nilssen, T. 1987. The breeding performance of Puffins *Fratercula arctica* on Røst, Northern Norway, 1979-1985. Fauna norvegica Series C, Cinclus **10**: 21-38.

Anthony, V.C., and Waring, G.T. 1980. Estimate of herring spawning stock biomass and egg-production for the Georges Bank-Gulf of Maine Region. Northeast Fisheries Science Center, Northwest Atl. Fish. Organ. Sci. Counc. Res. Doc. 1980b;80/1X/135 Ser. No. N209.

Bakun, A., Babcock, E.A., and Santora, C. 2009. Regulating a complex adaptive system via its wasp-waist: grappling with ecosystem-based management of the New England herring fishery. ICES J. Mar. Sci. **66**(8): 1768–1775. doi:10.1093/icesjms/fsp073.

- 696 Barrett, R.T., and Furness, R.W. 1990. The prey and diving depths of seabirds on Hornø, North Norway
697 after a decrease in the Barents Sea capelin stocks. *Ornis Scand.* **21**(3): 179-186. Available from
698 <https://www.jstor.org/stable/3676777> [accessed 10 January 2017].
- 699 Becker, P., and Chapdelaine, G. 2003. Further development of seabird monitoring. *In* Seabirds as
700 monitors of the marine environment. *Edited by* Tasker, M.L. and Furness, R.W. ICES Cooperative
701 Research Report No. 258. 52-60.
- 702 Bell, R.J., Richardson, D.E., Hare, J.A., Lynch, P.D., and Fratantoni, P.S. 2015. Disentangling the effects of
703 climate, abundance, and size on the distribution of marine fish: an example based on four stocks from
704 the Northeast US shelf. *ICES J. Mar. Sci.* **72**(5): 1311–1322. doi:10.1093/icesjms/fsu217.
- 705 Berkeley, S.A., Hixon, M.A., Larson, R.J., and Love, M.S. 2004. Fisheries sustainability via protection of
706 age structure and spatial distribution of fish populations. *Fisheries* **29**(8): 23-32. doi:10.1577/1548-
707 8446(2004)29[23:FSVPOA]2.0.CO;2.
- 708 Boyar, H.C., Marak, R.R., Perkins, F.E., and Clifford, R.A. 1973. Seasonal distribution and growth of larval
709 herring (*Clupea harengus* L.) in the Georges Bank-Gulf of Maine area from 1962 to 1970. *J. Cons., Cons.*
710 *Perm. Int. Explor. Mer* **35**(1): 36-51. doi:10.1093/icesjms/35.1.36.
- 711 Brander, K.M. 2007. Global fish production and climate change. *Proc. Natl. Acad. Sci. U. S. A.* **104**(50):
712 19709-19714. doi:10.1073/pnas.070205.
- 713 Breton, A.R., and Diamond, A.W. 2014. Annual survival of adult Atlantic Puffins *Fratercula arctica* is
714 positively correlated with Herring *Clupea harengus* availability. *Ibis* **156**(1): 35–47.
715 doi:10.1111/ibi.12100.
- 716 Cairns, D.K. 1987. Seabirds as indicators of marine food supplies. *Biological Oceanography* **5**(4): 261–
717 271. doi:10.1080/01965581.1987.10749517.

- Cardinale, M., Möllmann, C., Bartolino, V., Casini, M., Kornilovs, G., Raid, T., Margonski, P., Grzyb, A.,
Raitanemi, J., Gröhsler, T., and Flinkman, J. 2009. Effect of environmental variability and spawner
characteristics on the recruitment of Baltic herring *Clupea harengus* populations. Mar. Ecol. Prog. Ser.
388:221-234. <https://doi.org/10.3354/meps08125>
- Christensen, N.L., Bartuska, A.M., Brown, J.H., Carpenter, S., D'Antonio, C., Francis, F., Franklin, J.F.,
MacMahon, J.A., Noss, F.R., Parsons, D.J., Peterson, C.H., Turner, M.G., and Woodmansee, R.G. 1996.
Report of the Ecological Society Committee on the scientific basis for ecosystem management. Ecol.
Appl. **6**(3): 665-691. doi:10.2307/2269460.
- Convention on Biological Diversity. Nd. Generic and specific indicators for assessing progress in the
attainment of the Aichi biodiversity targets, including an assessment of their main characteristics
[online]. Available from <https://www.cbd.int/doc/strategic-plan/strategic-plan-indicators-en.pdf>
[accessed 5 December 2016].
- Cook, A.S.C.P., Dadam, D., Mitchell, I., Ross-Smith, V.H., and Robinson, R.A. 2014. Indicators of seabird
reproductive performance demonstrate the impact of commercial fisheries on seabird populations in
the North Sea. Ecol. Indic. **38**: 1–11. doi:10.1016/j.ecolind.2013.10.027.
- Corten, A. 2013. Recruitment depressions in North Sea herring. ICES J. Mar. Sci. **70**(1): 1-15.
doi:10.1093/icesjms/fss187.
- Crawford, R.J.M., Sabarros, P.S., Fairweather, T., Underhill, L.G., and Wolfaard, A.C. 2008. Implications
for seabirds off South Africa of a long-term change in the distribution of sardine. Afr. J. Marine Sci **30**(1):
177–184. doi:10.2989/AJMS.2008.30.1.18.468.
- Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J.M., Furness, R.W., Mills, J.A.,
Murphy, E.J., Österblom, H., Paleczny, M., Piatt, J.F., Roux, J.-P., Shannon, L., and Sydeman, W.J. 2011.

- 740 Global seabird response to forage fish depletion—one-third for the birds. *Science* **334**(6063): 1703–
741 1706. doi:10.1126/science.1212928.
- 742 Department of Fisheries and Oceans. 2015. 2015 Assessment of 4VWX herring. DFO Can. Sci. Advis.
743 Sec. Res. Doc. 2015/040.
- 744 Department of Fisheries and Oceans. 2016. 4VWX herring 2016 update report. DFO Can. Sci. Advis.
745 Sec. Sci. Resp. 2016/036.
- 746 Deroba, J. 2015. Atlantic Herring Operational Assessment Report 2015. U.S. Dept. Commer., Northeast
747 Fish. Sci. Cent. Ref. Doc. 15-16.
- 748 Diamond, A.W. 2009. Vicissitudes of the tern colony on Machias Seal Island. *NB Naturalist* **36**(3): 116-
749 117.
- 750 Diamond, A.W. 2012. Managing for migrants. *In* Advancing an ecosystem approach in the Gulf of
751 Maine. *Edited by*: Stephenson, R.L., Annala, J.H., Runge, J.A., and Hall-Arber, M. Am. Fish. Soc. Symp. 79.
752 Amer. Fisheries Soc., Bethesda, MD. Pp. 311-320.
- 753 Diamond, A.W., and Devlin, C.M. 2003. Seabirds as indicators of changes in marine ecosystems:
754 Ecological monitoring on Machias Seal Island. *Environ. Monit. Assess.* **88**(1): 153–175.
755 doi:10.1023/A:1025560805788.
- 756 Dickey-Collas, M., Engelhard, G.H., Rindorf, A., Raab, K., Smout, S., Aarts, G., van Deurs, M., Brunel, T.,
757 Hoff, A., Lauerburg R.A.M., Garthe, S., Haste Andersen, K., Scott, F., van Kooten, T., Beare, D., and Peck,
758 M.A. 2013. Ecosystem-based management objectives for the North Sea: riding the forage fish
759 rollercoaster. *ICES J. Mar. Sci.* **71**(1): 128-142. doi:10.1093/icesjms/fst075.
- 760 Duffy, D.C. 1983. Environmental uncertainty and commercial fishing: effects on Peruvian guano birds.
761 *Biological Conservation* **26**(3): 227-238. doi:10.1016/0006-3207(83)90075-7.

- 762 Durant, J.M., Anker-Nilssen, T., and N.C. Stenseth. 2003. Trophic interactions under climate fluctuations:
763 the Atlantic Puffin as an example. *Proceedings: Biological Sciences* **270** (1523): 1461-1466.
- 764 Efron, B., and R. Tibshirani. 1993. An introduction to the bootstrap. *Monographs on Statistics and*
765 *Applied Probability* 57. Chapman and Hall, Boca Raton, FL.
- 766 Einoder, L.D. 2009. A review of the use of seabirds as indicators in fisheries and ecosystem
767 management. *Fisheries Research* **95**(1): 6–13. doi:10.1016/j.fishres.2008.09.024.
- 768 Fogarty, M.J. 2014. The art of ecosystem-based fishery management. *Can. J. Fish. Aquat. Sci.* **71**:479-
769 490.
- 770 Frederiksen, M., Jensen, H., Daunt, F., Mavor, R. A., and Wanless, S. 2008. Differential effects of a local
771 industrial sand lance fishery on seabird breeding performance. *Ecol. Appl.* **18**(3): 701–710.
772 doi:10.1890/07-0797.1.
- 773 Friedland, K.D., Leaf, R.T., Kane, J., Tommasi, D., Asch, R.G., Rebuck, N., Ji, R., Large, S.I., Stock, C., and
774 Saba, V.S. 2015. Spring bloom dynamics and zooplankton biomass response on the US Northeast
775 Continental Shelf. *Cont. Shelf Res.* **102**: 47-61. doi:10.1016/j.csr.2015.04.005.
- 776 Gaston, A.J., Bertram, D.F., Boyne, A.W., Chardine, J.W., Davoren, G., Diamond, A.W., Hedd, A.,
777 Montevecchi, W.A., Hipfner, J.M., Lemon, M.J.F., Mallory, M.L., Rail, J.-F., and Robertson, G.J. 2009.
778 Changes in Canadian seabird populations and ecology since 1970 in relation to changes in oceanography
779 and food webs. *Environ. Rev.* **17**: 267–286. doi:10.1139/A09-013.
- 780 Golet, W.J., Cooper, A.B., Campbell, R. and Lutcavage, M. 2007. Decline in condition of northern bluefin
781 tuna (*Thunnus thynnus*) in the Gulf of Maine. *Fish. Bull.* **105**: 390-395.

- 782 Golet, W.J., Record, N.R., Lehuta, S., Lutcavage, M., Glauradi, B., Campbell, R., and Pershing, A.J. 2015.
783 The paradox of the pelagics: why bluefin tuna can go hungry in a sea of plenty. *Mar. Ecol. Progr. Ser.*
784 **527**: 181-192.
- 785 Green, D.B., Klages, N.T.W., Crawford, R.J.M., Coetzee, J.C., Dyer, B.M., Rishworth, G.M., and Pistorius,
786 P.A. 2015. Dietary change in Cape gannets reflects distributional and demographic shifts in two South
787 African commercial fish stocks. *ICES J. Mar. Sci.* **72**(3): 771–781. doi:10.1093/icesjms/fsu203.
- 788 Greenstreet, S.P.R., Becker, P.H., Barrett, R.T., Fossum, P., and Leopold, M F. 2000. Consumption of pre-
789 recruit fish by seabirds and the possible use of this as an indicator of fish stock recruitment. *In* *Diets of*
790 *seabirds and consequences of changes in food supply. Edited by* Furness, R.W., and Tasker, M.L. ICES
791 Cooperative Research Report no. 232. 6-17.
- 792 Hare, J.A., and Kane, J. 2012. Zooplankton in the Gulf of Maine – a changing perspective. *Am. Fish. Soc.*
793 *Symp.* **79**:115-135.
- 794 Harris, M.P., and Hislop, J.R.G. 1978. The food of young puffins *Fratercula arctica*. *J. Zool. Lond.* **185**:213-
795 236.
- 796 Hislop, J.R.G., Harris, M.P., and Smith, J.G.M. 1991. Variation in the calorific value and total energy
797 content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. *J. Zool. Lond.*
798 **224**:501-517.
- 799 Hsieh, C., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M., and Sugihara, G. 2006. Fishing elevates
800 variability in the abundance of exploited species. *Nature* **443**: 859-862. doi:10.1038/nature05232.
- 801 Iles, T.D. 1971. The retention inside the Bay of Fundy of herring larvae spawned off the southwest coast
802 of Nova Scotia. Selected papers from the 1971 annual meeting. International Commission for the
803 Northwest Atlantic Fisheries Redbook Part **3**: 93-103.

- 804 Jodice, P.G.R., Roby, D.D., Turco, K.R., Suryan, R.M., Irons, D.B., Piatt, J.F., Shultz, M.T., Roseneau, D.G.,
805 Kettle, A.B., and Anthony, J.A. 2006. Assessing the nutritional stress hypothesis: Relative influence of
806 diet quantity and quality on seabird productivity. *Mar. Ecol.: Prog. Ser.* **325**: 267–279.
807 doi:10.3354/meps325267.
- 808 Johnson, S.A., Ober, H.K., and Adams, D.C. 2017. Are keystone species effective umbrellas for habitat
809 conservation? A spatially explicit approach. *Journal for Nature Conservation* 37:47–55.
- 810 Jordaan, A., Chen, Y., Townsend, D.W., and Sherman, S. 2010. Identification of ecological structure and
811 species relationships along an oceanographic gradient in the Gulf of Maine using multivariate analysis
812 with bootstrapping. *Can. J. Fish. Aquat. Sci.* **67**: 701-719.
- 813 Kenney, R., Scott, G., Thompson, T., and Winn, H. 1997. Estimates of prey consumption and trophic
814 impacts of cetaceans in the USA northeast continental shelf ecosystem. *J. Northw.*
815 *Atl. Fish. Sci.* **22**: 155–171. doi: 10.1.1.555.4576.
- 816 Libby, D., and Yuen, M. 2013. Review of the fishery management plan for Atlantic Sea Herring (*Clupea*
817 *harengus harengus*) for the 2012 fishing year. Atlantic States Marine Fisheries Commission.
- 818 Massias, A., and Becker, P.H. 1990. Nutritive value of food and growth in Common Tern *Sterna hirundo*
819 chicks. *Ornis Scand.* **21**(3): 187–194. Available from <https://www.jstor.org/stable/3676778> [accessed 10
820 January 2017].
- 821 Mazerolle, M.J. 2015. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)
822 [online]. R package version 2.0-3. <http://CRAN.R-project.org/package=AICcmodavg> [accessed 1 June
823 2014].
- 824 McFadden, D. 1974. Conditional logit analysis of qualitative choice behaviour. *In* *Frontiers in*
825 *econometrics*. Edited by Zarembka, P. Academic Press, New York. NY. Pp. 105-142.

- 826 Mills, K.L., Laidig, T., Ralston, S., and Sydeman, W.J. 2007. Diets of top predators indicate pelagic juvenile
827 rockfish (*Sebastes* spp.) abundance in the California Current System. Fisheries Oceanography **16**(3): 273–
828 283. doi:10.1111/j.1365-2419.2007.00429.x.
- 829 Monaghan, P., Uttley, J.D., and Okill, J.D. 1989. Terns and sandeels: seabirds as indicators of
830 changes in marine fish populations. J. Fish Biol. Suppl. A, **35**: 339-40. doi:10.1111/j.1095-
831 8649.1989.tb03080.x.
- 832 Montevecchi, W.A., and Myers, R.A. 1996. Dietary changes of seabirds reflect shifts in pelagic food
833 webs. Sarsia **80**: 313-322. doi:10.1080/00364827.1996.10413606.
- 834 Northeast Fisheries Science Center. 2012. 54th Northeast regional stock assessment workshop (54th
835 SAW) assessment report. U.S. Dept. Commer., Northeast Fish. Sci. Cent. Ref. Doc. 12-18.
- 836 Ottersen, G., Stige, L.C., Durant, J.M., Chan, K.S., Rouyer, T.A., Drinkwater, K.F., and Stenseth N.C. (2013)
837 Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and
838 temperature. Mar. Ecol. Prog. Ser. **480**:205-225. <https://doi.org/10.3354/meps10249>
- 839 Overholtz, W.J., Jacobson, L.D., Melvin, G.D., Cieri, M., Power, M., Libby, D., and Clark K. 2004. Stock
840 Assessment of the Gulf of Maine-Georges Bank Atlantic Herring complex, 2003. U.S. Dept. Commer.,
841 Northeast Fish. Sci. Cent. Ref. Doc. 04-06.
- 842 Paine, R.T. 1995. A conversation on refining the concept of keystone species. Conservation Biology 9:
843 962-964.
- 844 Parsons, M., Mitchell, I., Butler, A., Ratcliffe, N., Frederiksen, M., Foster, S., and Reid, J.B. 2008. Seabirds
845 as indicators of the marine environment. ICES J. Mar. Sci. **65**(8): 1520–1526.
846 doi:10.1093/icesjms/fsn155.

- 847 Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean
848 environmental temperature in 175 fish stocks. ICES J. Mar. Sci. **39**(2): 175-192.
849 doi:10.1093/icesjms/39.2.175.
- 850 Payne, M.R., Stine, D.R., Worsøe, Clausen L., Munk, P., Mosegaard, H., and Nash, R.D.M. (2013)
851 Recruitment decline in North Sea herring is accompanied by reduced larval growth rates. Mar. Ecol.
852 Prog. Ser. **489**:197-211. <https://doi.org/10.3354/meps10392>
- 853 Pershing, A.J., Alexander, M.A., Hernandez, C.M., Kerr, L.A., Le Bris, A., Mills, K.E., Nye, J.A., Record, N.R.,
854 Scannell, H.A., Scott, J.D., Sherwood, G.D., and Thomas, A.C. 2015. Slow adaptation in the face of rapid
855 warming leads to collapse of the Gulf of Maine cod fishery. Science **350**(6262): 809-
856 812. doi:10.1126/science.aac9819.
- 857 Pikitch, E., Boersma, P.D., Boyd, I.L., Conover, D.O., Cury, P., Essington, T., Heppell, S.S., Houde, E.D.,
858 Mangel, M., Pauly, D., Plaganyi, E., Sainsbury, K. and Steneck, R.S. 2012. Little fish, big impact: managing
859 a crucial link in ocean food webs. Lenfest Ocean Program, Washington, DC.
- 860 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Team. 2016. nlme: Linear and nonlinear mixed
861 effects models [online]. R package version 3.1-127. Available from [http://CRAN.R-](http://CRAN.R-project.org/package=nlme)
862 [project.org/package=nlme](http://CRAN.R-project.org/package=nlme) [accessed 15 November 2016].
- 863 R Core Team. 2014. R: A language and environment for statistical computing [online]. R Foundation for
864 Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org/> [accessed 1 June
865 2014].
- 866 Regehr, H.M., and Montevecchi, W.A. 1997. Interactive effects of food shortage and predation on
867 breeding failure of black-legged kittiwakes: indirect effects of fisheries activities and implications for
868 indicator species. Mar. Ecol.: Prog. Ser. **155**: 249–260. doi:10.3354/meps155249.

- 869 Reid, R.N., Cargnelli, L.M., Griesbach, S.J., Packer, D.B., Johnson, D.L., Zetlin, C.A., Morse, W.W., and
870 Berrien, P.L. 1999. Essential Fish Habitat Document: Atlantic herring, *Clupea harengus*, life history and
871 habitat characteristics. National Oceanic and Atmospheric Administration Technical Memorandum
872 NMFS-NE-126.
- 873 Rijnsdorp, A.D., Peck, M.A., Engelhard, G.H., Möllmann, C., and Pinnegar, J.K. 2009. Resolving the effect
874 of climate change on fish populations. ICES J. Mar. Sci., **66**(7): 1570–1583. doi:10.1093/icesjms/fsp056.
- 875 Scopel, L.C., and Diamond, A.W. 2017. The case for lethal control of gulls on seabird colonies. J. Wildl.
876 Manage **81**(4): 572-580. doi: 10.1002/jwmg.21233
- 877 Scopel, L.C., and Diamond, A.W. Predation and food-weather interactions drive colony collapse in a
878 managed metapopulation of Arctic Terns (*Sterna paradisaea*). Can. J. Zool. In press.
- 879 Singh, R., Dalton, A., Knox, D., Macintyre, A., and Melvin, G.D. 2016. 2015 Evaluation of Northwest
880 Atlantic Fisheries Organization (DAFO) divisions 4VWX herring. DFO Can. Sci. Advis. Sec. Res. Doc.
881 2016/073.
- 882 Skern-Mauritzen, M., Ottersen, G., Handegard, N.O., Huse, G., Dingsør, G.E., Stenseth, N.C., and Kjesbu,
883 O.S. 2016. Ecosystem processes are rarely included in tactical fisheries management. Fish and Fisheries
884 **17**: 165–175. doi:10.1111/faf.12111.
- 885 Smith, P.C., Pettigrew, N.R., Yeats, P., Townsend, D.W., and Han, G. 2012. Regime shift in the Gulf of
886 Maine. Am. Fish. Soc. Symp. **79**:185-203.
- 887 Stephenson, R.L. 2012. A perspective on advancing ecosystem research for the Gulf of Maine. Am.
888 Fish. Soc. Symp. **79**:409-415.

- 889 Stephenson, R.L., Lane, D.E., Aldous, D.G., and Novak, R. 1993. Management of the 4WX Atlantic
890 herring (*Clupea harengus*) fishery: an analysis of recent events. Can. J. Fish. Aquat. Sci. **50**(12): 2742-
891 2757. doi:10.1139/f93-299.
- 892 Stephenson, R.L., Power, M.J., Clark, K.J., Melvin, G.D., Fife, F.J., and Paul, S.D. 1998. 1998 Evaluation of
893 4VWX herring. DFO Can. Sci. Advis. Sec. Res. Doc. 98/52.
- 894 Stephenson, R.L., Power, M.J., Laffan, S.W., and Suthers, I.M. 2015. Tests of larval retention in a tidally
895 energetic environment reveal the complexity of the spatial structure in herring populations. Fisheries
896 Oceanography **24**(6): 553-570. doi:10.1111/fog.12129.
- 897 Stevenson, D.K., and Scott, M.L. 2005. Atlantic herring, *Clupea harengus*, life history and habitat
898 characteristics. National Oceanic and Atmospheric Administration Technical Memorandum NMFS-NE-
899 192.
- 900 Suryan, R.M., Irons, D.B., Brown, E.D., Jodice, P.G.R., and Roby, D.D. 2006. Site-specific effects on
901 productivity of an upper trophic-level marine predator: Bottom-up, top-down, and mismatch effects on
902 reproduction in a colonial seabird. Prog. Oceanogr. **68**(2-4): 303–328. doi:10.1016/j.pocean.2006.02.006
- 903 Sydeman, W.J., Mills, K.L., Santora, J.A., Thompson, S.A., Bertram, D.F., Morgan, K.H., Wells, B.K.,
904 Hipfner, J.M., and Wolf, S.G. 2009. Seabirds and climate in the California Current – a synthesis of
905 change: troubling trends or meandering variability? California Cooperative Oceanic Fisheries
906 Investigations Reports **50**: 82–104. Available from
907 <https://137.110.142.7/publications/CR/2009/2009Syd.pdf> [accessed 10 January 2017].
- 908 Thompson, S.A., Sydeman, W.J., Santora, J. A., Black, B. A., Suryan, R.M., Calambokidis, J., Peterson,
909 W.T., and Bograd, S.J. 2012. Linking predators to seasonality of upwelling: Using food web indicators

- 910 and path analysis to infer trophic connections. *Prog. Oceanogr.* **101**(1): 106–120.
911 doi:10.1016/j.pocean.2012.02.001.
- 912 Townsend, D.W., Rebeck, N.D., Thomas, M.A., Karp-Boss, L., and Gettings, R.M. 2010. A changing
913 nutrient regime in the Gulf of Maine. *Cont. Shelf Res.* **30**:820-832.
- 914 Transboundary Resource Assessment Committee. 2009. Gulf of Maine-Georges Bank herring stock
915 complex. Status report 2009/04.
- 916 Travis, J., Coleman, F.C., Auster, P.J., Cury, P.M., Estes, J.A., Orensan, J., Peterson, G.H., Power, M.E.,
917 Steneck, R.S., and Wootton, T.J. 2014. Integrating the invisible fabric of nature into fisheries
918 management. *Proc. Natl. Acad. Sci. U. S. A.* **111**(2): 581–584. doi:10.1073/pnas.1305853111.
- 919 Tupper, M.H., Anthony, V.C., Chenoweth, S.B., and MacCluen, H.A. 1998. Biology and assessment of Gulf
920 of Maine Herring Stocks. Gulf of Maine Aquarium, Portland, ME.
- 921 Wanless, S., Harris, M.P., Redman, P., and Speakman, J.R. 2005. Low energy values of fish as a probable
922 cause of a major seabird breeding failure in the North Sea. *Mar. Ecol. Progr. Ser.* **294**:1-8.
- 923 Wootton, R.J. 1998. Ecology of teleost fishes. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- 924 Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. Mixed effects models and
925 extensions in ecology with R. Springer, New York, NY.

926
927 Table 1. Relative Atlantic herring age-1 cohort strength among seabird colonies and fishery data. Boxes indicate strong (red) or weak (blue)
928 cohorts for a particular seabird colony-species pair, or for cohorts as defined by the American stock assessment model. Fishery cohorts are
929 listed by raw abundance and by quartile. Colonies include Machias Seal Island (MSI), Petit Manan Island (PMI), Matinicus Rock (MR), Seal Island
930 NWR (SI), Eastern Egg Rock (EER), Pond Island NWR (PI), Jenny Island (JI), Outer Green Island (OGI), and Stratton Island (STI). Seabirds are Arctic
931 tern (ARTE), common tern (COTE), Atlantic puffin (ATPU), and razorbill (RAZO).

932 Table 2. List of seabird-fishery predictive models with a prediction error <0.2. Models are ranked by
 933 prediction error. All models are considered strong potential bioindicators.

Fishery Category	Fishery Description	Seabird Colony	Seabird Species	Seabird Data Type	Lag	Prediction Error	SE	Pseudo- R^2	Slope	SE	N
Acoustic	Bay of Fundy	Machias Seal Is.	C. Tern	Proportion	+1	0.03	0.00	1.14	1.00	0.08	8
Model	Spawning Stock	Matinicus Rock	Razorbill	Mass/feed	+5	0.05	0.01	1.00	1.09	0.16	5
Landings	Combined	Machias Seal Is.	C. Tern	Mass/hr	+4	0.08	0.00	0.94	0.64	0.11	11
Landings	Fixed	Machias Seal Is.	C. Tern	Proportion	-2	0.13	0.01	0.86	0.62	0.12	12
Model	Recruits, USA	Matinicus Rock	C. Tern	Mass/hr	0	0.13	0.01	0.87	1.07	0.13	9
Model	Spawning Stock	Jenny Is.	C. Tern	Mass/feed	+5	0.13	0.01	0.91	1.07	0.16	8
Acoustic	Georges Bank	Machias Seal Is.	C. Tern	Mass/hr	+4	0.15	0.01	0.73	1.03	0.14	11
Weight	At-age 1	Seal Is.	Puffin	Avg. mass	+5	0.15	0.02	0.91	0.82	0.24	6
Model	Recruits, USA	Matinicus Rock	Puffin	Proportion	0	0.17	0.02	0.86	1.33	0.22	7
Acoustic	Bay of Fundy	Pond Is.	C. Tern	Proportion	+3	0.18	0.01	0.76	0.97	0.22	9
Landings	Combined	Petit Manan Is.	C. Tern	Proportion	0	0.18	0.01	0.80	0.54	0.15	12
Landings	Mobile, USA	Stratton Is.	C. Tern	Mass/hr	+5	0.18	0.02	0.87	0.64	0.19	8
Acoustic	Georges Bank	Machias Seal Is.	A. Tern	Mass/hr	+4	0.19	0.01	0.65	0.88	0.14	11

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935

Table 3. Rankings of 13 fishery data types for potential use as indices of predator food availability in the Gulf of Maine and Bay of Fundy region. Ranking criteria included the number of seabird species included in cross-validated models (four total), the number of seabird colonies included in cross-validated models (nine total), the number of geographic regions encompassed by the models (three total), the number of cross-validated models with slopes and pseudo- $R^2 > 0.5$, and the number of cross-validated models with prediction error < 0.2 represented by each data type.

Category	Description	# Species	# Colonies	# Regions	# Models >0.5	# Error <0.2	Potential?
Model	Spawning Stock Biomass	4	8	3	10	2	High
Acoustic	Bay of Fundy (Canada)	4	5	3	6	2	High
Weight	At-age 1	3	5	2	12	1	Moderate
Landings	Mobile, USA	3	5	2	7	1	Moderate
Model	Recruits, Canada	3	5	2	7	0	Moderate
Landings	Fixed, New Brunswick	3	3	2	6	1	Moderate
Model	Recruits, USA	2	2	1	4	2	Low
Acoustic	Georges Bank (USA)	2	1	1	4	2	Low
Weight	At-age 3-5	3	3	2	4	0	Low
Weight	At-age 3+	2	1	1	4	0	Low
Landings	Combined (USA Mobile, all Fixed)	2	2	1	3	2	Low
Weight	Growth increment 2-3	2	3	2	3	0	Low
Landings	Mobile, New Brunswick	0	0	0	0	0	Poor

942

Figure 1. Stages of Atlantic herring life cycle and timing of peak mortality from seabirds and fisheries.

Herring hatch in the fall (age 0, not shown), and become age 1 on January 1; fall-spawned herring do not overlap with the seabird breeding season at age 0. Seabirds target age-1 herring in summer, and, to a lesser extent, age-2 herring the following summer. The fixed-gear fishery primarily catches age-2 herring, and the mobile-gear fishery catches a range of fish cohorts, especially ages 3-5.

Figure 2. Map depicting the Gulf of Maine-Bay of Fundy region, the nine seabird colonies in this study, spawning grounds of Atlantic herring, and locations of acoustic surveys. Colonies are annotated as follows: Stratton Island (STI), Outer Green Island (OGI), Jenny Island (JI), Pond Island National Wildlife Refuge (PINWR), Eastern Egg Rock (EER), Matinicus Rock (MR), Seal Island National Wildlife Refuge (SINWR), Petit Manan Island (PMI), and Machias Seal Island (MSI). Colonies in green are considered

western, colonies in red are considered central, and colonies in pink are considered eastern. Adapted from Overholtz et al. 2004; NEFSC 2012; DFO 2016.

Figure 3. Mean weights-at-age for the (A) American stock assessment and (B) Canadian stock assessment. American data include 1965-2011, while the Canadian data include 1965-2015.

Figure 4. Top ranked models showing relationships between seabird diet data and American (blue) and Canadian (orange) acoustic surveys in the Gulf of Maine and Bay of Fundy region. Common and Arctic tern diet data at Machias Seal Island (MSI) predicted acoustic surveys at Georges Bank four years later, while common terns at Pond Island (PINWR) predicted acoustic surveys from the Bay of Fundy three years later. Dashed lines suggest proposed larval movements from spawning areas toward seabird

970 colonies, where seabirds consume juvenile herring. Solid lines indicate connectivity back to natal
971 grounds.

Draft

973 Figure 5. Links between Canadian fishery data and seabird diets in the Gulf of Maine and Bay of Fundy
974 region, based on cross-validated regression models. Two types of fishery data represented the age-1
975 cohort (age-1 recruitment, weight-at-age 1, upper panel), and one was linked to older cohorts (acoustic
976 survey, lower panel). The blue and orange arrows indicate links between age-1 data and seabird
977 colonies; the blue arrow indicates a significant relationship with both sets of data, whereas the orange
978 arrow shows a link with just one. The black arrows show ties back to the Bay of Fundy acoustic data
979 three years later, suggesting movement back to Canada three years later. Spawning areas are shown in
980 blue polygons, where acoustic surveys are performed.

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