Varied breeding responses of seabirds to a regime shift in prey base in the Gulf of Maine

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ABSTRACT: Seabirds consume forage fish, which are keystone species in many marine ecosystems. The Junk Food Hypothesis proposes that high-lipid prey should produce better reproductive performance by seabirds. In the Gulf of Maine, changes in the forage fish community followed rapid warming post-2005 and included a decline in high-lipid Atlantic herring *Clupea harengus*. We studied 3 species of alcid (Atlantic puffin *Fratercula arctica*, razorbill *Alca torda*, common murre *Uria aalge*) over 23 yr at 3 colonies to assess changes in chick diet and its relationships with reproductive success. Puffin and razorbill chick diet changed over time; puffin diet was highly variable taxonomically, whereas razorbill diets were more consistent, showing proportional changes within fewer taxa. For puffins and razorbills, herring was replaced by sand lance *Ammodytes* spp. and other taxa with lower energy density. Puffins did not require high-lipid fish to breed successfully, but diet–reproduction relationships became unpredictable following extremely warm winters (2013 and 2016). Razorbills and murres provisioning with low-lipid fish showed reduced chick condition and breeding success. We concluded that razorbills and murres need higher-quality diets than puffins, which more frequently exploited lower-lipid food during food shortages. However, puffin reproductive output was much more vulnerable to ocean warming owing to their longer breeding season and more varied diet. Different responses of closely-related species to changes in prey are driven by differences in chick-development strategies with clear implications for using seabirds as environmental indicators.

KEY WORDS: Nutritional stress hypothesis · Forage fish · Energy density · Alcids · Seabirds · Breeding success · Ocean warming · Indicators

1. INTRODUCTION

Seabirds are apex marine predators subsisting entirely on food from the sea. They nest on land and bring marine prey to their chicks while being constrained to foraging within a limited distance from the colony; as such, they are 'central place foragers' (Boyd et al. 2017), not able to follow food freely as they can when not breeding (Diamond 1978). Large colonies are liable to deplete prey close to the colony through density-dependent competition, leading to reduced prey density around the colony, often referred to as 'Ashmole's halo' (Ashmole 1963, Birt et al.

1987). Likely effects of this process include an inverse relationship between colony size and productivity (Gaston et al. 1983, Hunt et al. 1986, Cairns 1989) and spatial distribution of colonies that reduce potential overlap of foraging areas (Furness & Birkhead 1984).

Forage fish are important prey for seabirds and other marine predators, with a keystone role (Paine 1995) funnelling nutrients between plankton and larger vertebrates in a so-called 'wasp-waist' trophic system (Bakun 2006, Breton & Diamond 2014). While many seabird diet studies have focused on the quantity of preferred prey (e.g. Cury et al. 2011 and references therein), the quality of prey can be equally im-

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portant for marine predators (Rosen & Trites 2000, Golet et al. 2007, Kadin et al. 2012). Quality and quantity are related directly; the biomass of prey required by a predator is inversely proportional to its quality (Rosen 2009). Thus, the nutritional requirements of predators can be met by larger amounts of low-quality prey, smaller amounts of high-quality prey, or a combination of the two. The Junk Food Hypothesis predicts that low food quality causes lower reproductive performance in predators (Rosen & Trites 2000, Jodice et al. 2006). The usual proxy for quality is lipid content because lipids contain more energy per gram than carbohydrates or protein (Ricklefs 1974) and the energetic cost of processing food is lowest for lipids (Blaxter 1989 in Rosen 2009). Different prey taxa tend to have constant relative values of lipid content (Bradstreet & Brown 1985, Budge et al. 2002), but lipid content varies intraspecifically both seasonally and annually (Lane et al. 2011) as well as regionally (Budge et al. 2002), and annual differences may be correlated with breeding performance of seabird predators (Diamond & Devlin 2003, Wanless et al. 2005).

Although inaccessible at sea for most of the year, seabirds can be accessed by researchers when they come to land to breed. Behavioral and demographic characteristics in these colonies can be measured relatively efficiently, and changes in these responses are the basis of using seabirds as indicators of changes in marine environments (Cairns 1987, Einoder 2009, Durant et al. 2009). Many studies examine seabird responses (population size, breeding success ['productivity'], chick growth rate, time budgets) in relation to changes in abundance of their main prey (Cury et al. 2011 and references therein); fewer studies assess the relationship between chick diet and other measures of prey abundance such as catch per unit effort or standing stock biomass (Parsons et al. 2008, Buren et al. 2012, Scopel et al. 2018), yet this linkage is implicit in using seabirds as indicators.

Fish abundance is obviously affected by fisheries (Scheffer et al. 2005) but also by changing environmental conditions, including temperature and chemical changes induced by global warming (Heath et al. 2012); these may act simultaneously with fishing, making their effects difficult to disentangle (Bell et al. 2015). Fish respond directly to temperature in many ways, including moving deeper in the water column or changing distribution (Rose 2005, Rijnsdorp et al. 2009, Corten 2013). Thus, rising temperatures can have great effects on seabirds by affecting fish (Sydeman et al. 2015); for example, many seabirds have shown recent declines in breeding success due to changes in distribution of forage fish (Bar-

rett et al. 2006, Foster & Marrs 2012, Miles et al. 2015), leading to listing European populations of Atlantic puffin *Fratercula arctica* as Endangered in 2015 (www.iucnredlist.org/details/22694927/0).

The Gulf of Maine (GOM) is a semi-enclosed shelf sea extending from Cape Cod, MA, in the southwest to the Bay of Fundy in the northeast (Fig. 1). The GOM has changed in many ways as its human population has expanded, historically due largely to overfishing (Steneck 1995, Jackson et al. 2001, Steneck et al. 2013) and more recently to changes in ocean circulation associated with global warming (Greene & Pershing 2007, Smith et al. 2012, Pershing et al. 2015). The surface waters of the GOM are warming faster than most of the world's oceans (Mills et al. 2013). While seabird populations have not declined here, as the same species have in Europe, seabirds in the GOM have shown major shifts in diets after 2000 (Diamond & Devlin 2003, Breton & Diamond 2014, Symons 2018) and again since 2010 (Kress et al. 2016, Scopel et al. 2018).

In the GOM, the keystone forage fish, for seabirds and many other marine predators, was Atlantic herring *Clupea harengus* (Bakun 2006, Diamond 2012), the species with the highest lipid content (Budge et al. 2002). The proportion of 1-group (juvenile) herring in the diet of breeding seabirds has declined since its predominant position in the 1990s (Diamond
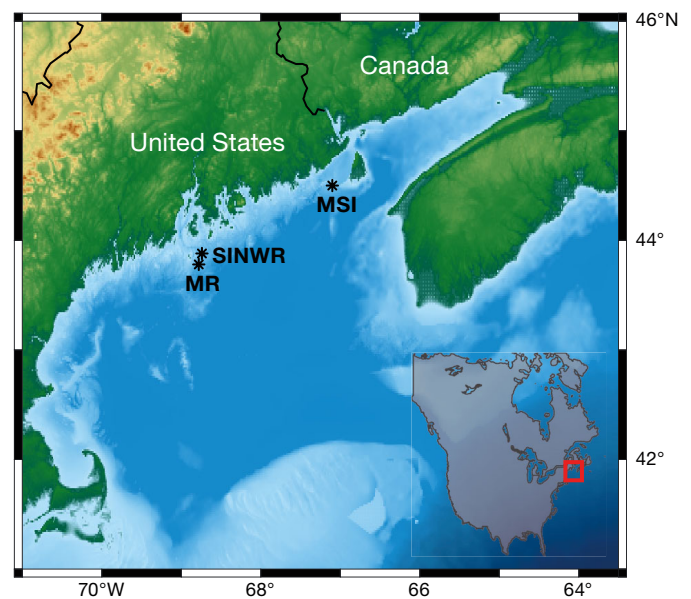

Fig. 1. The Gulf of Maine region, including the 3 study colonies: Machias Seal Island, New Brunswick (MSI); Seal Island National Wildlife Refuge, Maine (SINWR); Matinicus Rock, Maine (MR). We used data for Atlantic puffins *Fratercula arctica* from all 3 colonies, for razorbills *Alca torda* from MSI and MR, and for common murres *Uria aalge* at MSI only
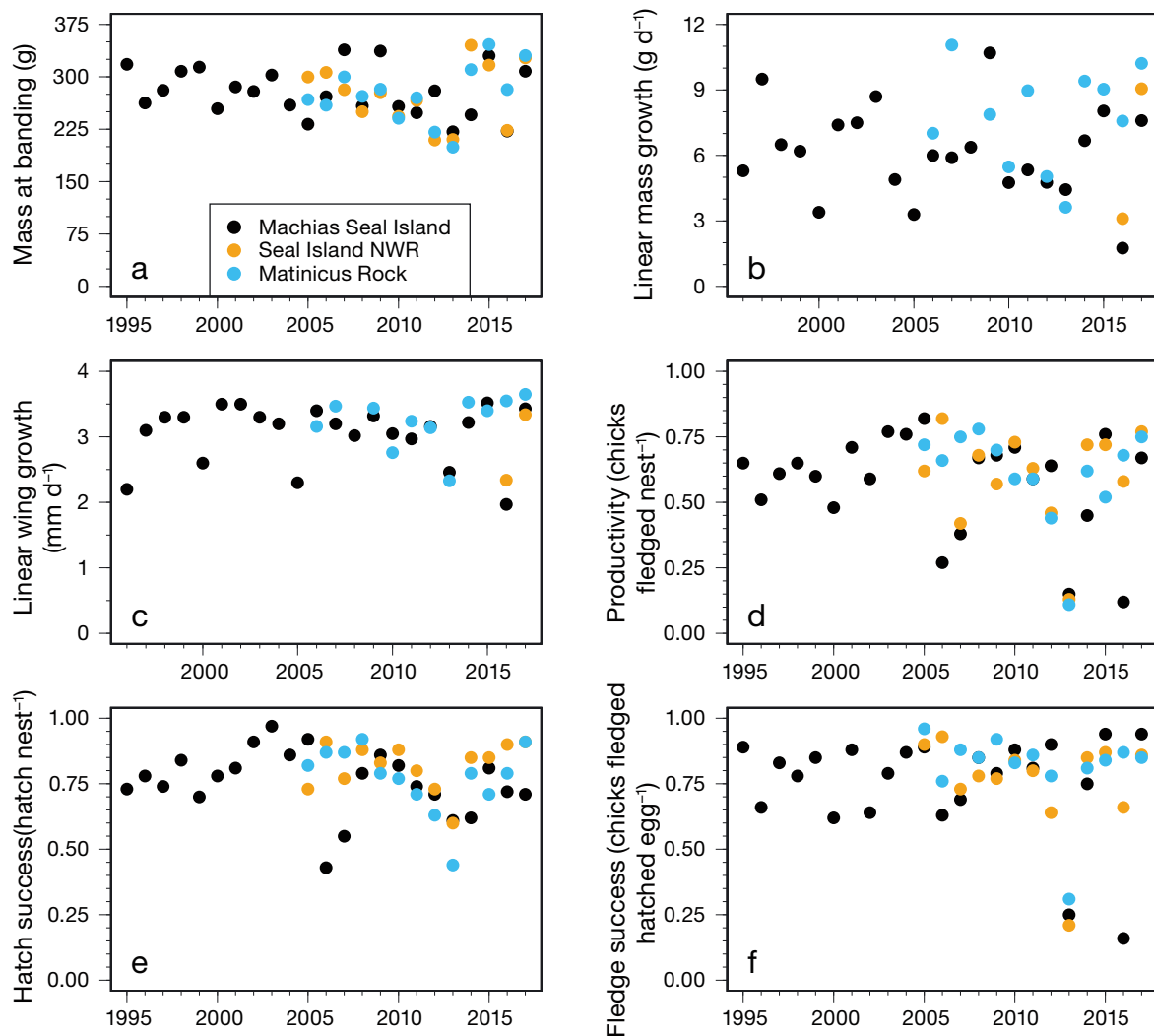
Fig. 2. Measures of chick condition and reproductive success for Atlantic puffins *Fratercula arctica* at 3 colonies in the Gulf of Maine, 1995–2017

& Devlin 2003, Breton & Diamond 2014) and early 2000s (Kress et al. 2016), raising concerns about the sustainability of both herring and seabird populations (Scopel & Diamond 2018, Scopel et al. 2018). Declines in several demographic responses associated with feeding conditions—including productivity (breeding success), chick growth, fledging condition (Figs. 2 & 3), and post-fledging survival—coincide with the loss of the highest-quality prey (Kress et al. 2016, Whidden 2016). Herring has been replaced in seabird diets by other juvenile fish such as butterfish *Poronotus triacanthus*, sand lance *Ammodytes* spp., and white hake *Urophycis tenuis*, but since 2010 also by species not previously recorded in seabird diets including haddock *Melanogrammus aeglefinus* and redfish *Sebastes* spp., both

of which are also commercially fished (Kress et al. 2016; our Fig. S1). These species differ in nutritional quality, raising the question: Are these 'new' taxa in seabird diets nutritionally adequate compared with the herring on which seabirds used to feed?

Previously, we explored relationships between seabird diet and fisheries measures of Atlantic herring in the GOM (Scopel et al. 2018) and documented changes in diet, survival and condition of puffin chicks at 3 GOM colonies (Kress et al. 2016); here, we address relationships between chick diet and seabird responses commonly used in studies of seabirds as indicators, using 3 seabird species breeding on 3 islands spanning a range of 150 km in the GOM. The study species are alcids (family Alcidae), which feed by pursuit diving underwater. Compared with Kress
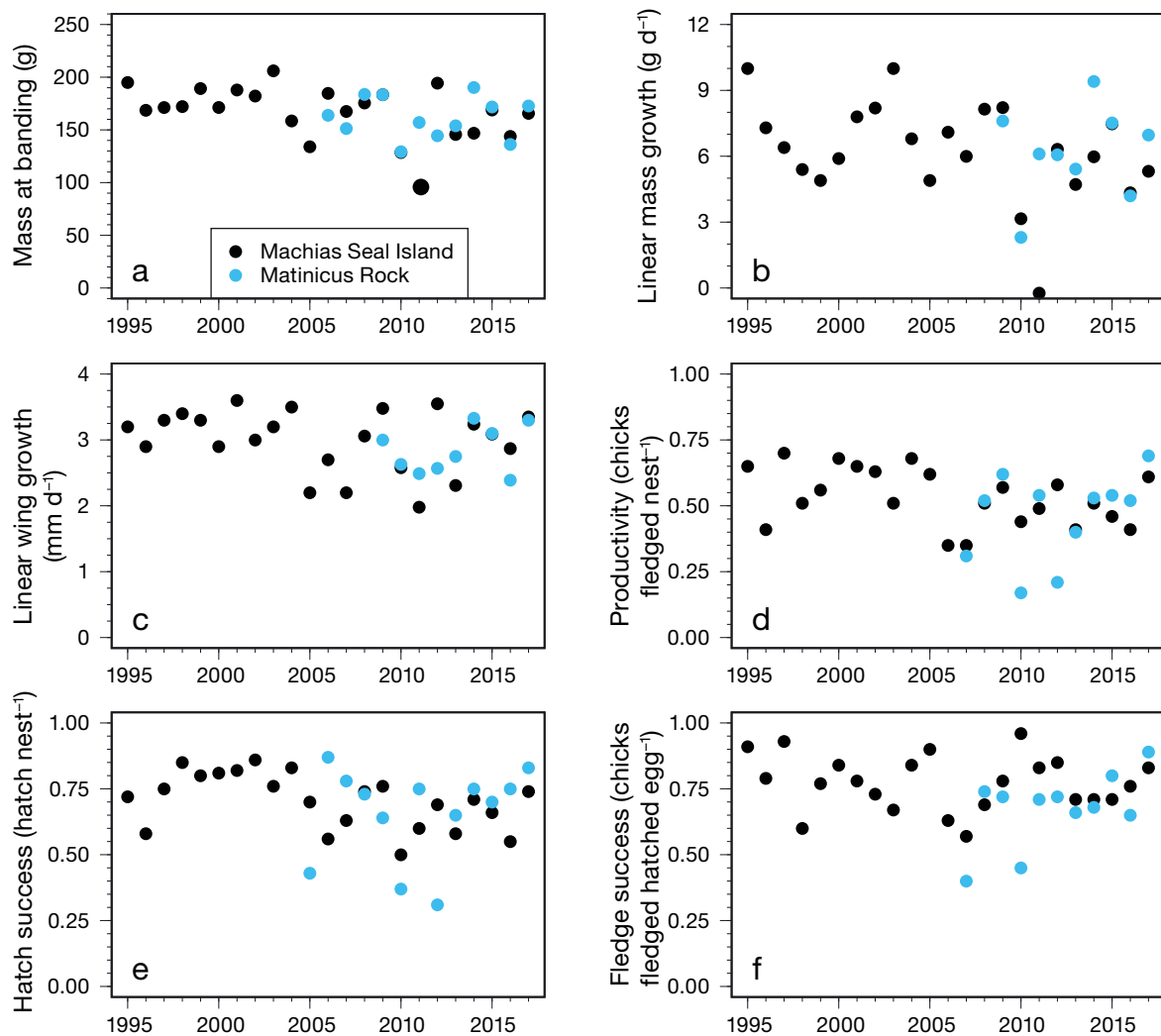
Fig. 3. Measures of chick condition and reproductive success for razorbills *Alca torda* at 2 colonies in the Gulf of Maine, 1995−2017

et al. (2016), our time series is longer, we add data from the largest colony in the region, treat diet data by mass not number, add 2 study species and more environmental variables, and explicitly model relationships between diet and measures of reproductive output.

Our objective in this paper is to explore the effects of changes in chick diet on reproductive success of 3 species of alcid in the Gulf of Maine and Bay of Fundy. Specifically, we

1. Quantify changes in chick diet pre-2010 and 2010 onwards;

2. Compare the importance of new vs. old taxa;

3. Compare the importance of low-lipid vs. high-lipid taxa; and

4. Quantify the influence of weather, predation pressure, and sea conditions.

2. MATERIALS AND METHODS

2.1. Study area

We analyzed chick diet and reproductive data from 3 seabird colonies in the GOM: Matinicus Rock, Maine, USA (MR); Seal Island National Wildlife Refuge, Maine, USA (SINWR); and Machias Seal Island Migratory Bird Sanctuary, New Brunswick, Canada (MSI). MR and SINWR are 14 km apart in Penobscot Bay, ~150 km from MSI at the mouth of the Bay of Fundy (Fig. 1). All 3 islands are within 30 km of the Maine coast. We analyzed data from puffins *Fratercula arctica* at all 3 colonies, razorbills *Alca torda* at MR and MSI, and common murres *Uria aalge* at MSI. Common murres colonized MSI in 2003 and MR in 2018, but data were collected systematically on MSI

only beginning in 2013. MSI supports the largest alcid colony in the GOM region (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m626p177_supp.xlsx). Study colonies are described in more detail by Diamond & Devlin (2003) and Kress et al. (2016), and years of data collection are in Table S2.

2.2. Study species

Of the 3 species in this study, Atlantic puffins are the smallest, averaging 435 g. They incubate a single egg in an underground burrow or rock crevice for ~40 d, followed by a prolonged chick rearing period ('semi-precocial' fledging strategy), typically lasting between 38 and 44 d but up to 69 d in poor years. After the chick reaches 10 d of age, both parents forage throughout the rearing period. Chicks fledge alone at night; on MSI, some chicks wander near the lighthouse at night and are collected on the lawn, banded, measured, and released. Adult puffins on MSI are captured in May, where adult mass can serve as a proxy of pre-breeding condition. Over 2 yr, MSI puffins foraged on average 38 km from the island, often over deep water (Symons 2018).

Razorbills are larger than puffins, averaging 690 g. They nest among granite boulders on all islands, with an incubation period of 35 to 39 d followed by chick-rearing for only 16 to 21 d. After fledging, the male adult provisions the chick at sea. During chick-rearing, one parent forages while the other guards the chick from predators and poor weather. Razorbills typically fledge in late June to early July on MR and early to mid-July on MSI. Adults from MSI foraged on average 19 km from the colony in 2 yr, nearer the coast and in shallower water than puffins (Symons 2018).

Murres are the largest of the study species, averaging 960 g, and nest under boulders. Phenology and behavior are very similar to razorbills, with fledging typically in early-mid July. There are no data on murre foraging behaviour in the GOM.

2.3. Chick diet

Data were collected visually in 3 h observation stints from blinds each breeding season (Kress et al. 2016, Scopel et al. 2018). Diet data were converted into mass using length-mass relationships following Scopel et al. (2018). We developed taxon-specific estimates of mass (g) per feeding (hereafter 'mass per feed') and proportion of total mass for each colony, seabird species, and year; although proportions are a common form of diet representation, they are 0–1 bound and depend on the other taxa consumed, which can bias estimates. Feeding rates for study plots (number of feedings per hour) were calculated for each year and site.

Puffins experienced major diet shifts over the course of study (Kress et al. 2016); since 2010, puffins at MR and SINWR have consumed several taxa that were not major parts of the diet before 2010 (Table S3). Three species were first observed in chick diets in 2010 or later (redfish *Sebastes* spp., haddock *Melanogrammus aeglefinus*, rough scad *Tracharus lathami*); 4 other species were observed rarely before 2010 (Atlantic saury *Scomberesox saurus*, bluefish *Pomatomus saltatrix*, mackerel *Scomber scombrus*, squid *Illex* spp.) but were observed more frequently thereafter (Table 1). Some newer taxa represented >1% of the diet during a single season only. We were specifically interested in the potential effect of these 'new' taxa. Juvenile gadoids, which are hard to identify, were grouped into a single taxon ('haddock') which was dominated by haddock *M. aeglefinus* after 2010. We were also interested in the relative importance of high-fat and low-fat or difficult-to-consume taxa, especially for puffins because of their long chick-rearing period (Table S4).

Table 1. Occurrence and perceived value of prey taxa in alcid diets in the Gulf of Maine region. Value here is indicated by predicted effects on reproductive outcomes (see Section 2.8). Prey taxa that were observed throughout the time series are classified as 'old'; taxa that first appeared or greatly increased in prominence in the diet after 2009 are considered 'new'. See Table S4 in the Supplement for complete fat content values

Prey taxon	Atlantic puffin	Razorbill	Common murre	Time period	Fat content	Value
Atlantic herring	X	X	X	Old	High	Excellent
Sand lance	X	X	X	Old	High	Excellent
White hake	X	X	X	Old	Low	Moderate
Butterfish	X	X	X	Old	High	Poor
Euphausiids	X	X		Old	Low	Poor
Larval fish	X	X	X	Old	Low	Poor
Redfish	X			New	High	Excellent
Haddock/pollock	X	X	X	New	Low	Moderate
Rock gunnel			X	New	Low	Moderate
Bluefish	X			New	Low	Moderate
Atlantic saury	X			New	High?	Moderate
Rough scad	X			New	High?	Moderate
Mackerel	X			New	Low	Moderate
Squid	X		X	New	Low	Poor

2.4. Chick growth, condition, and reproductive success

Field crews at each colony followed permanently marked puffin and razorbill burrows. Murres could not be systematically monitored, so the only reproductive metric is chick condition, determined at banding (see below). Puffin nests were checked at weekly intervals in May and early June for clutch initiation; burrows with an egg were considered active. From mid-June, active burrows were checked at intervals according to site and year: at MR and SINWR, puffin burrows were visited every 5 to 18 d prior to 2013, thereafter every 3 to 5 d; at MSI, burrows were checked at hatch, at least twice during the period of linear growth (see below), and at fledging. Razorbill nests were checked at 3 to 5 d intervals. Burrows where contents could not be determined unambiguously were removed from analysis. Puffin chicks not yet fledged when field crews departed were treated as fledged if the last wing chord measurement was >100 mm; razorbill chicks reaching 12 d or a minimum wing of 50 mm were considered fledged. We calculated both productivity (chicks fledged per active nest) and fledge success (chicks fledged per hatched egg).

Chick growth rates (wing chord [mm; Pyle 1997] and mass [g]) were derived annually by regressing measurements against chick age during the linear growth period (Days 10–30 for puffins, Days 5–15 for razorbills). Chick growth was not recorded on all islands in all years.

Measures of chick condition (mass [g] and condition [mass wing chord^{-1}]) were obtained from marked burrows and opportunistic banding of random chicks. Precise ages could not be determined at random burrows, but crews targeted older chicks. Razorbills and murres were likely between 11 and 16 d old, whereas puffins showed a wider range owing to their longer breeding season. At monitored burrows, we used the latest measurement in the linear growth period (razorbills) or closest to Day 35 (puffins).

At MSI, estimates of condition were calculated of fledging puffins on the lawn at night. We compiled mean mass and condition of fledging chicks for comparison with size-at-banding data.

2.5. Environmental variables

We compiled variables to represent weather, predation pressure, and sea conditions. Although alcid chicks are typically sheltered at our sites, precipitation can affect thermoregulation (Vongraven et al. 1987), and we included total rainfall in June to represent early chick-rearing (late rearing for razorbills at MR, where they nest earlier than at MSI) and in July to represent late chick-rearing. Predation pressure by gulls (*Larus argentatus* and *L. marinus*) and ravens *Corvus corax* is represented by the proportion of depredated tern *Sterna* spp. eggs at each colony, as tern nests are especially susceptible to predation (Scopel & Diamond 2018). To account for potential environmental effects on prey availability, we included sea surface temperature (SST) from island measurements recorded daily at noon in May, June, and July. Prey quality and availability in May will affect females forming eggs (Perrins 1970), and summer temperatures can affect breeding success, through prey availability for chicks (Carroll et al. 2015, Descamps et al. 2017).

2.6. Analytical approach: quantification of changes to alcid chick diets

Using proportional representations of diet, we created diet profiles for puffins and razorbills in PRIMER v. 6.1.15 (PRIMER-E). Data were normalized, and a resemblance matrix was created using Euclidean distances. We identified *a priori* an apparent dietary shift in 2010, when haddock first started to appear in chick diets in the GOM; we thus created a dummy variable identifying periods before 2010 and periods during 2010 and after. We used 2-way ANOSIMs with colony and time as factors. For global Rs >0.1, we performed a SIMPER test to identify taxa driving differences between groups.

2.7. Data preparation: diet–reproduction relationships

Missing data in chick growth measurements precluded them from being analyzed directly, but we incorporated them into a principal component analysis (PCA) of chick condition. To estimate missing values, we used expectation-maximization (EM) methods in PRIMER, using mean chick condition and chick mass as correlating variables (Tabachnick & Fidell 2013). A PCA was then performed on chick mass at banding, condition at banding, linear mass growth, and linear wing growth. PC1 represented 84.6% of the variation in the data for puffins and 79.9% for razorbills. In both cases, we rescaled the

PCs so that high values corresponded to years of better chick growth (hereafter 'condition PC').

The data for 1995 adult puffin mass in May on MSI were also missing, and the 1999 mean was unusually high with small sample size; we used EM and the above chick condition variables to generate estimates for these 2 years.

Correlations between predictor variables were assessed for each species, where correlations >|0.5| were examined closely and rejected if >|0.7| (Tabachnick & Fidell 2013). In the puffin data, multicollinearity was observed between some new taxa; we grouped probable high-fat 'new' taxa (Table 1: rough scad and Atlantic saury) and lower-fat new taxa (bluefish, mackerel, and squid) together. Redfish and haddock were represented independently owing to their prevalence and our interest in their value. For razorbills, proportional herring *Clupea harengus* estimates were highly correlated with hake *Urophycis tenuis* and sand lance, so these variables were not modeled together (see Section 2.8). Murre diet data suffered from high multicollinearity in mass per feed data; we thus used proportional data only. Haddock and herring were also strongly correlated (−0.78).

2.8. Analytical approach: diet–reproduction relationships

We performed general or generalized linear regressions on seabird chick diet and reproductive data, compared using Akaike's Information Criterion corrected for small sample sizes (AICc). We used seabird chick condition and reproductive data as responses and used diet and environmental variables as predictors. A categorical island effect was included for puffin and razorbill analyses. All data were normalized and analyzed in R (v. 3.1.2). Normal responses — including mass at banding, condition at banding, mass at fledging, condition at fledging, and condition PC — were analyzed using the lm() function. Binary data—fledge success, productivity, and hatch success — were analyzed using the glm() function. All generalized linear models (GLMs) used the binomial family and logit link.

Global models were fit for each response variable. Diet was estimated as both mass per feed and proportion of total mass (all identified items), so we compared the fit of each type and modeled just one when possible. As razorbills had multicollinearity issues with proportional data, proportional models were fit with herring or hake and sand lance; the best fit of each was retained, in addition to the best fitting mass

per feed model. For murres, owing to small sample size, we created a series of global models for each response variable, limited to 3 variables per model.

We considered qualitative–quantitative interactions for island–diet effects, as well as quadratic terms for environmental or diet data; all main effects were included (Aiken & West 1991). In addition to acceptable diagnostic plots of residuals, leverage, and influence, for normal response variables we considered fit appropriate once we reached a minimum R^2 of 0.7; for GLMs, we tried to get $\hat{c}$ (overdispersion) as close to 1 as possible, based on the ratio of residual scaled deviance to residual df (Agresti 2007). We also report goodness of fit based on G^2 (Agresti 2007). Hatch success models typically had poor fit and are not considered further. Global models and fit statistics are listed in Appendix S1 in the Supplement at www.int-res.com/articles/suppl/m626p177_supp.xlsx.

Owing to potential autocorrelation, we also tested alternative modeling structures for each analysis. For all response variables, we used generalized least squares regression with a varIdent variance structure on island or year categorical variables, using the gls() function in package nlme (Pinheiro et al. 2017). We also used a linear mixed-effects model with year as a random factor, using function lme() in package nlme for normal response variables and function glmer() in package lme4 for binary response variables (Bates et al. 2015).

During global model fitting, puffin models showed consistent strongly negative outliers with data points from 2013 and 2016 across all response variables; attempts to account for this variation using predictor variables or alternative modeling structures failed. These seasons were notable for late nesting, poor chick growth, and poor fledging condition, so we highlighted these years using a dummy variable 'bad year'. For all puffin analyses, we then created global models with and without this variable.

For puffins, after selecting a global model structure, we substituted different variable combinations to compare the importance and fit of groupings of diet taxa, in effect creating a short list of global models. We assessed the importance of high-lipid taxa and new taxa using these combinations (Table S5).

Once global models were finalized, we ran each global model through the dredge function in package MuMIn (Barto 2014); we removed models with a ΔAICc >10 and those with pretending variables (Anderson 2008, p. 65) and collated results where multiple global models were used to generate our confidence set. QAICc was used for GLMs where $\hat{c}$ was >1. Where

applicable for puffin models, the best-fitting new and high-lipid taxon groupings were selected, with all remaining structures removed. For puffins, 2 confidence sets were generated for each response variable, with and without the bad year variable. For razorbills, either mass per feed or proportional data were selected for the final confidence set. Diagnostics of the top-ranked model in each confidence set were checked for obvious outliers, leverage, or influence.

2.9. Variable assessment: diet–reproduction relationships

Once a confidence set was generated, we created an AICc table using package AICcmodavg (Mazerolle 2016); where applicable, $\hat{c}$ was adjusted. We pared our confidence set down to 95% based on cumulative model weight, then performed model averaging with shrinkage (Anderson 2008). We reported effect sizes, considering any of at least |0.10| to be biologically relevant (Martínez-Abraín 2008). For interactions or quadratic terms, main effects were reported regardless of effect size.

2.10. *A posteriori* analysis: identifying bad years for puffins

Following the diet–reproduction analyses, we identified variables that might predict when bad years occur for puffins (Table S6). We compiled 2 sets of variables: one representing the condition of adults following the overwintering period, and one representing conditions during chick rearing. Owing to limited data from MR and SINWR, we compiled one dataset for MSI only and one for all islands. Data representing pre-breeding adult condition included adult mass in May (MSI), mean monthly overwintering SST (September to May) from the closest grid point to each island in the Optimal Interpolated SST dataset by the National Oceanic and Atmospheric Administration (www.ncei.noaa.gov/erddap /griddap/ncdc_oisst_v2_avhrr_by_ time_zlev_lat_lon.html), and early-season breeding indices (occupancy [MSI], mean lay date [MSI], hatch success). Data representing conditions during chick rearing included

chick condition (mass at banding, mass at fledging [MSI], condition at banding, condition at fledging [MSI], mass growth rate), productivity, adult foraging (feeding rate, biomass provisioning rate), and summer SST (June–July, recorded at the island). We performed a PCA on each dataset. PCs were inspected for high scores in 2013 and 2016 to indicate bad years; PC1 was used throughout. A third dataset was compiled using variables with factor loadings >|0.1| from these 2 PCs, to give an index for the entire breeding season.

3. RESULTS

3.1. Atlantic puffin *Fratercula arctica*: diet quantification

The ANOSIM showed no meaningful difference between colonies (global R = −0.015, p = 0.54), and some support for a dietary shift (global R = 0.103, p = 0.075). We thus performed a SIMPER test on the time grouping only. No taxon was a major driver of group dissimilarity over time, with all contributing about equally (Table 2). Herring *Clupea harengus*, euphausiids, hake *Urophycis tenuis*, and larval fish decreased over time, replaced by butterfish *Poronotus triacanthus*, sand lance *Ammodytes* spp., and new taxa.

3.2. Atlantic puffin: diet–reproduction relationships

For each response variable representing alcid reproductive success and chick condition, 2 model sets

Table 2. Relative changes in Atlantic puffin *Fratercula arctica* diets at colonies in the Gulf of Maine before and after 2010. Mean values are by percentage of total mass in the diet. Entries are ordered by their contribution to group dissimilarity

Taxon	Time period	Mean (1995–2009)	Mean (2010–2017)	Change	% Contribution to group dissimilarity
Haddock/pollock	New	0.57	20.69	+20.12	9.83
Atlantic herring	Old	47.80	23.67	−24.14	8.09
Butterfish	Old	3.04	9.43	+6.39	8.08
Redfish	New	0.00	3.54	+3.54	7.95
Bluefish	New	0.01	2.02	+2.01	7.57
Rough scad	New	0.00	1.08	+1.08	7.53
Squid	New	0.16	0.88	+0.72	7.46
White hake	Old	33.18	21.79	−11.40	7.42
Atlantic saury	New	0.37	1.44	+1.06	7.37
Mackerel	New	0.00	0.52	+0.52	7.36
Euphausiids	Old	0.68	0.36	−0.33	7.17
Sand lance	Old	10.90	13.00	+2.10	7.11
Larval fish	Old	3.28	1.60	−1.68	7.06

were created, with and without the bad year dummy variable. Productivity models had poor fit, and because productivity combines effects from the incubation and chick growth periods, which were already modeled separately, we dropped productivity from the analysis.

For confidence sets, complete summaries of model-averaged effect sizes, and plots of quadratic effects, please see Appendix S2 in the Supplement. Biologi-

cally relevant effects (Fig. 4) include 6 cases where the bad year variable markedly improved fit; hatch success was the only response for which the bad year variable did not have the greatest effect size, although the effect was still biologically relevant (Fig. 4g). We therefore consider models with the bad year variable to be superior. Some differences in relevant predictors are apparent when comparing the 2 analyses (Table S7); most notably, euphausiids

Fig. 4. Biologically relevant effect sizes in reproduction−diet models for Atlantic puffins *Fratercula arctica* in the Gulf of Maine. All effects are from the analysis with the bad year variable included. Effects are on a normalized scale. Error bars are 95% CI (based on SE). [2]Indicates quadratic terms. Cond. band.: condition at banding; Cond. fledging: condition at fledging; Condition PC: principal component of condition variables; MSI: Machias Seal Island; SI: Seal Island National Wildlife Refuge, SST: sea surface temperature. Interactions between variables designated by ×

became more important when bad years were accounted for, showing strongly negative curvilinear effects on all 7 response variables. Redfish *Sebastes* spp. also had greater positive support among condition variables and changed in sign from negative to positive for fledge success. Several variables received reduced support and had smaller effect sizes with the bad year variable included, most notably butterfish, May adult mass, SST, and rain in July.

The strongest effect sizes across both analyses were always negative, and negative linear effects were usually at least twice as large as positive effects (Fig. 4). Curvilinear effects were typically negative and declined to a threshold (Appendix S2). Condition responses were explained by fewer variables, while reproductive success models were more complicated and included more dietary, environmental, and categorical variables.

Generally, older and low-fat taxa were important in both analyses, more than new or high-fat taxa. Euphausiids had the strongest and most consistent negative effects, while butterfish had a consistent negative effect on chick condition. Larval fish positively affected 3 reproductive success variables. Older and high-lipid taxa, including sand lance and herring, and low-lipid but common hake and haddock *Melanogrammus aeglefinus* (and mixed juvenile gadoids) each showed biologically relevant effects on only one response variable. Among the less common new taxa, fat content drove value. Redfish had positive effects on 4 responses and was the only new taxon with no negative effects. Atlantic saury *Scomberesox saurus* and rough scad *Tracharus lathami* had positive effects on 2 reproductive success variables but 2 negative effects on condition; bluefish *Pomatomus saltatrix*, mackerel *Scomber scombrus* and squid *Illex* spp. negatively affected 3 response variables. May SST and July rain each affected one response variable when the bad year variable was included.

Differences between colonies were supported via the categorical island effect, which was important in describing hatch and fledge success. SINWR performed equally well or marginally better than MR, but MSI had notably lower responses.

3.3. *A posteriori* analysis: bad years for puffins

The MSI-only dataset had more variables for the early condition period, but PC1 scores were similar between analyses, so we report scores from the complete dataset. In the early-condition PCA, years with

negative scores on PC1 were clustered after 2010 (Fig. 5a). The lowest score at each island occurred in 2013, followed by 2016 at MSI and 2012 at MR and SINWR. Variation was stratified into 2 time periods (Fig. S2): PC1 had stronger loadings by winter SST and the earliest measures of breeding from the MSI-only dataset (occupancy, May adult mass; Figs. S3 & S4), while PC2 had stronger loadings by spring SST and hatch success, better representing late incubation.

In the late-season PCA, negative scores on PC1 were more variable over time but became more com-
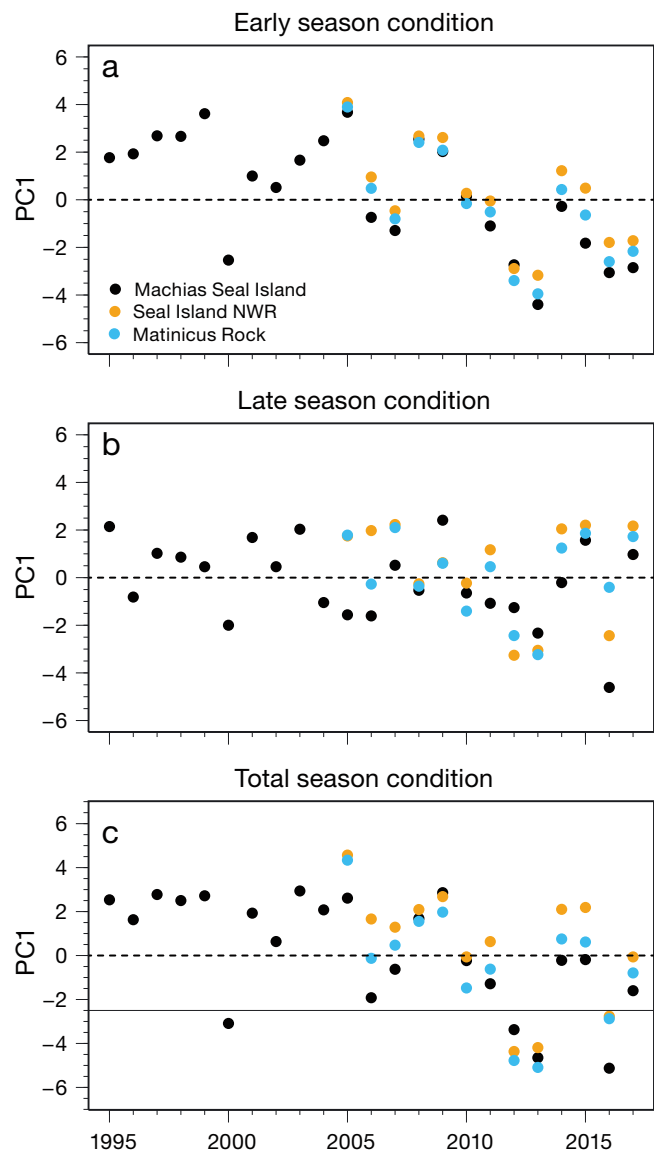

Fig. 5. Scores from principal component 1 identifying (a) early-, (b) late-, and (c) total-season condition of adult puffins *Fratercula arctica* at 3 colonies in the Gulf of Maine. Solid line in panel (c) is cut-off for especially poor years

mon after 2009 (Fig. 5b). Minimum scores varied by colony: 2013 at MR, 2012 at SINWR, and 2016 at MSI. Measures of breeding during chick-rearing had stronger loadings than SST or mass per feed.

In the total-season PCA, negative scores on PC1 were more common beginning in 2010 (Fig. 5c). The lowest scores by colony mirror late-season condition, but the difference between colonies in poor years was much smaller; 2012, 2013, and 2016 were poor at all sites. The strongest loadings on PC1 were measures of winter SST, followed by late-season breeding variables; PC2 represented seasonal timing.

3.4. Razorbill *Alca torda*: diet quantification

The ANOSIM identified differences between colonies (global R = 0.282, p = 0.005) and time periods (global R = 0.400, p = 0.009) for razorbills. The SIMPER test accounted for colony and time period. Herring was the most frequently consumed taxon at both colonies, but razorbills at MR consumed more white hake, haddock, and butterfish, while those at MSI consumed more herring and larval fish (Table 3). Over time, herring decreased at both colonies and was replaced by larval fish, sand lance, butterfish, hake, and haddock.

3.5. Razorbill: diet–reproduction relationships

Six response variables were analyzed. All biologically relevant main effects for razorbill condition models were negative (Fig. 6a–c). Diet variables were more common and had stronger mean effect sizes than environmental variables. Among the reproductive success models, only one positive main effect was found — a combined herring and sand lance measure, which appeared in fledge success

and hatch success models (Fig. 6e,f). Diet and environmental variables were equally common, and the mean magnitudes of the effects were similar. As in puffin models, most curvilinear effects were negative (Appendix S2). Provisioning data represented by mass per feed were similarly ranked but typically superior to measures by proportion, except for models of condition at banding and hatch success for which proportional diet fit much better.

Diet variables segregated strongly by response type. Euphausiids, butterfish, and haddock negatively affected all 3 chick condition variables. Larval fish, hake, and haddock negatively affected at least one measure of reproductive success. July rain was the most important environmental effect, followed by May SST and June rain.

3.6. Common murre *Uria aalge*

We investigated 2 condition variables; in both cases, the intercept-only model received the most support and no models were within 10 AICc units, so no effect sizes were generated. Univariate models received more support than multivariate models, so we ranked the univariate models relative to each other, noting the sign of effect. Effect sizes were still calculated, but we retained only models with an effect size within 2 orders of magnitude of the top-ranked univariate model (Appendix S2).

Within our univariate models, 4 represented diet; 3 positive variables represented butterfish, sand lance, and squid, and 1 negative variable represented a combined haddock and hake measure ('gadoids'). Two environmental variables were also ranked; SST in July showed a positive relationship, and rain in July negative. The 3 highest ranked variables, based on relative effect sizes, were gadoids, sand lance, and rain in July.

Table 3. Relative changes in razorbill *Alca torda* diets at colonies in the Gulf of Maine (Machias Seal Island, MSI, and Matinicus Rock, MR) before and after 2010. Mean values are by percentage of total mass in the diet. Entries are ordered by their contribution to group dissimilarity

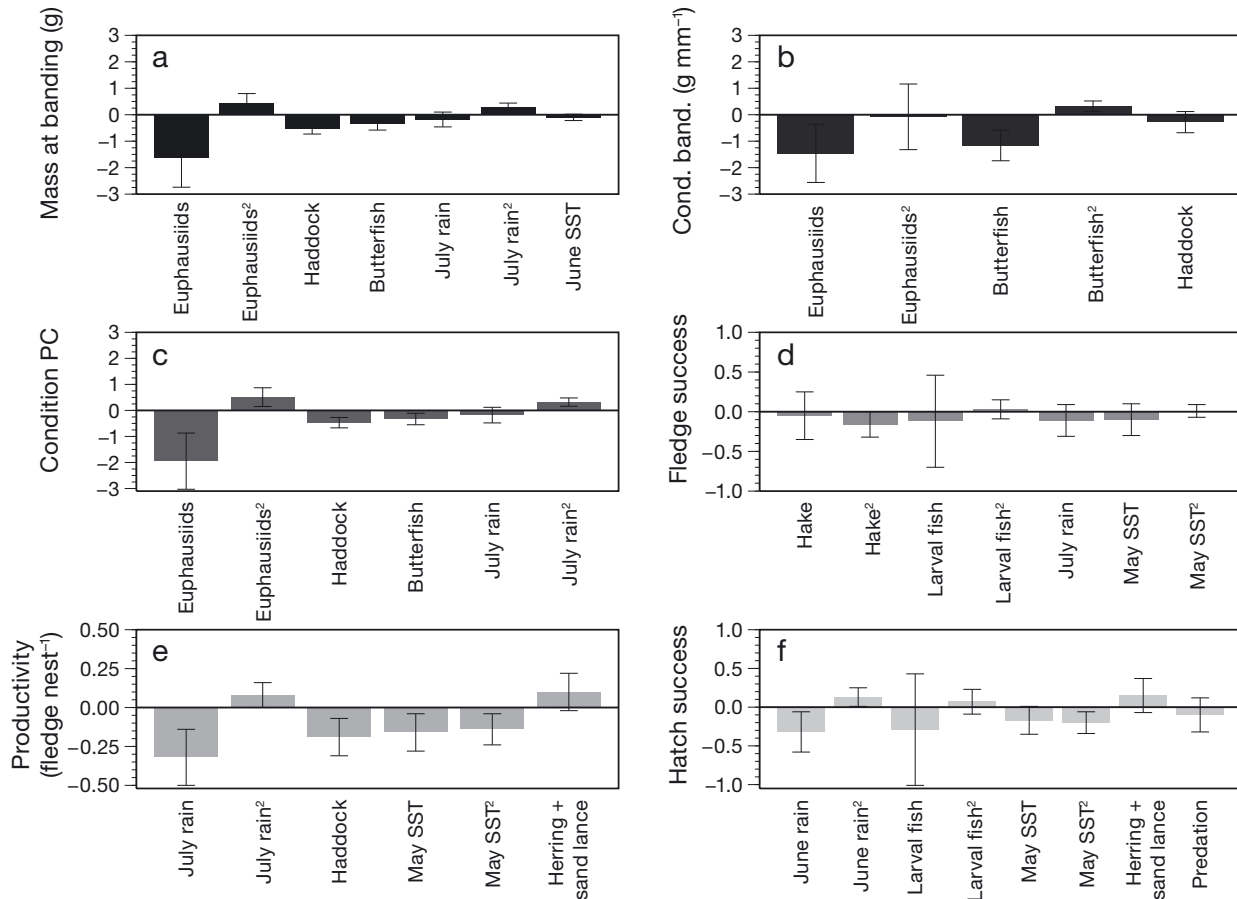| Taxon	Mean (1995–2009)	Mean (2010–2017)	Change	% Contribution to group dissimilarity	Mean (MSI)	Mean (MR)	Difference
Larval fish	1.31	3.06	+1.76	21.03	3.15	0.21	2.94
Sand lance	12.60	21.04	+8.44	17.25	15.96	17.04	1.08
Atlantic herring	65.09	42.62	−22.46	15.23	63.97	39.42	24.54
Euphausiids	0.04	0.02	−0.02	13.61	0.01	0.06	0.05
Butterfish	1.48	8.75	+7.27	13.57	2.69	8.30	5.61
White hake	17.42	20.11	+2.70	10.15	13.30	28.02	14.72
Haddock/pollock	2.07	4.39	+2.32	9.16	0.92	6.95	6.03

Fig. 6. Biologically relevant effect sizes in reproduction–diet models for razorbills *Alca torda* in the Gulf of Maine. Effects are on a normalized scale. Error bars are 95% CI (based on SE). [2]Indicates quadratic terms. SST: sea surface temperature. See Fig. 4 for explanation of axis labels

3.7. Community dynamics

Table 4 presents cross-species comparisons of all effects, ordered by prey category. Across all responses, we calculated the mean effects of each diet taxon on reproduction for each seabird species (Table S8), categorizing the effective value of prey type to seabird chicks (Table 5). Euphausiids were the worst available prey to all 3 seabird species. Butterfish were negative prey for puffins and razorbills but were positive for murres. Four taxa scaled with seabird body size: larval fish, hake, and haddock, all low-lipid prey, lost value as body size increased, whereas sand lance, a high-lipid prey, became more valuable. High-lipid herring were top-ranked prey for razorbills but were neutral for murres and had no effect for puffins, in spite of their abundance in puffin chick diet. Most new taxa were consumed by puffins only and ranked as neutral or negative. Environmental effects were most important to razorbills, but rain in July negatively affected all 3 seabirds.

4. DISCUSSION

All 3 seabird species showed distinct differences in their chick diets. Changes after 2010 reflected a consistent replacement of high-lipid taxa with lower-lipid prey. Puffins *Fratercula arctica* showed high interannual variability and a strong shift from herring *Clupea harengus* and hake *Urophycis tenuis* toward newer taxa, especially haddock *Melanogrammus aeglefinus* (and mixed juvenile gadoids). Razorbills *Alca torda* consumed most of the same prey during the time series, replacing herring with older taxa that were often high-lipid. Murres *Uria aalge* consumed several unique species and avoided small-sized prey. Reproductive responses of the alcids were generally consistent with predictions of the Junk Food Hypothesis, except that we typically found negative effects of low-lipid prey on seabirds, rather than positive support for high-lipid fish, i.e. 'junk' food was more influential than 'good' food. In the North Sea, comparable changes in chick diet of the same alcid species

Table 4. Comparison of effect sizes representing reproduction–diet relationships for 3 alcid species in the Gulf of Maine. Effects for puffins and razorbills are strongly negative (dark brown, >−0.5), weakly negative (light brown, <−0.5), weakly positive (light green, <0.5), or strongly positive (dark green, >0.5). Unshaded effects are <|0.1| but are part of quadratic terms or interactions. Effects for murres are shown as having more support (dark gray, <1 order of magnitude of the highest ranked effect size) or less support (light gray, <2 orders of magnitude). Old taxa were common in diets pre-2010, whereas new taxa were observed primarily in 2010 or later. SST: sea surface temperature; Cond.: condition; Cond. PC: principal component of condition variables; Prod.: productivity (chicks fledged per egg laid). Interactions between variables designated by ×

Variable	AP Mass at banding	AP Cond. at banding	AP Cond. PC banding	AP Mass at fledging	AP Cond. at fledging	AP Fledge success	AP Hatch success	RB Mass at banding	RB Cond. at banding	RB Cond. PC banding	RB Fledge success	RB Prod.	RB Hatch success	CM Mass at banding	CM Cond. at banding
Bad Year (2013, 2016)	−	−	−	−	−	−	−								
Old, high-lipid															
Butterfish	+	−	−	−						−				+	
Butterfish²	+	+		+					+						
Herring							−	−							
Herring²							+								
Herring × island (MSI)							+								
Herring × island (Seal)							−								
Herring + sand lance										+		+	+	+	−
Sand lance						+									
Old, low-lipid															
Euphausiids	−	−	−	−	−	−	−	−	−	−	−				
Euphausiids²	+	+	+	+	+	+	+	+	+	+	+				
Hake							−				−				
Hake × island (MSI)							+								
Hake × island (Seal)							−				−				
Hake²						−	−				+				
Haddock + Hake												−		−	
Larvals				+	+	+	+					−	−		
Larvals²						−	−				+		+		
New, high-lipid															
Redfish	+	+	+			−	−								
Saury + scad	−					+	+								
New, low-lipid															
Bluefish + squid + mackerel					+	+									
Haddock						−	−	−	−	−		−			
Haddock²							+								
Saury + scad + bluefish + mackerel + squid			−												
Squid	+						−							+	
Environmental															
Island (MSI)		−				−	−								
Island (Seal)															
Feeding rate	+														
Predation					−				−	−	−	−	−	+	−
July rain						−			−	−	−				
July rain²					+	+		+	+	+		+	+		
June rain													−		
June rain²												−	+		
May SST											−	−	−		
May SST²											+		−		
June SST	−														
July SST														+	

Table 5. Comparison of prey value for 3 alcid species in the Gulf of Maine region. Taxa are designated based on their value to chicks of each seabird species. 'Value' reflects species-specific responses to changes in prey abundance, based on observed relationships between prey taxa and reproduction or chick condition. Baseline species had no measured effect size but made up a majority of diet. See Section 3.7. for explanation of value

Value	Atlantic Puffin	Razorbill	Common Murre
Highest	Redfish	None	Sand lance
Positive	Larval fish	Atlantic herring Sand lance	Butterfish
Neutral/ baseline*	Atlantic saury Rough scad Sand lance Atlantic herring* Haddock* White hake*	Larval fish White hake	Atlantic herring Rock gunnel Squid
Negative	Bluefish Butterfish Mackerel Squid	Butterfish Haddock	Haddock White hake
Lowest	Euphausiids	Euphausiids	Euphausiids Larval fish

occurred; high-lipid sandeels *Ammodytes marinus* were replaced by high-lipid clupeids, but reproductive success did not decline because the 'dietary quality of the alternative prey are all broadly comparable in energetic value' to sandeels (Wanless et al. 2018, p. 203).

The diverse reproductive responses by different alcid species in the GOM to the same prey demonstrate that lipid content alone is not enough to define the value of a prey taxon to a particular predator. We suggest that lipid content and energy density are best regarded as traits of prey rather than as defining its 'quality' to a predator; the value of prey to a predator is reflected in the predator's reproductive response to the prey, rather than being an intrinsic characteristic of a prey taxon. We therefore propose the term 'value' of prey as distinct from lipid content, energy density, or 'quality' and defined by a species' reproductive responses to changing amounts of the taxon in the chick diet.

4.1. Changes in the marine environment

The environmental context for our study is important. The GOM has undergone at least 3 climate-driven regime shifts since the 1980s from a combination of local atmospheric warming and remote forcing

from the rapidly warming Arctic Ocean (Greene et al. 2013). Concurrent northward movement of the Gulf Stream has caused widespread warming in the northeast Atlantic, with dramatic effects on seabirds there including reduced breeding success (Foster & Marrs 2012, Frederiksen et al. 2013, Miles et al. 2015). The changes in alcid diet we document here are best discussed in this context and suggest similar changes may be beginning in the northwest Atlantic.

In the early 2000s, the Labrador Current brought increased flows of cold, fresh, nutrient-poor water from increased melting in the Arctic (Townsend et al. 2010) into the GOM, changing its circulation patterns (Greene & Pershing 2007, Smith et al. 2012). Nutrient status has also declined in recent years (Peppin et al. 2013), and changes in plankton communities indicate reduced feeding conditions for planktivorous fish (Johnson et al. 2018), on which many seabirds feed. The copepod *Calanus finmarchicus* has declined in both abundance and lipid content; it is the most lipid-rich prey of many larval fish and the major prey of endangered North Atlantic right whales *Eubalaena glacialis* (McKinstry et al. 2013). Many right whales formerly spent summers feeding on these copepods in the Bay of Fundy, but since 2011 have largely abandoned it and moved north (Pace et al. 2017). Linkages between declines of *C. finmarchicus* and seabirds have also been identified in the northeast Atlantic (Frederiksen et al. 2013).

The decline of *C. finmarchicus* and right whales coincided with seabird diets changing markedly in the GOM; we therefore suggest that the diet shifts we observed were driven by recent oceanographic changes impoverishing the marine food web, cascading upward to affect seabirds through their prey, including changes in fish distribution (Rose 2005, Nye et al. 2009, Pinsky et al. 2013). Ocean warming and recovery from overfishing have moved redfish *Sebastes* spp. into foraging areas around the 2 southernmost colonies, partially mitigating the decline in herring there, but redfish have not yet reached the most northerly colony of MSI.

4.2. Prey value to alcid chicks in the GOM

Our calculated prey values showed inconsistent correlations with lipid content. Small, low-lipid euphausiids were a universally poor choice; their presence in the chick diet was negative for puffins and razorbills, and murres avoided them completely. This pattern is perhaps related to the higher salt content of euphausiids; processing euphausiids may require fully devel-

oped salt glands in chicks, as in common eiders *Somateria mollissima* (DeVink et al. 2005). The high flight cost of alcids also makes it energetically inefficient for them to feed their chicks such small and low-quality prey; this would be especially true for murres, less so for razorbills and least for puffins, as reflected in the proportion of euphausiids each species consumed. The presence of euphausiids in alcid chick diet indicates a dearth of alternative prey and is cause for concern however small the proportion (see also Kauffman 2012), though not necessarily so in smaller-bodied terns (Laridae) (Scopel & Diamond 2018).

Four prey taxa showed changes in value scaling with seabird body size. Low-lipid hake, haddock, and larval fish were worse for larger alcids, while sand lance *Ammodytes* spp., a high-lipid fish, was neutral for puffins and highest-ranked for razorbills and murres. Based on flight costs and prey-loading (Wanless et al. 2018), we would expect puffins to be the least selective regarding the energy density of their prey, consistent with these findings. Razorbills and murres, with increasing flight costs and chick guarding needs (Gaston & Jones 1998), have more constraints on the prey that they provide to chicks (Burke & Montevecchi 2008). While both puffins and razorbills brought fewer herring in 2010 and later, razorbills fed more high-lipid prey as replacements and were less likely to bring in new taxa than puffins. Single-loading murres, whose feeding rate and bill load size are limited by high flight costs (Elliott et al. 2013), rarely brought in small low-lipid prey and were negatively affected by low-lipid gadoid prey, indicating that prey size is an important component of their foraging needs during chick rearing.

Other prey had values inconsistent with their lipid content. Butterfish *Poronotus triacanthus* are rich in lipids and positively influenced murre chick condition, but negatively affected chick condition of puffins and razorbills, likely because they are too deep-bodied for young chicks to swallow. Low-lipid (Table S4) and large-bodied squid *Illex* spp. had negative effects on puffins, were avoided by razorbills, but were neutral for murres. While the shape and energy density of squid may have been unappealing to smaller and multi-prey loading puffins and razorbills, a large squid would make an efficient meal for a single-prey loading murre parent, despite the lower fat content. Finally, high-lipid herring was a neutral yet initially abundant prey for puffins, neutral for murres, and highest-ranked but with a small effect size for razorbills. Herring are widely regarded as one of the best available prey in the GOM (Golet

et al. 2007, Pikitch et al. 2012, Breton & Diamond 2014) and made up the majority of seabird diets in the GOM when they were abundant (Diamond & Devlin 2003, Kress et al. 2016). There was also a strong negative correlation between gadoids and herring in the murre diet, indicating that murres may have consumed low-lipid prey only when herring were not available. We therefore suggest that many of the taxa that showed no statistical effect, and which are typically numerous in chick diet — namely white hake (for puffins), sand lance, and herring — constitute a high-value 'baseline' that is the foundation of alcid diets in this region (see Cury et al. 2011). Fluctuations of these baseline taxa did not typically explain changes in alcid reproductive success and chick condition; it was the taxa replacing them that best explained the reproductive responses we measured. Baseline taxa are thus more challenging to rank owing to their prevalence, but when new taxa become more abundant we can judge their quality relative to the baseline.

The remaining new taxa were consumed only by puffins and were irregular components of their diet. Their value scaled directly with their lipid content. High-lipid redfish were the highest ranked taxon for puffins, but the remaining taxa were either neutral or negative. These new taxa appeared in puffin diets only in years when hake, herring, and sand lance made up <80 % of the diet by mass; their modest contribution to total mass in these years and absence in the diet of other seabirds further suggests that puffins may have consumed them owing to a lack of preferred prey, rather than unusually high abundance of these new taxa. Even for the generalist puffins, most new taxa were not adequate replacements to baseline prey, and their presence in the diet may indicate difficult foraging conditions.

The different responses to poor-quality prey by the 3 seabirds have implications for using seabirds as indicators of environmental change. The longer growth period of puffin chicks on land (compared with razorbills and murres) allows them to survive short periods of food shortage by reducing metabolic rate (Kitaysky 1999) and accumulating subcutaneous fat when food is plentiful (Øyan & Anker-Nilssen 1996); extended (or 'retarded; Barret & Rikardsen 1992) fledging periods are well known as a response to food shortage in puffins (Eilertsen et al. 2008, Harris & Wanless 2011, Whidden 2016) but not razorbills or murres. Puffins' prolonged rearing period at the colony allows chicks to endure short periods of low-quality food and still fledge successfully, albeit in poor condition with reduced survival prospects (Kress et al. 2016, Whidden

2016). Puffins, whose breeding seasons on land can be extended if food is short, require a stable and persistent prey base (e.g. herring, hake, haddock, or sand lance) that does not need to be of high energy density, so long as it is accessible. Razorbills and murres, however, with their shorter chick-rearing period on land, evidently rely more on high-quality prey. The higher flight cost of murres requires greater selectivity of high-energy prey compared with the more generalist puffins (Burke & Montevecchi 2008) with their smaller flight costs; razorbills are intermediate in both flight cost and prey selectivity. Furthermore, only one razorbill or murre adult forages for chicks while the other guards the young, whereas adult puffins can forage simultaneously because the chick is protected by its underground nest site. Razorbills and murres are thus further restricted in their foraging relative to puffins. The different responses of each species are consistent with the constraints of optimal foraging (Orians & Pearson 1979) increasing with energetic demands, driven by differences in foraging costs and patterns of chick development. Ultimately, different species exposed to the same changing prey field can respond differently despite broadly similar foraging methods.

4.3. Spatial variability: puffins and razorbills

Colony-specific effects influenced the reproductive success of puffins. At MSI, chicks were smaller, and hatch and fledge success were lower than at the colonies in Penobscot Bay; MSI's colony is 10-fold larger than the others (Table S1). We attribute the poorer chick condition and lower reproductive success on MSI to more intense density-dependent competition for food. This idea is supported by negative correlations between chick fledging mass and colony size across the North Atlantic (Gaston & Jones 1998, p. 291).

Razorbills showed inter-colony differences in chick diet but no inter-colony differences in reproductive measures. Despite breeding on the same islands as puffins, razorbills did not consume the newer taxa that puffins did and showed less interannual variability in chick diet. Razorbill diet was more specialised than puffins; herring, sand lance, and hake dominated diet at both colonies and appeared adequate to meet the energetic needs of chicks in most years. MSI supports 5-fold as many razorbills as MR, yet the relative colony size did not seem to affect razorbill reproductive success. In spite of razorbills' higher foraging costs, they appeared more capable of meet-

ing their chicks' energetic needs compared to puffins. Other studies of razorbill diets had difficulty linking them with independent measures of fish abundance (Harris & Wanless 1986, Frederiksen et al. 2006, Scopel et al. 2018), possibly because razorbills can adjust their time budgets to account for changes in provisioning needs (Furness & Tasker 2000). Despite evidence that razorbills did need high-fat fish to be successful, the negative impacts of low-lipid prey were not as drastic as in puffins.

4.4. Low reproductive success: puffins

The bad year variable helped to explain anomalous puffin responses in 2013 and 2016, revealed by strongly negative residuals during model fitting; given the chick diet in those years, puffins underperformed their expected reproductive success. These years corresponded with poor puffin reproductive success, but for different reasons.

The early-season condition PCA revealed poorer incoming adult condition after 2010 (Fig. 5a); this effect was driven by winter SST, presumably affecting puffins' overwinter food supply, and was strongest in 2013. The 2012–2013 winter featured mass mortality events and unusual movement patterns of razorbills (Brinkley 2013, Robben et al. 2014, A. Diamond pers. obs.) and a wreck of puffins and razorbills at Cape Cod (A. Diamond pers. obs); at MSI, laying in 2013 was the latest on record and birds were in poor condition, abandoning breeding during incubation or early chick-rearing.

The late-season condition PCA identified a different pattern during chick rearing, driven by summer prey quality. This describes differences between colonies in 2012 and 2016, where prey quality was worse at particular colonies. In 2012, despite high summer SST, model residuals were unremarkable despite poor breeding success at MR and SINWR, where chick diets featured new taxa and butterfish. Meanwhile, puffin chicks at MSI consumed a typical herring-hake diet, and breeding success was normal. Conversely, 2016 began as a typical season, but rapid temperature increases in June and July led to very low provisioning rates at MSI and SINWR in July, and chick growth stalled at MSI. MR and SINWR experienced food shortage but had fair to average success, bolstered by newer taxa, especially redfish at MR. Redfish mitigated challenging environmental conditions there but were not found at MSI, where chick condition and productivity were the lowest on record. The late-season PCA indicated that adults in

poor incoming condition can be 'rescued' by high-quality prey, as they were in 2015 and 2017 (Fig. 5b); incoming condition in 2013 was evidently too poor to be rescued by high-quality prey.

Combining both time periods, poor overwinter conditions in 2013 and poor summer conditions of 2012 and 2016 were equally weighted by the PCA (Fig. 5c), indicating that there are multiple ways for these catastrophic breeding seasons to arise. All 3 summers were preceded by warm winters, which we identify as the strongest indicator of bad years for puffins. Out of 13 years, MSI had the lowest late-season condition score of the 3 colonies 9 times; the studied colonies at MR and SINWR are smaller and consume a wider suite of prey, and thus may be more resilient to prey fluctuations. These results underscore the potential importance of range shifts (Rose 2005, Nye et al. 2009, Pinsky et al. 2013), especially of incoming alternative prey; if these have high energy density and are of suitable size, predators may breed successfully even when baseline prey are scarce, but lower-quality replacements can lead to reduced breeding performance under the same environmental conditions.

4.5. Environmental effects

We found that rainfall had a universally negative effect on alcid chicks, especially razorbills and murres during chick rearing. This effect is likely directly related to thermoregulation of chicks at the more exposed nests of razorbills and murres.

Each species also responded differently to SST. Increasing water temperature can induce fish to shift distribution (Rose 2005, Nye et al. 2009, Pinsky et al. 2013, Poloczanska et al. 2016), reduce growth rate and recruitment (Deutsch et al. 2015, Pershing et al. 2015), or dive to deeper, cooler water (Pinsky et al. 2013); any of these responses might affect their availability to seabird predators. Puffins showed strongly negative relationships between SST and breeding measures, where the breeding stage was associated with that month's SST. This strong temporal coupling suggests that temperatures affect fish (and the puffins' ability to obtain prey) directly over short time scales. SST in May negatively affected razorbills' reproductive success, but this relationship would be concentrated on adults before hatch; this suggests that razorbill success is determined primarily from their pre-breeding condition. Razorbills may travel longer distances to forage as SST increases (Shoji et al. (2014); longer foraging trips would be energetically expensive and likely indicate local food short-

age. For murres, where only chick condition was examined, July SST had a positive relationship with condition, in contrast to the other alcids. If warmer water drives fish deeper or increases their activity, the greater diving ability of murres (Piatt & Nettleship 1985) would allow them to track these fish best.

4.6. Environmental outlook

Recent marine heatwaves (Mills et al. 2013, Pershing et al. 2018) and the corresponding diet shift of our study species indicate that the GOM has undergone a regime shift since 2010, at least in terms of seabird chick diet. The GOM temperature anomaly in 2010 exceeded all anomalies recorded since 1980 (Pershing et al. 2018, their Fig. 4a), and anomalies have remained unprecedentedly high thereafter. Johnson et al. (2018) identified major changes to the Scotian Shelf and eastern GOM beginning in 2010, including increases in temperature and stratification, and decreases in deep nutrients and plankton abundance. Changes in plankton community composition to smaller organisms reduce transfer efficiency, and negatively affect forage fish and their predators. Each seabird species is likely to deal with these changes differently, related to their life history and behaviour.

Puffins are the most flexible in terms of dietary needs but have the longest breeding seasons and are the most affected by heatwaves. As temperatures increase, prey will move deeper and will be difficult for puffins to catch. This may explain why razorbills were able to switch to hake after 2010, while puffins at the same colonies delivered fewer hake and switched to newer taxa that razorbills avoided. Puffins have recently decreased their occupancy rates at MSI, indicating skipped breeding seasons, and have had multiple low-productivity seasons driven by high SST. Differences between MSI and the Penobscot Bay colonies also suggest that puffins at MSI are approaching a limit: further increases to the razorbill and murre populations in tandem with high SST could reduce the size of the puffin colony there.

Trends in razorbill reproduction at MSI indicate reduced breeding success since 2006, yet the population in the GOM continues to grow. Herring, while formerly preferred, have been only partially replaced by high-lipid sand lance; razorbills now bring more gadoids, which reduce reproductive success, but their effect has been small. Should high SST persist and diet shifts continue, razorbills may face future reductions in breeding output; future monitoring

should carefully consider diet composition, adult foraging behaviour, and reproductive metrics.

Although our murre data encompass only 5 yr from MSI, murre chicks were negatively affected by small or low-lipid prey. Murres have the highest constraints on their foraging behaviour (Burke & Montevecchi 2008) yet are able to raise chicks on low-lipid prey if the prey size is large enough. Squid were more abundant in years of high SST, indicating a potential boon to murres. Murre chicks also benefited from higher SST in July, which, when combined with their growing regional population, suggests that murres may thrive in the future.

Rain negatively affected all 3 species, especially razorbills and murres. While alcids in the GOM nest in sheltered sites, the greater exposure of razorbill and murre nests could negatively affect chicks and further constrain the foraging choices of adults by requiring them to spend more time brooding chicks. There are clearly interactions with the environment that we have not fully described. Closer examination of relationships between juvenile forage fish and environmental conditions would be an excellent area of future study, particularly as it relates to energetics of adult puffins. The influence of winter sea conditions on puffins also indicates an urgent need to determine the diets of adults, which might differ significantly from those of chicks.

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