Contrasting phenological and demographic responses of Atlantic Puffin (*Fratercula arctica*) and Razorbill (*Alca torda*) to climate change in the Gulf of Maine

Heather L. Major¹,* , Sarah E. Durham¹, Natalia Fana¹, Joy E. Rivers¹, and Antony W. Diamond²

The Gulf of Maine is warming faster than most of the world’s ocean and is also the southern-most limit for nesting, cold-adapted Atlantic Puffin (*Fratercula arctica*) and Razorbill (*Alca torda*). Beginning in 1995, the Atlantic Laboratory for Avian Research has collected annual data on phenology, productivity, and fledgling body condition for puffins and Razorbills nesting at Machias Seal Island. Here, we aimed to quantify changes in these measures of breeding performance and assess whether they are related to environmental conditions. As predicted, we found that all measures of breeding performance (except puffin fledge date) have changed between 1995 and 2020, and in many cases, puffins and Razorbills are responding differently. Specifically, hatch date has retreated for puffins (occurring approximately 1 week later in 2011–2020 than in 1995–2004) and advanced for Razorbills (occurring approximately 1 week earlier in 2011–2020 than in 1995–2004). We found that environmental conditions were important predictors for measures of breeding performance, but importance of environmental conditions differ both between the species and among the measures of breeding performance. As the climate continues to warm, we expect continued changes in breeding performance of puffins and Razorbills. Further research is needed to understand the reasons for differences between the 2 species and the impacts of continued warming.

**Keywords:** Alcidae, Sea surface temperature, Hatch date, Fledge date, Reproductive success, Body condition

**Introduction**

Many ecosystems are undergoing dramatic changes associated with anthropogenic climate change resulting in varied impacts on marine life (Poloczanska et al., 2013; Poloczanska et al., 2016). Documented regime shifts (e.g., Wernberg et al., 2016; Morse et al., 2017), and changes to the distribution of species (e.g., Walther et al., 2002; Perry et al., 2005; Cristofari et al., 2018), phenology (e.g., Kharouba et al., 2018), and demographics (e.g., Jenouvrier et al., 2018; Hipfner et al., 2020; Price et al., 2020) are widespread. Changes in sea surface temperature (SST) noted around the globe are of particular concern as many marine species, and in particular marine birds, are adapted to live in limited thermal ranges (Cairns et al., 2008; Sunday et al., 2012; Grady et al., 2019). Climate change (including changing SSTs) has resulted in observed reorganizations of marine species and ecosystems (e.g., Beaugrand, 2004; Hays et al., 2005; Albai et al., 2018) and ecological mismatches (e.g., Hipfner, 2008; Watanuki et al., 2009). For example, in the Isle of May, documented changes in the timing of lesser sandeel (*Ammodytes marinus*) reproduction resulted in a shift in phenology of 6 species of seabird that rely on sandeels reaching a certain size to provision their chicks (Burthe et al., 2012). However, even with a shift in phenology, adult birds were unable to shift their nesting phenology sufficiently and began feeding their young smaller sandeel, with negative consequences to their own reproductive success (Burthe et al., 2012).

Marine birds play an important role in the marine ecosystem because they are top consumers and can be used as indicators of the marine environment (Cairns, 1987; Piatt et al., 2007). Marine birds can be used to detect changes in the availability of their prey species (Cairns, 1987; Diamond and Devlin, 2003) and used to monitor anthropogenic impacts such as pollution (Furness and Camphuysen, 1997; Burger and Gochfeld, 2004), climate change (Diamond and Devlin, 2003; Grémillet and Boulinier, 2009), and fisheries (Einoder, 2009).

Waters in the Bay of Fundy/Gulf of Maine are rapidly warming, with documented marine heat waves in the last
10 years and regime shifts in 2006 and 2010 (Mills et al., 2013; Chen et al., 2014; Pershing et al., 2015; Kress et al., 2016; Scopel et al., 2019). In this region, the impacts of climate change and ocean warming are being noted in the marine inhabitants (e.g., Morse et al., 2017; Scopel et al., 2019; Staudinger et al., 2019). At Machias Seal Island, the Atlantic Laboratory for Avian Research (ALAR) has been monitoring the demographics of nesting seabirds since 1995. Many of the seabird species breeding at Machias Seal Island, in particular Atlantic Puffin (*Fratercula arctica*; hereafter “puffin”) and Razorbill (*Alca torda*), are cold-adapted species, nesting at the southern extent of their global ranges in the Gulf of Maine (Diamond and Devlin 2003; Gaston et al., 2009; Lavers et al., 2020; Lowther et al., 2020). Thus, these species are at particular risk from climate change and ocean warming. In fact, previous work in the Gulf of Maine has revealed important linkages between measures of seabird biology and climate-related changes in prey species and availability and environmental conditions (Kress et al., 2016; Whidden, 2016; Scopel et al., 2019).

Puffins and Razorbills are widely distributed in the North Atlantic with breeding populations in Greenland, Iceland, United Kingdom, France, Norway, Russia, and along the Atlantic coast of Canada and United States of America (Lavers et al., 2020; Lowther et al., 2020). Populations of both species in the Western Atlantic are thought to be stable or increasing (Wilhelm et al., 2015). Yet, over the last 26 years, researchers on Machias Seal Island and other Gulf of Maine islands have observed changes in chick growth and diet, productivity, and phenotype that are likely related to changes in prey (Kress et al., 2016; Whidden, 2016; Scopel et al., 2018; Scopel et al., 2019; Depot et al., 2020). In the Bay of Fundy/Gulf of Maine, puffins and Razorbills feed on adult and larval sand lance (*Ammodrtes* sp.), white hake (*Urophycis tenuis*), Atlantic herring (*Clupea harengus*), Atlantic butterfly (*Peprilus triacanthus*), and haddock (*Melanogrammus aeglefinus*; Scopel et al., 2019; ALAR, personal communication, 2019). Although puffins and Razorbills are closely related, they differ in some important biological aspects, primarily their strategies of chick development. Puffin chicks are semi-precocial, requiring adult provisioning for up to 40 days until the chick departs the nesting site alone (Gaston, 1985). Razorbills have a more intermediate strategy, where chicks require adult provisioning throughout chick development, but the chick departs the island with their male parent after 16–22 days and completes development at sea with that parent (Gaston, 1985). Further, Scopel et al. (2019) found that puffin chick diet is more variable than Razorbill chick diet, but because puffin chicks remain at the colony longer, they are more likely to be affected by marine heat waves, especially because these heat waves occur mostly in late summer (Pershing, 2020) after Razorbills have left the colony. In both species, the condition of adults when they arrive at the nesting colony at the start of the breeding season is an important determinant of productivity in that year (Scopel et al., 2019). Puffins and Razorbills acquire nutrients for eggs by a combination of income and capital breeding (Bond and Diamond, 2010). Thus, prey quality and availability in the late winter and early spring play a major role in the breeding success of these species (Durant et al., 2003; Scopel et al., 2019).

Here, our goals were to (1) quantify the changes we have observed in phenology and productivity for sympatrically nesting Atlantic Puffins and Razorbills and (2) evaluate whether changes in these metrics are related to changing environmental conditions (e.g., SST) in the Gulf of Maine. SST threshold temperatures are advancing by about 0.5 d/yr, and warming trends are weakest in winter, positive May–June, and strongest (approximately 1.0°C/decade) in late summer (July–September; Thomas et al., 2017). Based on relationships identified by Durant et al. (2003), Whidden (2016), and Scopel et al. (2019), we predict that (1) early in the nesting season, increases in SST during winter (September–February) and spring (March–May) result in a delay in hatch date and a decrease in hatch success, and (2) increases in spring air temperature and precipitation similarly result in decreased hatch success. For measures associated with the chick rearing period (i.e., fledge date, fledge success, and puffin fledgling body condition), when both species are restricted to forage near the nesting colony, we predict that increases in SST during summer, air temperature, precipitation, and decreased quality of prey (as defined in Scopel et al., 2019) feed to chicks result in declines in fledging success, delayed fledge date, and decreased fledgling body condition, especially in puffins because of their longer exposure to late summer conditions.

**Materials and methods**

**Study site**

Machias Seal Island is a small island (9.5 ha) located at the mouth of the Bay of Fundy, Canada (Figure 1), and is a designated Migratory Bird Sanctuary. During the summer, it supports the most diverse suite of nesting seabirds in the Canadian Maritimes, including Atlantic Puffin, Razorbill, Common Murre (*Uria aalge*), Common Tern (*Sterna hirundo*), Arctic Tern (*Sterna paradisaea*), Leach’s Storm-petrel (*Hydrobates leucourous*), and Common Eider (*Somateria mollissima*). Researchers from ALAR at the University of New Brunswick have conducted research and monitoring of the nesting seabirds at Machias Seal Island in each year since 1995. Populations of Atlantic Puffin and Razorbill were last estimated as approximately 8,500 and 3,000 pairs, respectively, in 2019, representing a stable population of puffins and increasing population of Razorbills (ALAR, personal communication, 2019).

**Seabird data collection**

Since 1995, we have collected numerous measures of seabird biology annually at MSI. Here, we focus on 3 of those measures (phenology, productivity, and fledgling body condition).

**Phenology—Hatch date**

For puffins and Razorbills, hatch date was determined from permanently marked nest sites that are checked for the presence or absence of an egg during the month of May. All nest sites that had an egg (i.e., “active” nests) are...
rechecked every few days around the estimated date of hatch, which is calculated as 37 days (puffins) and 35–37 days (Razorbills) from the date an egg is first observed. Hatch date is classified as “known” when a new chick is found that is wet and/or has bits of eggshell attached to its down, or “estimated,” when age is based upon the size and weight of the chick when first found in comparison with those classified as “known.” In each year, we note the total number of nest sites among our permanent set that are active. We then calculate an estimate of nest site occupancy as:

$$\text{Occupancy} = \frac{\# \text{active nest sites}}{\# \text{permanently marked nest sites}}.$$ 

Because our permanently marked nest sites were first marked in 1995, there are no occupancy data for that year. Our analyses of hatch date use the time series 1996–2020.

**Phenology—Fledge date**

Puffin chicks fledge at night, when many are attracted to the light from the light station and congregate on the mown lawn around the light station where they are easily captured. Beginning just before the predicted fledge date for chicks in our monitored burrows (i.e., 35 days after the first monitored chicks hatch), crews begin nightly surveys of the lawn in front of the light station for fledgling puffins (checks begin just after dark and continue at half-hour intervals until sunrise). All captured puffin fledgers are banded, measured, and weighed before being released near the water. This practice provides unique data on the timing of peak puffin fledge from the colony and an estimate of body condition of puffin fledgers on the night they depart the island. Here, we use data from the lighthouse fledgers to relate environmental conditions with fledge date and body condition. Because puffins continue to fledge after our crews have left the island, we miss the latest fledgers. Our estimate of mean fledge date is therefore biased early. However, our data collection method does capture the peak of puffin fledge in each year; thus, any bias would be slight and consistent over our time series. Fledge date is not recorded in Razorbills because attempting to do so would disrupt the chick–parent bond, as the male parent takes the chick to sea in daylight.

**Productivity**

Permanently marked nest sites described in our phenology section are also used for productivity. Here, marked sites are checked for presence of an egg when crews arrive on the island in May and are rechecked for hatching as described above. After hatch, during chick brooding and

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**Figure 1.** Map showing location of Machias Seal Island and 48 grids from which sea surface temperature (SST) was extracted. Map showing location of Machias Seal Island and the 48 grids that were used in estimating SST in winter (September–February), spring (March–May), and summer (June–July). DOI: https://doi.org/10.1525/elementa.2021.00033.f1
provisioning, sites are rechecked approximately once a week until the chick disappears or is found dead. A chick is considered fledged if it survives 35 days (puffins) or 9–11 days (Razorbill). We calculate productivity as:

$$\text{Productivity} = \frac{\# \text{chicks fledged}}{\# \text{eggs laid}}.$$

Here, we assess changes over time for productivity but treat hatch and fledge success separately in relation to environmental conditions because they occur at different times of the year and are subject to changing environmental influences (Scopel et al., 2019). Hatch success is calculated as:

$$\text{Hatch Success} = \frac{\# \text{chicks hatched}}{\# \text{eggs laid}}.$$

And fledge success is calculated as:

$$\text{Fledge success} = \frac{\# \text{chicks fledged}}{\# \text{chicks hatched}}.$$

Note that productivity data are subject to more uncertainty in Razorbills than in puffins because of the shorter and more variable fledging period of Razorbills.

### Body condition

We developed a puffin fledger body condition index (BCI) using the scaled mass index method outlined by Peig and Green (2009, 2010) for our lighthouse fledgers. In brief, we calculated the values of extreme outliers (i.e., mass and wing chord measurements greater and less than 3 \times \text{interquartile range}) and excluded them from the dataset. Next, we log-transformed our mass and wing chord data for the entire 26-year dataset (i.e., 1995–2020) and used the ‘model2’ program (Legendre, 2018) in the R studio environment (R Core Team, 2020; RStudio Team, 2020) to perform a ranged major axis regression (RMA) on the log-transformed data. Using the equation developed by Peig and Green (2009), we calculated the predicted body mass for each individual (including those that were considered extreme outliers in the first step) and calculated BCI as the difference between the observed and predicted mass. Here, a positive value denotes an individual that is heavy for its body size and is therefore considered in good condition and a negative value one that is light for its body size and is in poor condition. There are no equivalent data for Razorbills.

### Chick prey quality

Over the chick-rearing period, observations of prey species and size are recorded during multiple 3-h prey watches each year; these data are then used to calculate the total biomass of each prey species brought into the colony for chicks (see Scopel and Diamond, 2018; Scopel et al., 2019, for detailed methods). We calculated prey quality as the proportion of the total biomass of prey brought into the colony for chicks that was of poor quality (prey was assigned as poor, moderate, or high quality with reference to Scopel et al., 2019).

### Environmental data

Each day on MSI we record daily precipitation amount (mm), and air temperature (min and max °C); here, we used total precipitation amount expressed as millimeters per day and mean minimum daily temperature between May 15–June 15 as “spring” (for both puffins and Razorbills), June 16–August 5 as “summer” for puffins, and June 16–July 15 as “summer” for Razorbills (because most Razorbills leave the island by mid-July). In 2020, due to COVID-19, we were unable to begin our studies on MSI until July 4; thus, for both puffins and Razorbills, our record of summer precipitation and summer air temperature begins July 4, 2020 (no data on spring precipitation or air temperature were collected). We downloaded SST data from the National Oceanic and Atmospheric Administration (NOAA) Physical Sciences Laboratory website (https://www.psl.noaa.gov). Specifically, we extracted SST data from the NOAA Optimum Interpolation (IO) SST V2, which contains monthly means for 1981–2020 on a 1° latitude by 1° longitude grid. For both species, we extracted SST for 2 grids (i.e., grids 2 and 3; Figure 1) surrounding MSI for the months of June and July in 1995–2020 (i.e., during the breeding season when nesting adults remain close to MSI; see Baran, 2019, and M Dodds, unpublished data; termed “summer”). For puffins, we extracted SST from 39 grids (i.e., grids 9–48; Figure 1) in the Gulf of Maine for the months September–February (when puffins are located in the southern Gulf of Maine near Cape Cod, see Baran, 2019; termed “winter”). For Razorbills during the same time period, we extracted SST from 13 grids (i.e., grids 1–13; Figure 1) in the Gulf of Maine because most Razorbills tend to be resident in the Gulf of Maine all year (M. Dodds unpublished data). For these same 13 grids, we extracted SST for the months of March–May (when both species are present in the Gulf of Maine and returning to MSI; termed “spring”). Our value for SST was calculated as the median value over the range of grids and months sampled. Finally, we downloaded the North Atlantic Oscillation Index (NAO [DJFM]; PC-based) from the NCA/UCAR Climate Data Guide Website (Hurrell, 2005, 2020) for each year in our dataset.

### Statistical analyses

All statistical analyses were conducted using the R Studio Environment (v. 3.5.2) and used an information theoretic approach. Here, we used the R package “MuMIn” (Barton, 2020) and ranked models using Akaike’s Information Criterion (AIC) for small sample sizes (AICc), AIC, weights ($\omega_o$) were used to evaluate model likelihood (Burnham and Anderson, 2002). We used model averaging, from the R package “MuMIn”, and the “natural average” method as described by Burnham and Anderson (2002) and Grueber et al. (2011), to draw inference from our dataset when the top supported candidate model received less than 90% of the total weight among candidate models (Johnson and Omland, 2004). Specifically, we use weighted parameter estimates, unconditional standard errors, and relative variable importance (termed “relative importance”; i.e., the sum of $\omega_o$) to draw inference from our dataset. Summary data are presented as means ± 95% confidence intervals.
To evaluate changes in phenology, productivity, and body condition between 1995 and 2020 (data from 2020 were excluded for puffin and Razorbill hatch success, as COVID-19 restrictions limited our data collection in that year) we used the “nlme” package in R (Pinheiro et al., 2020) and a series of generalized least square (GLS) models (for hatch date, fledge date, and BCI) and logistic regressions (hatch and fledge success). For our GLS models, we first ran the global model (i.e., the most highly parameterized model) fit by restricted maximum likelihood (REML) and checked model diagnostics. In all cases, models met assumptions of linearity except they showed temporal autocorrelation. To define the autocorrelation structure, we used an autoregressive moving average (ARMA) serial correlation structure. To find the optimal ARMA structure, we used all combinations for p and q from 0 to 5 and compared them with AIC. The model with the lowest AIC value was taken as containing the optimal ARMA structure (see Zuur et al., 2009, for more information). Finally, we incorporated the ARMA structure into all models in our a priori candidate model sets and ran each model as above but fit with maximum likelihood (ML).

Using the above procedure, we first tested whether our measures of seabird nesting biology: phenology, productivity, and BCI have changed over our 26-year dataset and whether changes were similar between the two species. When the interaction term “Species × Year” was identified as an important predictor, we conducted post-hoc analyses for each species separately to further evaluate how the measure of nesting biology had changed over our 26-year dataset. Here, we followed the same procedure as described above for AICc analysis with a candidate model set of two models (an intercept only model and a model with “Year” as the sole predictor; see Tables S1–S4). Next, when the term “Year” was included as an important predictor in our analysis of change over time, we evaluated the relationship between environmental variables and the observed changes. Here, we first performed Spearman’s rank correlation analysis using the “corrplot” package in R (Wei and Simko, 2017) for all environmental variables used in models for puffins and Razorbills, separately. Any variables with a correlation coefficient greater than 0.70 were considered to be strongly correlated and were not included in the same statistical model (see Tables S5 and S6). With our final list of candidate models (Table S7), we followed the steps outlined above to check model diagnostics, assess autocorrelation structure, and ran our a priori candidate model sets.

Results

Environmental conditions

Each of the environmental variables included in our analyses show cyclic variations between 1995 and 2020 and increases in almost all of them in that same time period (Figure 2).

Phenology—Hatch date

Over our time series, we have “known” and “estimated” hatch dates for 1,535 puffins (59 ± 7 per year) and 1,035 Razorbills (40 ± 4 per year). The earliest hatch date on record was May 31, 2013, and June 3, 2012 (and 2016), and the latest was August 1, 2005, and July 25, 2001, for puffins and Razorbills, respectively. In our models, the interaction term Year × Species was an important predictor for hatch date (Tables 1 and 2). Our post hoc analyses and trend data both show that mean hatch date has retreated (i.e., occurs later in more recent years) over the last 26 years in puffins (Figure 3A, Tables S1 and S2), from June 17 ± 1.07 days in the first 10 years to June 22 ± 0.84 days in the last 10 years. By contrast, in Razorbills, mean hatch date has advanced (i.e., occurs earlier in more recent years) over the last 26 years (Figure 3B, Tables S3 and S4), from June 26 ± 0.62 in the first 10 years to June 23 ± 0.68 days in the last 10 years.

For both puffins and Razorbills, we evaluated the relationship between hatch date and NAO, SST in winter (September–February) and spring (March–May; Tables 3–6), and nest site occupancy. Spring SST and NAO were important predictors of hatch date for both puffins and Razorbills; occupancy was also an important predictor for puffins (Tables 4 and 6). For both species, hatch date advanced as spring SST increased; for puffins, hatch date advanced with increasing occupancy and retreated as NAO increased, the relationship with NAO was opposite for Razorbills (Tables 3–6).

Phenology—Fledge date

Between 1995 and 2020, we have fledge dates for 5,195 (200 ± 43 per year) lighthouse fledglings (puffins only). The earliest peak fledge date on record was July 19, 1998, and the latest was August 26, 1995 (and 2013). Our statistical analyses show year was not an important predictor of fledge date (Tables 1 and 2), and our data show no change in fledge date with time (Figure 3C; puffin fledge date in the first 10 years of our study was August 7 ± 0.28 days and August 7 ± 0.45 days in the last 10 years).

Productivity

To date, we have monitored 3,256 nesting burrows (1,827 for puffins: mean 73 ± 6 per year and 1,429 for Razorbills: mean 57 ± 3 per year) for hatch success (i.e., the proportion of eggs laid that hatch), and 2,170 nesting burrows (1,230 for puffins: mean 49 ± 6 per year and 940 for Razorbills: mean 38 ± 3 per year) for fledge success (i.e., the proportion of hatched chicks that fledge). Overall mean productivity between 1995 and 2019 was 55% ± 6% for puffins and 54% ± 4% for Razorbill. For puffins, the highest productivity on record (75%) occurred in 2015 and the lowest (16%) in 2013; the corresponding numbers for Razorbills are 72% in 1997 and 10% in 2007. Our statistical analysis shows Year was the most important predictor for productivity (Table 1) and productivity has decreased for both species over time (Table 2; Tables S1–S4). That decline is apparent in our dataset that shows a decline in productivity from 60% ± 5% in the first 10 years of our study to 51% ± 13% in the last 10 years for puffins and from 63% ± 6% in the first 10 years of our study to 47% ± 4% in the last 5 years for Razorbills (Figure 4A and B).
Productivity—Hatch success
Between 1995 and 2019, mean hatch success was 75% ± 3% for puffins and 71% ± 3% for Razorbills. For puffins, the highest hatch success on record (86%) occurred in 2009 and the lowest (56%) in 2006 and 2014. For Razorbills, the highest hatch success on record (86%) occurred in 2002 and 2004 and the lowest (55%) in 2016. The interaction term Year × Species was an important predictor for hatch success (Tables 1 and 2), and in both puffins and Razorbills, hatch success declined between 1995 and 2019 (Figure 4C and D; Tables S1–S4). For puffins, mean hatch success was 79% ± 3% in the first 10 years of our study and 72% ± 5% in the last 10 years. For Razorbills, mean hatch success was 78% ± 4% in the first 10 years and 64% ± 4% in the last 10 years.

For both puffins and Razorbills, our statistical analyses show that spring air temperature, spring SST, spring precipitation, and NAO were important predictors of hatch success and that hatch success decreased with spring air temperature, SST, and precipitation; the relationship with NAO differed between the 2 species and was negative for puffins and positive for Razorbills (Tables 3–6). For Razorbills, winter SST was also an important predictor of hatch success, which decreased as winter SST increased (Table 5 and 6).

Productivity—Fledge success
Mean fledge success between 1995 and 2020 was 74% ± 7% for puffins and 78% ± 3% for Razorbills. For puffins, the highest fledge success on record (93%) occurred in 2015 and the lowest (23%) in 2016. The corresponding figures for Razorbills are 93% in 1997 and 58% in 2011. Year was the most important predictor of fledge success (Table 1), and both species show declines in fledge.
success over time (Table 2, Figure 4E and F). For puffins, mean fledge success has declined from 79% ± 5% in the first 10 years to 70% ± 16% in the last 10 years, and for Razorbills, mean fledge success has gone from 83% ± 4% in the first 10 years to 74% ± 4% in the last 10 years.

For both puffins and Razorbills, we evaluated the relationship between fledge success and mean hatch date, summer air temperature, summer precipitation, and prey quality. For puffins hatch date, summer air temperature and summer precipitation were important predictors of fledge success, and fledge success decreased with increases in these variables (Tables 3 and 4). For Razorbills, summer precipitation and prey quality were important predictors of fledge success, and fledge success decreased as both variables increased (Tables 5 and 6).

**Body condition**

Over our time series (1995–2020), a total of 5,195 (200 ± 43 per year) fledging puffins have been captured, measured, and BCI calculated. Mean BCI over our time series was −1.49 ± 0.95; the highest was in 2000 (132.91) and the lowest in 2016 (−236.88). Our statistical analyses show year was an important predictor of BCI and that BCI has decreased with time (Tables 1 and 2, Figure 3D). Our data show that mean BCI has gone from 9.47 ± 1.07 in the first 10 years of our study to −23.98 ± 2.27 in the last 10 years. Our statistical analyses showed that summer air temperature, summer SST, summer precipitation, and fledge date were important predictors of BCI (Tables 3 and 4). Specifically, we found that BCI decreased as each of these variables increased (Tables 3 and 4).
Sympatric species of cold-water marine predators would be expected to show comparable responses to ocean warming, especially given the rate of warming in the Gulf of Maine. Puffins and Razorbills breeding together at 2 North Sea colonies have both responded by breeding later, despite spring coming earlier (Wanless et al., 2009). Yet at MSI, both species responded to earlier springs with opposite changes in timing, despite showing reduced productivity.

In the Bering Sea, Black-legged Kittiwakes *Rissa tridactyla* and Thick-billed Murres *Uria lomvia* also show opposite responses to ocean warming (Byrd et al., 2008); kittiwake breeding advanced and productivity increased, but Thick-billed Murres either showed no change in timing or productivity (St. George Island) or nested later with reduced productivity (St. Paul Is.). Byrd et al. (2008) attribute the different responses by the 2 species in part to a difference in feeding zone (kittiwakes at the surface, murres in deep water), but our results show that very different responses can also occur in 2 pursuit-diving species.

The Gulf of Maine is warming faster than most of the world’s ocean (Pershing et al., 2015), shifts in seabird diet were noted in 2000 and 2009 (Diamond and Devlin, 2003; Breton and Diamond, 2014; Kress et al., 2016; Scopec et al., 2018; Symons, 2018), and marine heat waves have occurred in 2012, 2016, and 2020 (Mills et al., 2013; Pershing et al., 2018; Pershing, 2020). Puffins and Razorbills are closely related, cold-adapted species, nesting at

### Table 2

Summary results of model-averaged hatch date, hatch success, fledge date (puffin only), fledge success, and fledgling BCI (puffin only), and environmental conditions at Machias Seal Island, New Brunswick between 1995 and 2020 (1995–2019 for reproductive success and hatch success) DOI: https://doi.org/10.1525/elementa.2021.00033.t2

| Parameter | Estimate | Unconditional SE | Relative Importance |
|-----------|----------|------------------|---------------------|
| Hatch date |          |                  |                     |
| (Intercept) | 174.918  | 0.897            |                     |
| Year | 0.014 | 0.008 | 0.99 |
| Species (RAZO) | 1.045 | 0.596 | 1.00 |
| Species (RAZO) × Year | -0.022 | 0.005 | 0.99 |
| Fledge date |          |                  |                     |
| (Intercept) | 218.609  | 2.151            |                     |
| Year | 0.002 | 0.021 | 0.27 |
| Reproductive success |          |                  |                     |
| (Intercept) | 41.656  | 13.408           |                     |
| Year | -0.021 | 0.007 | 1.00 |
| Species (RAZO) | 30.414 | 21.132 | 0.27 |
| Species (RAZO) × Year | -0.015 | 0.011 | 0.27 |
| Hatch success |          |                  |                     |
| (Intercept) | 31.207  | 16.372           |                     |
| Year | -0.015 | 0.008 | 1.00 |
| Species (RAZO) | 35.350 | 22.896 | 0.92 |
| Species (RAZO) × Year | -0.018 | 0.011 | 0.92 |
| Fledge success |          |                  |                     |
| (Intercept) | 33.733  | 17.525           |                     |
| Year | -0.018 | 0.007 | 0.91 |
| Species (RAZO) | 15.286 | 26.160 | 0.19 |
| Species (RAZO) × Year | -0.009 | 0.014 | 0.16 |
| Fledgling BCI |          |                  |                     |
| (Intercept) | -5.325  | 3.652            |                     |
| Year | -0.122 | 0.035 | 0.98 |

Important parameters are in bold font. BCI = body condition index.

*Effect sizes have been standardized on 2 standard deviations following Gelman (2008).*

### Discussion

Sympatric species of cold-water marine predators would be expected to show comparable responses to ocean warming, especially given the rate of warming in the Gulf of Maine. Puffins and Razorbills breeding together at 2 North Sea colonies have both responded by breeding later, despite spring coming earlier (Wanless et al., 2009). Yet at MSI, both species responded to earlier springs with opposite changes in timing, despite showing reduced productivity.

In the Bering Sea, Black-legged Kittiwakes *Rissa tridactyla* and Thick-billed Murres *Uria lomvia* also show opposite responses to ocean warming (Byrd et al., 2008); kittiwake breeding advanced and productivity increased, but Thick-billed Murres either showed no change in timing or productivity (St. George Island) or nested later with reduced productivity (St. Paul Is.). Byrd et al. (2008) attribute the different responses by the 2 species in part to a difference in feeding zone (kittiwakes at the surface, murres in deep water), but our results show that very different responses can also occur in 2 pursuit-diving species.
the southern extent of their range in the Gulf of Maine (Lavers et al., 2020; Lowther et al., 2020), and changes in chick diet and other measures of their nesting biology have been observed and related to the changes noted above (e.g., Whidden, 2016; Scopel et al., 2018; Scopel et al., 2019). Our results show that all measures of puffin and Razorbill nesting biology have declined between 1995 and 2020 and changes in these parameters are related to environmental conditions in the Gulf of Maine/Bay of Fundy, as predicted. In all cases, important predictors of puffin and Razorbill nesting biology were similar, but measures included for both puffins and Razorbills (i.e., hatch date, hatch success, and fledge success) showed important differences in their responses, including opposite relationships with environmental conditions. Why these differences occurred is intriguing.

Throughout, we used measures of environmental conditions as a proxy for general changes in the ecosystem; our measures are in many cases (e.g., with SSTs) indirect measurements of the variables affecting puffin and Razorbill breeding biology. In the Northwest Atlantic, the early onset of spring due to climate change is characterized by warmer ocean waters earlier in the season (Mills et al., 2013). In response, some adult and larval fish species in the Gulf of Maine region have shifted their phenology to match this earlier spring; others have shifted their phenology later (Walsh et al., 2015). If the primary prey that puffins and Razorbills feed to their chicks have shifted their phenology, it would make sense for these birds to follow with a shift in their phenology, similar to the findings of Burthe et al. (2012) in the North Sea. Our data show that for hatch date, Razorbills and puffins have shifted their phenology both earlier (Razorbills) and later (puffins). In both cases, this change in phenology has resulted in reduced hatch success. Although this finding is puzzling (i.e., retreated and advanced hatch dates), comparable differences have been found for other sympatric seabird species (e.g., Byrd et al., 2008).

Sorensen et al. (2009) suggested that Cassin’s Auklets (Ptychoramphus aleuticus) need to achieve a threshold body condition before they initiate breeding. Winter is
an energetically expensive period for many birds (Fort et al., 2009), when they need to recover from the breeding season, complete molt, and begin preparing for the next breeding attempt. If prey availability during winter is poor, birds may delay their arrival to the breeding colony, arrive in suboptimal condition (which is known to delay breeding; Norris and Marra, 2007), or fail to breed (shown as reduced occupancy). Here, our proxy for changes in the ecosystem in winter (i.e., winter SST) has increased between 1995 and 2020 in regions where both puffins and Razorbills overwinter. Warmer SSTs are associated with poor food availability as fish grow slower, dive deeper, and/or move northward to cooler waters (Lekve and Stenseth, 2005; Frederiksen et al., 2011). Thus, we predicted that puffins and Razorbills nesting at MSI should begin breeding later, which would be observed in later hatch dates. Our results show an overall trend toward later hatching in puffins, similar to the findings of previous studies at MSI (e.g., Whidden, 2016), and suggest that puffins may be having difficulty obtaining enough energy-rich food to recover from the previous breeding season, molt, and prepare for the next breeding season. To further consider this, we included both winter SST and occupancy as predictors in our models of hatch date; if a threshold size is required before initiating breeding, we should see a reduction in occupancy and a delay of hatch date in years when environmental conditions during winter are poor. This prediction was supported for puffins but not Razorbills. In the Western North Sea, puffins and Razorbills were found to lay later in response to changes in prey availability, but there was no relationship between breeding phenology and winter SST (Wanless et al., 2009; Burthe et al., 2012). Winter SST in our study ranged from approximately 7°C to 10°C (for puffins) but in the Western North Sea ranged from approximate 5.5°C to 7°C (Burthe et al., 2012), so although the 2 regions are warming at a similar rate, SST is cooler in the North Sea than the Gulf of Maine, so presumably closer to any physiological

### Table 3. Top 5 candidate models describing the relationship between Atlantic Puffin hatch date, hatch success, fledge success, and fledgling BCI with environmental conditions at Machias Seal Island, New Brunswick during 1995–2020 (1996–2020 for hatch date and 1995–2019 for hatch success) DOI: https://doi.org/10.1525/elementa.2021.00033.t3

| Model Predictors | k | ΔAICc | ΔAICw | w0 |
|------------------|---|--------|-------|----|
| Hatch date ARMA correlation structure: ~1|Year, P = 1, q = 1 | | | |
| Occupancy + Spring SST | 6 | 9,500.16 | 0.00 | 0.24 |
| Occupancy + NAO + Spring SST | 7 | 9,500.37 | 0.21 | 0.22 |
| Occupancy + NAO | 6 | 9,500.71 | 0.55 | 0.18 |
| Occupancy | 5 | 9,501.32 | 1.16 | 0.14 |
| Occupancy + NAO + Winter SST | 7 | 9,502.51 | 2.35 | 0.07 |
| Hatch success Models weighted by # of nests with eggs | | | | |
| Spring Air Temp + Spring Precipitation | 3 | 149.76 | 0.00 | 0.38 |
| NAO + Spring Air Temp + Spring Precipitation | 4 | 150.86 | 1.09 | 0.22 |
| Spring SST + Spring Precipitation | 2 | 152.10 | 2.34 | 0.12 |
| Winter SST + Spring Air Temp + Spring Precipitation | 4 | 152.44 | 2.68 | 0.10 |
| Spring Precipitation | 2 | 153.16 | 3.40 | 0.07 |
| Fledge success Models weighted by # of nests with hatched eggs | | | | |
| Hatch Date + Summer Air Temp | 3 | 220.75 | 0.00 | 0.51 |
| Hatch Date + Summer Air Temp + Summer Precipitation | 4 | 222.10 | 1.35 | 0.26 |
| Hatch Date + Summer Air Temp + Prey Quality | 4 | 222.79 | 2.04 | 0.18 |
| Hatch Date + Summer Precipitation | 2 | 227.36 | 6.61 | 0.02 |
| Hatch Date | 2 | 227.66 | 6.91 | 0.02 |
| Fledgling BCI ARMA correlation structure: ~1|Year, p=2, q=2 | | | |
| Fledge Date + Summer Air Temp | 8 | 48,719.47 | 0.00 | 0.34 |
| Fledge Date + Summer Air Temp + Summer Precipitation | 9 | 48,720.45 | 0.98 | 0.21 |
| Fledge Date + Summer Air Temp + Prey Quality | 9 | 48,721.35 | 1.88 | 0.13 |
| Fledge Date + Summer Precipitation + Summer SST | 2 | 48,722.13 | 2.66 | 0.09 |
| Fledge Date + Summer Air Temp + Summer Precipitation + Prey Quality | 10 | 48,722.14 | 2.67 | 0.09 |

SST = sea surface temperature.
thresholds of these cold-water species. Razorbill hatch date at MSI did not show a relationship with winter SST or occupancy, even though increases in winter SST and decreases in occupancy were similar to those experienced by puffins. This suggests that prey availability during winter is not as important, or hasn’t changed as much, as it has for puffins in the Gulf of Maine. Further, different than in the North Sea, at MSI, our results suggest Razorbills are able to meet all energetic and nutritional requirements necessary to initiate breeding, not just at the same time, but earlier in more recent years. Perrins (1970) suggested that birds might begin breeding whenever they are physiologically able to do so. Thus, Razorbills at MSI are meeting the energetic requirements of building an egg earlier than in previous years. With rises in SST and noted changes in the Gulf of Maine ecosystem, we find this puzzling. Walsh et al. (2015) found similarly contrasting phenological trends in fish larvae. We posit that because Razorbills consume larger fish than puffins, Razorbill prey may be feeding from a different part of the planktonic prey field. Thus, the difference in phenological change between puffin and Razorbill hatch date might come from lower down the food chain. We suggest that further study into puffin and Razorbill prey, especially during the non-breeding season, is required.

Breeding in seabirds is timed such that chick rearing aligns with peak resource availability (Lack, 1954); individuals that initiate laying early tend to be those that are older, are physiologically able to produce an egg earlier, and in better body condition (Perrins, 1970), that is,
those most likely to match prey availability and successfully fledge a chick. Interestingly, hatch date for Razorbills at MSI has advanced, which normally would suggest higher productivity and fledge success, but our results showed declining fledge success at the same time as advancing hatch date. Further study is required to fully understand the relationship between hatch date and fledge success.

Despite being closely related sympatric species, important differences in life history may result in distinct challenges for puffins and Razorbills, both direct and indirect, to overcome in response to climate change. Puffins have a longer chick development period on the breeding colony than Razorbills who are considered “fledged” much earlier than puffins, and many aspects of their development, including a true measure of fledging success (i.e., gaining independence from their parents), remain unknown. Puffin chicks might, therefore, be more susceptible to increases in air temperature during chick development and food availability around the breeding colony (as hypothesized by Sealy, 1973).

For puffins, high summer air temperatures may decrease the amount of time adults spend at the nest and increase time spent at sea, in order to minimize their own thermoregulatory costs (Oswald et al., 2008), leaving chicks unguarded and vulnerable to predation (Visser, 2002). Once homoiothermic, puffin chicks are often left unguarded but reside in burrows that are difficult for avian predators, such as gulls (Larus spp.), to access (Hudson, 1979; Lowther et al., 2020). Razorbills reside in crevices that can be open and relatively easy for predators to access but are often guarded throughout chick provisioning (Lavers et al., 2020; S. Symons, unpublished data). Thus, according to the ideas put forward by Visser (2002) and Oswald et al. (2008), Razorbill fledge success should be negatively related and puffin fledge success should have no relationship to air temperature. Yet, our results show the opposite (i.e., no relationship with Razorbills and a negative relationship with puffins). Oswald and Arnold (2012) suggest that chicks are much more prone to overheating than adults, thus for puffins, increased thermoregulatory costs incurred by chicks in response to higher temperatures may decrease fledge success. For Razorbills, our result showing no relationship between air temperature and fledge success requires further study but could be due to adults providing some protection against excess temperatures and/or that Razorbill burrows benefit from wind as they are more open than puffin burrows.

Interestingly, although we found that puffins appear to be adjusting their hatch date, we didn’t find an important change in fledge dates across years. This is contrary to what was found in a previous analysis by Whidden  

| Model Predictors                                      | k  | AICc | AAIc | w0  |
|------------------------------------------------------|----|------|------|-----|
| **Hatch date ARMA correlation structure: ~1|Year, P = 5, q = 1** |    |      |      |     |
| NAO + Spring SST                                     | 10 | 6648.52 | 0.00 | 0.38|
| NAO + Winter SST + Spring SST                        | 11 | 6650.19 | 1.67 | 0.17|
| Occupancy + NAO + Spring SST                         | 11 | 6650.27 | 1.74 | 0.16|
| Spring SST                                           |  9 | 6651.36 | 2.84 | 0.09|
| Occupancy + NAO + Winter SST + Spring SST            | 12 | 6652.06 | 3.54 | 0.07|
| **Hatch success Models weighted by # of nests with eggs** |    |      |      |     |
| Winter SST + Spring Air Temp                         |  3 | 143.23 | 0.00 | 0.30|
| Winter SST + Spring Air Temp + Spring Precipitation  |  4 | 143.28 | 0.05 | 0.29|
| Winter SST + Spring Precipitation                    |  3 | 145.00 | 1.77 | 0.12|
| Winter SST + Spring SST + Spring Precipitation       |  4 | 145.57 | 2.34 | 0.09|
| Winter SST                                           |  2 | 146.83 | 3.59 | 0.05|
| **Fledge success Models weighted by # of nests with hatched eggs** |    |      |      |     |
| Null                                                 |  1 | 128.98 | 0.00 | 0.17|
| Prey Quality                                         |  2 | 129.04 | 0.06 | 0.16|
| Summer Precipitation                                 |  2 | 129.09 | 0.11 | 0.16|
| Prey Quality + Summer Precipitation                  |  3 | 129.87 | 0.89 | 0.11|
| Summer Air Temp                                      |  2 | 130.77 | 1.79 | 0.07|

SST = sea surface temperature.
(2016), who found a significant increase in fledge date (i.e., later fledge dates in more recent years) between 1995 and 2013, but with very small effect size. We do note a general trend in our data suggesting a small increase of which may reduce hatch success. As mentioned above, it is interesting that we have not observed a delay in the chick-rearing and provisioning period (Nettleship, 1992; Gaston, 1985). Our current results suggest that puffins at MSI, despite laying later (based on later hatch dates), are most likely not extending the time of chick-rearing and provisioning, instead showing reduced chick body condition upon fledge. Other studies have found prolonged puffin fledging periods (Anker-Nilssen, 1987; Barrett and Rikardsen, 1992) related to food stress (Øyan and Anker-Nilssen, 1996). Despite the considerable changes in diet over the years, we have seen very few years with prolonged fledging periods on MSI; even in heat wave summers of 2013 and 2016, the “bad years” identified by Scopel et al., 2019, fledging periods were at or close to the long-term mean of 45 days (ALAR, unpublished data), though the condition of fledgers was the lowest recorded. We recommend further research to identify the drivers of fledge date for puffins at MSI, as it has been shown to affect juvenile survival (Whidden, 2016). It may be that puffins need to fledge by a certain date in order to survive the storms that usually begin in late August (Balling and Cerveny, 2003).

In addition to the phenological impacts of warming, we found that as spring air temperature increased, hatch success decreased for both species. Hatch success in birds is determined not only by the quality of the egg itself (i.e., resources put into producing the egg) but also on the time adults spend incubating that egg and the consequences of egg neglect to embryo development (Webb, 1987). During spring (here May–June), both puffins and Razorbills are initiating laying and incubating their eggs that typically hatch mid to late June. When air temperatures during this time are high, adults may spend more time on the water to reduce their own thermoregulatory costs (Durant et al., 2005) and therefore spend less time incubating their eggs (Oswald et al., 2008), which in turn can reduce hatch success (Yorio and Boersma, 1994). Diving seabirds such as puffins and Razorbills are especially vulnerable to heat stress as they experience a wide range of temperatures whereby they must minimize heat gain while breeding on land and minimize heat loss while foraging in cold ocean waters. Thus, heat stress is a likely factor contributing to our observed decrease in hatch success with increasing air temperatures during incubation. Additionally, we found that precipitation had a high relative importance for puffin and Razorbill hatch success. High amounts of precipitation can flood burrows and chill eggs, decreasing hatch success (Rodway et al., 1998). Our results agree with those of other studies on puffins in the Gulf of Maine in which hatch success declined with increasing spring SST and precipitation (Scopel et al., 2019). For Razorbills, we found an inverse relationship between hatch success and NAO. When NAO is positive, winter conditions are characterized by increasing levels of storm activity (Hurrell and Dickson, 2005), which may reduce Razorbills’ ability to forage (Finney et al., 1999; Durant et al., 2005; Diamond et al., 2020). If Razorbills are unable to access the quantity and quality of prey required during winter to maintain or improve their body condition, their reduced body condition early in the breeding season could result in delayed laying, the production of lower quality eggs (i.e., eggs with low energy and nutrient content), and/or egg neglect, all of which may reduce hatch success. As mentioned above, it is interesting that we have not observed a delay in Razorbill breeding, as we have for puffins. We have yet to identify the reason for this relationship but recommend continued monitoring and further studies investigating phenology at MSI.

### Table 6. Summary results of model-averaged Razorbill hatch date, hatch success, and fledge success, and environmental conditions at Machias Seal Island, New Brunswick, between 1995 and 2020 (1996–2020 for hatch date and 1995–2019 for hatch success) DOI: https://doi.org/10.1525/elementa.2021.00033.t6

| Parameter          | Estimate | Unconditional SE | Importance |
|--------------------|----------|------------------|------------|
| Hatch date         |          |                  |            |
| (Intercept)        | 176.389  | 0.660            |            |
| NAO                | −0.658   | 0.285            | 0.81       |
| Spring SST         | −1.627   | 0.533            | 0.96       |
| Winter SST         | 0.222    | 0.418            | 0.31       |
| Occupancy          | 30.584   | 62.922           | 0.26       |
| Hatch success      |          |                  |            |
| (Intercept)        | 0.903    | 0.059            |            |
| Winter SST         | −0.101   | 0.036            | 0.88       |
| Spring Air Temp    | −0.103   | 0.045            | 0.66       |
| Spring Precipitation | −0.024  | 0.013            | 0.56       |
| Spring SST         | −0.075   | 0.049            | 0.13       |
| NAO                | 0.029    | 0.025            | 0.03       |
| Fledge success     |          |                  |            |
| (Intercept)        | 1.270    | 0.077            |            |
| Prey Quality       | −5.870   | 3.979            | 0.42       |
| Summer Precipitation | −0.023  | 0.016            | 0.40       |
| Summer Air Temp    | −0.039   | 0.056            | 0.25       |
| Hatch Date         | 0.000    | 0.002            | 0.18       |

Important parameters are in bold font. SST = sea surface temperature.

*Effect sizes have been standardized on 2 standard deviations following Gelman (2008).*
Our measure of body condition in puffin fledglings decreased in parallel with increases in summer air temperature, precipitation, and SST (i.e., puffins fledged in worse condition in hot, wet summers). The impacts of increasing air temperature and precipitation are likely direct in that they may increase the amount of energy chicks spend on thermoregulation, which then cannot be used to grow and increase body mass (Durant et al., 2005), resulting in reduced body condition. Similarly, periods of heavy precipitation have been linked to lowered body temperature, suggesting heavy precipitation also increases thermoregulatory costs to chicks (Vongraven et al., 1987). It appears there is a trade-off between extending the nestling period to reach a certain size and departing “on time” but at a smaller size. Extending the nestling period could result in increased heat stress on the colony and/or departing the colony too late to miss the cyclonic storms that often begin arriving in late August (Balling and Cerveny, 2003). Given the impacts of increasing SST on the prey base, it is not surprising that as summer SST increases, puffin chick condition declined, as reduced feeding is associated with reduced growth (Harris, 1978; Barrett and Rikardsen, 1992; Visser, 2002). An experimental study of puffin chick growth under varying food availability showed that when food intake was reduced, growth of several morphological measurements including body mass and wing length was similarly reduced, albeit not equally (Øyan and Anker-Nilssen, 1996).

**Conclusion**

Here, we show that 2 closely related cold-adapted species, with similar breeding and winter distributions in the Northwest Atlantic, are responding differently to some of the same environmental changes. Although our study focuses on 2 species in 1 geographic area, it is an important reminder that the response of individual species to climate change may differ in unexpected ways. Our study serves as an example of the types of changes we should expect to observe over larger geographical areas in the future. Specifically, as the Gulf of Maine continues to warm, it is imperative to continue monitoring these 2 populations to further our understanding of why they are responding differently and what aspects of their biology contribute to their response. Throughout, we focused on effects of environmental conditions as an indicator of change in the

**Figure 4. Reproductive success of puffins and Razorbills during 1995–2020.** Summary of puffin (ATPU) productivity, hatch success, and fledge success between 1995 and 2019 (1995–2020 for fledge success) at Machias Seal Island. Data are values calculated from our permanently marked nests; light gray line is a loess trend line with 95% CIs. DOI: https://doi.org/10.1525/elementa.2021.00033.f5
ecosystem; effects of changes in prey communities are described elsewhere (Scopel et al., 2019). Durant et al. (2003) found sea temperature and salinity were important predictors of puffin nesting period (i.e., number of days a chick spends in the nest from hatch to fledge) and fledging success. We did not include salinity or nesting period in our analyses but suggest that future work test the importance of these variables, along with stratification, for the MSI populations of puffins and Razorbills.

We have documented changing phenology and reduced breeding success in both Razorbills and puffins, and reduced body condition in fledging puffins, at a colony on the southern edge of the species’ ranges, over 26 years in one of the fastest-warming ocean ecosystems in the world. These changes can be viewed as early warnings of likely population decline if the ocean continues warming at this or a faster rate, as it is predicted to do (IPCC, 2018).

Data accessibility statement
All datasets generated by this project have been deposited into Dataverse (Major, Heather; Diamond, Tony, 2021, "Machias Seal Island ATPU RAZO data 1995-2020," https://doi.org/10.25545/US68YN).

Supplemental files
The supplemental files for this article can be found as follows:

Table S1. Candidate models assessing change in Atlantic Puffin hatch date, reproductive success, and hatch success at Machias Seal Island, New Brunswick, between 1995 and 2020 (1995–2019 for reproductive success and hatch success).

Table S2. Summary results of model-averaged Atlantic Puffin hatch date, reproductive success, hatch success, and year at Machias Seal Island, New Brunswick, between 1995 and 2020 (1995–2019 for reproductive success and hatch success). Important parameters are in bold font.

Table S3. Candidate models assessing change in Razorbill hatch date, reproductive success, and hatch success at Machias Seal Island, New Brunswick, between 1995 and 2020 (1995–2019 for reproductive success and hatch success).

Table S4. Summary results of model-averaged Razorbill hatch date, reproductive success, hatch success, and year at Machias Seal Island, New Brunswick, between 1995 and 2020 (1995–2019 for reproductive success and hatch success). Important parameters are in bold font.

Table S5. Spearman rank correlation coefficients for all environmental variables included in our candidate models evaluating the relationships between Atlantic Puffin phenology, productivity, and fledging body condition (puffins only) between 1996 and 2020. Correlation coefficients >0.70 are highlighted in gray; these were considered important and not included in any candidate models together. Major et al Supplemental info.docx

Table S6. Spearman rank correlation coefficients for all environmental variables included in our candidate models evaluating the relationships between Razorbill phenology, productivity, and fledging body condition (puffins only) between 1996 and 2020. Correlation coefficients >0.70 are highlighted in gray; these were considered important and not included in any candidate models together. Major et al Supplemental info.docx

Table S7. List of a priori candidate model sets evaluating the relationships between puffin and Razorbill phenology, productivity, and fledging body condition (puffins only) (1) between 1995 and 2020 (hatch success to 2019) and at Machias Seal Island, New Brunswick, Canada and (2) with environmental conditions. Models with a “1” were run for puffins only, those with a “2” were run for Razorbills only. Major et al Supplemental info.docx

Acknowledgments
Over the 26 years of this project, numerous graduate students and field assistants assisted in collecting these data; we are grateful to all of them for their attention to detail, hard work, and care. We are thankful to Captains Andy Patterson and Peter Wilcox for providing vessel transport to and from the island, and the Machias Seal Island light keepers for their help and friendship. We thank Andrew Kennedy, Garry Donaldson, and Sabina Wilhelm from the Canadian Wildlife Service for their continued support in our work on Machias Seal Island. We thank 2 anonymous reviewers for their helpful comments.

Funding
This project was funded by grants and contributions from Environment and Climate Change Canada, Natural Sciences and Engineering Research Council of Canada, the New Brunswick Wildlife Trust Fund, and the University of New Brunswick to AWD and HLM.

Competing interests
No competing interests exist.

Author contributions
Contributed to conception and design: HLM, SED, NF, JER, AWD.
Contributed to acquisition of data: HLM, SED, AWD.
Contributed to analysis and interpretation of data: HLM, SED, NF, AWD.
DRAFTED AND/OR REVISED THE ARTICLE: HLM, SED, NF, JER, AWD.
APPROVED THE SUBMITTED VERSION FOR PUBLICATION: HLM, SED, NF, JER, AWD.

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