Impacts of a rapidly warming environment on incubation and nestling periods of Atlantic Puffins (*Fratercula arctica*) on Machias Seal Island

by

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A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

Bachelor of Science with Honours in Environmental Biology

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SAINT JOHN

March, 2022

ABSTRACT

The Gulf of Maine (GOM) is warming faster than most of the world's oceans, cold-adapted seabirds such as Atlantic Puffins (*Fratercula arctica*), that are nesting at the southernmost extent of their range in the GOM, are at reproductive risk. Since 1995, researchers from the Atlantic Laboratory for Avian Research (ALAR) have collected various environmental and demographic data for puffins nesting on Machias Seal Island and have observed changes in their phenology. Specifically, puffins are now hatching later than early in the time series but fledge date has not changed. Here, I investigate changes in puffin incubation and nestling periods and how these periods are reacting to changing environmental conditions in the GOM. I found that sea surface temperatures and the North Atlantic Oscillation affect incubation periods, while hatch date and precipitation affect nestling periods. This study provides a groundwork for further research into the reproductive flux that seabirds are experiencing.

DEDICATION

To my parents and Fatima – thank you for always being there for me.

ACKNOWLEDGEMENTS

My deepest thanks to Dr Heather Major for introducing me to the world of marine birds; her patience, expertise, and supervision throughout this research project has opened the door for academia for me. Her constant support and encouragement are what made me see this project completed.

I would also like to thank M Sobana for encouraging me to take on a research project and for believing in me to complete this undertaking. I will cherish the support she has given me for the rest of my academic life.

STATEMENT OF RESEARCH CONTRIBUTION

Data for this project was collected by researchers in the Atlantic Laboratory for Avian Research (ALAR) at the University of New Brunswick (UNB), who have been collecting data on Machias Seal Island (MSI) since 1995. Due to the COVID-19 pandemic I was not able to participate in the field data collection. In late summer of 2021, I was given access to the Atlantic Puffin productivity data and extracted lay, hatch, and fledge dates, allowing me to calculate both incubation and nestling periods (together termed ‘breeding periods’). In early 2022, I was provided the environmental data collected on MSI and from online climate databases. With this data, I completed statistical analyses (with the help of Dr. Major) evaluating the relationships between environmental variables and breeding periods for Atlantic Puffins on MSI. Finally, I wrote my thesis with the editorial help of Dr. Major.

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INTRODUCTION

Anthropogenically-induced climate change has caused changes in ocean-atmosphere oscillations (Hurrell et al. 2003; Wang & Schimel 2012), affecting various marine ecosystems (Drinkwater et al. 2003). Interest in how marine ecosystems are responding to these changes is growing, and in particular their resiliency with regards to marine heatwaves (Smale et al. 2019; Cheung & Frölicher 2020). Marine heatwaves are defined as short periods (five or more days) of higher water temperatures, higher than the 90^{th} percentile of a 30-year baseline period (Hobday et al. 2016; Oliver et al. 2021). Marine heatwaves have been known to cause drastic changes in a marine ecosystem and are now longer and occur more frequently (Garrabou et al. 2009; Oliver et al. 2018). With the projected increases in average global temperatures (Lyon et al. 2021) there is concern regarding the survivability of marine species to changing temperatures (Saunders et al. 2014; Carrozza et al. 2018). Apart from this, there is growing evidence that species collapses in marine ecosystems are occurring and more will be driven by rapid climate change (Yacine et al. 2020).

Warming marine environments present a challenge to many top predators (Bond & Lavers 2014; Tanaka et al. 2021). For example, seabirds can be used as indicators of marine ecosystem health (Cairns 1986; Piatt et al. 2007; Hazen et al. 2019). Metrics such as abundance, diet, breeding success, and phenology of seabirds contribute to our understanding of how ecosystems are changing (Diamond & Devlin 2003; Sydeman & Bograd 2009). Reproductive success, for example, has been shown to be affected by oceanographic conditions (Catry et al. 2013; Scopel & Diamond 2017; Scopel et al. 2019). Breeding phenology (the timing of reproductive events) among seabirds has been observed to change in response to changes in the availability of prey in the marine ecosystem (Bond et al. 2011; Scopel et al. 2019).

Anthropogenic activities and changing prey availability are among factors responsible for the listing of more than 300 species of seabirds by the International Union for the Conservation of Nature (IUCN), and their situation is worsening (Croxall et al. 2012). For example, a study by Sandvik et al. (2005), suggested that survival rates of seabirds were correlated with prey availability that was driven by changes through the food chain. Birds have high metabolisms, maintaining their internal temperature close to 40°C (Gill et al. 2019). Cold-adapted seabirds, in particular, have poor heat tolerance (Choy et al. 2021). It can be difficult for these birds to adapt to rapid changes in temperatures and heat stress/death from overheating can easily occur.

Pershing et al. (2015) found that the Gulf of Maine is warming faster than most of the world's oceans. This rapid warming has presented consequences in the region, in particular, the collapse of the Gulf of Maine Atlantic cod (*Gadus morhua*) fishery. Other studies suggest that a "trophic mismatch" may be occurring in this region (Song et al. 2010; Morse 2021). Phytoplankton sit at the bottom of the food web, if they are not present when their predators expect them to be, those predators (and others up the food chain) either need to adapt, move into areas where prey remain, or adjust their phenology to match that of the phytoplankton. Thus, changes in one level of a food chain can result in a rippling to the rest of the chain (Edwards & Richardson 2004; Thackeray 2012). Warming in the Gulf of Maine is expected to continue at above average rates (Saba et al. 2016). Thus, monitoring changes within the ecosystem and understanding their drivers may enhance our ability to predict and mitigate those impacts and implement management practices in other areas that may experience rapid warming in the future.

Most seabirds nesting in the Gulf of Maine are cold-adapted species living at the southern extent of their range. For example, alcids (Alcidae) are the second most abundant nesting seabirds in the Gulf of Maine (GOMSWG 2018) and all three nesting species (Atlantic Puffin

Fratercula arctica, Common Murre *Uria aalge*, and Razorbill *Alca torda*) do so at the southern-most extent of their global range (Lavers et al. 2020; Lowther et al. 2020; Ainley et al. 2021). Nevertheless, the breeding populations of Atlantic Puffin (hereinafter "puffin") and Razorbills on Machias Seal Island are stable (puffins) and increasing (Razorbills; ALAR unpublished data).

Puffins nesting in the Eastern North Atlantic Ocean (Europe), have experienced population declines due in part to a lack of prey (Barrett & Rikardsen 1992; Anker-Nilssen et al. 2003) and nest predation (Lock 2006). Conservation and restoration efforts have been extensive, such as the removal of nest predators on Lundy Island (Appleton et al. 2006). Conversely, populations in Eastern Canada are stable and have not experienced the same declines. In North America, the largest puffin colonies are on Great Island, Witless Bay, Newfoundland (Wilhelm et al. 2015). The population in the Gulf of Maine is small in comparison, but may act as an early indicator of how puffins will react to climate change. In the Gulf of Maine, researchers have found that with warming oceans, prey consumed by puffins has shifted from energy-dense fish, like Atlantic herring (*Clupea harengus*) to lower quality (i.e., less-energy dense) prey (Scopel et al. 2019). This switch coincides with reduced reproductive output and a change in phenology of puffins (Durant et al. 2003; Scopel et al. 2019; Major et al. 2021). For example, puffin eggs hatch almost 2 weeks later today than in the 1990s, but fledge date (i.e., the date chicks depart the colony for the winter) has not changed (Major et al., 2021), suggesting a retraction (or shortening) of the nesting season.

Measures of reproductive success, such as the length of incubation and nestling periods, are an indicator of ecosystem change among other auks (Harding et al. 2007). The suggestion that the nesting season is shortening on Machias Seal Island is surprising, particularly as it seems that the shortening is occurring during the nestling period (Major et al. 2021). Previous studies have found that declining prey quality, as has been observed at Machias Seal Island, results in prolonged nestling periods for puffins (Anker-Nilssen 1987; Barrett and Rikardsen 1992; Øyan & Anker-Nilssen 1996), and reduced fledging success (Durant et al. 2003). Here, my goal is to quantify changes to puffin incubation and nestling periods at Machias Seal Island between 1995 – 2021 and investigate if these changes are related to changing environmental conditions in the Gulf of Maine. I hypothesize that changing environmental conditions (i.e., sea surface temperature, precipitation, and air temperatures) are indicators of changing prey availability and stress for Atlantic Puffin adults and chicks. I predict that incubation and nestling period duration are related to environmental conditions. Specifically, I predict that in years with poor environmental conditions (i.e., high SST, air temperatures, and heavy precipitation -all indicators of poor prey quality/quantity) breeding period duration will increase. During the incubation period, poor environmental conditions will result in females having less energy to devote to the egg during its development resulting in a poor-quality egg that is less likely to hatch, or adults will leave the egg unattended more often to self-provision, resulting in delayed hatching and a longer incubation period. During the nestling period, poor environmental conditions will result in a prolonged nestling period as observed in previous studies (see above).

METHODS

Study Site: Machias Seal Island

Data for this study were collected annually on Machias Seal Island during 1995 - 2021 by various members of the Atlantic Laboratory for Avian Research (ALAR). Machias Seal Island is a small (9.5 ha) island located 18 kilometers southwest of Grand Manan Island (Figure 1), between the mouth of the colder Bay of Fundy and the warmer Gulf of Maine. ALAR researchers are present on the island during May to August, except in 2020 and 2021 when COVID-19 restrictions delayed access to July (2020) and June (2021). The visitation window coincides with the breeding period of Atlantic Puffins nesting on the island, allowing researchers to collect demographic, diet, and phenological data.

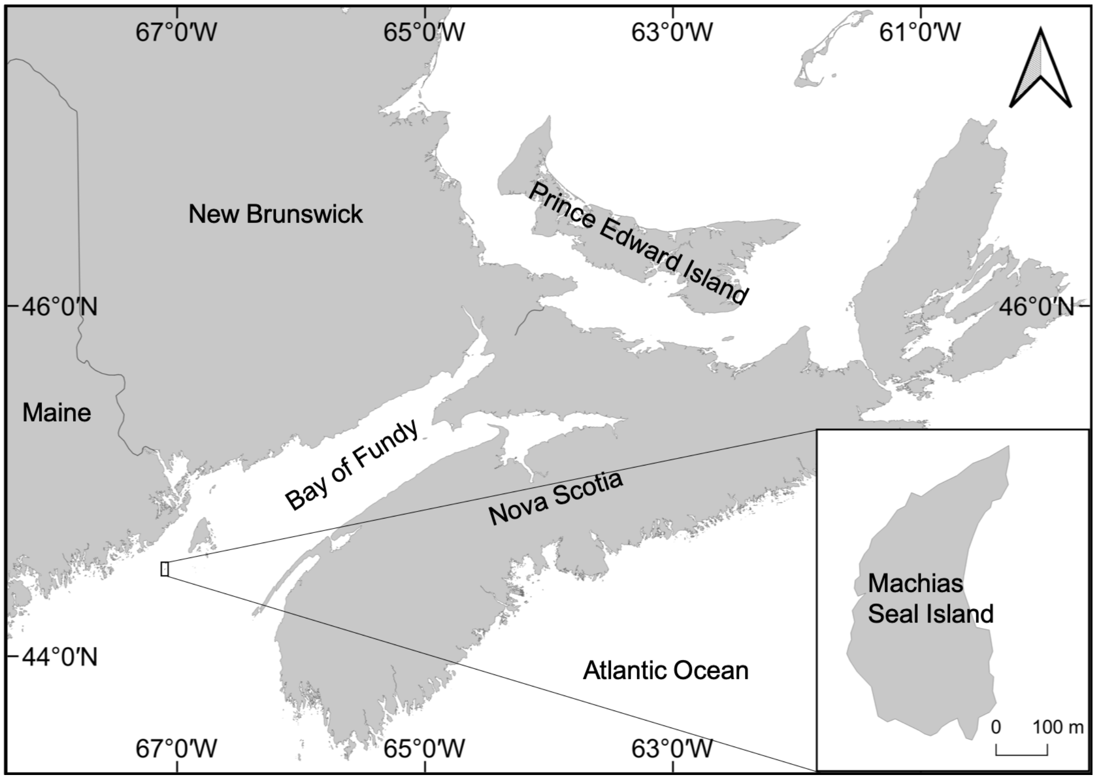

Figure 1. The location of the study site (Machias Seal Island) in the Gulf of Maine and the mouth of the Bay of Fundy.

Data Collection

Each year between 70 and 100 permanently marked burrows are regularly visited to collect data on lay, hatch, and fledge date, and hatch and fledge success. Atlantic Puffins lay one egg in May. During the first visit to each permanently marked burrow, ALAR researchers note if an egg is present or not. If an egg is found, the nest is marked as “active” and re-checked for hatch at the predicted hatch date (i.e., 37 days after the egg is found) (cite). If an egg is not found, the burrow is visited once every seven days until the peak of hatching, when the burrow is marked as “inactive”. Because some eggs are laid before the arrival of ALAR researchers and exact lay dates within the seven-day period between nest checks are unknown, lay date is estimated. If the egg was already present in the nest before the first check, the lay date of this egg cannot be used due to having an unknown lay date. If there was an egg laid in the subsequent nest checks, the lay date is estimated to be the date between the date the egg was first observed and the previous nest check. As this midpoint is between the weekly nest checks, lay dates are estimated to be plus or minus 3.5 days from its actual lay date. As for the hatch dates, this study uses the known hatch dates that the ALAR researchers have collected, which are chicks that were found on the day they hatched, which are noted due to the presence of eggshells attached to their down or wet down feathers. For the fledge dates, this is noted dependent on the chick checks which are conducted at the end of the breeding season. Fledge date is estimated to be the date between the chick was last seen in its burrow and the last chick check.

To calculate the number of days in the incubation and nestling periods, I subtracted 1) hatch date from lay date (incubation period) and 2) fledge date from hatch date (nestling period) for each puffin burrow in each year from 1995 – 2021 (incubation periods were not calculated for 2020 and 2021 because of the date ALAR researchers arrived on island).

Environmental Data

Following Major et al (2021), I used daily environmental data collected on MSI by ALAR researchers (i.e., precipitation and minimum and maximum air temperatures). Specifically, I first defined seasonal periods: “spring” defined as May 15 to June 15 of any given year; and “summer” defined as June 16 to August 5. For each period, I calculated total daily rainfall amount by summing the total daily precipitation and used the median daily minimum air temperature. Sea surface temperature (SST) data was retrieved from the National Oceanic and Atmospheric Administration (NOAA) Physical Sciences Laboratory (PSL) website (https://www.psl.noaa.gov). Specifically, I used NOAA Optimum Interpolation (IO) Sea Surface Temperature V2, that contains monthly means for 1981-2021 on a 1° latitude by 1° longitude grid. Again, following Major et al. (2021) I used data from grids 2 and 3 for the months of June to August (representing summer), 39 grids (grids 9 – 48) for the months of September to February (representing winter), and 13 grids (grids 1 – 13) for the months of March to May (representing spring; Figure 2). I downloaded the winter North Atlantic Oscillation Index (hereinafter “NAO”) from the NCAR/UCAR Climate Data Guide Website (Hurrell, 2021), for the months of December, January, February, and March for each year in my dataset.

To evaluate changes in incubation and nestling periods in relation to environmental variables, I used “spring” environmental variables for incubation period as this season reflects the time in which Atlantic Puffins lay and incubate their eggs. In addition, I included Winter SST as a proxy for food availability during egg production period, as adult body condition can impact the quality and lay date of an egg. For the nestling period, I used “summer” environmental variables and prey quality (based on Scopel et al. 2019, as the proportion of low-quality prey fed to chicks in each year).

Statistical Analysis

A priori candidate model sets were created based off environmental variables and the breeding periods, where the incubation and nesting periods had 32 and 28 models respectively, including intercept only null models (Tables 1 and 3). To assess the relationship between incubation and nestling periods and environmental conditions, generalized least squares (GLS) models were first run, fit by restricted maximum likelihood (REML) on my global (i.e., most highly parameterized model) models and check for linear fit and temporal autocorrection using the "*nlme*" package (Pinheiro et al. 2021). As temporal autocorrelation was found in the dataset, I defined the autocorrelation structure using an autoregressive moving average (ARMA) serial correlation structure, following the methods outlined in Zuur et al. (2009). Incubation and nestling periods were identified using 15 ARMA correlation structures and the structure with the lowest AIC value was used. Finally, I standardized the environmental variables following Gelman (2008) and ran each model in my two candidate model sets with the ARMA serial correlation structure described above but fit with maximum likelihood (ML). If the weight of my top ranked model was less than 0.9, I used model averaging (package "*MuMIn*"; Bartoń 2020) and the resulting parameter estimates, parameter likelihoods, and unconditional standard errors to draw inference from my data (following Johnson & Omland 2004 and Grueber et al. 2011).

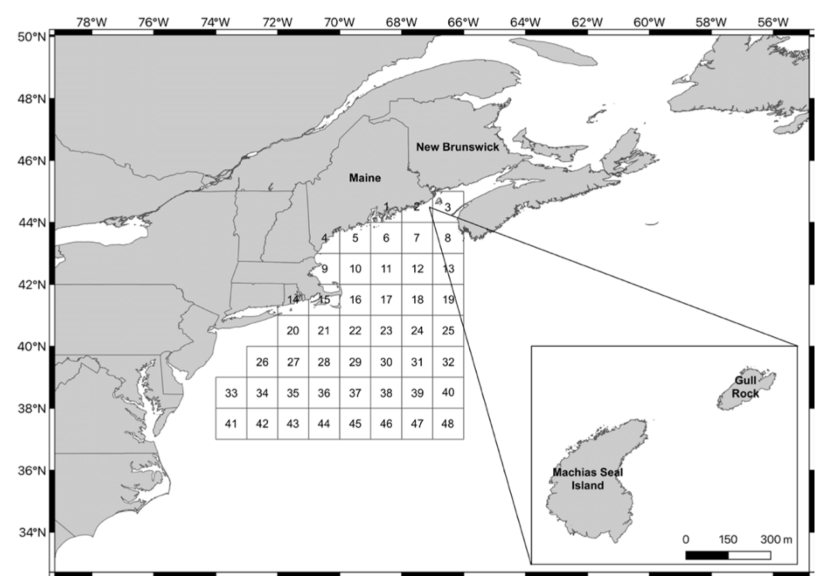

Figure 2. Map from Major et al., 2021 showing the location of Machias Seal Island and 48 grids from which SST was extracted.

RESULTS

Environmental Conditions

Environmental conditions at Machias Seal Island from 1995 to 2021 show a cyclical trend throughout the time period and are generally increasing (Figure 3).

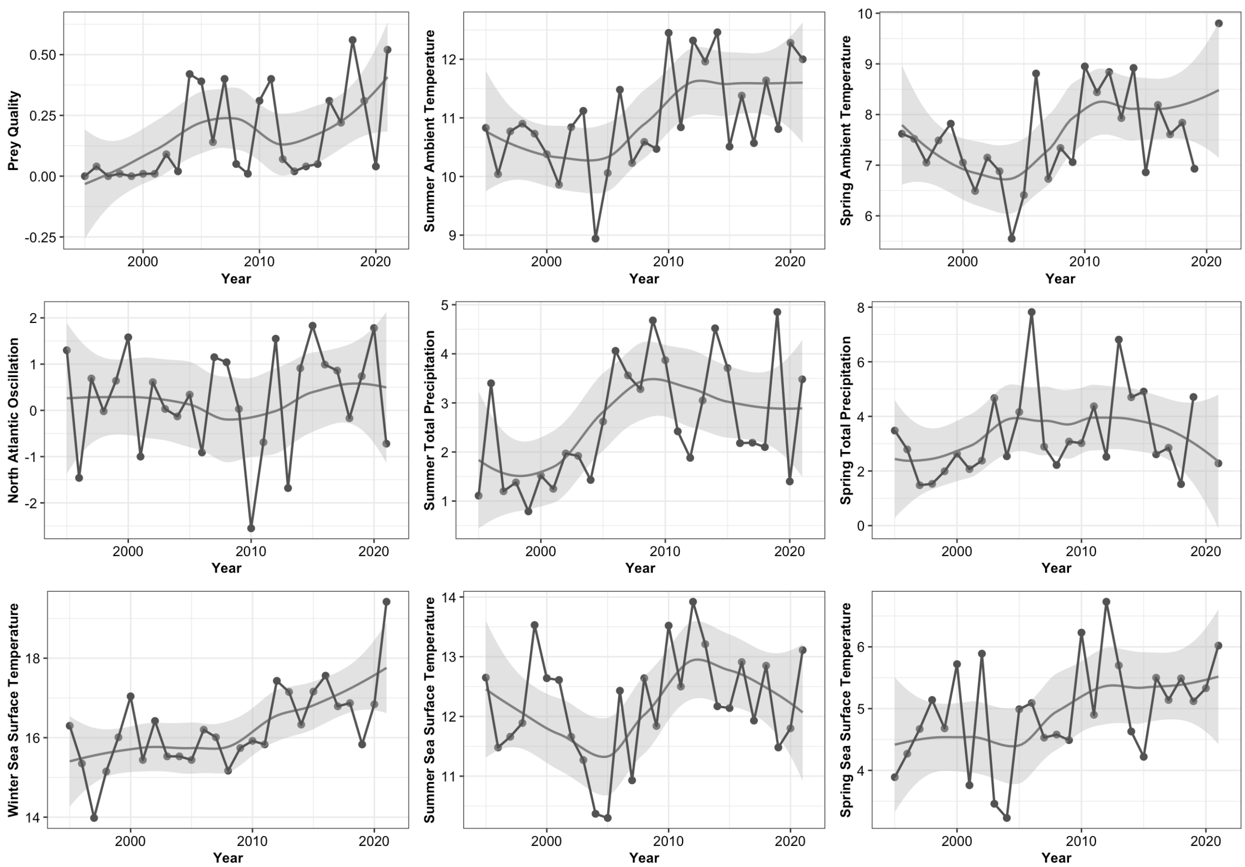

Figure 3: Environmental variables observed in the study; in which sea surface temperatures were collected for winter, summer, and spring seasons, total precipitation and ambient temperatures collected in summer and spring, and prey quality in summer, and North Atlantic Oscillation (climate variable) calculated yearly.

Incubation Periods

For this study, there were 790 incubation periods extracted from 1995 to 2021. Due to COVID-19 restrictions, the ALAR crew was unable to access MSI until after peak hatch in 2020, thus incubation periods for all years except 2020 were included in my analysis. In general, incubation periods have increased with time, though there is high variability in the years 1995 to 2000 (Figure 4). The trend from 2001 onwards appear to be stable or slightly increasing. For the time series, the mean incubation period was 38.98 (± 2.99) days, with the mean longest incubation period occurring in 2007 (47.70 ± 1.40 days) and the mean shortest incubation period occurring in 2000 (34.37 ± 1.10 days).

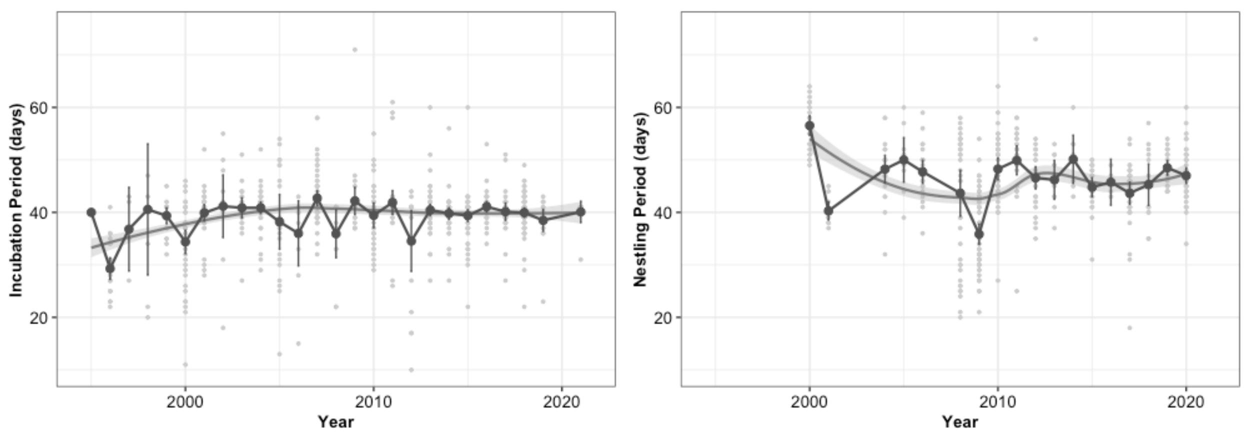

Figure 4. Incubation and Nestling periods for Atlantic Puffin (Fratercula arctica) chicks on Machias Seal Island, from 1995 to 2021

Model averaged parameter estimates showed that Spring Sea Surface Temperatures (SST) and North Atlantic Oscillation (NAO) were statistically important, and both included the interaction term 'Year' (Table 2). These results suggest that incubation periods change with time, but those changes are moderated by NAO and spring SST. For the incubation period models, 17 models sum up to 90% of the AIC weights. The top candidate model contained the interaction term NAO × Year and Spring Sea Surface Temperatures × Year (Table 1).

Table 1. Top 6 (of 32) a priori candidate model sets for incubation periods, in which ranking is based off AIC_c weights (ω_i), for ARMA correlation structure of $p = 3, q = 3$.

Model	df	logLik	AIC_c	ΔAIC	ω_i
NAO × Year + Spring SST + Year	13	-2498.720	5023.905	0	0.298
NAO × Year	11	-2501.800	5025.944	2.039	0.108
NAO × Year + Spring Rain × Year + Spring SST × Year	15	-2497.750	5026.111	2.206	0.099
Year	9	-2504.060	5026.348	2.443	0.0879
NULL	8	-2505.370	5026.919	3.014	0.066
Spring Temperature × Year	11	-2502.950	5028.232	4.337	0.034

Table 2. Summary of model-averaged variables assessing the relationship between incubation period and environmental conditions for Atlantic Puffins (*Fratercula arctica*) on Machias Seal Island, New Brunswick (highlighted parameters correspond to models that do not bound zero) during 1995 – 2021 (except 2020).

Parameter	Estimate	Std. Error
(Intercept)	39.175	0.541
NAO	-0.108	0.195
Year	0.016	0.007
Spring SST	-0.293	0.162
NAO × Year	-0.006	0.002
Spring SST × Year	1.761E-03	0.791E-03
Spring Precipitation	-0.020	0.108
Spring Precipitation × Year	0.893E-03	1.174E-03
Spring Air Temperature	-0.280	0.305
Spring Air Temperature × Year	2.154 E-03	2.371 E-03
Winter SST	-0.013	0.089
Winter SST × Year	0.000	0.000

Nestling Periods

For this study, there were 457 nestling periods observed, however due to changes in field protocols over the years and the date of departure from the island in some years ALAR researchers did not record fledge dates in some years. Thus, it was not possible to extract nestling periods for 1995 to 1999, 2002 to 2003, and 2007. Fledge success in 2021 was poor, only 3 chicks from monitored burrows were marked as fledged, because they were alive after 35 days, but none of these chicks had fledged before the crew left the island and most were small with no feathers (ALAR unpublished data). Thus, I did not include nestling periods for 2021.

In general, nestling periods have remained the same over time (Figure 4), with the longest mean nestling period occurring in 2000 (56.54 ± 1.83 days) and the shortest mean nestling period occurring in 2009 (35.85 ± 1.91). The mean nestling period for the time series was 46.58 (± 2.73) days.

My statistical analyses showed that, the top supported model was the NULL model that received 35% of the total model weight. Model averaged parameter estimates show a negative correlation between hatch date, precipitation, and nestling periods, indicating that as chicks hatch later and with increasing precipitation in the summer nestling periods were shorter (Table 4). Although, the effect of summer precipitation was moderated by year.

Table 3. Top 6 (of 28) *a priori* candidate model sets for nestling periods, in which ranking is based off AIC_c weights (ω_i), for ARMA correlation structure of $p = 2$, $q = 2$.

Model Predictors	df	logLik	AIC_c	ΔAIC	ω_i
NULL	7	-1517.010	3048.274	0	0.358
Hatch Date + Summer Rain	8	-1516.820	3049.961	1.687	0.154
Hatch Date + Prey Quality	8	-1516.940	3050.194	1.920	0.137
Hatch Date + Summer Temperature	8	-1517.000	3050.330	2.056	0.128
Hatch Date × Year + Summer Temperature × Year + Summer Rain × Year	13	-1512.470	3051.767	3.493	0.062
Hatch Date + Summer Temperature + Summer Rain	9	-1516.790	3051.989	3.715	0.056

Table 4. Summary of model-averaged variables assessing the relationship between nestling period and environmental conditions for Atlantic Puffins (*Fratercula arctica*) on Machias Seal Island, New Brunswick (highlighted parameters correspond to models that do not bound zero) during 2000 – 2020.

Environmental Conditions	Estimate	Std. Error
Intercept	46.691	1.195
Hatch Date	-0.015	0.002
Summer Precipitation	-0.246	0.401
Prey Quality	8.823	21.953
Summer Air Temperature	0.353	0.769
Year	-0.001	0.021
Hatch Date × Year	0.000	0.000
Summer Air Temperature × Year	0.008	0.012
Summer Precipitation × Year	0.012	0.006
Prey Quality × Year	-0.24	0.317

DISCUSSION

Rapidly changing environmental conditions in the Gulf of Maine and Bay of Fundy have been implicated in the change of many marine species in the region (Staudinger et al. 2019). The findings of this study partially support my prediction that in years of poor environmental conditions, breeding periods will be prolonged. I found that incubation periods have increased (become longer) but nestling periods have not changed. Further, I found duration of incubation period was negatively related to spring SST and NAO and duration of nestling period was negatively related to hatch date and precipitation. The result that nestling period has not changed was surprising given previous research for Atlantic Puffin nestlings (e.g., Anker-Nilssen 1987; Barrett and Rikardsen 1992; Øyan & Anker-Nilssen 1996) but is consistent with the results from Major et al. (2021) that hatch dates have advanced at MSI (i.e., occur later) but fledge dates have not changed. Further, the result that nestling period duration is negatively related to precipitation is perplexing, increased precipitation results in lower fledge success (Major et al. 2021) and have been shown to increase the amount of time some adult seabirds spend foraging, thus adults spend less time brooding and feeding nestlings (Pistorius et al. 2015).

Specifically, I found that as SST increases, incubation periods become longer and as precipitation in the summer increases, nestling periods become shorter (and changes with Year). This is notable as we have observed a step change in the amount of precipitation in 2006 – this year had the highest amount of precipitation on record and since then, the amount of rainfall has been higher before. An analysis between nestling periods before this step change occurred (in 2006) and nestling periods after this step change can provide a more robust justification on how precipitation has affected nestling periods. Although Major et al. (2021) did not assess how environmental variables impact fledge date, their results for hatch date are again similar to mine (i.e., hatch date occurred later with increasing spring SST. It is surprising that the nestling period has not changed as most studies assessing the impacts of decreased quality and availability of prey suggest that nestlings should remain at the nest longer (Durant et al. 2006; Harding et al.

2007; Bertram et al. 2017;). Equally unexpected, was that an increase in summer precipitation was related to shorter nestling periods.

Increased rainfall at MSI over the past decade (ALAR unpublished data) may negatively impact chick survival, as excessive rainfall may cause burrows to flood (or collapse). If chicks are exposed to rainfall and their down feathers wet, they can experience hypothermia (Wilhelm et al. 2013). Breeding failures have been observed amongst Short-tailed Shearwaters (*Puffinus tenuirostris*) and Wedge-tailed Shearwaters (*Puffinus pacificus*) that have experienced heavy rainfall (Tiller et al. 2000). Similar effects of rainfall have been seen among chicks belonging in the family Alcidae, where rainfall negatively affects chick development during chick rearing (Scopel et al. 2019). My prediction that increased rainfall during incubation would increase the duration of the incubation period was not supported. It is unclear why this would be, but given eggs are incubated and increased rainfall should not pose a threat to adult puffins, perhaps it does not change their incubation behaviour. Further, when a burrow is flooded or collapsed due to rainfall, those eggs would not hatch and therefore are not included in my analysis. Thompsoan and Furness (1991) found that adult Manx Shearwaters (*Puffinus puffinus*) lay eggs in burrows that are least likely to flood. Other seabirds, such as Tristram's Storm Petrel (*Oceanodroma tristrami*), have been observed to abandon their eggs due to the amount of precipitation (McClelland et al. 2008).

It is notable that winter SSTs did not affect incubation periods as the purpose of using SST was to act as a proxy for food availability for adults prior to starting the breeding season. Major et al. (2021) found that winter SSTs affected hatch success among Razorbills on MSI (but not puffins) – in which hatch success decreased as winter SSTs increased. Moreover, Hansen et al. (2021) suggest that winter SST affects the quantity of eggs laid in a given breeding season ("nest occupancy"). This would require the analysis of how environmental conditions are affecting nest occupancy, in which this study did not do. Meanwhile, the poor correlation between winter SST and incubation periods may suggest that winter SST is not a good proxy for adult body condition prior the start of the breeding season. Spring SST, on the other hand, has been observed to impact incubation period. Spring SST may indicate the availability of prey during the incubation period and may act as a proxy for egg neglect during times when adults are required to spend more time at sea self-provisioning.

Evidence from Cassin's Auklets (*Ptychoramphus aleuticus*) at Triangle Island, British Columbia, Canada show that rates of egg neglect are affected by wind speed, in which periods of strong winds increase the rate of egg neglect (Ronconi and Hipfner 2009). Wind speeds affect a seabird's ability to forage effectively. Further, strong winds affected the time at which Common Guillemot (*Uria aalge*) chicks departed their colonies (Johansen 2017) and incubation periods varied as a response to wind speeds among Ancient Murrelets (*Synthliboramphus antiquus*); where incubation periods increased as wind speeds increased (Shoji et al. 2011). I recommend future studies evaluate the relationship between wind speed and incubation and nestling periods.

While NAO is typically used as an index of large-scale climate oscillations, most of the literature covering seabirds and climate use NAO (e.g., Sydeman et al. (2012)). As discussed by Mesquita et al. (2015), the use of NAO as a climate proxy can lead to incorrect climate relationship interpretations due to unlinked ecological processes to NAO. Other climate variables, like the Atlantic Multidecadal Oscillation (AMO), may be a better alternative and I suggest future studies test for an effect of AMO due its long-term (60-year) cycles (Edwards et al., 2013). In Alheit et al. (2014), AMO provides a proxy for complex climate processes in the North Atlantic that involves other climate variations (such as NAO).

Due to trophic mismatch occurring in the Gulf of Maine (Song et al. 2010; Morse 2021;), puffins are now investing more energy foraging – possibly further than usual (Fayet et al. 2021) – and have changed their prey preferences to reflect what is currently available in the ecosystem (Scopel et al. 2019; Depot et al. 2020). Findings from Major et al. (2021) suggest that chicks are leaving the island with lower body condition (i.e., fledging lighter than would be predicted by their wing chord length) and are smaller overall (Georgantopoulos 2020), correlating well with the idea that they have a shortened nestling period and therefore are leaving before they have reached “full size”. However, the long-term implications of early departure of fledglings from the colony remain unclear. Future research should focus on understanding the implications on juvenile survival and adult body size.

Each season, ALAR researchers depart the island before all chicks have fledged, thus, the true length of the nestling period remains unknown. However, at the time of departure, ALAR researchers know the proportion of the permanently marked burrows that have fledged and generally do not depart the island until at least 90% of chicks have departed. Consequently, the missing data points are important to understand the full length of the nestling period but remain a small portion of the individual chicks overall. Thus, my data capture most of the nestling periods and the late departing chicks that are missed are excluded in every year.

Here, I found that Atlantic Puffin incubation periods have increased in length, but nestling periods have not. Overall, my findings suggest that even though nestling puffins are being fed lower quality prey and growing more slowly (ALAR unpublished data), they continue to depart the island at roughly the same time as early in our time series. This observation runs contrary to the published literature on puffin nestling periods and deserves further study. Perhaps there is an innate push to depart the colony by a certain date. One driver could be the start of the

North Atlantic cyclone season, as these seasonal weather events bring heightened levels of precipitation in a short time span and can cause mass-mortality events at sea (Clairbaux et al. 2021). Perhaps puffin chicks need to depart the island with sufficient time to ensure their survival during the cyclone season. Further study is required to investigate whether puffins are under constraints to depart the colony before a particular time and how that might be modulated. The rapidly warming Gulf of Maine can provide much needed insight on how top marine predators are impacted by changes to their environment.

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