EFFECTS OF ENVIRONMENTAL CONDITIONS ON EGG-LAYING DATES IN ATLANTIC PUFFIN *FRATERCULA ARCTICA*

by

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ABSTRACT

Climate change trends may have an impact on the timing of seasonal activities, and in particular the phenology of Atlantic Puffins. The purpose of this study was to investigate if changes in environmental conditions, such as Sea Surface Temperature (SST), are responsible for the observed delay in egg laying at Machias Seal Island (MSI), New Brunswick. I used monthly means for SST and egg laying dates over a period of 24 years (1995-2018) from MSI. I used general linear models in an AIC_c framework and found a positive relationship between egg laying dates and SST over time. I suggest continued long-term monitoring to assess future changes and the puffin's ability to continue to adapt to those changes.

DEDICATION

I dedicate this thesis to my husband and our two sweet little girls, Madeline and Judy.

Work hard and never stop dreaming!

STATEMENT OF RESEARCH CONTRIBUTION

All of the data for my project was collected by graduate students and technicians working for Drs. Tony Diamond (1995-2018) and Heather Major (2016-2018) on Machias Seal Island. I searched the Machias Seal Island (MSI) database and collated the egg laying dates for Atlantic puffins from 1995 to 2018 into one spreadsheet. I double-checked the data for errors (and corrected them when they were found) and re-formatted it to ensure the format was consistent among years. I downloaded the National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation Sea Surface Temperature (OISST) V5 dataset from the NOAA Research/Earth Science Research Laboratory, Physical Sciences Division and retrieved the data using the R Studio Environment (R version 1.0.136, www.r-project.org) with the interface to Unidata netCDF format data files package, (R package ncdf4, version 1.16; Pierce 2017). I completed the statistical analysis using an information theoretic approach and Generalized Linear Model with a Poisson distribution, in R Studio. Finally, I interpreted the results and wrote the thesis with editorial comments from Dr. Heather Major and S. Erin Whidden.

ACKNOWLEDGEMENTS

This project would not have been possible if it wasn’t for the unlimited support, patience and guidance of my supervisors, Dr. Heather Major and S. Erin Whidden. Thank you for believing in me and for supporting me no matter of the situation or circumstances. Thank you to my family, my husband and our little girls for their unlimited and unconditional love and support. I would also like to thank Mark Dodds, Sam Sweeney, Crystal Prieur, Kyle John Lefort and Demissew Gebreyohannes, for their advice and help throughout this journey. Finally, thank you to the members of ALAR lab for the data I have used for this project. UNBSJ thank you for the opportunity!

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List of Symbols, Nomenclature or Abbreviations

ALAR: Atlantic Laboratory for Avian Research

IUCN: International Union for Conservation Nature

MSI: Machias Seal Island

NAO: North Atlantic Oscillation

NOAA: National Oceanographic and Atmostpheric Administration

OISST: Optimum Interpolation Sea Surface Temperature

SST: Sea Surface Temperature

WNAO: Winter North Atlantic Oscillation

Introduction

Climate Change

Across the globe a changing climate may alter biological systems, impacting all levels of biological organization from ecosystems to populations to individual organisms. The global alteration of ocean ecosystem functioning is due to the rising levels of CO_2, most from anthropogenic sources (Nagelkerken and Connell 2015). CO_2 is a greenhouse gas that traps heat in the atmosphere, as CO_2 concentrations increase, atmospheric temperatures increase and so do ocean temperatures (Marshac 2016). Climate change can have a large ecosystem impact on the chemical, physical, and biological properties of the ocean, from the shifting of species distributions, phenology, and extirpation/extinction (Howes *et al.* 2015).

Sea surface temperature (SST) acts as an indicator of climate change (Thomas *et al.* 2017; Alexander *et al*. 2018) and has a considerable impact on the marine ecosystem (Taboada and Anadón 2012). Climate change can affect a population directly through its effects on metabolic and reproductive processes and/or indirectly through prey, predators, and competitors (Durant, 2003; Durant 2007). For example, changes in environmental conditions, such as SST, act primarily on prey availability and distribution (Howells *et al.* 2017) with many of these prey species being sensitive to very small changes in temperature (Diamond and Devlin 2003). Understanding how SST affects aspects of marine bird breeding phenology, which is dependent on prey availability, is fundamental to our understanding of the ecosystem and its health.

Marine birds as Indicators

Marine birds play an important role in the marine ecosystem because they are top consumers (Diamond and Devlin 2003). They are the most accessible top marine predator and cover large expanses of the sea while foraging within a short period of time, making them excellent sampling tools. Marine birds can therefore be used to detect changes in the availability of their prey species (Cairns, 1988; Diamond and Devlin 2003) and are used to monitor anthropogenic impacts such as pollution (Furness and Camphusen 1997) including heavy metals, petroleum products, plastic particles (Schreiber and Burger 2002), climate change (Grémillet and Boulinier 2009), and the effects of fisheries (e.g., bycatch and overfishing; Einoder 2009). Some examples include, assessments of bioaccumulation of heavy materials in the marine environment (Furness and Rainbow 1990; Dauwe *et al*. 1999), effects of oil spill in the marine environment (Wiese and Ryan 2003; Moreno et al. 2013), and presence of plastic particles (Ryan and Fraser 1988; Ryan 2008; Van Franeker 2011; Van Franeker and Law 2015).

The Atlantic Puffin

The Atlantic Puffin (*Fratercula arctica*) is a medium sized auk and is the only puffin native to the Atlantic Ocean. Atlantic Puffins are listed as vulnerable on the International Union for Conservation of Nature (IUCN) red list (BirdLife International 2018) due to declining populations (mostly in Europe). They are widely-distributed in the North Atlantic with breeding populations in Greenland, United Kingdom, France, Norway, Russia, and along the Atlantic coast of Canada and United States of America (Harris and Wanless 2011). The Atlantic Puffin spends the fall and winter months at sea, returning to shore in late April to breed. They choose to nest on rocky, isolated islands where there is limited disturbance and the absence of mammalian predators. Puffins feed on capelin (*Mallotus villosus*), sandeel (*Ammodytes marinus*), white hake (*Urophycis tenuis*), Atlantic herring (*Clupea harengus*), Atlantic butterfish (*Peprilus triacanthus*), haddock (*Melanogrammus aeglefinus*), and larval American sandlance (*Ammodytes americanus*; Harris and Wanless 2011; Atlantic Laboratory for Avian Research 2018 unpublished data). The Atlantic Puffin starts breading at the age of four, laying a single egg with both parents sharing incubation duties (Gaston and Jones 1998). They lay their egg in an underground burrow or a crack in a cliff face, the incubation period lasts approximatively 41 days (Harris and Wanless, 2011).

Egg Production

Egg production is energetically costly for females (Williams 2005), thus availability of prey is crucial during the time females are making the egg. Puffins are intermediate breeders, meaning they use a combination of income and capital breeding (income- using reserved nutrients and capital- using locally derived nutrients; 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 Atlantic Puffins (Durant 2003).

An increase in SST along the North Pacific has been strongly associated with reduced breeding success in Ancient Murrelets (*Synthliboramphus antiquus*) part of the auk family (Gaston and Smith 2001). SST was correlated with decreased growth and fledging success in another auk species, the Tufted Puffin (*Fratercula cirrhata;* Gjerdrum et al 2003). At Machias Seal Island (MSI), New Brunswick (Figure 1) researchers from the

Atlantic Laboratory for Avian Research (ALAR) at the University of New Brunswick have noticed a change (delay) in mean egg lay dates for the Atlantic Puffin over the past 24 years. Recent ocean warming trends, increase the concerns over the sustainability of the Atlantic Puffins in the Bay of Fundy and Gulf of Maine (Melvin *et al*. 2009). SST during January-May period in the eastern Atlantic Ocean has been strongly associated with adult puffin survival at four colonies (Grosbois *et al*. 2009). At the same time this change in egg lay dates has occurred, the Bay of Fundy and Gulf of Maine have been rapidly warming (Lima and Wethey 2012, Belkin 2009; Friedland and Hare 2007).

The objective of my research is to determine if environmental conditions (i.e., SST) are driving the change in egg lay date in Atlantic Puffins at MSI. I hypothesize that if environmental conditions (i.e., SST) have a direct impact on prey availability and puffins are intermediate breeders, then a change in SST (in April, when females are making the egg) will affect the time energy/prey is available for egg production and therefore lay dates. Based on the hypothesis, I predict that an increase in SST will cause a delay in egg lay date of Atlantic Puffins at MSI.

Methods

Study area

Data were compiled from the MSI Migratory Bird Sanctuary (44°30' N, 67°06' W, Figure 1) in the Bay of Fundy, Canada, by members of ALAR over a period of 24 years (1995 – 2018). MSI is a small island (9.5 ha) situated 19 km south of Grand Manan Island and 10 km off the coast of Maine (Diamond and Devlin 2003). The island is considered home to the largest puffin breeding colony in the Gulf of Maine (Gaston et al. 2009). The island has a breeding population of approximately 6000 breeding pairs of Atlantic Puffins (ALAR unpublished data).

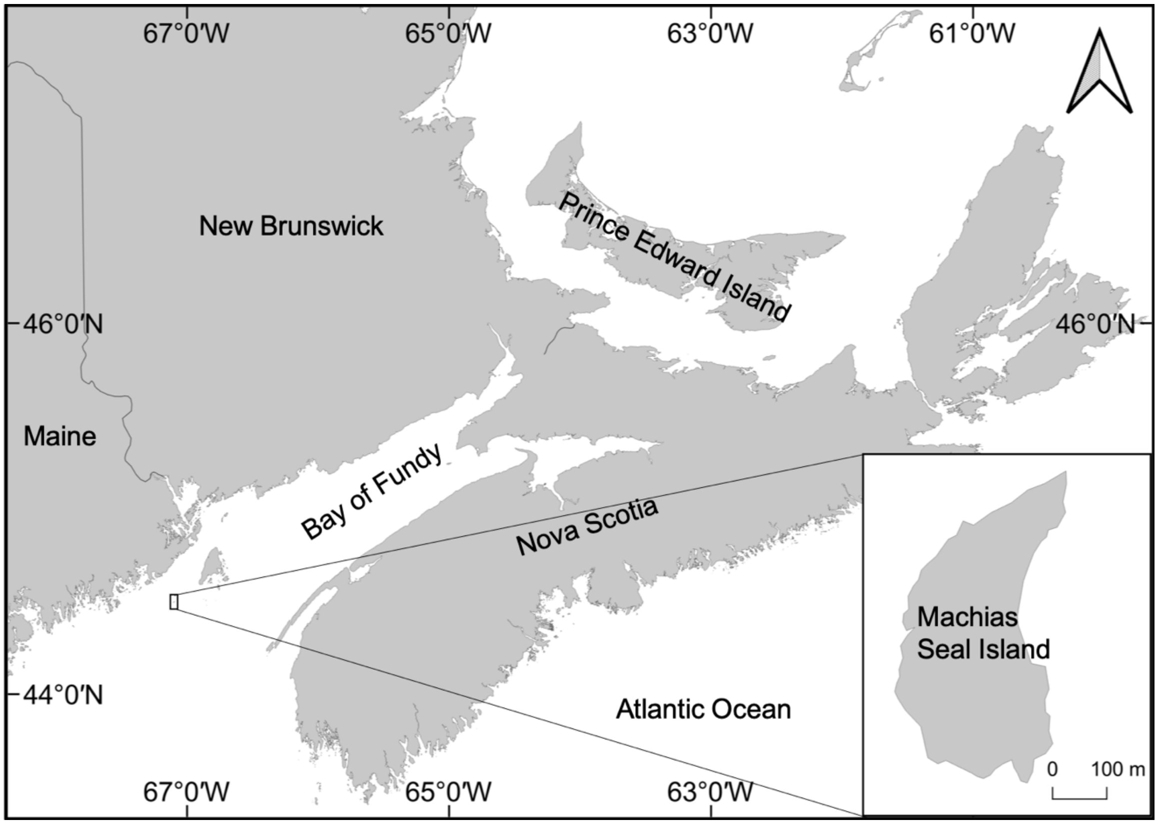

Figure 1. Map of Atlantic Canada and surrounding areas showing the location of Machias Seal Island.

Long-term monitoring of puffins at MSI is consistent and has used the same methods each year since 1995 (Diamond 1997). For puffins, monitoring includes, checking marked puffin burrows for the presence or absence of an egg during the month of May and June on a weekly basis. Egg lay dates are determined by 1) noting the first date an egg was observed in a burrow, and 2) back-calculating 37 days from the observed hatch date, often considering chick size. Here, I used a combination of these two methods, where inconsistencies between dates estimated using the two methods are resolved using the rule of parsimony (termed final adjusted egg lay dates) for all active puffin burrows with a hatched egg over a period of 24 years (1995 - 2018).

Sea Surface Temperature

To evaluate changes in SST, I downloaded the National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation Sea Surface Temperature (OISST) V5 dataset from the NOAA Research/Earth Science Research Laboratory, Physical Sciences Division (https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.ersst.v5.html). I retrieved the data using the R Studio Environment (R version 1.0.136, www.r-project.org) with the Interface to Unidata netCDF Format Data Files package, (R package ncdf4, version 1.16; Pierce 2017), which is a format for exchanging or distributing climate data. The dataset contains monthly means for SST from 1995 – 2018 on a 2 × 2 grid (2° latitude by 2° longitude), I used data for the grid that most closely overlapped with the location of MSI (i.e., grid coordinates V67, 146), that corresponds to the monthly mean SST in the North Atlantic within a range of approximatively 100 km radius from the breeding colony at MSI. I based this range on previous studies that used geolocators to investigate the foraging areas of Atlantic Puffins (Scheneider 1990; Anker-Nilssen and Lorentsen 1990; Stone et al.1992; Hilton et al. 2000, Harris et al. 2012).

Data analysis

To examine the relationship between egg laying dates and SST between 1995 – 2018, I used an information theoretic approach and generalized linear models (R version 1.0.136, www.r-project.org) with a Poisson distribution and considered five *a priori* candidate models (see Table 1) composed of the parameters of interest (i.e., year, SST, and the interaction term year*SST) including an intercept only null model. I ranked models using Akaike's Information Criterion (AIC) for small sample sizes (AIC_c) and AIC_c weights (ω_i) were used to evaluate model likelihood (Burnham and Anderson 2002). Parameter likelihoods, estimates, and standard errors were used to draw inference from the data. All summary data are presented as means with 95% confidence intervals.

Results

Mean Atlantic Puffin egg laying date on Machias Seal Island during 1995-2018 was May 14th (range April 18th – June 22nd). The earliest date (April 18th) occurred in 2011 and the latest in 2005 with an overall trend of egg laying dates becoming later with time (Figure 2). Similarly, mean monthly SST in April (1995-2018) during that same period averaged 4.5 (range 3.0 – 6.4) and has also increased with time (Figure 2).

Of my five candidate models, the global model (that included the interaction term year*SST) received virtually all the weight among models (~99%; Table 1). The parameter estimates and standard errors suggest that a change in egg laying date with SST and year (Table 2).

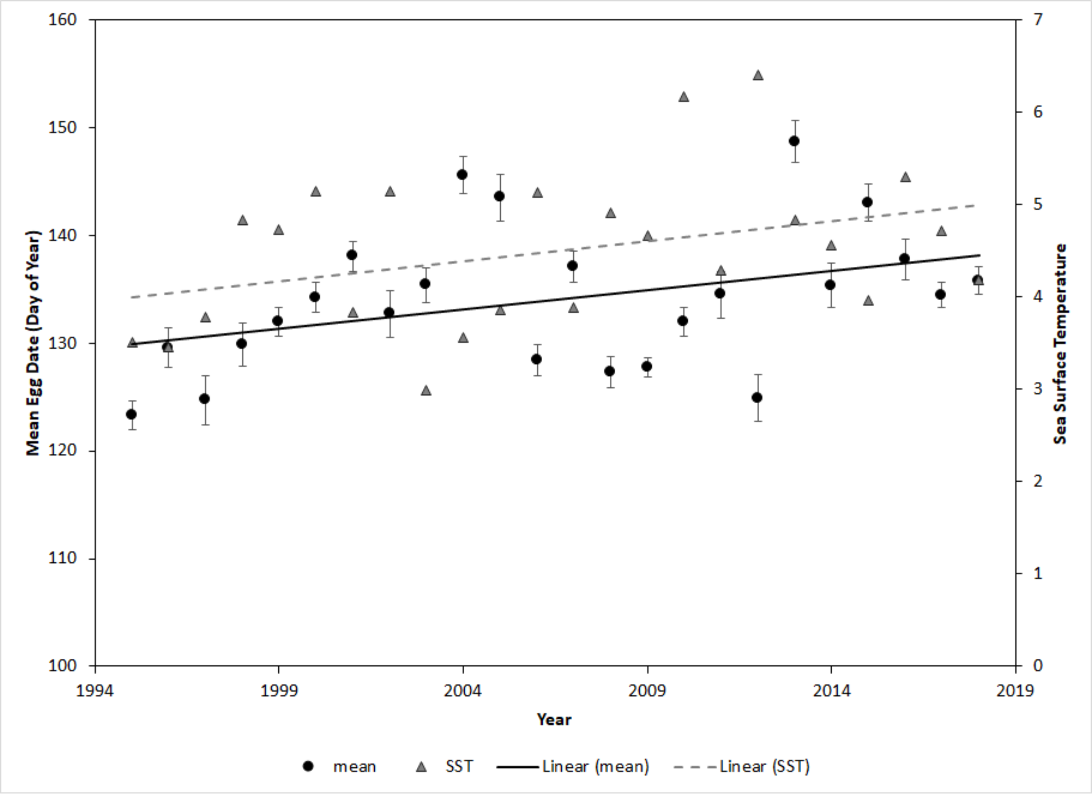

Figure 2. Mean egg laying dates (± 95% CI; black circles) for nesting Atlantic Puffins (*Fratercula arctica*) at Machias Seal Island, NB during 1995-2018 and mean monthly sea surface temperature (gray triangles) in a 2° x 2° grid around Machias Seal Island for the month of April. Lines of best fit (black for mean egg laying date and dashed gray line for SST) are shown to represent trends over time.

Table 1. Comparison of five generalized linear models describing the interaction between SST* Year and Atlantic Puffin (*Fratercula arctica*) egg laying dates at Machias Seal Island between 1995-2018.

Model	**k**	**AICc**	**AICW**
Egg Lay Date = Year + SST + Year*SST	5	9808.609	0.988
Egg Lay Date = Year + SST	4	9817.515	0.012
Egg Lay Date = Year	3	9870.783	0.000
Egg Lay Date = SST	3	9874.625	0.000
Egg Lay Date = null	2	9902.298	0.000

Table 2. Parameter likelihoods, estimates, and standard errors (SE) included in the top candidate models describing the relationship between Atlantic Puffin (*Fratercula arctica*) egg laying dates at Machias Seal Island between 1995-2018 and year, SST, and the interaction term Year*SST.

Parameter	**Likelihood**	**Estimate**	**SE**
Intercept	1.000	-18.270	4.993
Year	1.000	0.012	0.002
SST	1.000	4.012	1.123
Year*SST	0.988	-0.002	0.001

Discussion

Overall, my results suggest that the observed delay in egg laying dates is related to an increase in SST over that same time period (i.e., between 1995 – 2018). This supports my hypothesis that environmental factors (i.e., SST) have an impact on puffin prey availability and therefore the ability for female puffins to produce an egg, leading to a change (delay) in egg lay dates. Previous research has found that timing of egg laying in Common Murres (*Uria aalge*) is positively correlated with winter North Atlantic Oscillations WNAO (Votier *et al.* 2009). Advanced egg laying in response to climate changes was also noted in Common Eiders (*Somateria mollissima*) where eggs were laid later in response to milder winters (D'alba *et al*. 2009). Further, a study by Barrett *et al*. (2012) suggests that changes in egg volume of Atlantic Puffins breeding in Europe is in response to changes in SST and NAO. However, a similar study of puffin egg volumes over 140 years in Atlantic Canada did not find this same trend (Lefort 2017).

Puffins are among the first seabirds to lay their eggs in the eastern North Atlantic (Harris and Wanless 2011) and the ones that adjust their breeding pattern according to prey availability. This makes them excellent indicators of changes due to climatic fluctuations in the marine environment. Durant *et al.* (2005; 2007) show that climate change indirectly affects the breeding phenology and reproductive success of puffins through prey availability and abundance. Increases in SST and continuous warming of Bay of Fundy and Gulf of Maine creates a mismatch between food requirements prior to egg laying and food availability and can affect survival and reproductive success (Durant *et al.* 2007). Warmer waters affect the abundance and availability of the two main species of fish that puffins feed upon, white hake and Atlantic herring (Harris and Wanless 2011) where the availability of herring has been positively correlated with the annual survival of adult Atlantic Puffins (Breton and Diamond 2013). With SST rising, warmer waters are expected to shift the prey's range towards northern colder waters. According to the puffin's life history, when environmental conditions are unfavorable and food availability is scarce, the cost of reproduction is high and they may forego reproduction, favouring self-preservation (Cubaynes *et al.* 2010). With a continuous rapidly changing climate the Bay of Fundy and Gulf of Maine's diverse ecosystem may approach a state where it can no longer support populations of cold-water seabirds such as puffins (Breton and Diamond 2013). Given the results of my study, further warming in the Bay of Fundy will result in either a distinct change in the timing of the egg laying for puffins or their inability to continue to nest in the region entirely.

The lay dates used here are calculated based on hatch date and puffin chick measurements. In some cases, when an egg was not observed early in incubation (thus the date of first observing the egg is not useful in determining lay date) hatch dates are used to calculate a lay date. Additionally, there can be a discrepancy between the date an egg was first observed, and the calculated lay date based on hatch date and chick measurements. In these cases, egg lay date is determined using all of the available information and the researchers own discretion. This of course means that there are no lay dates for eggs that do not hatch. Because the timing of incubation is not strictly 37 days (that is the long-term average), by using these methods to estimate egg lay date we can be reasonably accurate and precise over time, but we are missing the potential of interesting information regarding changes in incubation timing with a changing climate and there is the potential for bias in our resulting egg lay dates. I recommend future studies document the timing of egg laying and the consideration of several other measures be taken into account, for example, recording the date the first puffin is observed carrying a fish to the burrow.

My analyses reveal that changing SST is affecting egg lay dates of Atlantic Puffins at MSI, therefore the observation that puffins are laying their eggs later in the breeding season in response to the SST holds true. Atlantic Puffins are listed as vulnerable (BirdLife International 2019) and thus far, they have successfully adapted to warming waters by adjusting their phenology. However, whether they are able to continue to adapt is unknown. The rapidly warming Bay of Fundy and Gulf of Maine waters may be a future contributing factor to further changes in puffin breeding phenology, and possibly their extirpation from the area. These results carry a significant importance for the conservation of the Atlantic Puffins in the Bay of Fundy and Gulf of Maine. Finally, I recommend conducting similar modeling at other colonies to see if climate change affects the timing of egg laying in puffins. Getting a better understanding of how the advanced egg lay dates will affect the size of the egg, its quality (e.g., energy content), its likelihood of survival to hatch, and the viability of the resulting chick. Future research is required to assess the effects of climate change on prey availability and abundance and its contrasting thermal preferences. It is important to monitor the future changes in the climate change that affect seabirds in the Eastern Canada.

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