CHANGES IN ATLANTIC PUFFIN *FRATERCULA ARCTICA* EGG VOLUME IN EASTERN CANADA

by

Kyle John Lefort

A THESIS PREPARED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF

Bachelor of Science with Honours in Marine Biology

Supervisor: H.L. Major Ph.D., Department of Biological Sciences

THE UNIVERSITY OF NEW BRUNSWICK

SAINT JOHN

April 2017

ABSTRACT

In several species of single-egg laying seabirds such as the Atlantic Puffin (*Fratercula arctica*), changes in resource availability prior to egg laying can result in changes in egg size. Long-term decline in egg volume has been observed at two Norwegian colonies and has been attributed to changes in environmental conditions and forage fish stocks. The purpose of this study was to investigate whether similar long-term changes in egg volume have occurred in eastern Canada (1877-2016), and to investigate the relationship between sea surface temperature (SST) and egg volume (1985-2016). This was accomplished by compiling a dataset of Atlantic Puffin egg volume in the Bay of Fundy, Gulf of St. Lawrence, Newfoundland, and Labrador from museum specimens and numerous researchers, and using model averaged AIC_c to quantify changes in egg volume through time. Results revealed that there has been no change in egg volume in eastern Canada but that regional variation in egg volume does occur. These results suggest that North American and Norwegian Atlantic Puffin populations are experiencing different trends: egg volume has decreased in Norway and has remained stable in North America. Additional research must be completed to better understand the factors driving the Norwegian decline, whether other European populations have experienced a similar decline, and what this might mean for the long-term viability of the population.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

ACKNOWLEDGEMENTS

INTRODUCTION

A Changing Climate

Climate change has the potential to influence a variety of marine ecological processes and, in turn, the spatiotemporal distribution and abundance of many marine species worldwide (Hoegh-Guldberg and Bruno 2010; Hazen *et al.* 2013). A rise in the concentration of atmospheric greenhouse gases has increased mean global temperatures and has resulted in an increase in energy absorption by the world's oceans (Hansen *et al.* 2006). Changes in oceanic chemical and physical conditions due to a changing climate have resulted in a wide range of biological responses which are reflected in fluctuations in the productivity of marine ecosystems, altered food web dynamics, and shifting species distributions (Hoegh-Guldberg and Bruno 2010; Hofstede *et al.* 2010). Changes in sea surface temperature (SST) have considerable impacts on the marine ecosystem and are an important indicator of climate change (Taboada and Anadón 2015). Globally, SST has increased by 0.6°C over the past 100 years (Hoegh-Guldberg and Bruno 2010), and it is predicted that mean global SST will increase by 1-6°C by 2100 (Pachauri *et al.* 2007; Rosenzweig *et al.* 2008). These changes are, however, more pronounced in certain areas such as in the North Atlantic Ocean (Taboada and Anadón 2015).

The North Atlantic Ocean

Extensive warming of the North Atlantic Ocean has been documented since the 1980s (Lima and Wethey 2012; Taboada and Anadón 2015). The highest warming

1

rates, with values greater than 0.5°C per decade, have occurred along the Gulf Stream front, the subpolar gyre, the Labrador Sea in the northwestern Atlantic Ocean, and the European continental shelf in the northeastern Atlantic Ocean (Taboada and Anadón 2015). These warming temperatures not only impact the spatiotemporal distribution and abundance of many marine species, but may also cause greater ecological impacts due to cascading effects throughout the trophic network (Hoegh-Guldberg and Bruno 2010; Hazen *et al.* 2013). For many marine species, increasing SST may result in increased metabolic rates, which can influence population growth as well as ecosystem processes such as larval dispersal (O'Connor *et al.* 2007). Certain organisms can acclimatize to these changing temperatures and environmental conditions, within limits. Outside of these limits, when acclimation is no longer biologically possible, mortality increases, fitness is reduced, and populations decline or are driven to local extinction (Hochachka and Somero 2002). For example, increasing SST in the Gulf of Maine is associated with the collapse of the Gulf of Maine cod (*Gadus morhua*) fishery (Pershing *et al.* 2015).

Marine Birds as Indicators

 The ease of study of marine birds, due to their wide range and colonial breeding, make them excellent indicators of change in marine ecosystems (Piatt *et al.* 2007; Durant *et al.* 2009). More importantly, marine birds often represent the top of the trophic network, thus, changes in lower trophic levels or in the physical environment are likely to be expressed in their population demographics (e.g. reduced seabird breeding success can be an indicator of decreased prey abundance; Bost and Le Maho 1993).

Additionally, marine birds are influenced by anthropogenic pressures such as overexploitation of their prey species or pollution (Bost and Le Maho 1993).

Marine Bird Egg Production

Many species of marine birds optimize the timing of reproduction and migration with periods of favorable environmental conditions (e.g., light, temperature, precipitation, prey availability; Lack 1968; Stenseth and Mysterud 2002). In the marine ecosystem, predators high in the food web, such as many marine birds, have high metabolic requirements during breeding, and environmental conditions have a direct impact on marine bird food availability (Watanuki *et al.* 2009). An excellent example of this is the climate-forced seasonal mismatch between the hatching of Rhinoceros Auklets (*Cerorhinca monocerata*) and the availability of anchovy (*Engraulis japonicus*), described by Watanuki *et al.* (2009). These results can be generalized beyond this one study: the phenological mismatch between predator energy requirements and prey availability is a wide-spread phenomenon in marine ornithology (Suryan *et al.* 2006; Durant *et al.* 2007; Hipfner 2008; Gaston *et al.* 2009). Marine birds can regulate the energy invested into, and the timing of reproduction in response to changing environmental conditions and food availability (Watanuki *et al.* 2009; Barrett *et al.* 2012). This is accomplished by adjusting laying dates, clutch size, and in the case of species that lay a single egg, egg size (Watanuki *et al.* 2009; Barrett *et al.* 2012).

Egg production is energetically expensive for females, and egg size varies in response to the amount of energy available to invest into reproduction (Christians 2002; Williams 2005). Consequently, food availability immediately prior to and during egg

production is important in determining egg size (Drent and Daan 1980; Jacobs *et al.* 2009). An additional potential factor influencing egg size is the physiological status of the female, which is also influenced by environmental conditions and food availability, though this relationship has not been thoroughly investigated (Christians 2002; Williams 2005).

The Atlantic Puffin

Atlantic Puffins (*Fratercula arctica*) are a widely-distributed seabird in the North Atlantic Ocean, and therefore, an excellent candidate species with which to assess environmental changes in this area (Lowther *et al.* 2002; Harris and Wanless 2011). The European population of Atlantic Puffins is estimated between 9.5 million and 11.6 million individuals (BirdLife International 2016), approximately half of which breed in Iceland (Lowther *et al.* 2002). Outside of Iceland, additional breeding areas are located throughout the North Atlantic Ocean in Greenland, Great Britain, France, Norway, Russia, and Atlantic Canada (Lowther *et al.* 2002). The North American population is estimated between 700,000 and 800,000 individuals (Rodway *et al.* 1996; Chardine 1999), though, population trends outside of Europe are considered poorly understood (BirdLife International 2016). In North America, the diet of Atlantic Puffins is comprised primarily of small fish such as capelin (*Mallotus villosus*), Atlantic herring (*Clupea harengus*), and white hake (*Urophycis tenuis*; Lowther *et al.* 2002). Atlantic Puffins breed monogamously, nesting in excavated burrows or rock crevices where females lay a single egg annually (Lowther *et al.* 2002). Atlantic Puffins display bi-parental care, with

both parents incubating the egg, which takes approximately 40-45 days to hatch (Lowther *et al.* 2002).

Atlantic Puffin Egg Size

Barrett *et al.* (2012) investigated the long-term decline in Atlantic Puffin egg size at two Norwegian colonies and associated this decline with changes in climate conditions, mainly through SST, and forage fish stocks. They suggested that declining egg size may reduce the success of future breeders and have negative impacts on populations. This is particularly pertinent as the Atlantic Puffin is listed as Vulnerable on the IUCN Red List (BirdLife International 2016). Additionally, in Europe, Atlantic Puffin populations are predicted to decrease by 50-79% between 2000 and 2065; In North America, there is comparatively limited information on population trends (BirdLife International 2016).

The objective of this study was to investigate long-term changes in Atlantic Puffin egg size in eastern Canada in response to changing environmental conditions, and more specifically, increasing SST in the Western North Atlantic (Taboada and Anadón 2015). I hypothesized that increasing SST in the Western North Atlantic would result in considerable ecosystem changes (e.g., decreasing food availability) and a change in Atlantic Puffin egg size. Subsequently, I predicted a decrease in the size of Atlantic Puffin eggs in eastern Canada between 1877 and 2016.

METHODS

Study Area and Egg Measurements

Atlantic Puffin eggs were collected from breeding colonies in eastern Canada over the course of 140 years (1877-2016). This study included eggs from nine Atlantic Puffin colonies that were grouped into four regions: Bay of Fundy (BOF), Gulf of St. Laurence (GSL), Labrador (LAB), and Newfoundland (NFL; Figure 1, Appendix 1). Analyses were based on region and not colony because several of the colonies had very small sample sizes ($n < 10$) or had measurements recorded during only one year; to avoid excluding this data, colonies in the same geographic areas, that would be exposed to similar oceanographic conditions, were grouped into regions (Figure 1).
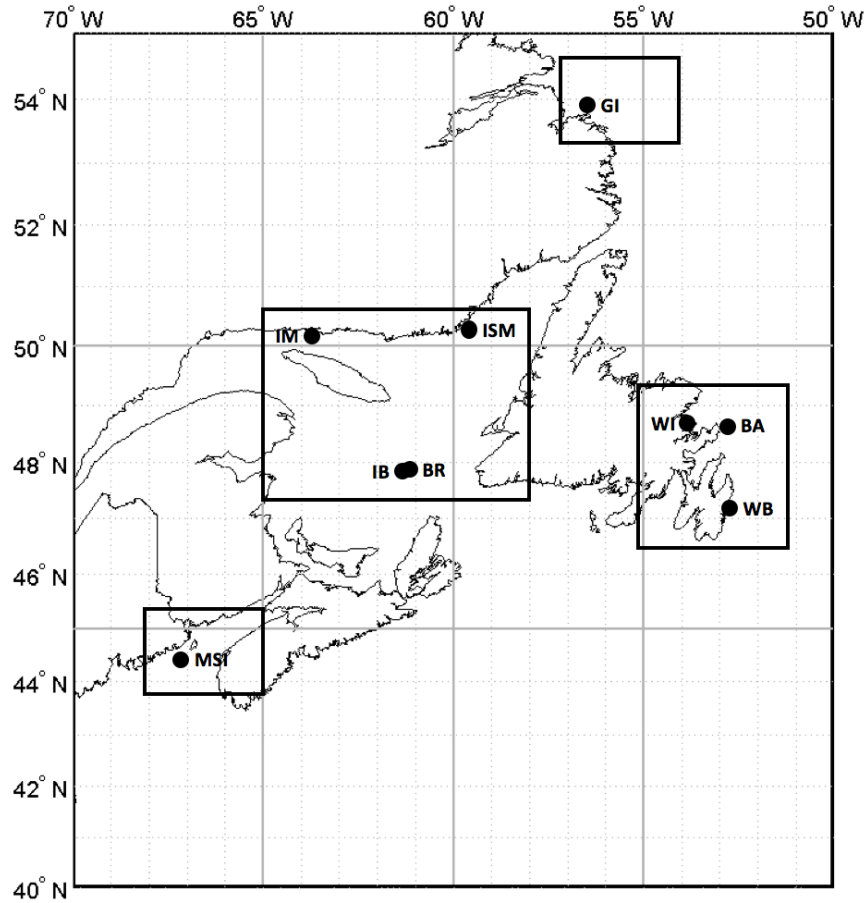
Figure 1. Atlantic Puffin breeding colonies in eastern Canada used as study sites (indicated by the black dots) in the following four regions (indicated by the black boxes): Bay of Fundy (Machias Seal Island [MSI]), Gulf of St. Lawrence (Bird Rocks [BR], Île Brion [IB], Île de Mingan [IM], and Île Sainte-Marie [ISM]), Newfoundland (Baccalieu [BA], Wolf Island [WI], and Witless Bay [WB]), and Labrador (Gannet Islands [GI]).

Eggs were collected by numerous researchers and either added into museum collections where they were measured by AL Bond (Royal Ontario Museum, n = 18; The Provincial Museum of Newfoundland and Labrador n = 6), KJ Lefort (New Brunswick Museum; n = 16), or Carnegie Museum personnel (Carnegie Museum, n = 33), or were

collected for research projects by the Canadian Wildlife Service (CWS) Toxicology

Program and were measured by CWS personnel. Additional eggs were measured by

researchers at breeding colonies and returned to their nesting burrows or were obtained

from the literature (see Appendix 1). In all cases, maximum length and breadth of

individual eggs were recorded (n = 1809) to the nearest 0.1 mm using calipers. Egg

volume was then calculated using the equation:

$$Volume = K{\times}L{\times}B^2 \quad \text{(Hoyt 1979)}$$

where the constant K = 0.507 (egg shape typical of Charadriiformes species), L is egg

length, and B is egg breadth.

Sea Surface Temperature

Mean weekly SST was obtained from the National Oceanic and Atmospheric

Administration (NOAA) Optimum Interpolation database

(https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html), and was

extracted 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; Pierce

2015). SST data was only available post 1981, which limited the analysis to four

colonies: Machias Seal Island (MSI), Île Sainte-Marie (ISM), Gannet Islands (GI), and

Witless Bay (WB), each located in one of the four regions. Mean SST was calculated

during the three weeks leading up to egg laying as it corresponds to time spent at the

colony and the time in which energy can be invested into egg development (Bond 2007;

Bond and Diamond 2010). Mean egg laying dates were based on published accounts of

phenology from each colony, and mean SST was calculated over an area spanning 2°

latitude by 3° longitude surrounding each colony (Table 1). This corresponds to an

approximate 100 km radius from the colony: the distance that an Atlantic Puffin could

potentially travel from the colony in search of food (Pearson 1968; Corkhill 1973; Anker-

Nilssen and Lorentsen 1990).

Table 1. Mean sea surface temperature (SST) latitude and longitude ranges and mean

egg laying dates calculated following a literature review of the four colonies for which

SST data was available: Machias Seal Island (MSI), Île Sainte-Marie (ISM), Gannet

Islands (GI), and Witless Bay (WB); asterisk (*) denotes unpublished data.

Colony	Latitude Range	Longitude Range	Mean Laying Date	Source
MSI	43°N - 45°N	66°W - 69°W	14th May	Lowther et al. 2002
ISM	49°N - 51°N	58°W - 61°W	19th May	Canadian Wildlife Service*
GI	53°N - 55°N	54°W - 57°W	26th June	Baillie & Jones 2003
WB	46°N - 48°N	50°W - 53°W	21st May	Baillie & Jones 2003 Calvert & Robertson 2002

Data Analyses

All statistical analyses were conducted using the R Studio Environment (R

version 1.0.136, www.r-project.org). To quantify changes in egg volume between 1877

and 2016 (*n* = 1809) linear mixed effect models (R package nlme; Pinheiro *et al.* 2017)

were used with region and year as fixed effects, and colony as a random effect. To

quantify changes in egg volume between 1985 and 2016 (*n* = 1536) in response to

changing SST, general linear models were used with year, colony, and SST as fixed

effects (note that in the SST analysis, colony and region can be used interchangeably

as each of the colonies is from a different region). An information-theoretic approach

was used and considered five and twelve *a priori* candidate models (Appendix II)

composed of combinations of the parameters of interest (including interactions between

parameters) and an intercept-only model. Models were ranked using Akaike's

Information Criterion (AIC) for small sample sizes, and AIC_c and AIC_c weights (ω_i) were

used to evaluate model likelihood (Burnham and Anderson 2002). Model averaging was

used to generate parameter estimates and unconditional standard errors when the best-

supported model received a weight less than 0.9 (Johnson and Omland 2004). These

were used with parameter likelihoods to draw inference from the data. All summary data

are presented as means with 95% confidence intervals.

RESULTS

General Trends

In total, 1809 Atlantic Puffin eggs were measured in eastern Canada between

1877 and 2016. The majority of these eggs (n = 1528; 85% of the total eggs measured)

were measured between 1985 and 2016. Mean (± SD) egg volume for eggs measured

between 1877 and 2016 was 63.3 ± 0.2 mL (range: 44.0 mL – 85.8 mL). Mean egg

volume for eggs measured between 1985 and 2016 was 63.3 ± 0.2 mL (range: 45.0 mL

– 85.8 mL). SST was highest in the Bay of Fundy, and varied among regions (range:

1.5°C – 8.0°C), although all regions exhibited a slight increase between 1985 and 2016

(Figure 2).
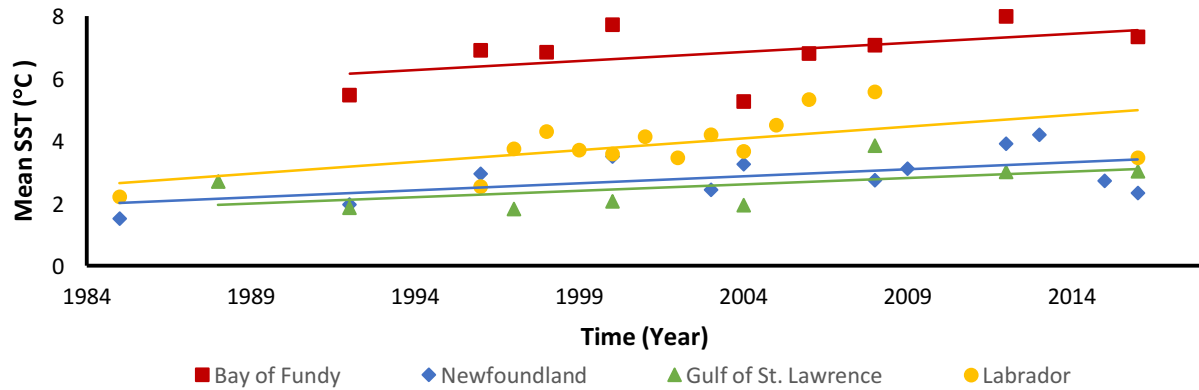
Figure 2. Mean sea surface temperature (SST) observed within a 100 km radius of each of four regions in eastern Canada during the three weeks leading up to Atlantic Puffin egg laying.

Changes in Egg Volume: 1877-2016

Overall trends in each of the four regions varied with slight positive changes in egg volume in the Bay of Fundy, Gulf of Saint Lawrence, and Labrador, and a slight decrease in Newfoundland (Figure 3). This trend was somewhat supported by the results from the model averaged AIC_c that showed variation in egg volume related to region in eastern Canada between 1877 and 2016 (Table 2A, Table 3A). Here, the top two candidate models received 92% of the total weight among models and weighted parameter estimates show region was the only parameter with a likelihood above 0.9 (Tables 2A, 3A). Weighted parameter estimates show that egg volume was smallest in the Labrador region and largest in Newfoundland, although parameter estimates from all regions except Newfoundland bound zero, suggesting that those effects are weak (Table 3A).

Changes in Egg Volume: 1985-2016

Overall trends in egg volume in each of the four regions were similar, remaining relatively stable or possibly decreasing slightly over time (Figure 3). This trend was supported by the results from the model averaged AIC_c that showed no change in egg volume in eastern Canada between 1985 and 2016 (Table 2B, Table 3B), and revealed that egg volume was not related to SST. Here, the top candidate model received 44% of the total weight among models and weighted parameter estimates showed region was the only parameter with a likelihood above 0.9 (Tables 2B, 3B). Note that all parameter estimates bound zero, suggesting that those effects are weak (Table 3B).
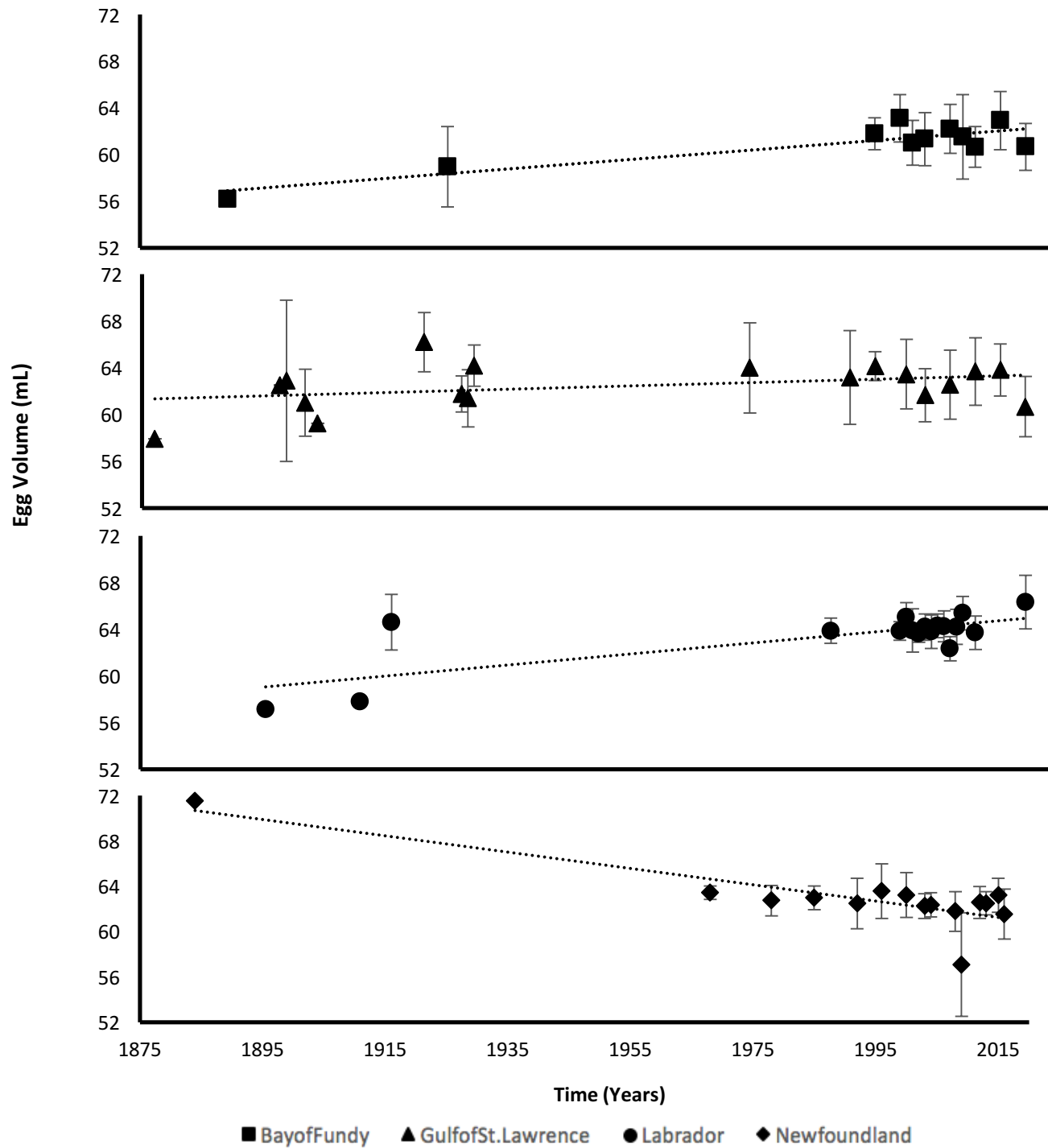
Figure 3. Changes in mean Atlantic Puffin annual egg volume (± 95% CI) observed in the Bay of Fundy, Gulf of St. Lawrence, Labrador, and Newfoundland between 1877 and 2016.

Table 2. A) Comparison of five candidate models describing the relationship between year, region, and the interaction between year and region with colony as a random effect and Atlantic Puffin egg volume in eastern Canada between 1877 and 2016. All models, including the null, include colony as a random term. B) Comparison of the top six of twelve candidate models describing the relationship between region, year, sea surface temperature (SST), the interaction terms year x region and region x SST, and Atlantic Puffin egg volume in eastern Canada between 1985 and 2016.

Model	n	k	AICc	Δ	ω_i
A					
EggVolume~Year+Region+Year*Region+(1|Colony)	1809	10	10678.32	0.00	0.759
EggVolume~Region+(1|Colony)	1809	6	10681.45	3.12	0.159
EggVolume~Year+Region+(1|Colony)	1809	7	10682.86	4.54	0.078
EggVolume~(1|Colony)	1809	3	10690.21	11.89	0.002
EggVolume~Year+(1|Colony)	1809	4	10691.42	13.10	0.001
B					
EggVolume~Region	1536	6	9119.20	0.00	0.443
EggVolume~Region+SST	1536	7	9120.88	1.68	0.192
EggVolume~Year+Region	1536	7	9121.05	1.85	0.176
EggVolume~Year+Region+SST	1536	8	9121.64	2.44	0.131
EggVolume~Year+Region+Year*Region	1536	10	9124.16	4.96	0.037
EggVolume~Region+SST+Region*SST	1536	10	9125.28	6.09	0.021

14

Table 3. Model averaged parameter likelihoods, estimates, and unconditional standard errors (SE) included in the candidate models describing the relationship between A) year, region, the interaction between year and region with colony as a random effect, and Atlantic Puffin egg volume in eastern Canada between 1877 and 2016; and B) region, year, sea surface temperature (SST), the interaction terms year x region and region x SST, and Atlantic Puffin egg volume in eastern Canada between 1985 and 2016.

Parameter	Parameter Likelihood	Weighted Estimate	Unconditional SE
A			
Intercept	1.00	21.54	44.87
RegionNewfoundland	1.00	80.05	59.85
RegionGulfofSt.Lawrence	1.00	44.14	47.55
RegionLabrador	1.00	-10.45	47.00
Year	0.84	0.02	0.02
Year:RegionNewfoundland	0.76	-0.04	0.03
Year:RegionGulfofSt.Lawrence	0.76	-0.02	0.02
Year:RegionLabrador	0.76	0.01	0.02
B			
Intercept	1.00	71.66	23.63
RegionNewfoundland	1.00	0.72	4.89
RegionGulfofSt.Lawrence	1.00	3.66	8.29
RegionLabrador	1.00	-1.85	10.38
SST	0.34	0.04	0.11
Year	0.34	-0.01	0.01
Year:RegionNewfoundland	0.04	0.00	0.00
Year:RegionGulfofSt.Lawrence	0.04	0.00	0.00
Year:RegionLabrador	0.04	0.00	0.01
RegionNewfoundland:SST	0.02	0.00	0.02
RegionGulfofSt.Lawrence:SST	0.02	-0.01	0.05
RegionLabrador:SST	0.02	0.01	0.03

DISCUSSION

The results from this study suggest that Atlantic Puffin egg volume in eastern Canada remained constant between 1877 and 2016. The hypothesis that increasing SST in the Western North Atlantic results in considerable ecosystem changes and a change in Atlantic Puffin egg size was not supported. Results show no relationship between SST and egg volume in eastern Canada between 1985 and 2016, but some regional variation in egg volume between 1877 and 2016. Such regional variation may be due to genetic differences among populations, or to variation in the physiological characteristics of females as a result of the quality and abundance of prey (Christians 2002).

Very few eggs (n = 270; ~15% of the total sample size) were collected before 1980, thus, changes in egg volume during these early years are perhaps not an accurate representation of the population at that time. For example, one egg collected on Wolf Island in 1884 had a volume considerably greater than the annual means of all other years in the Newfoundland region (12.4% larger than the next largest annual mean). Additional Atlantic Puffin eggs (*n* = 152) were located in museums (the majority of which were from the late 1800s – early 1900s) but were not measured due to time and financial constraints. It is possible that by including these specimens in the analysis, thereby increasing the sample size, the observed trends could change.

Contrary to Barrett *et al.*'s (2012) study, which found SST to be a driving factor in the egg volume decline observed at two widely separated Norwegian colonies, Hornøya and Hernyken, between 1980 and 2011, egg volume in eastern Canada does not

appear to be changing in response to SST. The geographic SST range used in this study was an approximate 100 km radius (2° latitude × 3° longitude) surrounding each of the colonies, based on the distance an Atlantic Puffin could travel in search of food during the nesting season (Corkhill 1973; Anker-Nilssen and Lorentsen 1990). The Norwegian study considered coastal topography and the foraging routes of puffins and selected smaller grids, spanning 1° latitude x 1° longitude. The different methodologies used in the selection of feeding grounds could be a factor in the contrasting results. This is further supported by the fact that SST commonly varied by $1 - 2°C$ between latitude x longitude grids in any given week in the area surrounding a single colony in the eastern Canadian study. Atlantic Puffins are not necessarily feeding in the entire 100 km radius, and mean SST of a smaller, more commonly used feeding ground might be a stronger predictor of egg volume. It should also be noted that Barrett *et al.* (2012) used monthly mean SST for the month of April (laying dates ranged from the 9th to 27th of May on Hornøya, and the 30th of April to the 9th of June on Hernyken), while this study used weekly mean SST in the three weeks prior to egg laying as this more accurately reflects SST and foraging conditions during egg development. This roughly corresponds to the first three weeks of May in the case of MSI, ISM, and WB, or the first three weeks of June in the case of GI. Bond and Diamond (2010) suggested that Atlantic Puffins invest nutrients acquired from wintering areas in the North Atlantic and/or during migration to the nesting colony into egg development, in addition to energy obtained from the colony and surrounding waters. Future research is required to determine the wintering areas of Atlantic Puffins and to investigate any relationship between the SST of wintering areas, migratory routes, and egg size.

This study suggests that the North American and Norwegian Atlantic Puffin populations are not experiencing the same egg volume trends: egg volume of the North American population has remained stable, while egg volume in the Norwegian population has declined (Barrett *et al.* 2012). The European Atlantic Puffin population is declining and are listed as Threatened by the International Union for the Conservation of Nature (BirdLife International 2015). Whether declining egg volume is a contributing factor is unknown. While the North American Atlantic Puffin population is relatively poorly understood (BirdLife International 2016), there is no evidence to suggest that such a population decrease is occurring (Wilhelm *et al.* 2015). Egg size is often correlated with offspring mass immediately following hatching (Christians 2002). While long-term studies are required (Christians 2002), there is evidence to suggest that egg volume influences offspring fitness, survival, and reproductive success (Gaston 1997, Krist 2011, Lee *et al.* 2012). This correlation is, as suggested by Barrett *et al.* (2012), often confounded by the correlation between egg size, the health of the female, and her ability to raise a chick. An alternate conclusion is that, in general, egg volume has remained stable, globally, and that the decline observed at Hornøya and Hernyken are the exception. Atlantic Puffins have a limited number of mechanisms by which they can adjust their parental investment, egg volume being the most plastic of these traits (Watanuki *et al.* 2009; Barrett *et al.* 2012). The obtained results suggest that Atlantic Puffins in eastern Canada are not adjusting their egg volume in response to changing environmental conditions; parental investment could, however, be adjusted by changing egg laying dates. This was observed on MSI between 1995 and 2016 where mean egg laying dates have varied between the 3rd and 28th of May, with the general trend

suggesting that egg laying is occurring later in the month (AW Diamond, unpublished data).

Future research is required to assess whether the trends observed at Hornøya and Hernyken are representative of European Atlantic Puffin populations, and if so, the drivers of this change and the population implications need to be identified. Likewise, if similar trends are found in other European populations, it would be prudent to continue to monitor North American populations for similar changes. Future research must focus on gaining an improved understanding of the relationship between egg volume, breeding success, and offspring fitness, and how climate change and resource availability might influence this relationship. This improved understanding is crucial in the future management and conservation of the species.

LITERATURE CITED

Anker-Nilssen T and Lorentsen SH. 1990. Distribution of Puffins *Fratercula arctica* feeding off Røst, northern Norway, during the breeding season, in relation to chick growth, prey and oceanographical parameters. Polar Research 8:67-76.

Baillie SM and Jones IL. 2003. Atlantic Puffin (*Fratercula arctica*) chick diet and reproductive performance at colonies with high and low capelin (*Mallotus villosus*) abundance. Canadian Journal of Zoology 81:1598-1607.

Barrett RT, Nilsen EB and Anker-Nilssen T. 2012. Long-term decline in egg size of Atlantic puffins *Fratercula arctica* is related to changes in forage fish stocks and climate conditions. Marine Ecology Progress Series 457:1-10.

BirdLife International. 2015. *Fratercula arctica* European Regional Assessment. The IUCN Red List of Threatened Species 2015. Retrieved from: http://www.iucnredlist.org/details/22694927/1

BirdLife International. 2016. *Fratercula arctica*. The IUCN Red List of Threatened Species 2016. Retrieved from: http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T22694927A82593109.en.

Bond AL and Diamond AW. 2010. Nutrient allocation for egg production in six Atlantic seabirds. Canadian Journal of Zoology 88(11):1095-1102.

Bond AL. 2007. Patterns of mercury burden in the seabird community of Machias Seal Island, New Brunswick. M.Sc. Thesis, University of New Brunswick, Fredericton, NB. 124 pp.

Bost CA and Le Maho Y. 1993. Seabirds as bio-indicators of changing marine

    ecosystems: new perspectives. Acta Oecologica 14(3):463-470.

Burnham KP and Anderson DR. 2002. Model selection and multimodel inference: a

    practical information-theoretic approach. 2nd Edition. New York: Springer-Verlag.

Calvert AM and Robertson GL. 2002. Using multiple abundance estimators to infer

    population trends in Atlantic Puffins. Canadian Journal of Zoology 80(6):1014-

    1021.

Chardine JW. 1999. Population status and trends of the Atlantic Puffin in North America.

    Bird Trends 7:15-17.

Christians JK. 2002. Avian egg size: variation within species and inflexibility within

    individuals. Biological Reviews of the Cambridge Philosophical Society 77:1-26.

Corkhill P. 1973. Food and feeding ecology of Puffins. Bird Study 20:207-220.

Drent R and Daan S. 1980. The prudent parent: energetic adjustments in avian

    breeding. Ardea 68:225-252.

Durant JM, Hjermann DØ, Frederiksen M, Charraissin JB, Le Maho Y, Sabarros PS,

    Crawford RJM and Stenseth NC. 2009. Pros and cons of using seabirds as

    ecological indicators. Climate Research 39:115-129.

Durant JM, Hjermann DØ, Ottersen G and Stenseth NC. 2007. Climate and the match

    or mismatch between predator requirements and resource availability. Climate

    Research 33:271-283.

Gaston AJ, Gilchrist HG, Mallory ML and Smith PA. 2009. Changes in seasonal events,

    peak food availability, and consequent breeding adjustment in a marine bird: a

    case of progressive mismatching. Condor 111:111-119.

Gaston AJ. 1997. Mass and date at departure affect the survival of ancient murrelet *Synthliboramphus antiquus* chicks after leaving the colony. Ibis 139:673-678.

Hansen J, Sato M, Ruedy R, Lo K, Lea DW and Medina-Elizade M. 2006. Global temperature change. Proceedings of the National Academy of Science 103(39):14288-14293.

Harris MP and Wanless S. 2011. The Puffin. London: T & AD Poyser.

Hazen EL, Jorgensen SJ, Rykaczewski RR, Bograd SJ, Foley DG, Jonsen ID, Shaffer SA, Dunne JP, Costa DP, Crowder LB and Block BA. 2013. Predicted habitat shifts of Pacific top predators in a changing climate. Nature Climate Change 3:234-238.

Hipfner JM. 2008. Matches and mismatches: ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. Marine Ecology Progress Series 368:295-304.

Hochachka PW and Somero GN. 2002. Biochemical Adaptation: Mechanism and Process in Physiological Evolution. New York: Oxford University Press.

Hoegh-Guldberg O and Bruno JF. 2010. The Impact of Climate Change on the World's Marine Ecosystems. Science 328(5985):1523-1528.

Hofstede RT, Hiddink JG and Rijnsdorp AD. 2010. Regional warming changes fish species richness in the eastern North Atlantic Ocean. Marine Ecology Progress Series 414:1-9.

Hoyt DF. 1979. Practical method of estimating volume and fresh weight of bird eggs. Auk 96:73-77.

Jacobs SR, Elliott KH, Gaston AJ and Weber JM. 2009. Fatty acid signatures of female

Brünnich's guillemots *Uria lomvia* suggests reliance on local prey for replacement

egg production. Journal of Avian Biology 40:327-336.

Johnson JB and Omland KS. 2004. Model selection in ecology and evolution. Trends in

Ecology and Evolution 19:101-108.

Krist M. 2011. Egg size and offspring quality: a meta-analysis in birds. Biological

Reviews of the Cambridge Philosophical Society 86:692-716.

Lack D. 1968. Ecological adaptations for breeding in birds. London: Chapman & Hall.

Lee DE, Warzybok PM and Bradley RW. 2012. Recruitment of Cassin's auklet

(*Ptychoramphus aleuticus*): individual age and parental age effects. Auk 129:124-

132.

Lima FP and Wethey DS. 2012. Three decades of high-resolution coastal sea surface

temperatures reveal more than warming. Nature Communications 3:704.

Lowther PE, Diamond AW, Kress SW, Robertson GJ and Russell K. 2002. Atlantic

Puffin (Fratercula arctica), The Birds of North America (P. G. Rodewald, Ed.).

Ithaca: Cornell Lab of Ornithology.

O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP and Weiss JM.

2007. Temperature control of larval dispersal and the implications for marine

ecology, evolution, and conservation. Proceedings of the National Academy of

Science 104(4):1266-1271.

Pachauri RK, Reisinger A and Core Writing Team. 2007. IPCC Climate Change 2007:

Synthesis Report. Retrieved from: www.ipcc.ch/pdf/assessment-

report/ar4/syr/ar4_syr.pdf.

Pearson TH. 1968. The feeding biology of sea-bird species breeding on the Farne

    Islands, Northumberland. Journal of Animal Ecology 37:521-552.

Pershing AJ, Alexander MA, Hernandez CM, Kerr LA, Le Bris A, Mills KE, Nye JA,

    Record NR, Scannell HA, Scott JD, Sherwood GD and Thomas AC. 2015. Slow

    adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod

    fishery. Science 350 (6262):809-812.

Piatt JF, Harding AMA, Shultz M, Speckman SG, Van Pelt TI, Drew GS and Kettle AB.

    2007. Seabirds as indicators of marine food supplies: Cairns revisited. Marine

    Ecology Progress Series 352:221-234.

Pierce D. 2015. ncdf4: Interface to Unidata netCDF (Version 4 or Earlier) Format Data

    Files. R package version 1.15, https://cran.r-

    project.org/web/packages/ncdf4/index.html.

Pinheiro J, Bates D, DebRoy S, Sarkar D and R Core Team. 2017. nlme: Linear and

    Nonlinear Mixed Effects Models. R package version 3.1-131, https://CRAN.R-

    project.org/package=nlme.

Rodway MS, Regehr HM and Chardine JW. 1996. Population census of breeding

    Atlantic Puffins at Great Island, Newfoundland in 1993-1994. St. John's, NL:

    Environment Conservation Branch, Canadian Wildlife Services, Atlantic Region.

Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu Q, Casassa G, Menzel A, Root TL,

    Estrella N, Seguin B, Tryjanowski P, Liu C, Rawlins S and Imeson A. 2008.

    Attributing physical and biological impacts to anthropogenic climate change.

    Nature 453:353-357.

Stenseth NC and Mysterud A. 2002. Climate, changing phenology, and other life history

    traits: Nonlinearity and match-mismatch to the environment. Proceedings of the

    National Academy of Science 99(21):13379-13381.

Suryan RM, Irons DB, Brown ED, Jodice PGR and Roby DD. 2006. Site-specific effects

    on productivity of an upper trophic-level marine predator: bottom-up, top-down,

    and mismatch effects on reproduction in a colonial seabird. Progress in

    Oceanography 68:303-328.

Taboada FG and Anadón R. 2012. Patterns of change in sea surface temperature in the

    North Atlantic during the last three decades: beyond mean trends. Climate Change

    115:419-431.

Watanuki Y, Ito M, Deguchi T and Minobe S. 2009. Climate-forced seasonal mismatch

    between the hatching of rhinoceros auklets and the availability of anchovy. Marine

    Ecology Progress Series 393:259-271.

Wilhelm SI, Mailhiot J, Arany J, Chardine JW, Robertson GJ and Ryan PC. 2015.

    Update and trends of three important seabird populations in the western North

    Atlantic using a geographic information system approach. Marine Ornithology

    43:211-222.

Williams TD. 2005. Mechanisms underlying the costs of egg production. Bioscience

    55:39-48.

Appendix I. Division of colonies into regions, latitude and longitude of the study colonies, and the source and number of eggs collected each year at these study colonies. Abbreviated sources are as follows: New Brunswick Museum Archives (NBM), Royal Ontario Museum (ROM), Carnegie Museum (CM), Provincial Museum of Newfoundland and Labrador (MNF), and the Canadian Wildlife Service Toxicology Program (CWS). Additional contributors with unpublished data are as follows: Dr. AL Bond (Royal Society for the Protection of Birds), Dr. GJ Robertson (Environment Canada), Dr. IL Jones (Memorial University of Newfoundland [MUN]), and Dr. WA Montevecchi (MUN); asterisk (*) denotes unpublished data.

Region	Colony	Latitude	Longitude	n	Year	Data Source
Bay of Fundy (BOF)	Machias Seal Island (MSI)	44°30'07"N	67°06'05"W	1	1889	NBM
				4	1924	NBM
				5	1992	NBM
				15	1992	CWS
				15	1996	CWS
				25	1998	Diamond*
				15	2000	CWS
				15	2004	CWS
				10	2006	Bond (2007)
				5	2008	NBM
				15	2008	CWS
				16	2012	CWS
				16	2016	CWS
Gulf of St. Lawrence (GSL)	Bird Rocks (BR)	47°50'18"N	61°08'44"W	1	1877	ROM
				5	1901	CM
				1	1903	ROM
				5	1920	CM
				3	1926	CM
				4	1927	ROM
				5	1928	ROM
	Île Brion (IB)	47°47'17"N	61°28'52"W	1	1897	ROM
	Îles de Mingan (IM)	50°12'30"N	64°07'29"W	1	1898	ROM

Region	Colony	Latitude	Longitude	n	Year	Data Source
				18	1928	CM
				5	1972	CWS
				5	1988	CWS
				13	1992	CWS
	Îles Sainte-Marie (ISM)	50°18'20"N	59°39'18"W	10	1997	CWS
				12	2000	CWS
				15	2004	CWS
				15	2008	CWS
				16	2012	CWS
				8	2016	CWS
	Unknown	-	-	2	1898	ROM
				2	1992	CWS
Labrador (LAB)	Gannet Island (GI)	53°56'23"N	56°33'48"W	1	1895	ROM
				1	1910	ROM
				2	1915	CM
				56	1985	Robertson*
				147	1996	Jones*
				50	1997	Jones*
				32	1998	Jones*
				166	1999	Jones*
				14	2000	CWS
				49	2000	Jones*
				50	2001	Jones*
				50	2002	Jones*
				51	2003	Jones*
				50	2004	Jones*
				50	2005	Jones*
				51	2006	Jones*
				15	2008	CWS
				16	2016	CWS
Newfoundland (NFL)	Baccalieu (BA)	48°08'13"N	52°48'04"W	60	1978	Montevecchi*
	Witless Bay (WB)	47°15'47"N	52°46'23"W	150	1968	Nettleship (1972)
				92	1985	Robertson*
				15	1992	CWS
				15	1996	CWS
				15	2000	CWS
				64	2003	Robertson*
				15	2004	CWS
				60	2004	Robertson*
				15	2008	CWS
				6	2009	MNF
				28	2012	Bond*
				52	2013	Robertson*
				50	2015	Robertson*

Region	Colony	Latitude	Longitude	n	Year	Data Source
				16	2016	CWS
	Wolfe Island (WI)	48°43'48"N	53°54'48"W	1	1884	NBM

Appendix II. A) Five candidate models describing the relationship between year, region, the interaction between year and region, and Atlantic Puffin egg volume in eastern Canada between 1877 and 2016. All models, including the null, include colony as a random term. B) Twelve candidate models describing the relationship between region, year, sea surface temperature (SST), the interaction terms year x region, year x SST, region x SST, and year x region x SST, and Atlantic Puffin egg volume in eastern Canada between 1985 and 2016.

Model
A
EggVolume~Year+Region+Year*Region+(1|Colony)
EggVolume~Year+Region+(1|Colony)
EggVolume~Year+(1|Colony)
EggVolume~Region+(1|Colony)
EggVolume~(1|Colony)
B
EggVolume~Year+Region+SST+Year*Region*SST
EggVolume~Year+Region+SST
EggVolume~Year+Region+Year*Region
EggVolume~Year+Region
EggVolume~Year+SST+Year*SST
EggVolume~Year+SST
EggVolume~Region+SST+Region*SST
EggVolume~Region+SST
EggVolume~Year
EggVolume~Region
EggVolume~SST
EggVolume~1