

**Changes in body size of Atlantic Puffins at Machias Seal Island (MSI) from 1995-2019**

by

Joy Georgantopoulos

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

**Bachelor of Science with Honours in Marine Biology**

Supervisor: Dr. Heather Major, Department of Biological Sciences

This work is licensed under the Creative Commons Attribution 4.0 International License. To view a copy of this license, visit: <http://creativecommons.org/licenses/by/4.0/> or send a letter to Creative Commons, PO Box 1866, Mountain View, CA 94042, USA.

THE UNIVERSITY OF NEW BRUNSWICK

SAINT JOHN

April, 2020

©Joy Georgantopoulos, 2020



This work is licensed under the Creative Commons Attribution 4.0 International License. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>

## ABSTRACT

Body size of fledging Atlantic Puffins (*Fratercula arctica*) at Machias Seal Island have been decreasing over the past 25 years (1995-2019) likely due to climate change. Using fledging size data archived in the Microsoft Access data base “seabird finder” I asked three questions: 1) have puffin fledgers gotten smaller in size (wing chord and mass) over the last 25 years, 2) can small fledgers continue to grow (in wing chord) after leaving the island, and 3) are adult Atlantic Puffins decreasing in size (wing chord). Using linear regressions, I found support for the hypothesis that fledgers are getting smaller with time and that small fledgers grow more after leaving the island than large fledgers. Finally, I found a marginally insignificant result suggesting that adult size is changing in response to fledging size (i.e., adults are becoming smaller with time).

## **DEDICATION**

To Mom and George, who pushed me to be my best, always.

## **ACKNOWLEDGEMENTS**

I would like to acknowledge Dr. Heather Major, my supervisor, who was a tremendous help throughout this whole process and also taught me a lot this year while writing my thesis. I would also like to acknowledge Dr. Tony Diamond, the MSI research crew, and the ALAR lab members who have gone out to the island, collected all of the data, and have done a lot of other very valuable research on the island. Finally, I would like to thank Environment and Climate Change Canada for their support. Research on Machias Seal Island is funded through a contribution agreement from Environment and Climate Change Canada to Drs. Diamond and Major. Annual Animal Use Protocols were obtained from the UNB Animal Care Committee.

## **STATEMENT OF RESEARCH CONTRIBUTION**

In September 2019, in conversation with Dr. Major, I decided to tackle the question of whether body size of Atlantic Puffin fledgers has changed over the past 25 years at Machias Seal Island. My part in this research was to bring together and analyze annual data on fledger body size that teams of scientists collected at Machias Seal Island annually beginning in 1995. This included querying the Microsoft Access database ‘Seabird Finder’ for all fledger and adult recapture data, and filtering all data not related to fledger body size and subsequent adult recaptures of those same individuals. With the help of Dr. Major, I completed my statistical analyses using R. I was then responsible for graphing the results, interpreting them, and writing and editing my thesis.

## Table of Contents

<a href="#">ABSTRACT</a> .....	ii
<a href="#">DEDICATION</a> .....	iii
<a href="#">ACKNOWLEDGEMENTS</a> .....	iv
<a href="#">STATEMENT OF RESEARCH CONTRIBUTION</a> .....	v
<a href="#">Table of Contents</a> .....	vi
<a href="#">List of Figures</a> .....	vii
<a href="#">Introduction</a> .....	1
<a href="#">Material and Methods</a> .....	6
<a href="#">Fieldwork</a> .....	6
<a href="#">Data Analysis</a> .....	6
<a href="#">Statistical Analysis</a> .....	8
<a href="#">Results</a> .....	9
<a href="#">Change in Fledgling Size</a> .....	9
<a href="#">Post-Fledgling Wing Chord Growth</a> .....	11
<a href="#">Change in Adult Size</a> .....	13
<a href="#">Discussion</a> .....	14
<a href="#">References</a> .....	18

## List of Figures

- [Figure 1. Map showing location of Machias Seal Island in the Bay of Fundy/Gulf of Maine.....](#) 7
- [Figure 2. Summary of the relationship between Atlantic Puffin fledgling mass \(in grams\) and wing chord \(in mm\) at Machias Seal Island between 1995 - 2019. Each point is the average for one year of data shown with 95% CIs. Linear trendline included to show the general relationship between mass and wing chord.....](#) 9
- [Figure 3. Summary of the mean \( \$\pm\$  95% CI\) of Atlantic Puffin fledger A\) wing chord and B\) mass measured at Machias Seal Island at the time of their departure from the island in 1995 – 2019. Linear trendline added to show general decrease with time.....](#) 10
- [Figure 4. Comparison of size \(wing chord in mm\) of fledgers \(age 0\) and recaptured adult Atlantic Puffins on MSI from 1995-2019.....](#) 12
- [Figure 5. Comparison of the change in Atlantic Puffin wing chord length \(in mm\) from fledger to adult. All data were collected between 1995 – 2019. Linear trendline included to indicate general negative relationship between change in wing chord length from fledger to adult and fledger wing chord length.....](#) 12
- [Figure 6. Comparison of Atlantic Puffin adult wing chord \(mm\) measurements taken when recaptured on MSI and the year they fledged. All data were collected between 1995 – 2019. Linear trendline to indicate the relationship between adult wing chord and fledge year.....](#) 13

## Introduction

Climate change like increases in both air and sea surface temperatures (SST), and more frequent heat waves is affecting ecosystems worldwide (IPCC, 2018). With respect to rising SST, marine ecosystems have become vulnerable and continue to face serious threats (Diamond and Devlin, 2003; Pershing et al., 2015). Some notable changes as a result of a warming environment include a change in prey source and an increase in competition for resources (Amey, 1992; Scopel et al., 2019). The Gulf of Maine is an area that is experiencing warming at a rate faster than most of the global oceans, at a rate of up to 99% faster (Pershing et al., 2015). This could have major negative impacts on the surrounding ecosystems and the organisms that live within them. This increased rate of warming is due to the position of the Pacific Decadal Oscillation (PDO, a 20-30 year, recurring, ocean-atmosphere climate pattern that is centred over pacific basin), Atlantic Multidecadal Oscillation (AMO, a 60-80 year natural pattern of climate based on the anomalies in sea surface temperatures), and the Gulf Stream (Mantua and Hare, 2001; Pershing et al., 2015; Wu et al., 2011).

This change in climate is affecting many species and there seems to be a trend in many species towards a smaller body size. Reductions in body size are now considered to be the third universal response to climate change, with the other two being change in phenology and change in distribution (Durant et al., 2007; Gardner et al., 2011; Visser and Both, 2005). Body size is directly related to resilience of a species and has direct effects on water requirements and energy for thermoregulation. The Bergmann rule is the tendency for mean body size to decrease with decreasing latitude, because smaller body sizes are beneficial in warmer climates as it is easier to remove heat due to the proportionally larger surface area and thinner boundary layers (Gardner et



al. 2011). Thus, this tendency could be occurring at higher latitudes as a mechanism to deal with increasing temperatures (Gardner et al., 2011). The actual change in body size could be genetic (i.e., adaptation) or phenotypic plasticity, with phenotypic plasticity being less of a long-term solution and genetic adaptations being better for long term success (Gardner et al., 2011; Gienapp et al., 2008). However, a probable reason for the shift in body size is change in quality and nutrition of food the organism receives. Temperature could be a factor by altering growing seasons or affecting temperature-dependent energy budget that can restrict feeding (Gardner et al., 2011; Ozgul et al., 2010). Also non-temperature related events could cause a change in food source, like habitat loss or fragmentation, changes in land or agricultural practices (Gardner et al., 2011; Schmidt and Jensen, 2005). The relationship of nutrition to body size has not been studied very extensively as it is difficult to get a direct assessment of many organisms. However, birds are very good organisms to study nutrient availability stress or environmental changes as they are easy to monitor in the marine environment thus making data easy to obtain and their feathers which can indicate conditions of environment based on what kind of state the bird was in during molt (i.e. while the feathers a growing), they do not provide much information once fully grown as this do not change metabolically (Gardner et al., 2011).

Atlantic Puffins (*Fratercula arctica*) are medium sized (~30 cm in length) pelagic seabirds that range throughout the North Atlantic Ocean (Harris and Wanless, 2011; BirdLife International, 2019). They have a native non-breeding distribution that reaches north of Spitsbergen (Norwegian archipelago) and extends south to around South Carolina, USA (Harris and Wanless, 2011; BirdLife International, 2019). In correlation with this distribution they do show a decline in body size in relation to latitude (i.e. as latitude decrease body size does as well) as predicted bgy the Bergman's rule (Lowther et al., 2002). However, their breeding range does

not extend as far south, with the Gulf of Maine being their southernmost extent (Harris and Wanless, 2011; BirdLife International, 2019). This limitation in breeding range is likely due to temperature, which directly relates to food supply (Diamond and Devlin, 2003). As is the case for most seabirds, during the breeding season adults are constrained to forage near the colony (Gaston, 2004). An ideal prey source for the Atlantic Puffin would be a very nutrient-rich, high-lipid food source, like Atlantic herring (*Culpea harengus*). In contrast, a poor food source would be a low nutrient, low lipid food source, like Euphausiids or larval fish (Scopel et al., 2019). Lipid is the main component of food used to measure energy because it contains more energy per gram than proteins or carbohydrates (Ricklefs, 1974; Scopel et al., 2019). This is beneficial because it means that the energy required to break down lipids is lower than carbohydrate or proteins (Blaxter, 1989; Scopel et al., 2019). The food being brought back to the colony to feed the chicks varies from year to year but over the past 25 years a visible change has been observed and herring has been almost completely lost from the diet of chicks (Diamond and Devlin, 2003; Scopel et al., 2019).

Body condition and growth can be affected by several factors: the prey being brought back to the colony to feed the chicks; and the prey available at sea when fledgers leave the colony. The observed shift to lower quality prey in recent years at colonies in the Gulf of Maine could result in a change in body condition as insufficient nutrients are gained, and this can ultimately lead to death (Elliot et al., 2016; Ydenberg et al., 1994). Wing chord and mass are often used as indicators of body condition in birds (Elliot et al., 2016; Morrison et al., 2008; Whidden, 2016). Wing chord is a structural measurement used to approximate the size of the bird, and is measured from the carpal joint at the bend of the wing to the tip of the longest primary feather. Condition is then measured as the ratio of mass to wing chord, where a bird with

a higher than average mass for the length of its wing chord is considered in good condition (i.e., it was able to consume enough nutrients to more than meet its metabolic requirements).

Atlantic Puffins display a semi-precocial pattern of chick development, where chicks require both parents to feed them until they gain independence (i.e., fledge; Ydenberg et al., 1994). Here, at the time of fledging, body condition (i.e., the ratio of mass to wing chord) is important, as there is a positive correlation between mass at time of fledging and juvenile survival (Whidden, 2016), which is likely due to the bird having a reserve of energy to draw upon when they are out at sea and may not have developed successful foraging skills yet.

In the Gulf of Maine, where the ocean is rapidly warming and changes in marine species have been noted (Pershing et al., 2018; Scopel et al., 2019), researchers at Machias Seal Island have examined the trend that the body size of fledging Atlantic Puffins appears to have declined (in both wing chord and mass) over the past 25 years and wondered if this decrease is significantly significant (Whidden, 2016, H Major personal communication). In a previous study by Whidden (2016) it was found that there was a significant decline in wing chord but not in mass at the time of fledge, this result is what my study will be building off of. The driving factors behind this change have not been investigated, but it is thought that changing prey availability and quality related to ocean warming is a likely factor. This is because if prey change (i.e. from nutrient dense herring, to species less nutrient dense like larval fishes) is having an effect on size of the puffins then it would be assumed to be more advantageous to be smaller thus requiring less energy to maintain a healthy body conditions. Making having a larger body less ideal as it would be more difficult to maintain a proper body condition. Thus, my primary objective is to quantify changes in body size (mass and wing chord) of fledgling and adult Atlantic Puffins at Machias Seal Island between 1995 – 2019. I will address this objective using

a three-pronged approach where I will 1) quantify changes in fledger body size with time; 2) assess whether individuals that fledge small are able to compensate for their smaller size by growing more after departing the island than individuals that fledge large; and 3) assess whether adult body size has changed over the same time period in response to fledger body size. I hypothesized that adult body size is a function of body size at the time of fledging, and predict that small fledgers are not able to compensate for their small size by growing more than large fledgers and therefore adult body size will decrease with a decrease in fledgling body size, thus resulting in a significant relationship between adult body size and year.

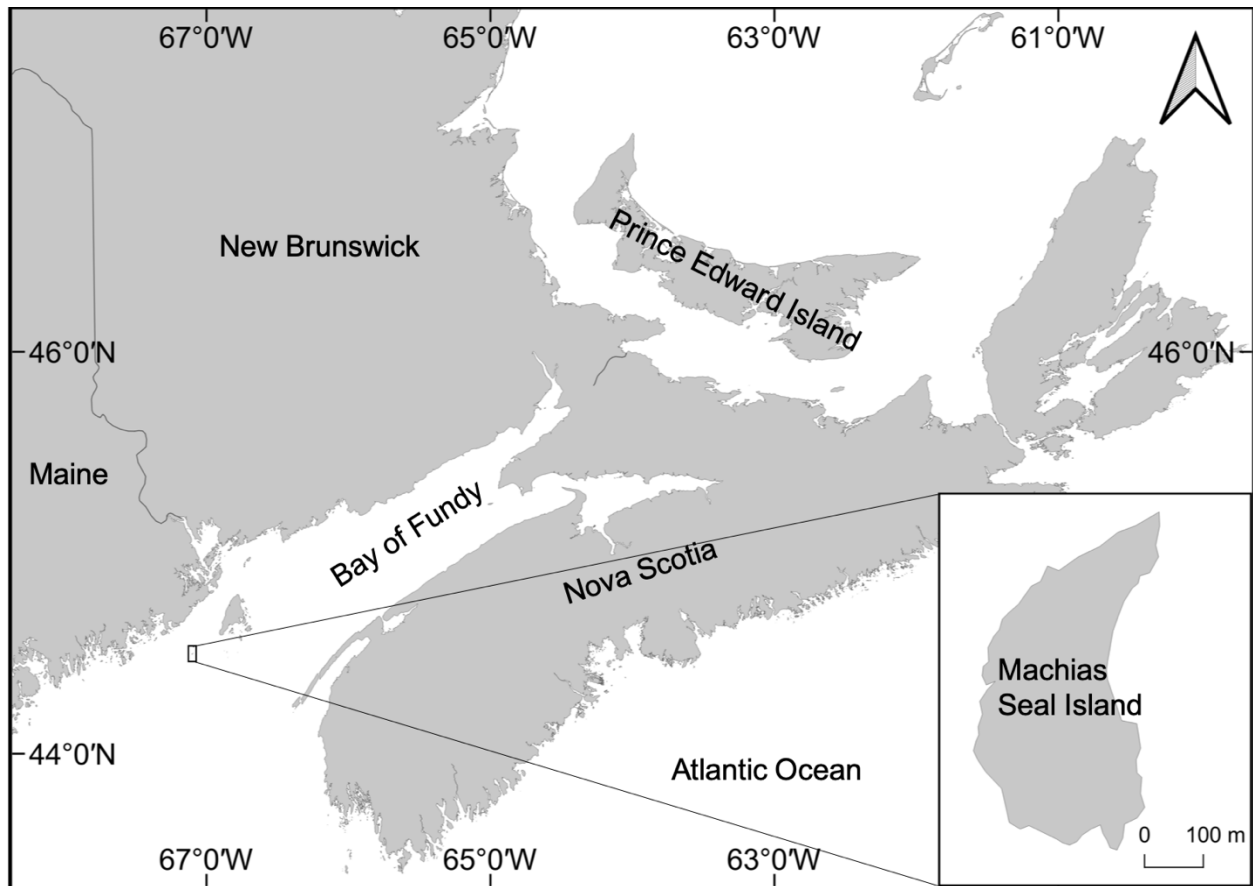
## **Material and Methods**

### **Fieldwork**

Machias Seal Island (MSI), designated as a federal Migratory Bird Sanctuary, is a small island (~9.5 hectares) located at the mouth of the Bay of Fundy and the edge of the Gulf of Maine (Figure 1). Members from the Atlantic Laboratory for Avian Research (ALAR) at the University of New Brunswick have been studying populations of seabirds, including Atlantic Puffins, at MSI since 1995. Data collection for Atlantic Puffins includes: capturing adults on the island using box traps (wooden boxes with a swivel lid, when a bird sits on the top of the box, the swivel spins depositing the bird inside the box, where it is retrieved); burrow ‘grubbing’ (pulling birds out of nesting burrows by hand); and capturing fledging chicks during their departure from the island. All captured individuals are banded with a uniquely coded Bird Banding Laboratory (BBL) stainless steel leg band and an alpha-numeric leg band (used to identify individuals in the field), and have morphometric measurements taken include mass to the nearest gram and wing chord to the nearest millimeter (see Diamond, 2014). Captured individuals are released back into their nesting burrow (those who were grubbed), on the rocks near where they were captured (box trapped), or directly into the ocean (fledgers).

### **Data Analysis**

All banding data from MSI is entered into an Access database called “Seabird Finder”. I queried the database for all capture and recapture measurements from Atlantic Puffins on Machias Seal island for the years 1995 – 2019. The data was exported as a Microsoft Excel



**Figure 1.** Map showing location of Machias Seal Island in the Bay of Fundy/Gulf of Maine.

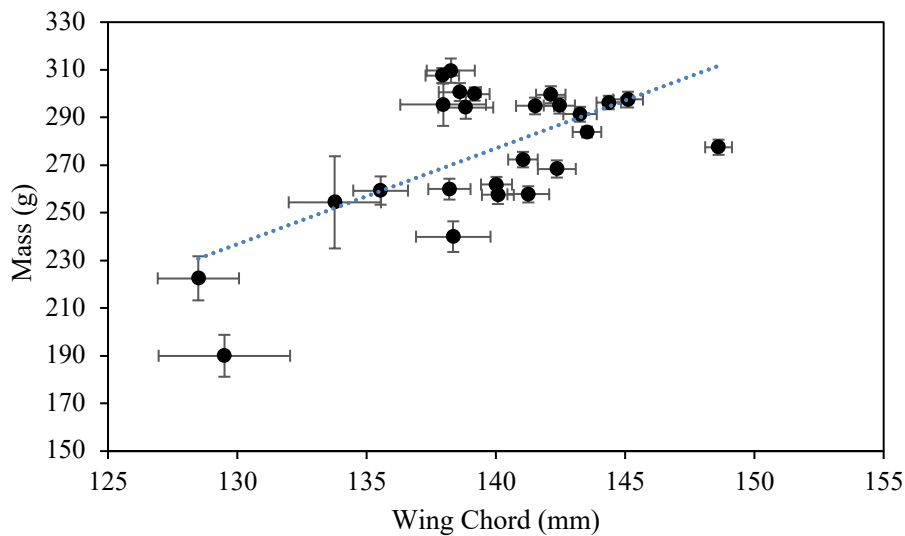
spreadsheet and includes both adult and chick measurements. I then manually separated adult and chick data within each worksheet for each of the 25 years. Finally, I discarded all unnecessary information, keeping measurements for wing chord, mass, and other identifying information (i.e., ID numbers, date of capture/ recapture, etc.).

## Statistical Analysis

All statistical analyses were completed in the R studio environment (R version 3.5.2). A separate analysis was run for each of my three questions. First, using a Multivariate Linear Regression (Wilks'  $\Lambda$ ), I tested whether the body size (i.e., measurements of mass and wing chord) of fledgers has changed between 1995 – 2019. Second, I tested whether fledglings that left the island smaller than average grew more before returning as adults than those that left the island larger. Here, I first queried the database for all individuals that were banded as a fledger and were subsequently recaptured as an adult. I calculated the difference between adult wing chord and fledger wing chord using a Linear Regression, I evaluated the relationship between fledger wing chord and the change in wing chord at the adult stage. Finally, using only data from individuals that returned to the island as adults, I used a Linear Regression to assess the relationship between adult wing chord and the year the individual fledged the island. All summary data are presented as means with 95% confidence intervals.

## Results

During 1995 – 2019 a total of 4,736 fledgling Atlantic Puffins were captured as they were departing MSI. The total number of fledgers measured in each year varied and averaged  $189 \pm 0.03$  (range 26 – 495). In general, there was variability in the size of puffin fledgers among years and puffins with larger wing chords were also heavier (Figure 2). Puffin fledgers were smallest in 2016 and largest in 2004.



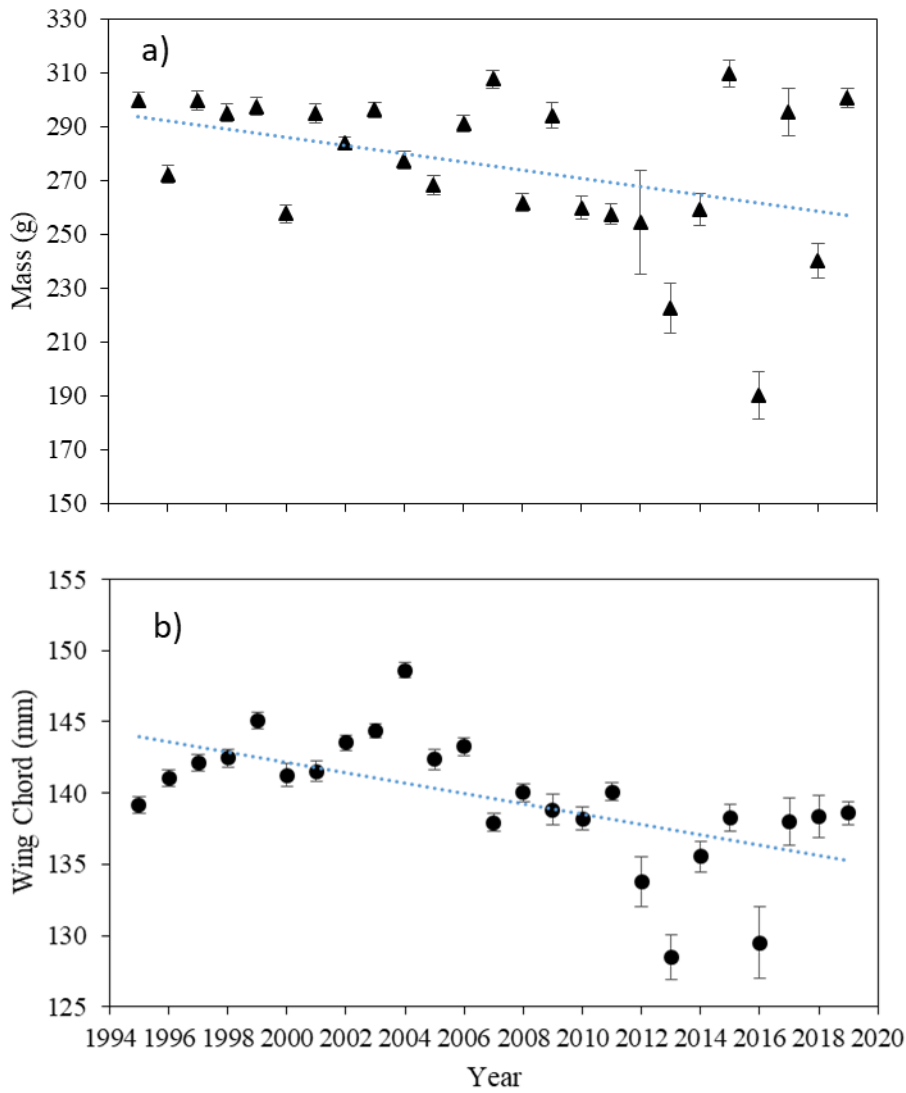
**Figure 2.** Summary of the relationship between Atlantic Puffin fledgling mass (in grams) and wing chord (in mm) at Machias Seal Island between 1995 - 2019. Each point is the mean for one year of data shown with 95% CIs. Included is a linear trendline to show the general relationship between mass and wing chord.

### Change in Fledgling Size

During 1995 - 2019, fledgers departing MSI averaged  $282.6 \text{ g} \pm 0.98 \text{ g}$  (range 123-495) in mass and  $141 \text{ mm} \pm 0.18 \text{ mm}$  (range 98-240) in wing chord. A multivariate linear regression



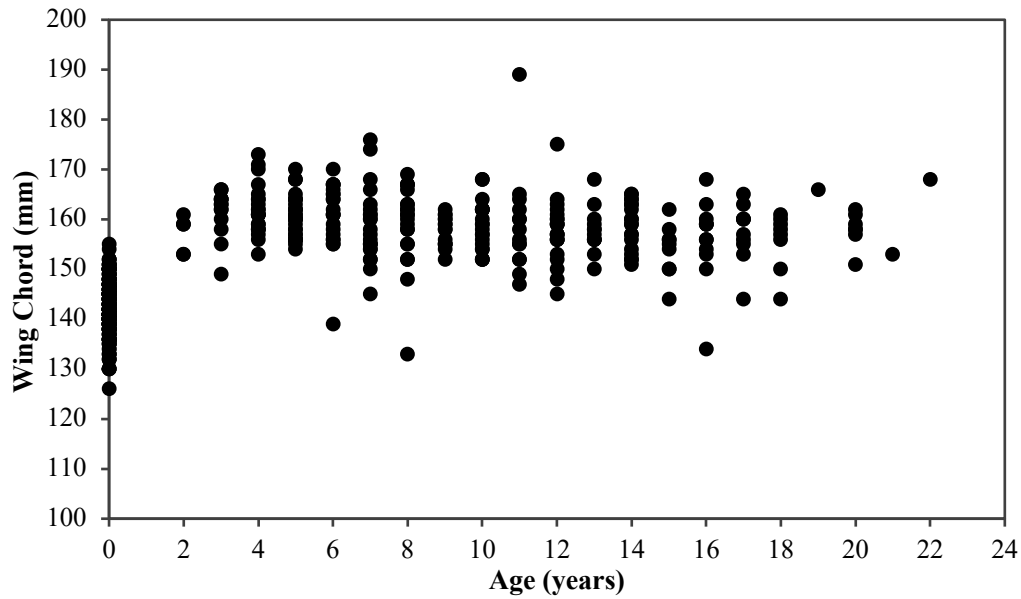
revealed that the body size of fledgers changes significantly with year (Wilks'  $\Lambda = 0.91$ ,  $F = 244.66$ ,  $df = 4,730$ ,  $p\text{-value} < 0.001$ ). Graphical examination of the data shows that both mass and wing chord of fledgers leaving Machias Seal Island are declining with time (Figure 3).



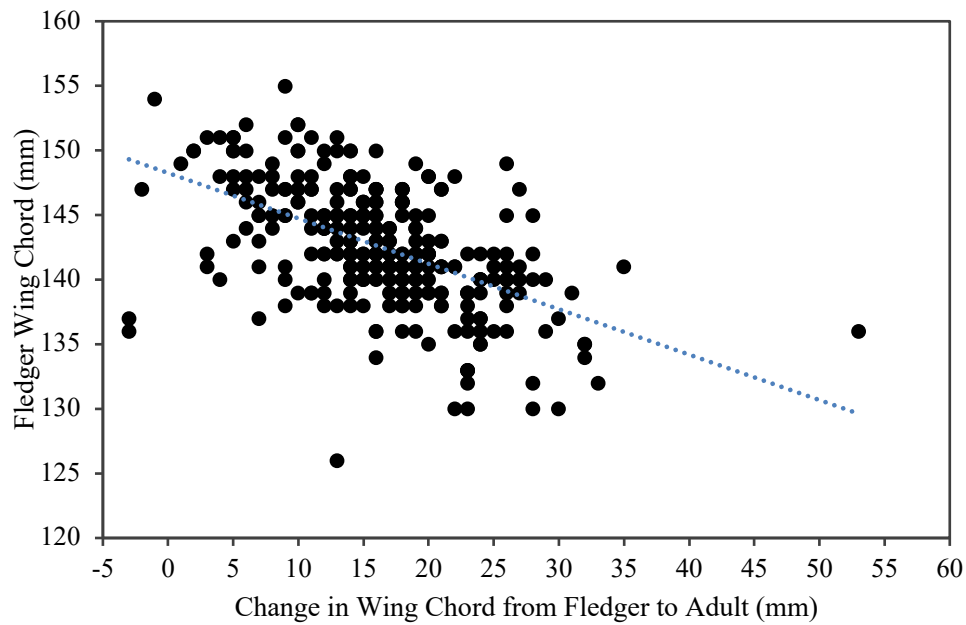
**Figure 3.** Summary of the mean ( $\pm$  95% CI) of Atlantic Puffin fledger A) wing chord and B) mass measured at Machias Seal Island at the time of their departure from the island in 1995 – 2019. A Linear trendline is included to show general decrease with time.

### **Post-Fledgling Wing Chord Growth**

During 1995 – 2019 a total of 229 individual adult Atlantic Puffins were recaptured on MSI that had also been measured as a fledger. For these individuals I have a record of their size (wing chord) at fledge and when they were recaptured as adults, including their age in years at the time of recapture. Recapture ages ranged from 2 to 22 years old and include 28 individuals recaptured and measured in two or more years. Overall, the mean change in wing chord from fledgling to adult was  $16.3 \text{ mm} \pm 0.85 \text{ mm}$ . In general, at the time of departure from MSI fledgers are smaller than adults, but once individuals are ~2 years old increases in wing chord length are not observed (Figure 4). However, linear regression assessing the relationship between change in wing chord from fledger to adult (Figure 5) shows that the post-fledging increase in wing chord was inversely related to fledging wing-length (i.e., longer-winged fledgers grew less than those fledging with shorter wings) ( $F=111.56$ ,  $df = 1$ ,  $p\text{-value}<0.001$ ).



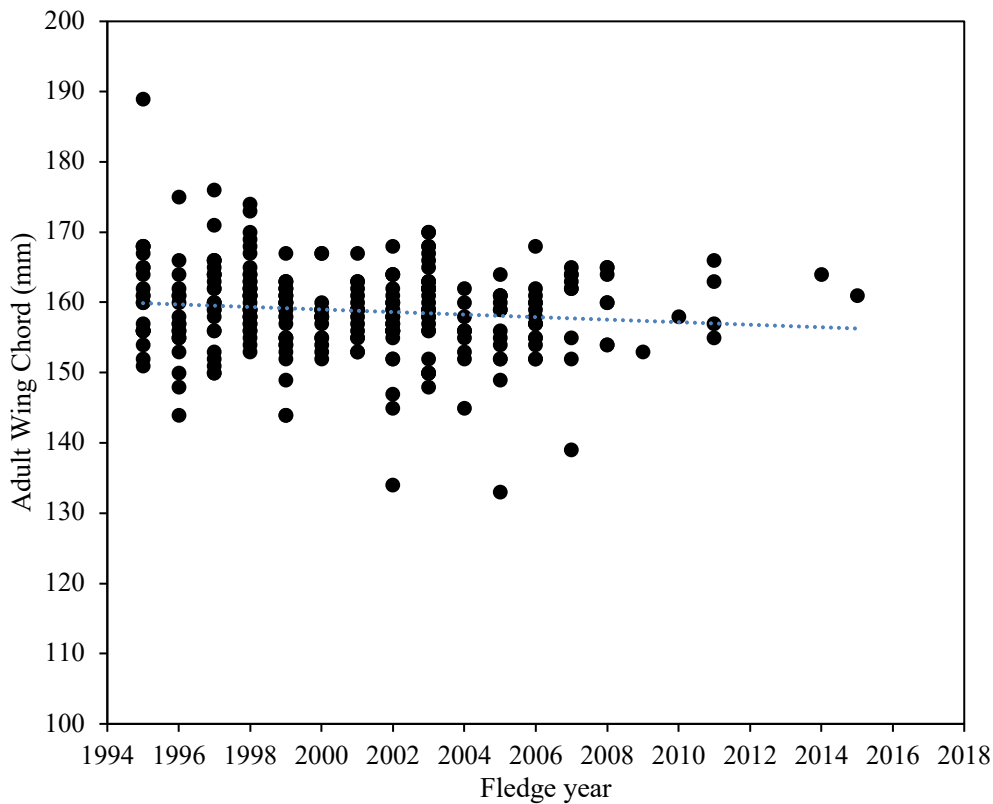
**Figure 4.** Comparison of size (wing chord in mm) of fledgers (age 0) and recaptured adult Atlantic Puffins on MSI from 1995-2019



**Figure 5.** Comparison of the change in Atlantic Puffin wing chord length (in mm) from fledger to adult. All data were collected between 1995 – 2019. A linear trendline is included to indicate general negative relationship between change in wing chord from fledger to adult and fledger wing chord.

## Change in Adult Size

Focusing on the 229 individual Atlantic Puffins that were recaptured at MSI after being measured as a chick, I found that adult wing chord length varied among years and averaged 159 mm  $\pm$  0.72 mm (range 133-189). Using a linear regression, I found a weak (i.e., non-significant, but very close to significant) negative relationship ( $F = 3.83$ ,  $df = 281$ ,  $p\text{-value} = 0.051$ ) between adult wing chord and the year of fledge.



**Figure 6.** Comparison of Atlantic Puffin adult wing chord (mm) measurements taken when recaptured on Machias Seal Island and the year they fledged. All data were collected between 1995 – 2019. Included is a linear trendline to indicate the relationship between adult wing chord and fledge year.

## Discussion

Over the last 25 years, researchers working on seabirds at Machias Seal Island have noted that the size (mass and wing chord) of Atlantic Puffin fledgers has been decreasing. The objective of my study was to quantify these changes and test how a change in body size at fledging might affect the size of individuals in adulthood. I found a significant negative relationship between fledger size and year, suggesting that fledgers are getting smaller with time (i.e. New fledgers are smaller than fledgers from the year before and this trend has continued over time); and that individuals that fledge the island small, grow more before they return as adults than those that leave the island large. Finally, I found no significant relationship between adult body size and the year of fledge, suggesting that adult body size has not decreased with time, however, I note that this relationship was only marginally non-significant, and suggests a weak underlying trend. My hypothesis that adult body size is a function of body size at the time of fledging, was therefore not supported; but the sample size for this test was quite small ( $n=229$ ) and given the dependence of p-values on sample size, a longer time series might well show a slight but significant trend.

Researchers on Machias Seal Island have noted a change in diet fed to chicks, with virtually no herring being brought into the colony in recent years (Scopel et al., 2019). Similar to studies on other species of alcids (e.g., Golet et al, 2000), Scopel et al. (2019) found that in years when high lipid prey (such as herring) are not available to puffin chicks, reproductive success may suffer through reduced chick growth and survival. This reduced growth in years with poor chick diet was also observed by Barrett and Rikardsen (1992) on a Norwegian colony, where they found that food shortages led to decreased growth of puffin chicks. Thus, changes in the quantity and quality of prey brought by adults for chicks at Machias Seal Island are likely the

cause of the observed decrease in body size in recent years, although this relationship should be tested. The impact of this relationship, in an area that is rapidly warming due to climate change, is concerning. With the rapid warming in mind, effects like the Bergmann rule may be an interesting area to explore and how effects of temperature are changing body size.

Morrison et al. (2009) found that Tufted Puffins (*Fratercula cirrhata*) at Triangle Island, BC with larger wing chord at fledging were more likely to return to their natal nesting site than individuals that fledged with smaller wing chords. They concluded that this suggested that individuals that fledged with a smaller wing chord had lower survival during the juvenile stage. Hipfner and Gaston (1999) found that mean mass of Atlantic Puffin fledgers varied more by year and colony than wing chord. Together with the Morrison et al. (2009) data this suggests puffins preferentially allocate energy and nutrients to wing chord growth over mass, which is an adaptive growth strategy (Morrison et al., 2009; O'Connor, 1977; Øyan and Anker-Nilssen, 1996). My results suggest this is not the case at Machias Seal Island, where both mass and wing chord were reduced. The impact this reduction in body size has on recruitment and juvenile survival has been tested and preliminary analyses found that lighter fledgers survived less well but the relationship requires further research (Whidden, 2016).

In general, it is believed that chicks should place resources into growing their skeletal structures before laying down fat stores (Ricklefs, 1983). Typically, chick growth follows a sigmoidal curve, with a period of rapid linear growth prior to reaching an asymptote prior to fledging (Gaston, 2004). At fledge individuals tend to have a heavier mass and shorter wing chord than adults (Gaston, 2004). The observation that puffin chicks fledge at or above adult body mass is believed to function as a fail-safe strategy, where chicks accumulate extra resources while being fed by their parents so that once they are at sea they can live off those resources until

they learn to forage for themselves (Roby, 1991; Weimerskirch et al., 2000). It is interesting that at Machias Seal Island, we don't see individuals leaving the island with similar wing chords (a measure of their structural size) across years but light in mass (a measure of their fat stores) when conditions are poor, which would indicate a poor body condition. Rather we see that individuals are leaving smaller in both wing chord and mass. Perhaps individuals are compensating for poor growth during the nesting phase by maintaining a consistent body condition (i.e., wing chord to body mass ratio) at fledge and are therefore better able to survive the post-fledging period. My current analyses do not answer this survival question, but I recommend it for future work.

The size advantage hypothesis states that larger body size gives individuals a physical advantage during competition for resources (Garnett 1981). Further, if the body size of a species is the direct result of evolutionary forces and adaptation, we can assume that there would be a selective advantage to attaining that size and individuals should allocate energy into structural growth. Thus, if individuals are fledging Machias Seal Island small, they might attempt to mitigate the effects of a reduced size by continuing to grow at sea, post fledge, which is what my data suggest. Further, this suggests that even though body size of fledglings has decreased over the last 25 years, the body size of adults should remain unchanged but only if they can perfectly compensate by post-fledging growth.

My final analysis evaluated the size of recaptured adults as a function of the year they fledged the island. If, as suggested above, individuals that leave the island small can compensate for their small size and continue to grow to an "ideal" adult size there should be no relationship between adult size and fledge year; this is what my data show, giving further support to the idea of compensatory growth post-fledge. However, I note that to be included in this analysis

individuals needed to recruit back to Machias Seal Island and be recaptured and measured. Out of all fledgers that have been captured and measured on Machias Seal Island since 1995, those that have been recaptured as adults account for only 5%. Further, puffins do not recruit to a nesting island until they are about five years old. Thus, my sample of adults only includes individuals up to and including 2015, but fewer than 15 individuals from fledge years after 2006 were recaptured as adults and average just one individual per year. Given the regime shifts in the Gulf of Maine in the early and mid-2000s (Morse et al. 2017), and in 2010 (Kress et al. 2016, Scopel et al. 2019), and the marine heat waves in 2012 and 2016 (Mills et al. 2013; Pershing et al. 2018), it is possible that the weak negative trend will continue as more data is added to this dataset. I think it is important to continue to study this relationship and I further suggest research into the relationship between fledging size, juvenile survival, recruitment, and nesting success as outlined in the work of Maness and Anderson (2013).



## References

- Amey, K.D. 1998. Seabirds as indicators of changes in availability and commercial weir landings of herring. *In*: 'Birds as indicators of change in marine prey stocks'. M.Sc. thesis, Biology Department, University of New Brunswick, Fredericton, N.B., Canada.
- Barrett, R.T., and Rikardsen, F. 1992. Chick growth, fledging periods and adult mass loss of Atlantic puffins *Fratercula arctica* during years of prolonged food stress. *Colonial Waterbirds*, 24-32.
- BirdLife International. 2019. Species factsheet: *Fratercula arctica*. Downloaded from <http://www.birdlife.org> accessed on 27/11/2019.
- Blaxter, K. 1989. Energy metabolism in animals and man. Cambridge University Press, Cambridge, UK.
- Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Diamond, A.W. 2014. Seabird research and monitoring on Machias Seal Island: Research and logistics protocols. Unpublished report. 121 pages.
- Diamond, A. & Devlin, C. 2003. Seabirds as Indicators of Changes in Marine Ecosystems: Ecological Monitoring on Machias Seal Island. *Environmental Monitoring and Assessment* 88: 153-181.
- Durant, J.M. Hjernmann, D.Ø. Ottersen, G., Stenseth, N.C. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33: 271-283.

- Elliott, K.H., Linnebjerg, J.F., Burke, C., Gaston, A.J., Mosbech, A., Frederiksen, M., and Merkel, F. 2017. Variation in Growth Drives the Duration of Parental Care: A Test of Ydenberg's Model. *The American Naturalist*. 189: 526-538.
- Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., and Heinsohn, R. 2011. Declining body size: a third universal response to warming?. *Trends in ecology & evolution*, 26: 285-291.
- Garnett, M. 1981. Body size, heritability and influence on juvenile survival among Great Tits, *Parus major*. *Ibis* 123: 31-41.
- Gaston, A.J. 2004. *Seabirds a natural history*. Yale University Press, New Haven NY.
- Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A., & Merilä, J. 2008. Climate change and evolution: disentangling environmental and genetic responses. *Molecular ecology*, 17: 167-178.
- Golet, G.H., Kuletz, K.J., Roby, D.D., and Irons, D.B. 2000. Adult prey choice affects chick growth and reproductive success in Pigeon Guillemots. *Auk* 117: 82-91.
- Harris, M. P., and Wanless, S. 2011. *The puffin*. Poyser Books.
- Hipfner, J. M., and Gaston, A.J. 1999. Timing of nest departure in the Thick-billed Murre and Razorbill: tests of Ydenberg's model. *Ecology* 80: 587-596.
- IPCC. 2018. Summary for Policymakers. In: *Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty* [Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X.

- Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield (eds.)]. World Meteorological Organization, Geneva, Switzerland, 32 pp.
- Johnson, J.B., and K.S. Omland. 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution* 19: 101–108.
- Lindstrom, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology and Evolution* 14: 343-348.
- Lowther, P. E., A. W. Diamond, S. W. Kress, G. J. Robertson, and K. Russell (2002). Atlantic Puffin (*Fratercula arctica*), version 2.0. In *The Birds of North America* (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA.  
<https://doi.org/10.2173/bna.709>
- Maness, T.J., and Anderson, D.J. 2013. Predictors of juvenile survival in birds. *Ornithological Monographs* 78: 1-55.
- Mantua, N.J. and Hare, S.R. 2002. The Pacific Decadal Oscillation. *Journal of Oceanography*. 58: 35-44.
- Metcalfe, N.B. and Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? *Trends in Ecology and Evolution* 16: 254-260.
- Metcalfe, N.B. and Monaghan, P. 2003. Growth versus lifespan: perspectives from evolutionary ecology. *Experimental Gerontology* 38: 935-940.
- Mills, K.E., Pershing, A.J., Brown, C.J., Chen, Y., Chiang, F.-S., Holland, D.S., Lehuta, S., Nye, J.A., Sun, J.C., Thomas, A.C., and Wahle R.A. 2013. Fisheries management in a changing climate: lessons from the 2012 ocean heat wave in the Northwest Atlantic. *Oceanography* 26: 191-195.

- Morrison, K.W., Hipfner, J.M., Gjerdrum, C., and Green, D.J. 2009. Wing length and mass at fledging predict local juvenile survival and age at first return in Tufted Puffins. *Condor*. 111: 433–441.
- Morse, R.E., Friedland, K.D., Tommasi, D., Stock, C., and Nye, J. 2017. Distinct zooplankton regime shift patterns across ecoregions of the U.S. Northeast continental shelf Large Marine Ecosystem. *Journal of Marine Sciences* 165: 77-91.
- O'Connor, R.J. 1977. Differential growth and body-composition in altricial passerines. *Ibis* 119:147–166
- Øyan, H.S., and Anker-Nilssen, T. 1996. Allocation of growth in food-stressed Atlantic Puffin chicks. *Auk* 113:830–841
- Ozgul, A., Childs, D. Z., Oli, M. K., Armitage, K. B., Blumstein, D. T., Olson, L. E., Shripad, T., and Coulson, T. 2010. Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, 466:482-485.
- Pershing, A.J., Alexander, M.A., Hernandez, C.M., Kerr, L.A., Le Bris, A., Mills, K.E., Nye, J.A., Record, N.R., Scannell, H.A., Scott, J.D., Sherwood, G.D., and Thomas, A.C. 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science*. 350: 809-812.
- Pershing, A.J., Mills, K.E., Dayton, A.M., Franklin, B.S., and Kennedy, B.T. 2018. Evidence for adaptation from the 2016 marine heatwave in the Northwest Atlantic Ocean. *Oceanography* 31: 152–161.
- Ricklefs, R.E. 1974. Energetics of reproduction in birds. *In*: Paynter RA (ed) *Avian energetics*. Nuttall Ornithology Club No. 15, Cambridge, p 152–297.

- Ricklefs, R.E. 1983. Avian postnatal development. *In: Avian biology*, vol. 7 (ed. D. S. Farner, J. R. King & K.C. Parkes), pp. 2-83. New York: Academic Press
- Roby, D.D. 1991. Diet and postnatal energetics in convergent taxa of plankton-feeding seabirds. *Auk* 108: 131-146.
- Scopel, L., Diamond, A., Kress, S., & Shannon, P. 2019. Varied breeding responses of seabirds to a regime shift in prey base in the Gulf of Maine. *Marine Ecology Progress Series* 626: 177-196.
- Schmidt, N. M., and Jensen, P. M. 2005. Concomitant patterns in avian and mammalian body length changes in Denmark. *Ecology and Society*, 10: 5-12.
- Visser, M.E, and Both, C. 2005. Shifts in phenology due to global climate change: The need for a yardstick. *Biological Sciences* 272: 2561–2569.
- Weimerskirch, H., Barbraud, C., and Lys, P. 2000. Sex differences in parental investment and chick growth in Wandering Albatrosses: fitness consequences. *Ecology* 81: 309-318.
- Whidden, S.E. 2016. Patterns of natal recruitment in the Atlantic Puffin (*Fratercula arctica*). M.Sc. thesis, UNB, 70pp. From Fredericton Biology Dept & ALAR.
- Wu, S., Liu, Z., Zhang, R., and Delworth, T.L. 2011. On the observed relationship between the Pacific Decadal Oscillation and the Atlantic Multi-decadal Oscillation. *Journal of Oceanography*. 67(1), 27–35.
- Ydenberg, R.C., Clark, C.W., and Harfenist, A. 1995. Intraspecific fledging mass variation in the Alcidae, with special reference to the seasonal fledging mass decline. *The American Naturalist*. 145: 412-433.