The effect of climate variability and prey abundance on chick growth in a subarctic Atlantic puffin (*Fratercula arctica*) colony

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Master of Science in Biodiversity, Evolution and Ecology

Autumn 2021

Preface

I would not have been able to complete this master thesis without the invaluable help from several people, who I can’t thank enough. I would like to especially thank my supervisor Geir Helge Systad, who has answered a countless number of emails, zoom-calls, and phone calls. Without his incredible knowledge and burning passion for seabirds, I would never have been able to piece together the “puffin puzzle”. I would also thank him for giving me the opportunity to work at Hjelmsøya since 2018, which has truly heightened my passion for seabirds!

I would also like to thank the incredibly patient Steven Guidos at NINA for invaluable assistance in using R and answering all my not so clever questions about statistics. Thank you to Øystein Varpe who took time to read through my drafts and give me great feedback.

I am eternally grateful for my closest friends who have given me constant support and listened to all my seabird facts, even though they don’t share the same passion as me. Thank you to K for his patience and calming words, he deserves an award as he has been the (periodically) unlucky person sharing an apartment with a slightly stressed master student. Lastly, thank you to F for being my therapist and personal trainer during a global pandemic.

Abstract

Annual fluctuations in chick growth are common in seabirds and the quick response chick growth shows to changes in the food sources makes seabirds good indicators for oceanographic and climatic conditions near the colony during the chick rearing period. In this thesis, the potential effect variation in both climate and prey abundance have on chick growth in the Atlantic puffin (*Fratercula arctica*) colony at Hjelmsøya, Northern Norway, was examined. I analyzed data on chick growth in the colony from the last 11 years and used North Atlantic Oscillation (NAO) and sea surface temperatures (SST) in the foraging area as proxies for food availability and species – specific prey biomass measure to examine which conditions best explained the yearly variability in chick growth. Further, I assessed if the explanatory conditions were changing throughout the nestling period or remained constant. My predictions were a) high SST and positive phases in winter NAO increases chick growth rates throughout the season b) higher initial egg volume results in higher growth rates providing chicks with an advantage compared to chicks hatched from smaller eggs c) lipid – rich fish species have a more positive effect on chick growth than lean fish species. I found that during the first 10 days after hatching, the growth rate was influenced differently by the various explanatory variables than later in the season. The first period after hatching, the NAO and SST had significant effects on the growth rate, however these changes throughout the season, and prey quality and quantity becomes the more influential features. Therefore, the variation in growth rate could best be explained by the indirect effects of climatic and oceanographic features, through the effects on prey abundance and quality.

This study examines a different side of the effect climatic and oceanographic variability, the viability of important fish stocks/prey abundance, and parental investment has on chick growth and survival. Thus, this study might be a starting point for future studies on exactly how chick growth in Atlantic puffin is influenced both indirectly and directly through trophic interactions.

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1. Introduction

Seabirds, being a group of marine top-predators, are recognized as long-lived species with relatively slow life histories (Durant, Anker-Nilssen and Stenseth, 2003; Sandvik and Erikstad, 2008). Some characteristics in long-lived species are delayed sexual maturity, high adult survival rate and low fecundity (Sandvik and Erikstad, 2008; Hovinen *et al.*, 2014). Multiple life-history traits are known to be affected by climatic conditions in the North Atlantic, such as chick growth, which has been proven to be more sensitive to short-term changes in prey availability relative to adult survival (Breton and Diamond, 2014; Hovinen *et al.*, 2014). Adult survival is expected to tolerate variability due to its high elasticity and importance in long-lived species (Sandvik *et al.*, 2005; Hovinen *et al.*, 2014). However, adult survival might still be vulnerable to changes in the environment (Sandvik *et al.*, 2005; Hovinen *et al.*, 2014), making the seabirds especially sensitive to environmental changes since any decrease in adult survival can have great potential effects on the total reproductive success of individuals (Sandvik and Erikstad, 2008).

Seabirds are considered good indicators for change in marine ecosystems since environmental variability is often reflected in their demographics, making it possible to monitor changes in lower trophic levels and understand marine trophic relationships (Furness and Camphuysen, 1997; Barrett, 2002; Barrett, Nilsen and Anker-Nilssen, 2012; Lefort *et al.*, 2021). Further, seabirds make great short-term indicators for prey abundance as their prey of choice reflects the prey availability in the foraging area (Barrett, 2002). The rapid response the growth rates of chicks have to changes in the prey base also makes seabirds good indicators for oceanographic conditions close to the foraging area during the nestling period (Barrett, 2002; Breton and Diamond, 2014).

Global climate changes are predicted to have the strongest effects in the Arctic, where multiple effects already are being observed: melting glaciers, increasing sea temperatures and decreasing range of sea ice (Hovinen *et al.*, 2014). Such changes have the potential to greatly affect nutrient cycling, species distribution and trophic interactions in the Arctic (Drinkwater, 2011; Hovinen *et al.*, 2014). The warm and saline water from the Atlantic Ocean is the main water source for the Arctic Ocean, hence playing an essential role in the heat and mass budget (Carton *et al.*, 2011). Recently, the increasing sea surface temperatures (SST) and reduction of sea ice coverage in the Arctic Ocean have been accompanied by an increase in the temperature and salinity of the Atlantic water flowing into the Nordic Seas (Carton *et al.*, 2011). The Atlantic water flowing into the Arctic is affected by the North Atlantic Oscillation (NAO) (Drinkwater, 2011; Hovinen *et al.*, 2014), as it refers to a shift of atmospheric mass between the Arctic and the Atlantic (J W Hurrell *et al.*, 2003). NAO is defined as the difference in atmospheric sea level pressure between Reykjavik, Iceland and Lisbon, Portugal (Hovinen *et al.*, 2014). A positive phase of the NAO indicates below normal heights and pressure in the higher latitudes of the North Atlantic and above-normal over the central North Atlantic (NOAA, 2021). Thus, the positive phase intensifies the westerlies blowing across the Atlantic, increasing the Atlantic water flowing into the Arctic (J W Hurrell *et al.*, 2003; Hovinen *et al.*, 2014). A negative NAO phase results in the opposite effects: weaker winds, less Atlantic water flowing into the Arctic, lower sea temperatures, more sea ice and ice algal growth, and later blooming in phytoplankton (Hovinen *et al.*, 2014).

Successful chick rearing in Atlantic puffins, having a clutch size of one, is predicted to be highly dependent on the quality and quantity of the prey brought to the chick (Durant, Anker-Nilssen and Stenseth, 2006). When considering the chick growth, both the quality and quantity of prey is determined by both environmental conditions and parental resources (e.g. body condition, time – budget etc.) (Durant, Anker-Nilssen and Stenseth, 2006; Barrett, Nilsen and Anker-Nilssen, 2012). It is expected that climatic variability influences both the parental resources and prey abundance, in which both are considered variables affecting chick growth (Durant, Anker-Nilssen and Stenseth, 2006). The timing of the peak in prey abundance varies between years and locations, causing the optimal timing of reproduction to concurrently vary (Joël M. Durant *et al.*, 2004).

The Atlantic puffin (from now on referred to as puffin), residing in a seasonal environment, is predicted to match optimal energy requirements through shifting their breeding phenology so it matches the abundance and phenology in their expected prey species (Burr *et al.*, 2016; Lefort *et al.*, 2021). Producing an egg costs the female a lot of nutrients and energy, especially since the puffin egg is one of the largest relative to body mass among seabirds, representing between 14 and 16% of a females body mass (Barrett, Nilsen and Anker-Nilssen, 2012; Lefort *et al.*, 2021). Yet, mismatches in these phenological shifts are common and seabirds are therefore able to vary the investment into the eggs to compensate for the mismatch, thus producing smaller eggs (Barrett, Nilsen and Anker-Nilssen, 2012; Lefort *et al.*, 2021). However, there is an positive correlation between egg size and the growth and survival of chicks (Barrett, Nilsen and Anker-Nilssen, 2012), meaning that producing a smaller egg is expected to cause a lower growth rate compared to the growth rate of a chick from a larger egg. Chicks hatching from larger eggs are also expected to weigh more, which may be a result of the chicks having a larger food reserve, that larger egg simply produces chicks with greater body mass, or that it is a combination of both (Birkhead and Nettleship, 1984).

The Barents Sea is inhabited by several of the puffin's potential prey species. During the nestling period the puffins are expected to be especially dependent on the spawning of several of these species; capelin (*Mallotus villosus*), cod (*Gadus morhua*), haddock (*Melanorammus aeglefinus*), Norwegian spring – spawning herring (*Clupea harengus*) and sandeels (*Ammodytes spp.)* (Vader *et al.*, 1990; Barrett, 2002; Durant, Anker-Nilssen and Stenseth, 2003). The growth and abundance in larval fish is affected by the fluctuations in the peak of plankton production (Durant, Anker-Nilssen and Stenseth, 2006). For example, the herring spawn drifts along the Norwegian coast between February and March, during the expected peak of plankton production (Durant, Anker-Nilssen and Stenseth, 2006).

The objective of this thesis is to examine the variation in chick growth, both between years and individual chicks, and to explore potential explanatory variables that can influence the growth rate in the Atlantic puffin chicks in the population at Hjelmsøya. This population has been formerly studied, and the monitoring of the population has been carried out since 1984. I will use chick and egg data collected over the last 11 years (2009-2020) to assess the influence of climate fluctuations may have on the population size. The data collected is expected to reflect short – time variability (for example caused by prey availability). Weather systems might be a source to the variability and timing of available food sources. NAO and SST is therefore included in the model. The prey choice and availability are explored in this thesis, since the food brought for the chicks are expected to be directly related to the growth rate. Prey quality is expected to be positively correlated to the growth rate, as high quality (lipid – rich) fish is predicted to quickly increase the chick body mass (Eilertsen, Barrett and Pedersen, 2008).

The predictions for this study are a) high SST and positive phases in winter NAO increases chick growth rates throughout the season b) higher initial egg volume results in higher growth rates providing chicks with an advantage compared to chicks hatched from smaller eggs c) lipid – rich fish species have a more positive effect on chick growth than lean fish species.

2. Material and methods:

2.1 Study species

Being the most numerous seabird breeding in mainland Norway, with an estimated 1,47 million breeding pairs (SEAPOP, 2021), the Atlantic puffin *Fratercula arctica* aggregate in large colonies along the coast from Rogaland in the south to East-Finnmark in the north (Figure 1) (Barrett, Nilsen and Anker-Nilssen, 2012). The Atlantic puffin belongs to the auks (Alcidae) and is, together with the Razorbill (*Alca torda*), the only auk species endemic to the North Atlantic (Harris and Wanless, 2011). As a pursuit-diving pelagic feeder, the Atlantic puffin usually forage far from land and to a depth of approximately 75 meters (Durant, Anker-Nilssen and Stenseth, 2003). Even though the puffin is thought to prey on any small fish, squids and crustaceans available, they are reliant on a predictable and relatively constant supply of energy-rich, shoaling fish within a relatively short distance to the colony during the chick rearing period (Harris and Wanless, 2011).

Figure 1: Map illustrating the global distribution of Atlantic puffin. The dark blue areas representing native, but non-breeding areas and the yellow areas native breeding areas (BirdLife International, 2021).

Seabirds are known to have high energy requirements and multiple species time energy demanding events, such as reproduction, with periods of optimal conditions and resources (Lefort *et al.*, 2021). The puffin is expected to prioritize self-maintenance, thus survival, over reproduction when under stressful conditions; such as a shortage in prey (Durant, Anker-Nilssen and Stenseth, 2003; Hovinen *et al.*, 2014). The timing and amount of prey available in the foraging area is extremely important for the puffins, when determining whether or not to initiate breeding (Durant, Anker-Nilssen and Stenseth, 2003). If they initiate breeding and not enough prey is available within the foraging area it can result in breeding failure, wasting a lot of energy for the adults, explaining why oceanographic variations are having such large effects on seabird populations (Durant, Anker-Nilssen and Stenseth, 2003).

2.2 Study site

The data is derived from fieldwork carried out on Hjelmsøya (71° 06’ N, 24° 44’E), an island in Finnmark, northern Norway. This field station is operated by The Norwegian Institute of Nature Research (NINA). Hjelmsøya is located between the northeastern part of the Norwegian Sea and the southwestern part of the Barents Sea. Thus, the island is influenced by both warm Atlantic water and cold Arctic water (Figure 2). The Barents Sea is an Arctic shelf sea and the largest of the Arctic marginal seas, sustaining higher trophic levels with high production and economically important fish stocks (Koenigstein, 2020). It is inhabited by several important prey species for the Atlantic puffin during the chick rearing period; cod, haddock, capelin, sandeels and herring (Barrett, 2002; Durant, Anker-Nilssen and Stenseth, 2003).

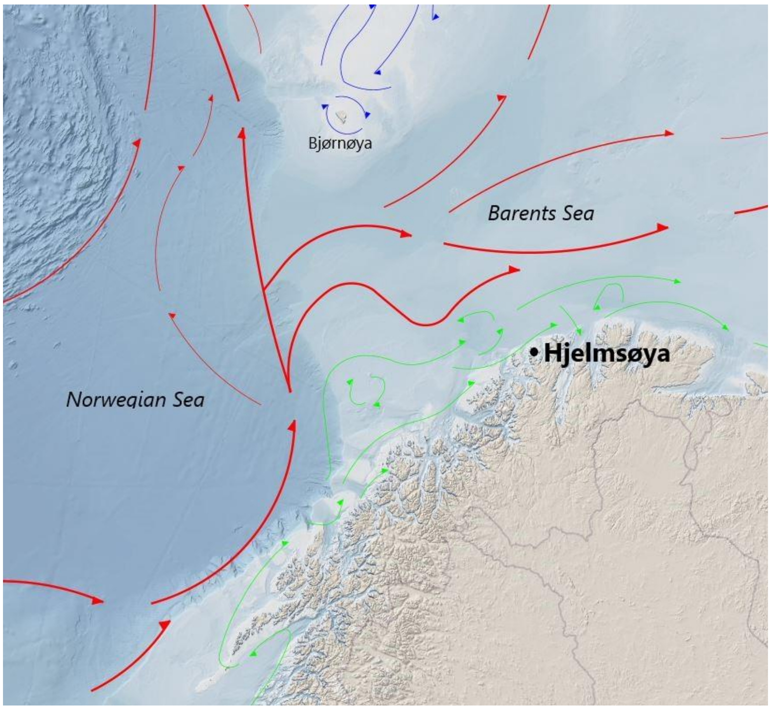

Figure 2: Schematic map illustrating oceanic currents along the northern part of the Norwegian coast. The study site is located at Hjelmsøya. Blue arrows represent Arctic currents, the red arrows are the Atlantic current and the light green arrows illustrates coastal currents. Map produced in kart.barentswatch.no (2021).

At Hjelmsøya, monitoring of seabird populations has been conducted annually since 1984. The Atlantic puffin colony is located on Staurfjellet on the north side of the island, stretching from Krykkjesjåen in the west to Finnkonneset in the East (Systad, 2021). It is estimated that about 80 000 pairs of puffins are breeding in the Hjelmsøya colony (Systad, 2021). Since the research program SEAPOP started in 2004, the research on the Hjelmsøya site has expanded and an ecological time-series of the breeding population has been established (Idsø, 2016; Systad, 2021).

2.3 Data collection

I used data collected during fieldwork in the years 2009 – 2020. The nests were later revisited in August, and this is consistent with the protocol from former seasons. Each season the goal is to have a sample size of 120 active nests.

The field worked in is the designated area for monitoring breeding success (71° 11,4' N, 24° 72,8'E). It is in this field an annual average of 110 puffin burrows (range from 70 – 125 nests) has been checked regularly (at 5-day intervals). This has been conducted during the breeding season, from the start of the month of June to mid-August. There is a break in the nest visits between ca 20th of July and 10 - 15th of August each season, checking the remaining chicks in August to estimate fledging weight and ringing of the chicks. In early June, during the first visits to the nests, the eggs were measured with sliding calipers (height and length ± 0,1mm) and weighted with a spring weight (± 1,0 g). Each active nest containing either an egg or an incubating bird was marked using white sticks numbered from 1 to 120 and placed at the nest entrance. This made it possible to monitor each individual nest through the season. Since the nests are in burrows, some were too deep to reach the actual nest and we had to dig holes to be able to get access to the egg or chick. To avoid the nests to be exposed to predation or weather we closed the holes with plugs made from surrounding vegetation, thus making the holes possible to reopen when revisiting the nests throughout the season.

All chicks were weighted and measured (wing length (maximum flattened chord, including down except for the tuft at the end), tarsometatarsus, and head and beak combined) during each visit. The chicks were measured until mid – July, corresponding to approximately age 15-20 days, and checked one last time in August around age 35 – 40 days just before the average departure period from the nests. The number of recorded chicks each season illustrates the yearly variation in hatching success (Table 1), however it was considered outside the scope and was not treated extensively in study.

Table 1: Number of chicks (n) recorded each season (2009 – 2020).

Year	Number of chicks (n)
2009	13
2010	6
2011	24
2012	29
2013	27
2014	60
2015	23
2016	62
2017	55
2018	56
2019	34
2020	34

2.4 Data processing

2.4.1 Growth rates, hatching date and egg volume

The hatching date for each chick was used to calculate the age, number of days after hatching, of each chick making it possible to follow the growth pattern closer. The individual hatching dates were estimated from visual observations during nest visits (such as active hatching or newly hatched chicks). As an example: If an egg had stars (hatching cracks), it was estimated that the hatching date was within the two next days. Thus, I had an estimated maximum hatching date. If hatching dates had low precision, 6 or more days, they were not included in the study.

The age of each individual chick was calculated by subtracting the estimated hatching date from the day of the last measurement.

$$Age\ (days) = Day_{of\ last\ measurement} - Hatchdate_{estimated}$$

The growth rate (g/day) for each chick was calculated by dividing the weight difference between the first and last measurement by the interval (in days) between measurements. The equation is:

$$Growthrate = \frac{Weight_{Max} - Weight_{Min}}{Age_{Maximum\ recorded} - Age_{Minumum\ recorded}}$$

The initial egg volume (V) for each egg was calculated using the measured egg length (L), height (B) and the constant K (0,51 in puffins) (Barrett, Nilsen and Anker-Nilssen, 2012). Initial egg volume was calculated and used as an individual based potential variable explaining the growth rate.

$$V = K \cdot L \cdot B^2$$

2.4.2 Environmental parameters

The NAO was used in this study as a large-scale parameter for climactic variations with the potential to influence the growth pattern in the puffin chick population at the Hjelmsøya colony (Idsø, 2016). In this thesis, winter NAO (December – March) was preferred since the noise ratio is highest during the winter (Sandvik *et al.*, 2005) and because it is a phenomenon affecting the movement of air and water masses influencing sea temperatures (James W Hurrell *et al.*, 2003; Joël M. Durant *et al.*, 2004). Other studies suggests that a 2 year lag in the winter NAO index influence adult survival in puffins (Sandvik *et al.*, 2005), however I chose to consider the winter NAO without lag as a proxy for the availability and distribution of fish larvae as it was expected to have a more direct effect on growth rate in chicks (Figure 3b), because the adults mainly feed the chicks with larvae hatched earlier the same year (Barrett, 2002). The NAO index reflects climactic variables such as wind speed, temperature in large portions of the Northern Hemisphere and precipitation (Durant, Anker-Nilssen and Stenseth, 2003; James W Hurrell *et al.*, 2003). I used the SST data to characterize variation in the temperature during the chick rearing period as a proxy for food availability. Mean SST for the chick rearing period (July and August) was used as a parameter for local oceanographic fluctuations affecting food availability and quality in the foraging area (Figure 3c and 3d). When assessing the fluctuation in SST it was important to limit the area to the expected foraging area, thus I chose to examine the SST in the area within longitude 15 - 30°E and latitude 70 - 72°N. The NAO and SST data was obtained from the National Centers for

Environmental Information (National Oceanic and Atmospheric Administration (NOAA)) databases (https://www.ncdc.noaa.gov).

The abundance of 4 prey species in the Barents Sea were included in the study and I chose to use age specific abundance, since the prey intended for the chick often consists of 0-group fish (fish in their first year) and smaller fish in general. The groups included in were 0-group capelin, the total stock biomass of capelin, 0-group herring, 1-3 group herring, 0-group cod, 0-group haddock. Due to the lack of data on sandeels, a common prey item brought for the chicks, they were not included in this study. The prey abundance data was provided by the International Council for the Exploration of the Sea (ICES) from the Working Group on the Integrated Assessments of the Barents Sea (WGIBAR).

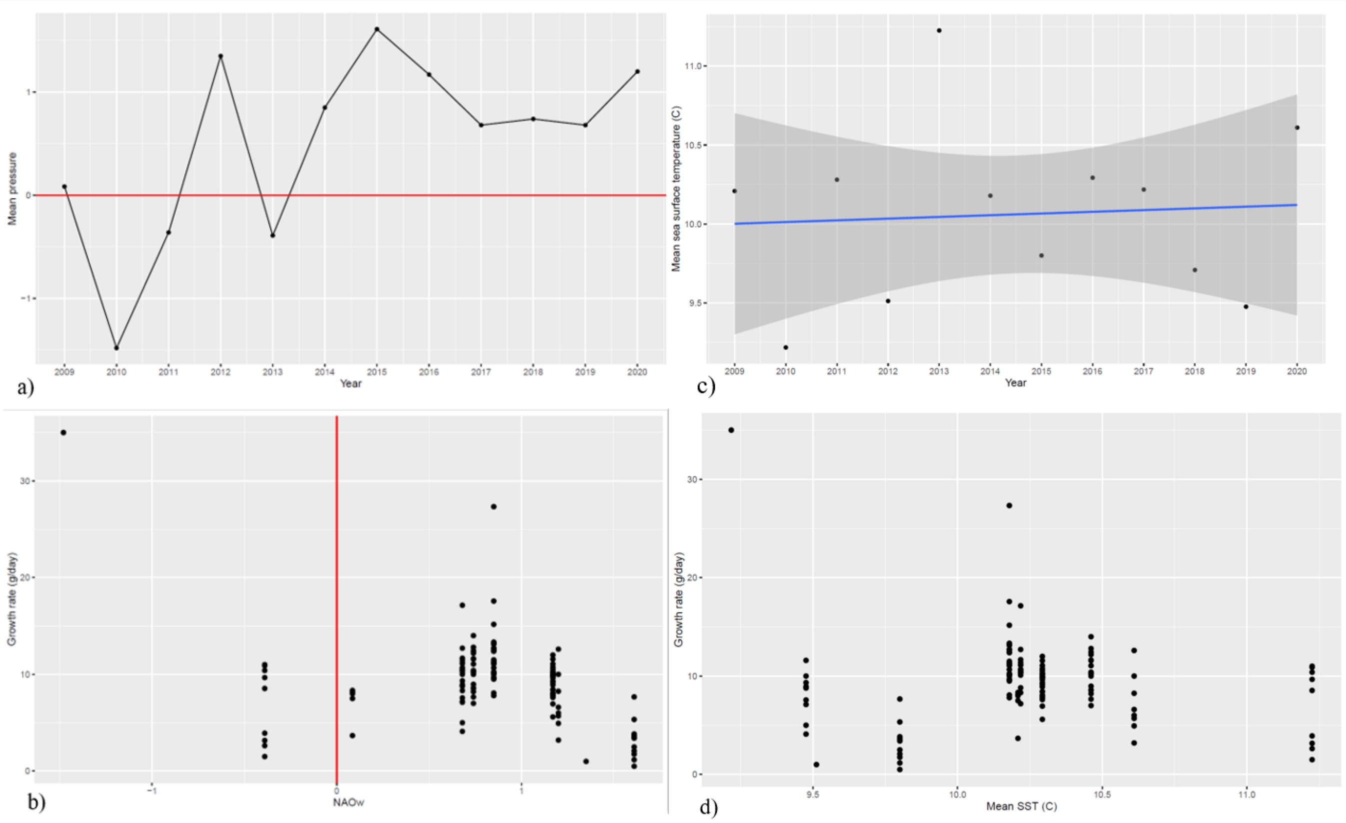

Figure 3: a) Yearly mean winter NAO (December - March) without lagged effect. The red line representing 0 difference in the pressure. b) The relationship between the growth rate (g/day) in each chick during the entire season and the winter NAO. Each vertical line of aggregated points represents one year. The figure shows that following positive winter NAO phases, the growth rate is higher, and more chicks are produced than during or close to negative phases. The red line representing 0 pressure difference. c) Yearly mean SST outside the Hjelmsøya colony, the graph illustrating how the average SST in July and August has increased over the last years. d) The relationship between growth rate in each chick during the entire season and the mean SST, showing how growth rate and number of chicks increase between the temperatures 10.0 and 10.5 degrees Celsius.

2.5 Data analysis

When analyzing the data, Akaike's Information Criterion (AIC) was used to identify potential models describing the relationship between the age specific growth rate, species specific prey abundance and the climatic parameters (SST and winter NAO). Since the sample size is finite, potential models was identified through comparing the AIC scores of multiple models through stepwise model selection (stepAIC). I chose to set the selection to both ways for stepwise regression. The objective of using stepAIC is to simplify the model without compromising the performance too much. StepAIC is a method of identifying the optimal set of variables in a model automatically in R. The variables with the higher AIC scores are recognized as contributing with more information than the ones with low AIC scores, resulting in variables with low scores to be excluded from the model. I identified the best-fitting models for both chicks in the age group 1 – 10 days and 1 – 40 days using this method. I chose to analyze the data from the 10 first days after hatching separately, as this period had the most data collected over multiple years. Also, I produced a chart correlation comparing the correlation between the variables, avoiding potential unsignificant variables seeming significant due to strong correlation. A linear model was also used to determine how growth rate varied each year based on the prey availability and climatic parameters.

R version 4.0.4 (R Core Team, 2021) was used for all statistical analyses, all figures were produced using the ggplot2 package (Wickham, 2016) and the model selection was conducted using the MASS package (Venables and Ripley, 2002).

3. Results

The models selected through the stepAIC method was considered in this study (see Table 2). Due to the high correlation between the plankton biomass and the different fish biomasses, it was excluded from the analysis.

Table 2: The two models selected as best-fitting for each analysis. Selected through the stepAIC method

Age group	Model formula
1 – 10 days	Growth_rate ~ Initial_Eggvolume + Cod_0_group + Herring_0_group + Herring_1-3+ Capelin_0_group + Capelin_TSB + Haddock_0_group + Mean_SST
1 – 40 days	Growth_rate ~ Initial_Eggvolume + Cod_0_group + Herring_0_group + Capelin_TSB + NAOw + Mean_SST

3.1 Chicks in age group 1 – 10 days

The models selected for chicks in the age 1 – 10 days contained variables were all of them, except adult herring (1 – 3 years old), were significant ($P < 0.05$) (Table 3). It suggests that during years with high abundance of herring larvae (0 group) and capelin (TSB), the growth rate decreased in the chicks during the 10 first days after hatching, having a negative effect on growth rate. However, in years with high mean SST, high initial egg volume and high abundance in the 0 – groups of cod, haddock, and capelin the growth rate increased. Winter NAO was not considered to have a significant effect during the 10 first days and therefore excluded during the model selection stage. The Adjusted $\boldsymbol{R^2}$ for this model was 0.62, indicating that 62 % of the variance in the growth rate can be explained by the variables selected collectively.

Table 3: Variable estimates of the best fitted model for chicks age group 1-10 days. Only variables with $P < 0.05$ are considered significant. Adjusted $\boldsymbol{R^2}$ = 0.621, F – statistic = 19.45 on 8. Residual standard error = 2.303 on 82 degrees of freedom.

Variable	Estimate	Std. Error	t-value	p-value + signif. codes
Intercept	-7.938e+01	1.080e+01	-7.347	1.35e-10***
Initial egg volume	8.118e-02	3.811e-02	2.130	0.036*
Mean SST	7.451e+00	9.801e-01	7.603	4.25e-11***
Cod 0-group	1.464e-02	1.562e-03	9.369	1.33e-14***
Herring 1-3	2.957e+03	1.587e+00	1.863	0.066 .
Herring 0-group	-8.851e-03	1.667e-03	-5.308	9.28e-07***
Capelin 0-group	4.567e-03	2.098e-03	2.177	0.0324*
Capelin TSB	-3.581e-03	4.865e-04	-7.361	1.27e-10***
Haddock 0-group	9.893e-03	4.290e-03	2.306	0.0236*

3.2 Chicks in age group 1 – 40 days

The model selected for the whole chick rearing period (1 – 40 days) suggests that high winter NAO and high abundance of capelin and herring (0 group) contribute to a decrease in the growth rate of the chicks at Hjelmsøya (Table 5). Further, high mean SST and high abundance of cod (0 group) correlate to higher growth rate throughout the chick rearing period. The initial egg volume was not considered significant in this model (P > 0.05). The adjusted $\boldsymbol{R^2}$ for the model was 0.357, therefore explaining approximately 36% of the variance in the growth rate.

Table 4: Variable estimates of the best fitted model for chicks in age group 1-40 days. Only variables with P < 0.05 are considered significant. Adjusted $\boldsymbol{R^2}$ = 0.357, F – statistics = 16,76 on 6. Residual standard error = 4,155 on 164 degrees of freedom.

Variable	Estimate	Std. Error	t-value	p-value + signif. codes
Intercept	-50.127	12.026	-4.168	4.96e-05***
Cod 0-group	0.009	0.001	6.566	6.52e-10***
Capelin TSB	-0.0037	0.0005	-7.02	5.45e-11***
NAOw	-2.916	0.947	-3.08	0.00245**
Herring 0-group	-0.0036	0.001	-3.648	0.00035***
Mean SST	5.533	1.0348	5.347	2.96e-07***
Initial egg volume	0.081	0.05047	1.607	0.11006

4. Discussion

Using chick, fish stock biomass, local SST and NAO data, this study aimed at testing the predictions that a) high SST and positive phases in winter NAO increases chick growth rates throughout the season b) higher initial egg volume results in higher growth rates providing chicks with an advantage compared to chicks hatched from smaller eggs c) lipid – rich fish species have a more positive effect on chick growth than lean fish species.

Chick growth has been proven to be more sensitive to short-term changes in prey availability and quality compared to other life – history traits, such as adult survival (Sandvik *et al.*, 2005; Hovinen *et al.*, 2014). Hence being greatly affected by climatic variability in the North Atlantic. As the effects of climate fluctuations on marine invertebrates and fish stocks are becoming increasingly documented, the indirect effects on mortality and growth rates in seabirds working through the food chain are better understood (Sandvik *et al.*, 2005). Oceanographic features such as fronts between water masses and currents mixing water from different depths have the potential to aggregate prey in certain areas (Jöel M. Durant *et al.*, 2004). Multiple frontal systems in the North Sea appear to be providing seabirds with predictable and abundant resources, yet these fronts are often seasonal and vary as a response to wind – induced mixing (Jöel M. Durant *et al.*, 2004), influenced by different NAO phases. During a positive NAO phase, there is an increased inflow of Atlantic water into the Barents Sea, which results in increased sea temperatures and earlier blooming of phytoplankton (Hovinen *et al.*, 2014). A negative NAO phase results in the opposite effects, hence the NAO is considered to significantly affect both weather and oceanic conditions, which in turn influences the dynamics and composition of the trophic levels in the Arctic Ocean (Drinkwater, 2011; Hovinen *et al.*, 2014). NAO indirectly produces variations in production, abundance and distribution of potential prey species (Jöel M. Durant *et al.*, 2004), through changes in features such as wind and current direction and strength. Seabirds are more likely to be affected by climate variability indirectly, through the changes in prey availability and trophic interactions (Durant, Anker-Nilssen and Stenseth, 2003; Jöel M. Durant *et al.*, 2004).

The relationship between oceanographic conditions and the duration of the chick rearing period in puffins can be explained if the length of the nestling period is a proxy for the food availability to the chick (Durant, Anker-Nilssen and Stenseth, 2006). In years where there is a mismatch in timing and/or abundance between fish and plankton, the fish arriving in the puffin’s foraging area is small and unable to school. This results in low accessibility and quality of the prey, contributing to low growth rates in the chicks and therefore extending the nestling period past the optimal range (estimated to be between 38 and 44 days after hatching) (Durant, Anker-Nilssen and Stenseth, 2006).

The local SST in the foraging area, which was considered in this study, plays a role in influencing which prey that is available and abundant in the area. The high SST also promoting growth in the prey within the area, as well as the time used foraging. If the local SST is too high or too low, the prey might be further away from the colony, increasing the cost of foraging for the adults. Puffins are piscivorous and their reproductive success is positively correlated to SST (Jöel M. Durant *et al.*, 2004), indicating that the high SST improves growth rates. Prey availability and SST is correlated, however changes in SST influences different prey species in varying ways (Jöel M. Durant *et al.*, 2004). For example, high SST tend to reduce plankton productivity and low SST can reduce growth in fish. The fluctuating SST and plankton biomasses, thus food availability for fish stocks, is a direct result from the climate oscillations affecting the Atlantic and Arctic water dynamics (Drinkwater, 2011; Koenigstein, 2020). Therefore, the Atlantic cod, Atlantic capelin, and herring populations have interdependent and climate – dependent variations in both abundance and productivity (Koenigstein, 2020). Also, since zooplankton is the food source for the fish stock, the zooplankton biomass is highly correlated with the fish species and was therefore excluded from the models used in this thesis. Zooplankton is considered as a very important, but indirect parameter influencing chick growth in seabirds, such as the puffin (Durant, Anker-Nilssen and Stenseth, 2003).

The marine food webs in the Northeast Atlantic are, on a global scale, among those most strongly subjected to human induced disturbance in the shape of fishing, pollution and climate change (Barrett, Nilsen and Anker-Nilssen, 2012). Even though the Barents Sea have low primary production, the water column is inhabited by several commercially important fish species which also is important prey species for the puffin: Atlantic cod, haddock, Atlantic capelin and herring (Forsgren *et al.*, 2009; Barrett, Nilsen and Anker-Nilssen, 2012; Koenigstein, 2020). All populations which have periodically collapsed, affecting whole ecosystems significantly (Barrett, Nilsen and Anker-Nilssen, 2012). The Norwegian puffin population usually prey on fish with a length between 30 to 60 mm (Barrett, 2002).

The capelin is a relatively small, schooling fish, spawning during from late March to early April along the Norwegian coast (Sakshaug, Mehlum and Gulliksen, 1994; Olsen *et al.*, 2010). After hatching, the capelin larvae ascend toward the sea surface where prevailing currents carries them in the direction of the nursery sites (Olsen *et al.*, 2010). The nursery sites tend to be in the western part of the Barents Sea, the same part as Hjelmsøya is in. During the early stages, the capelin larvae aggregate in the upper 40 m in the water column (Olsen *et al.*, 2010), easily available to the puffin. Northeast Arctic Cod spawns, among other locations, in coastal areas in western Finnmark and in Troms (Olsen *et al.*, 2010). The hatching peaks around mid – April, and during the summer the larvae grows into 0 – group cod (Olsen *et al.*, 2010). Both the larval stage and the 0 – group cod inhabit a large area in the Barents Sea, including the area around Hjelmsøya. Haddock is a gadoid and is abundant along the Norwegian coast and in the Barents Sea (Sakshaug, Mehlum and Gulliksen, 1994; Olsen *et al.*, 2010). Haddock spawns from March until June, with a peak in late April and early May (Olsen *et al.*, 2010). The haddock larvae have large variations in abundance and distribution resulting from migrating with the currents, but have a similar distribution as the cod (Sakshaug, Mehlum and Gulliksen, 1994; Olsen *et al.*, 2010).

Norwegian spring – spawning herring is mainly distributed along the Norwegian coast, where they spawn and reside as juveniles, and in the Barents Sea which is the main area for juveniles

(Durant, Anker-Nilssen and Stenseth, 2003; Olsen *et al.*, 2010). The herring spawns in February and March, and most of the larvae end up drifting into the Barents Sea (Durant, Anker-Nilssen and Stenseth, 2003; Varpe *et al.*, 2005). Both larvae and 0 – group herring is distributed in the same general area as Hjelmsøya and is expected to be a potential prey species for the Hjelmsøya puffins.

The sandeels are a group of fish rich in lipids, belonging to the Ammodytidae family. Little is known about the sandeels' life history, however they spawn during the winter, usually around new year (Staudinger *et al.*, 2020; Johnsen, 2021). The spawning sites is located between Vikingbanken, the Danish coast, The United Kingdom and Shetland (Johnsen, 2021), but local stocks is thought to spawn all along the Norwegian coast. The sandeel larvae in the North Atlantic lives in the water column during the 3 – 4 first months after hatching, reaching a length between 35 – 50 mm (Staudinger *et al.*, 2020), an ideal length for the puffin. The sandeels are recognized as essential forage fish and have an important role as prey in diets of higher trophic levels (Staudinger *et al.*, 2020). The sandeels are lipid – and protein – rich fish, and post – larval sandeels have been shown to contain a higher caloric count than capelin and herring of similar size (Staudinger *et al.*, 2020). The alcids in the Gulf of Maine have been observed replacing herring with the fat – rich sandeels, as they are able to dive deep enough to access the adult sandeels lower in the water column (Staudinger *et al.*, 2020). This might explain why sandeels have been observed to be a preferred prey species of the puffins at Hjelmsøya, as chicks fed lipid – rich fish have a higher growth rate, larger fat reserves and a shorter nestling period (Eilertsen, Barrett and Pedersen, 2008). It is also important to note that due to the lacking data on the sandeel biomass in the Barents Sea, I was unable to estimate the potential effect this fish stock have on chick growth in the Hjelmsøya colony. Nevertheless, a substantial amount of sandeels is observed during the sampling of prey loads each year, indicating that this is an important part of the chick diet at Hjelmsøya.

Figure 4: Picture of a puffin carrying a prey load consisting mainly of sandeels (Ammodytes spp.). Photo: Marthe Olsen, 2021.

Since the puffin feed at such high trophic levels, the populations breeding in the northeast Atlantic experience significant shifts in the ecosystem, leading to both short – and long-term reproductive failure and drops in the populations (Barrett, Nilsen and Anker-Nilssen, 2012). Annual monitoring of the puffin colonies since 1979 on the Norwegian sea coast has revealed a significant decline in the population, where the most dramatic decrease has been observed in the largest colony, Røst (Barrett, Nilsen and Anker-Nilssen, 2012). The Hjelmsøya colony and nearby colonies have not experienced a similar decline during the same period and have even had a slight incline in the population sizes (Fauchald *et al.*, 2015).

4.1 Chicks in age group 1 – 10 days

Initial egg volume was expected to be significant, especially right after hatching as it correlates to faster growth after hatching (Barrett, Nilsen and Anker-Nilssen, 2012), which it was. This indicates that larger eggs have a positive effect on growth rates in the Hjelmsøya colony, and is predicted to provide chicks with an advantage if prey availability is low (Barrett, Nilsen and Anker-Nilssen, 2012). However, higher initial egg volume might indicate that the parents have resources to produce larger eggs, thus resources to supply the chick with more food as well (Birkhead and Nettleship, 1984; Barrett, Nilsen and Anker-Nilssen, 2012).

The weight gain during the 10 first days after hatching is quite critical as it influences the length of the nestling period, which is optimal between the length of 38 – 44 days. Figure 5 illustrates the importance of prey availability and quality during the 10 first days, as the chick growth also influences chick survival rates. 2014 was a seemingly good year, with high growth rate, while 2013 and 2015 was seasons with very low growth in this period of time.

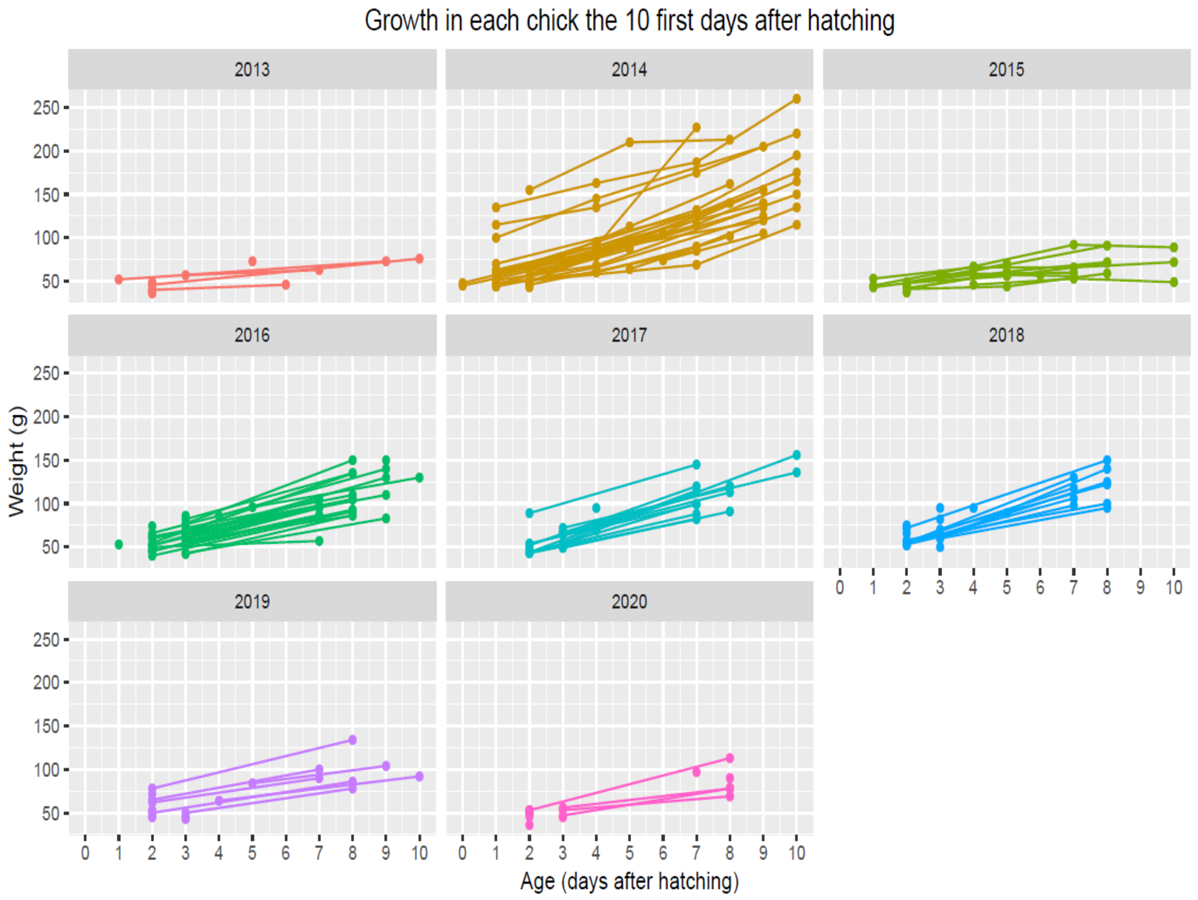

Figure 5: The growth (g/age) in each individual chick during the first 10 days after hatching, in the years 2013 – 2020. Years before 2013 was excluded due to inadequate measurements of the chicks.

4.1.1 Fish stocks

During the first 10 days after hatching, it was found that adult herring (age 1 – 3 years) had no significant effect on the growth rate in the puffin chicks. This result was somewhat expected as adult herring is more likely to be a part of the adult puffin diet rather than the chick diet, based on size compared to the chicks. The effect high amounts of adult herring might have on growth rates, will most likely be indirectly through the adults' body condition and time budgets.

This early after hatching, high amounts of spring-spawning herring (0 – group) and capelin (total stock biomass) seem to have a negative impact on chick growth, contradicting my prediction of the lipid-rich fish such as herring and capelin would be preferred, even though the effect size was low. This might indicate that neither the spring-spawning herring nor the capelin is the preferred choice of prey or easily available for the Hjelmsøya birds. This has been partly suggested already, as Idsø in 2016 compared the samples prey loads from 2009 – 2015 and observed that gadoids (cod and haddock) and sandeels were the most observed species intended for the chicks (Idsø, 2016). Another possible explanation for this relationship between herring, capelin and growth rate might be that the herring and capelin caught is usually in the larval stage and are quite small, and it is probably time-consuming gathering enough to feed the chick. This might make them less nutritionally desirable than larger prey such as the gadoids or the lipid – rich sandeels. In years with high abundance in the 0 – groups of cod, haddock and capelin, the growth rate was positively influenced. The cod biomass had the highest significance and higher effect size than the other variables, suggesting that this group is the more preferred, or available, prey for the puffins at Hjelmsøya. Gadoids are lean fish, however providing larger fish to the chick might be more efficient than foraging on smaller, fattier fish in the long run. Due to the puffins limited transport capacity and time – budget, they are expected to optimize the chicks energy in-take by selective foraging. By bringing back a few larger fish they provide the chick with more energy compared to many smaller, juvenile fish (Eilertsen, Barrett and Pedersen, 2008; Harris and Wanless, 2011). Further, as mentioned earlier the sandeels are not statistically accounted for in this study and plays an important role in the diet of these birds.

4.1.2 Environmental parameters

In this critical period after hatching, high mean SST have a significant, positive effect on chick growth. This coincides with my predictions. In Figure 3d, the relationship between growth rate and SST was illustrated. When comparing the relationship between SST and growth rate we can observe that the years where SST was between 10.0 and 10.5°C the number of chicks recorded and growth rate in each chick is higher. This is a possible indication of the puffins being well adapted to the average SST at Hjelmsøya, however in Figure 3c, we can see that the average SST is increasing annually. In this study, I used the actual SST values instead of residuals, making a linear model of the relationship between the mean SST and growth rates.

A study conducted on a puffin colony on Iceland observed that the SST were chick production peaked, during the 20th century, shifted to an average temperature of 0.24°C higher than before (Hansen *et al.*, 2021). It was suggested that this trend might be a potential response to an increasing SST. Due to the long generation time, it is likely that the puffins compensate through plastic behavioral responses (e.g. switching food sources) instead of evolutionary adaptations (Hansen *et al.*, 2021). My model shows that the effect size of the average SST is the largest out of the variables and is quite significant. This indicates that SST has a relatively large effect on the growth rate during the 10 first days after hatching. This can be explained by the direct effect SST has on lower trophic levels, influencing prey growth and abundance in the foraging area (Durant, Anker-Nilssen and Stenseth, 2003).

Interestingly, the winter NAO was considered insignificant for this time during the growth period and was excluded during the model selection stage. The expectation was that winter NAO have a more indirect effect on growth rate, as I considered it as a proxy for the prey abundance and location of fish spawning since seabirds are more likely to be affected by climate variability indirectly, through the changes in prey availability (Jöel M. Durant *et al.*, 2004). Therefore, this contradicted my prediction as I expected the NAO to be significant during the whole nestling period.

4.2 Chicks in age group 1 – 40 days

Interestingly, initial egg volume was significant during the 10 first days after hatching, but not when considering the whole season. This indicates that growth rates in chicks are positively affected from having larger eggs in the first, critical period right after hatching. However, it is not providing further advantages later in the season as the growth rate is thought to be more influenced by other parameter to a larger degree. This also suggests that having a larger egg initiates linear growth quicker (Barrett, Nilsen and Anker-Nilssen, 2012), increasing the initial growth rate rather than the overall growth rate.

Figure 6 illustrates the growth during the entire nestling period and the variation in weight close to fledging between chicks (around day 40). The August measurements from some years are not available as some of the August visits has been cancelled due to either variation in success, as in 2015 where the chick survival was extremely low, or bad weather making it impossible to get access to the colony before fledging.

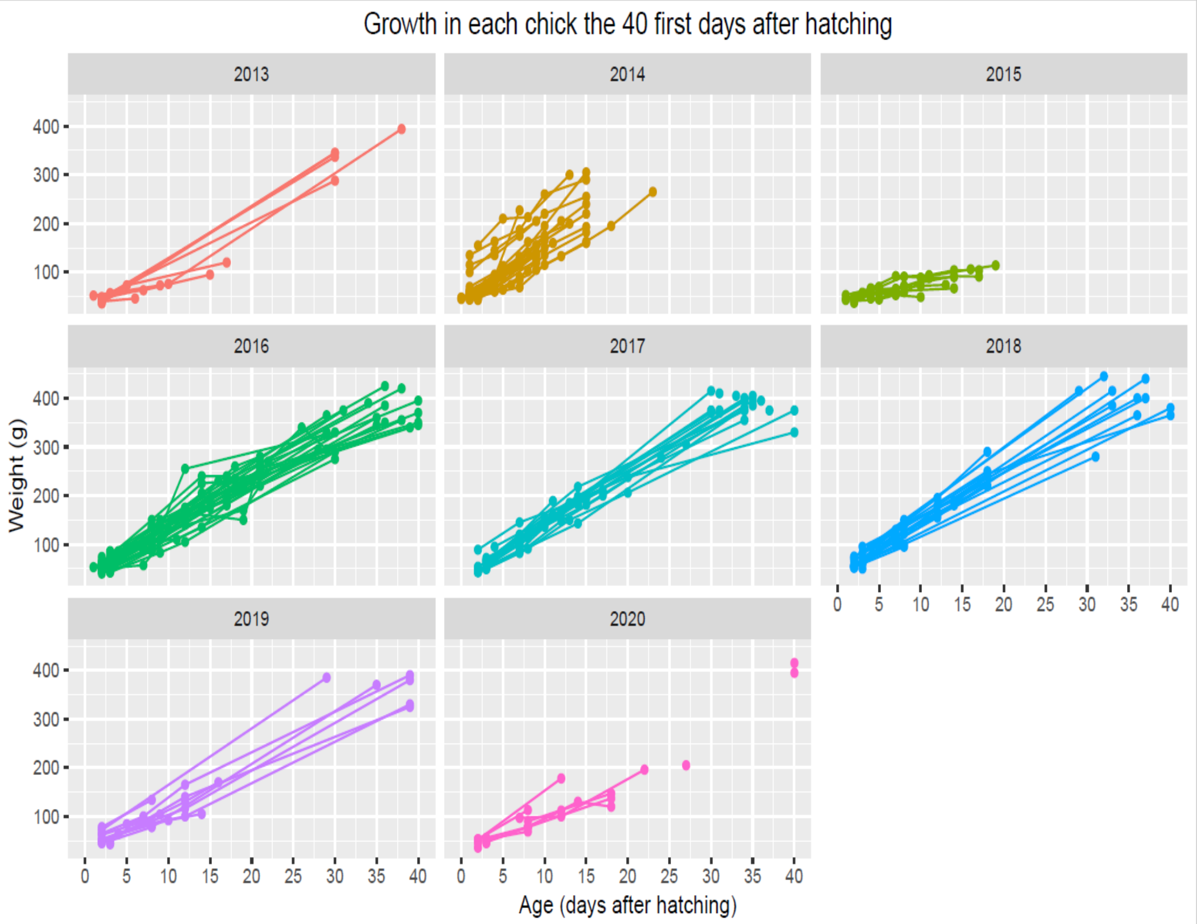

Figure 6: The growth (g/age) in each individual chick throughout the nestling period, in the years 2013 – 2020. The years before 2013 was excluded due to inadequate data.

4.2.1 Fish stocks

Throughout the whole chick rearing period, high abundance of capelin (total stock biomass) and spring-spawning herring (0 - group) have a negative impact on the growth rate, again contradicting my prediction that fat – rich fish positively affecting the chick growth. As mentioned earlier, this might be because neither capelin nor herring is the preferred prey, or because catching one larger gadoid is more effective for the adult and increasing the chick's growth rate rather than catching several smaller, juvenile herring. Further, the negative effect might also be caused, as mentioned earlier, that the Hjelmsøya puffins prefer sandeels to herring and capelin due to the high caloric count.

A high abundance of cod larvae is considered to have a positive impact on the growth rate, being quite significant. The effect size was rather low (0,006, however this again suggests that cod, even though being a lean fish, is a particular popular prey species for this colony due to the relationship with the growth rates.

4.2.2 Environmental parameters

A high winter NAO was shown to contribute to a decrease in chick growth when considering the whole season, contradicting my prediction. The interesting aspect is that winter NAO was insignificant for the growth during the 10 first days and considered significant when analyzing the growth rate from day 1 until fledging.

It has been shown that in the northeastern Atlantic, productivity in lower trophic levels is delayed with latitude (Burr *et al.*, 2016). Burr et al. (2016) observed that there also is a delay in hatching dates with latitude in puffins. Thus, the timing of hatching is expected to be relatively dependent on matching the peak in prey availability, which is expected to be influenced by NAO. In other studies, the effect of the NAO has been shown to become increasingly negative further north (Sandvik, Coulson and Sæther, 2008). If the winter NAO is high, this increases the amount of Atlantic water and Atlantic prey entering the Barents Sea. Feeding on Atlantic prey is not predicted to directly affect growth rates, as they are not expected to be less energetically valuable for the puffins. Although, the Atlantic prey can possibly affect the balance between the cost of foraging and the nutritional benefits (Descamps et al., 2019), being less desirable compared to more easily available, Arctic prey.

If there is a mismatch between hatching dates and when the fish larvae arrive in the foraging area, chick growth will be negatively affected due to a lack of available prey. A high winter NAO affects not only the distribution and quality of the prey, but it also influences the spawning areas. Warmer water can result in northwards shifts in spawning areas for Atlantic species, such as cod (Drinkwater, 2011), possibly changing the timing of larval drift passing the puffin colony. Stronger westerlies caused by the high NAO can cause a change in larval drift and retention time from the spawning sites to the colony (Fayet et al, 2021), thus amplify the mismatch between hatching and the peak in prey abundance. Since high winter NAO also have the potential to cause a mismatch in the timing and/or abundance between fish and plankton, the size and abundance of fish arriving in the puffin's foraging area is expected to be low, making the prey less available and more costly to gather. I could not find a clear correlation between the prey base, growth rate and NAO, indicating that changes in the prey abundance in the foraging area might be driven by local, small – scale variations, not only by large – scale shifts. However, the mismatch in timing between hatching and larval drift might be an explanation for the negative effect winter NAO has on growth rates.

Further, high mean SST throughout the season correlates to a higher growth rate, aligning with my predictions. The effect size was the largest out of all the variables in the model selected, suggesting that the SST have a very direct and significant effect on the chick growth during the whole chick rearing period. This was expected as the local SST is known to affect distribution and accessibility of fish larvae in the foraging areas (Drinkwater, 2011). If the temperatures in the Nordic Seas continue to increase, cod and capelin is expected to move even more North (Drinkwater, 2011), which does not necessarily have a negative effect on the Hjelmsøya colony. This might not have a direct impact on the chick growth at Hjelmsøya, as there only are small amounts of capelin observed in the chick diet, although it can greatly affect the chick growth indirectly through the adult diet. The adult puffins is thought to forage on capelin and therefore, a change in distribution have the potential to affect the adults body condition, which is proven to be positively correlated to chick growth rate (Rector *et al.*, 2014).

4.3 Conclusion

In this thesis, the results indicate that chick growth during the first period after hatching affects both survival and length of the nestling period. The growth in this period might not be as dependent on high-quality fish as much as quantity, however the lack of sandeel data might account for the high significance of lean fish species (haddock and cod). The results of this study also suggests that the different oceanographic and climatic conditions have higher significance throughout the nestling period, as it directly affects the prey abundance and availability. During the first period after hatching, having a higher initial egg volume was shown to have a positive effect on the initial growth rate. The effect of the egg volume seemed to even out and become more insignificant later in the season as food quality and amount became the more determining factors on the growth rate. However, larger eggs might indicate that the adults have extra resources to both produce a larger egg and to provide the chick with more food, giving the chick with an advantage during the whole nestling period compared to chick from smaller eggs.

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