

**Nest predation, reproductive investment, and
environmental variability in Atlantic puffin (*Fratercula
arctica*)**



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Cover photo: Atlantic puffin (*Fratercula arctica*) by Marthe Olsen

Abstract

For many species of birds, nest predation is one of the leading causes of reproductive failure. This has been especially apparent in island nesting seabirds, which have experienced rapid declines due to the introduction of mammalian predators. This study examines how nest predation varies between years in the Atlantic puffin (*Fratercula arctica*) colony at Hjelmsøya in Northern Norway. Further, we assess whether this variation can be linked to female condition and if this is affected by environmental fluctuations. To determine female condition, egg size was used as a proxy in this study. I found that predation rates were higher in years with lower egg volume. This indicates that: 1) Female condition is poor during seasons with low food availability, and they have less energy to invest in eggs. 2) If the perception of predation is high in the local area, females invest less in eggs because survival prospects and the reproductive value of offspring are low. The variation in egg size could best be explained by the indirect effects of climatic variables through the abundance of important prey. This study provides new insights into the connection between environmental conditions, parental investment, and predation in a puffin population. Therefore, this study may be a valuable asset for future conservation initiatives for this vulnerable species.

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1 Introduction

The trade-off between survival and reproductive success is the core of life-history theory (Santos & Nakagawa, 2012; Sousa & Marini, 2013). Parents need to balance investment in current offspring against their own survival and chances of reproducing in the future (Chalfoun & Martin, 2010; Erikstad et al., 1997). For seabirds, this trade-off is mainly affected by variation in predation risk and fluctuations in food availability (Oro, Pradel, & Lebreton, 1999). As seabirds are long lived species, life-history theory predict they should decrease parental investment during years with high predation pressure or when resources are scarce (Johnsen et al., 1994). During these years, offspring have low probabilities of survival and their reproductive value is low (Oro et al., 1999).

Nest predation is the main cause of reproductive failure in most species of birds, and this is likely to affect their reproductive strategies throughout their lifetime (Fontaine & Martin, 2006; Lima, 2009; Remeš et al., 2012). Predators can affect birds through lethal effects such as direct predation and consumption of prey and through non-lethal effects where individuals alter their behaviour in response to predation pressure (Cresswell, 2008). Studies have found that birds can evaluate predation risk and adapt their reproductive strategy accordingly (Fontaine & Martin, 2006; Forstmeier & Weiss, 2004). If the perceived predation risk is high, the reproductive value of current offspring is expected to be low. Parents are expected to invest less in their offspring by reducing clutch size, egg size, incubation efforts, and feeding rates (Chalfoun & Martin, 2010). This prediction is supported by empirical studies demonstrating increased investment in offspring where predators are actively eliminated from the area (Fontaine & Martin, 2006; Zanette et al., 2011).

For island nesting seabirds, the introduction of mammalian predators to breeding areas has been especially detrimental because seabirds lack defense mechanisms against these species (Iguar et al., 2007; Nordstrom & Korpimaki, 2004). Because many seabirds species are ground-nesting and hatch in dense colonies, they are easily targets and a great source of food for terrestrial predators (Ekanayake et al., 2015). The severe impacts of mammalian predators on seabird populations are well documented across the world (Hilton & Cuthbert, 2010; Nordström, 2003; Towns et al., 2011). Mink (*Neovision vision*) is an example of such an

introduced predator. The spread of mink throughout Europe happened after they escaped from fur farms, and because of its good swimming abilities, it was able to spread to offshore islands. Mink take eggs, kill chicks and even adults within the colony (Clode & Macdonald, 2002).

Balancing the reproductive investment of current offspring against future chances to reproduce is key to maximize individual fitness (Erikstad et al., 1997), and being able to invest accurate amounts of resources in current offspring is essential. Increased effort in current offspring can lead to an additional fitness cost, either by lowering adult survival or future reproductive output (Hanssen et al., 2005). For birds, reproductive investment involves incubation efforts, feeding and protection against predators. It also involves egg investment, which might be most important (Chalfoun & Martin, 2010). Egg production is an energy-demanding process, and egg size correlates with female weight or condition (Barrett et al., 2012). In addition, egg size can be related to the age and breeding experience of the female (Hargitai et al., 2005). Because egg production is such a costly process, resource availability before egg laying is likely to affect the female egg investment. Karell et al. (2008) found that eggs of Ural owls (*Strix uralensis*) were smaller in years where food was scarce compared to rich years. Females are more likely to produce larger eggs with sufficient food supply, and prey abundance prior to egg laying may likely affect egg size (Barrett, Nilsen, & Anker-Nilssen, 2012).

Food availability is highly dependent on climate, and climatic variations are considered one of the main drivers affecting phenology and the dynamic of seabird populations (Becker, Peery, & Beissinger, 2007). Seabirds time their reproductive activities to match periods of peak prey availability, and climatic fluctuations can therefore be the cause of mismatch between the timing of breeding and prey abundance (Durant et al., 2004). Long lived seabirds like the Atlantic puffin are closely linked to oceanographic features that affect resource abundance, making it crucial for them to time breeding to when prey arrives in their foraging area. Wrong timing of egg-laying and thus hatching leads to an incorrect estimation of available food resources, possibly causing reproductive failure that year (Durant, Anker-Nilssen, & Stenseth, 2003). Therefore, variation in climate may have a profound effect on their reproductive success (Durant et al., 2007). Unlike many bird species

that adjust clutch size in response to environmental fluctuations, puffins only lay one egg per year. Instead, they may adjust parental investment in the egg to balance costs with offspring benefits. They can also adjust chick investment, or skip breeding due to unfavorable conditions (Durant et al., 2007).

This study aims to examine annual variation in nest predation of Atlantic puffins and assess whether it is related to climatic variability and parental investment. To determine predation levels in the local area, nest were monitored each breeding season from 2007-2020. To evaluate levels of parental investment, egg size is used as a proxy in this study. To further explain the potential variation in egg size, environmental covariates known to affect seabirds in the North Atlantic are included in a multivariate regression analysis. This includes external environmental parameters like the winter NAO index and local SST, and biological parameters like the abundance important prey. If predation proves to be higher in years with lower food availability, this combination may have severe implications for the future success of the puffin population at Hjelmsøya.

In this thesis, I hypothesize that 1) Lower investment facilitates higher nest predation and 2) Investment in offspring is lower if food availability is scarce.

2 Material and methods

2.1 Study species

The Atlantic puffin (*Fratercula arctica*) is one of the most common seabirds in Norway and maybe the most well-known member of the auk family (Alcidae). The species is only found in the northern hemisphere and is endemic to the North Atlantic (Harris & Wanless, 2011). The species global distribution range from 50°N (Brittany) in North America to 80°N (Spitsbergen) (Figure 1). Individuals usually gather to breed and hatch in colonies on rocky islands or steep sea cliffs and excavate nesting burrows into the soil where possible. If not possible, they often nest under boulders or in cavities and cracks available in cliffs (Harris & Wanless, 2011). Females lay one single egg per breeding season, and individuals do not breed until they are 3 to 6 years old. They are agile divers and their prey generally consists of small schooling fish like herring and cod (Lowther et al., 2020).

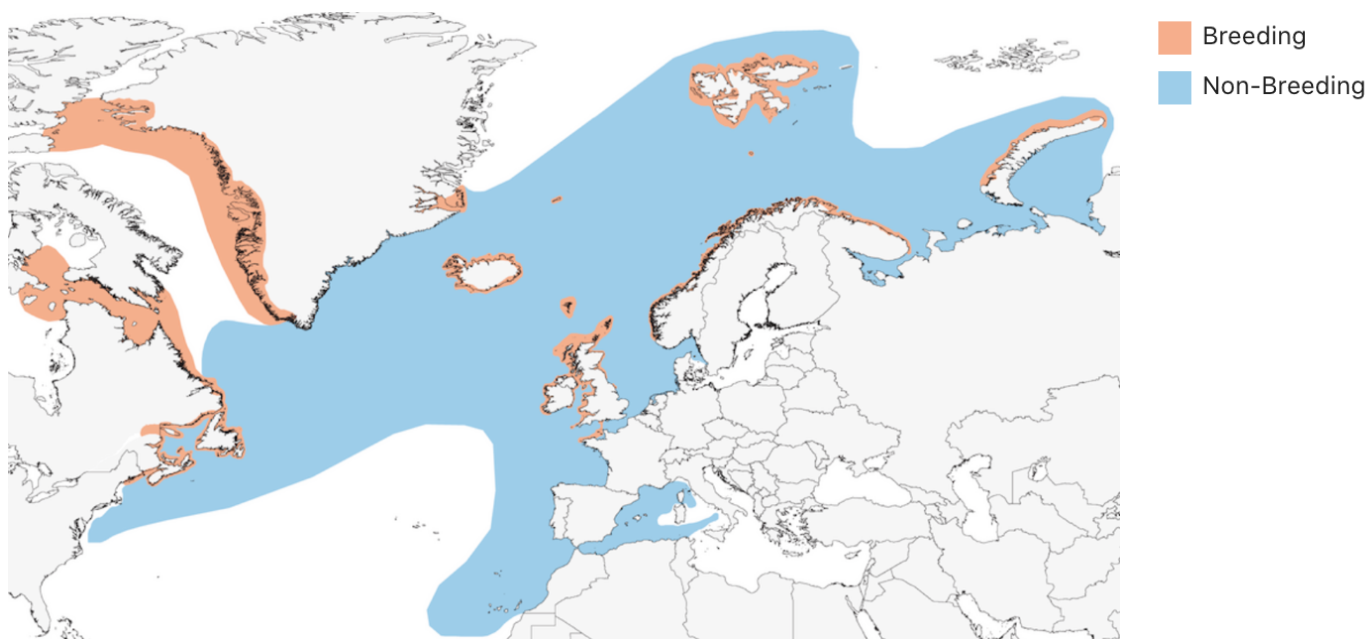


Figure 1: Global distribution of the Atlantic puffin during and outside the breeding season (Lowther et al., 2020).

Puffins in colonies at higher latitudes lay their eggs significantly later compared to colonies at lower latitudes (Burr et al., 2016). In Northern Norway this usually occur in late June or in the beginning of July (Burr et al., 2016). There can also be variations in egg-laying dates within and between colonies, which can often be associated with soil conditions. Egg-laying dates in northern colonies can be delayed by snow blocking nests or the presence of ice in the soil (Lowther et al., 2020). Both parents incubate the egg for approximately 40 days and share the feeding duty until the chick is ready to fledge. This usually happens when the chick is around 40 days old. However, this can vary between areas and quality of each breeding season (Lowther et al., 2020). The chick usually leaves the burrow and goes directly out to sea during nighttime, and at this point, they are completely independent of adults (Lowther et al., 2020). The Atlantic puffin is a long-lived seabird whose life-history traits include late maturity, few offspring and long generation lengths. Therefore, they are extra vulnerable to long term changes in the environment because it is difficult for them to fully recover once populations start to decline (Ricklefs, 1990).

In addition to the large threat posed by introduced predators to offshore islands, puffins have also been historically persecuted for their eggs, feathers, and meat. The species is considered as vulnerable because of its rapid decline across most of its European range, while trends outside Europe are still unknown (BirdLife International, 2021). This makes it especially important to protect and conserve the species, and there have already been several conservation initiatives to recover populations (Lowther et al., 2005). The Norwegian puffin population have also experienced declines, and has reduced from approximately 2 million pairs in 1980 to 1.5 million at present (Fauchald et al., 2015).

2.2 Study site

Hjelmsøya (71° 06' N, 24° 44' E) is an island located east in the Barents Sea in Troms and Finnmark county, Norway (Figure 2). Its location makes for an ideal breeding ground for various of seabird species (Sandvik et al., 2016). The Barents Sea is a relatively shallow ocean with depths ranging from 20-500 m (average depth 220m) (Bogstad et al., 2015). It is characterized by being a highly productive arctic and sub-arctic shelf sea, but this varies between seasons. Southern currents of Atlantic water bring large amounts of fish larvae from their spawning areas in the south, and large stocks of pelagic shoals such as cod, herring, haddock, and capelin can be found here (Reiertsen et al., 2019). These are all important food sources for seabirds during the breeding season and outside the breeding season in the south-western Barents Sea (Reiertsen et al., 2019).

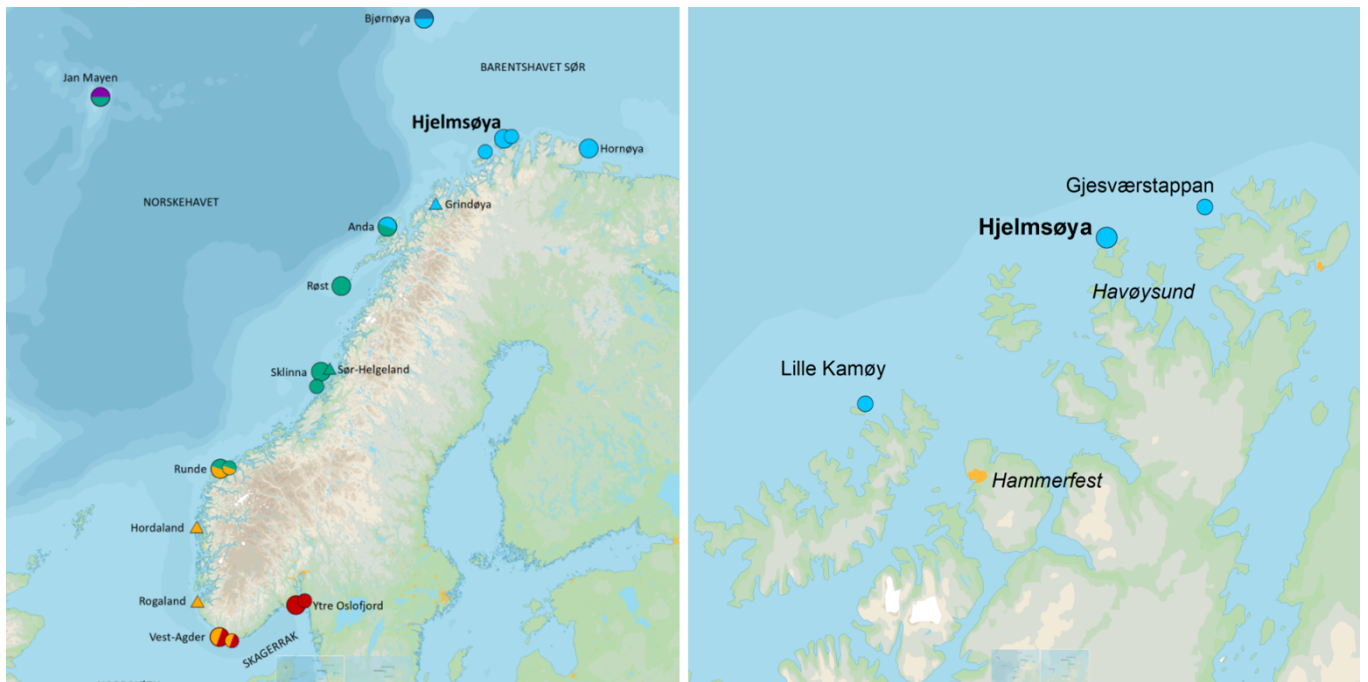


Figure 2: Map illustrating the location of Hjelmsøya. The island is situated north of mainland Norway, with feeding areas in the southwestern part of the Barents Sea.

The island of Hjelmsøya covers an area of 39 square kilometres and is one of several key-sites in the SEAPOP (Seabird Population Studies) monitoring system. Birds predominantly breed on the very north of the island (SEAPOP, n.d.). This area is categorised as a nature reserve with steep cliffs and slopes where thousands of birds lay their eggs. Several different seabird species nests on the island, such as the Razorbill (*Alka torda*), Common guillemot (*Uria aalge*), Black-legged kittiwake (*Rissa tridactyla*), among others, but the most numerous species is now the Atlantic puffin with more than 80 000 hatching pairs (SEAPOP, n.d.). Mink (*Neovision vision*) is one of the primary predators in the local area. Otter (*Lutra lutra*) is also a predator thriving here but is considered less severe compared to the mink. Some individuals though have been observed preying on chicks ready to leave the nest at Hjelmsøya, and other individuals have been spotted preying on adult puffins (Figure 3). Other potential predators are corvids, seagulls, and eagles, but as puffins shelter their eggs it is harder for them to access the nests (SEAPOP, n.d.).



Figure 3: Left: Mink captured with camera trap preying on an Atlantic puffin chick. Right: Otter observed killing an adult Atlantic puffin in the field. Photo: Eline Rypdal.

2.3 Field protocol

From 2007-2020, an average of 104 nests (ranging from 70-125 nests) were monitored to determine breeding success and predation rate. In a designated breeding success field, active nests (nests with eggs) were located and marked in the beginning of June. In the season of 2020, this was completed between the 5th and 15th of June, which is consistent with previous years. If some eggs were located too deep within the burrows to reach, they were made more accessible by digging holes (plugs) through the soil and into the nests. These were closed and covered with vegetation after length, width, and weight was measured for each egg. All measurements were made with sliding calipers (nearest 0.01 mm) and manual hanging scales (nearest 0.01 g). The plugs were then closed and properly covered to keep the nests insulated, and to keep predators away. Every nest was then inspected at regular intervals every five days throughout the breeding season until the end of July (usually between the 18th and 20th). If parents were present in nests, nests were not inspected to avoid any unnecessary disturbance. If eggs or chicks were missing from the nests, they were classified as predated. One last inspection was completed at the end of every breeding season in August before fledging. However, bad weather conditions in 2020 led to delays in the last nest inspection. This made it difficult to determine whether the chick had successfully fledged or been predated from the empty nest since the previous inspection in July.

2.4 Data selection

2.4.1 Egg volume and predation rate

Egg volume (V) was determined by the equation $V = KxLxB^2$, where $K = 0.51$ for puffins. K equals a constant calculated for different groups of birds and egg shapes, and L = length, and B = width (Barrett et al., 2012).

Predation rate was calculated for each individual year (Figure 4) by the following method:

$$\text{Predation rate} = \frac{\text{Chick predation rate}}{\text{Egg predation rate}}$$

Where chick predation rate was: $\frac{\text{Number of chicks predated}}{\text{Total number of nests}}$

And egg predation rate was: $\frac{\text{Number of eggs predated}}{\text{Total number of nests}}$

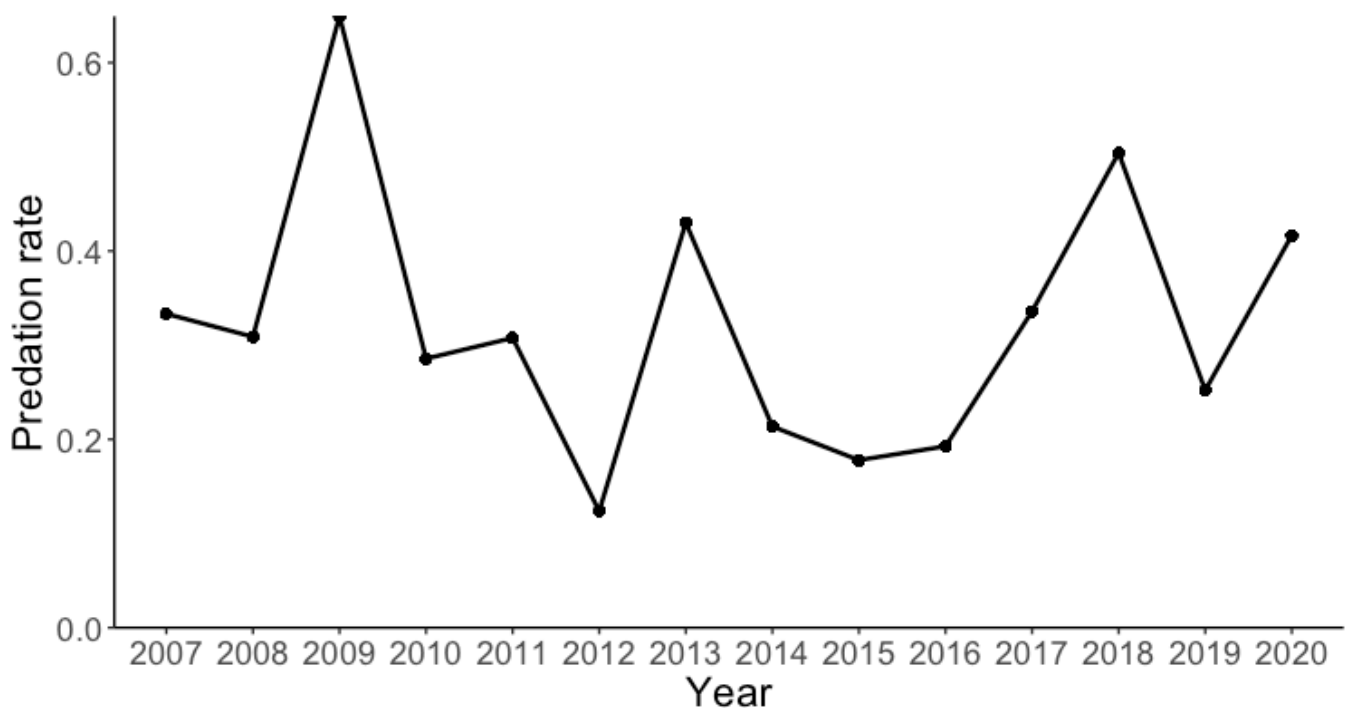


Figure 4: Annual variation in nest predation from 2007-2020 in the Atlantic puffin (*Fratercula arctica*) population at Hjelmsøya.

2.4.2 Environmental covariates

The winter NAO index (NAO_w, Des-March) was included as a large-scale climate parameter in this study. At Hjelmsøya, this index has previously shown to have indirect effects on the puffin population through the abundance of prey species (Idsø, 2016). Since environmental conditions predominantly influence the abundance of prey species during their first year of life (Barrett et al., 2012), the NAO_w indices in this study were set to the previous winter with one year lagged effect (NAO_{w_1lagged}). To assess small-scale local conditions, mean sea surface temperatures (SST) of months prior to the breeding season (February-April) were included in the analysis (Figure 5). Based on the location of Hjelmsøya and foraging routes of puffins, longitude was set from 15°-30°E and latitude was set from 70°-72°N. Age specific abundance of four prey species known to be of importance for puffins in Northern Norway were also included: Capelin TSB (total stock biomass) (*Mallotus villosus*), 1-3-class herring (*Clupea harengus*. L), 0-group herring, 0-group haddock (*M. aeglefinus*), and 0-group cod (*Gadus morhua*) (Barrett, 2002; Barrett et al., 2012) (Figure 5). Prey abundance data was provided by The International Council for the Exploration of the Sea (ICES). Data for monthly NAO indices and mean SSTs were obtained from online databases provided by the National Oceanic and Atmospheric Administration (NOAA; <https://www.ncdc.noaa.gov>).

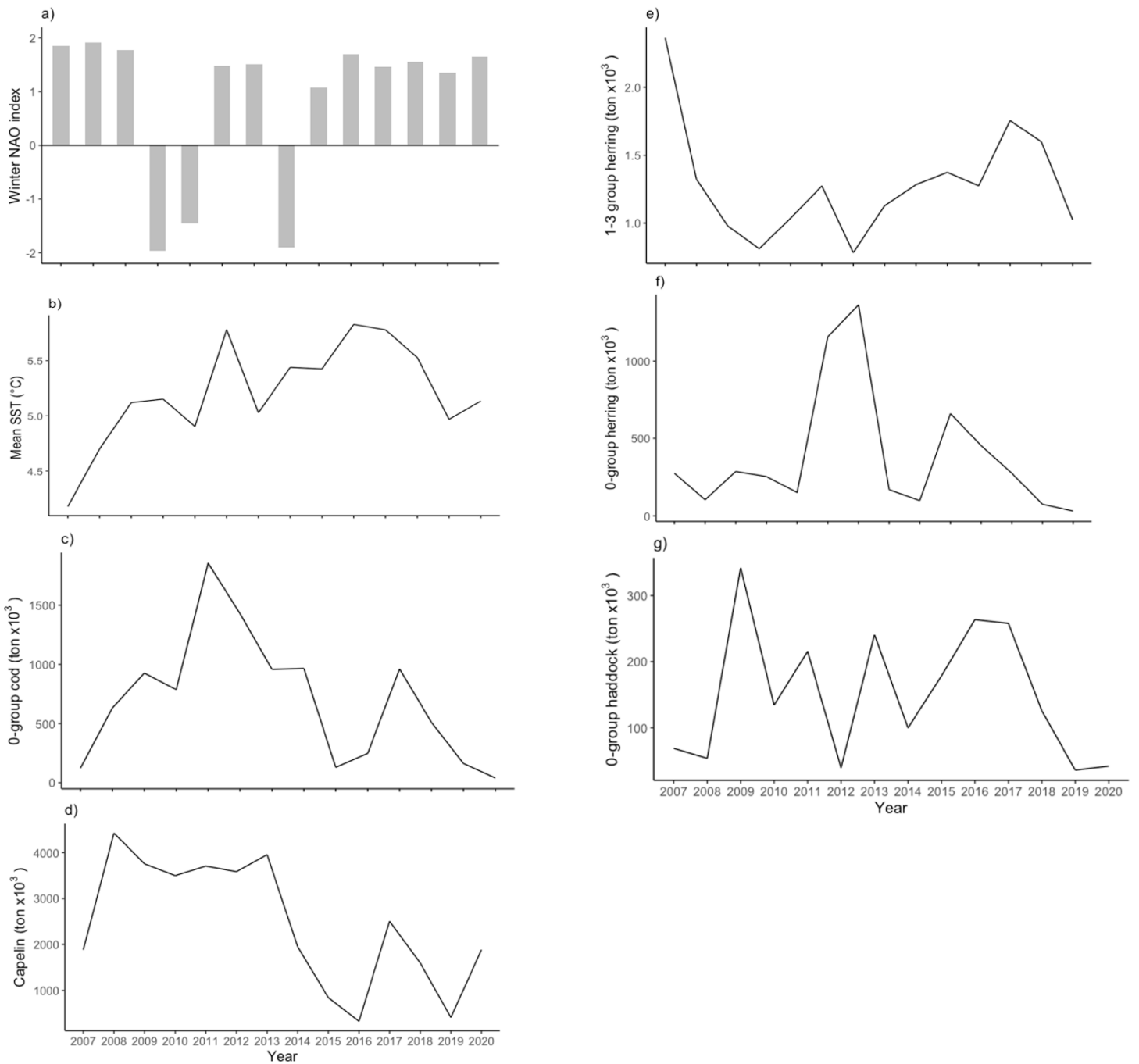


Figure 5: Time-series for the environmental covariates selected to model the variation in egg volume (e.g. quality of the season) for Atlantic puffins at Hjelmsøya from 2007-2020. a) Winter NAO index (Average from Des-March, with one year lagged effect), b) Mean SST (sea surface temperature) prior to the breeding season (Feb-April), d) Capelin TSB (total stock biomass) abundance , e) 1-3 group herring abundance, f) 0-group herring abundance, g) 0-group haddock abundance.

2.5 Data analysis

A generalized linear model (GLM) was used when evaluating the relationship between predation and egg volume. To determine the effects of the selected environmental covariates on egg volume, I used a separate multiple linear regression model. Egg volume was set as the response variable in all models and the environmental covariates were defined as predictors. I used Akaike's Information Criterion (AIC) to determine the best model suited for the data, where the best model was identified by the lowest AIC score. This was done using the forward selection method, where I started with a null model that only included the intercept. Next step was based on adding each variable one by one where the model with the lowest AIC score was kept before proceeding with the selection process. This step was repeated until adding more variables had no further improvement on the AIC score. A test of correlation was performed to ensure there was no correlation between the independent variables before performing the analysis (<0.60). Lastly, a linear model was used to assess how egg volume varied between years. All analyses were performed in the R environment (R Core Team 2019) version 1.2, and models were fitted using the tidyverse (Wickham, 2021) and lme4 (Bates et al., 2015) packages.

3 Results

There was a significant relationship between mean egg volume and predation rate ($n = 14$, $F = 9.07$, $P < 0.01$), where eggs were smaller in years with higher predation rates (Estimate = 0.0062 ± 0.002 SE) (Figure 6).

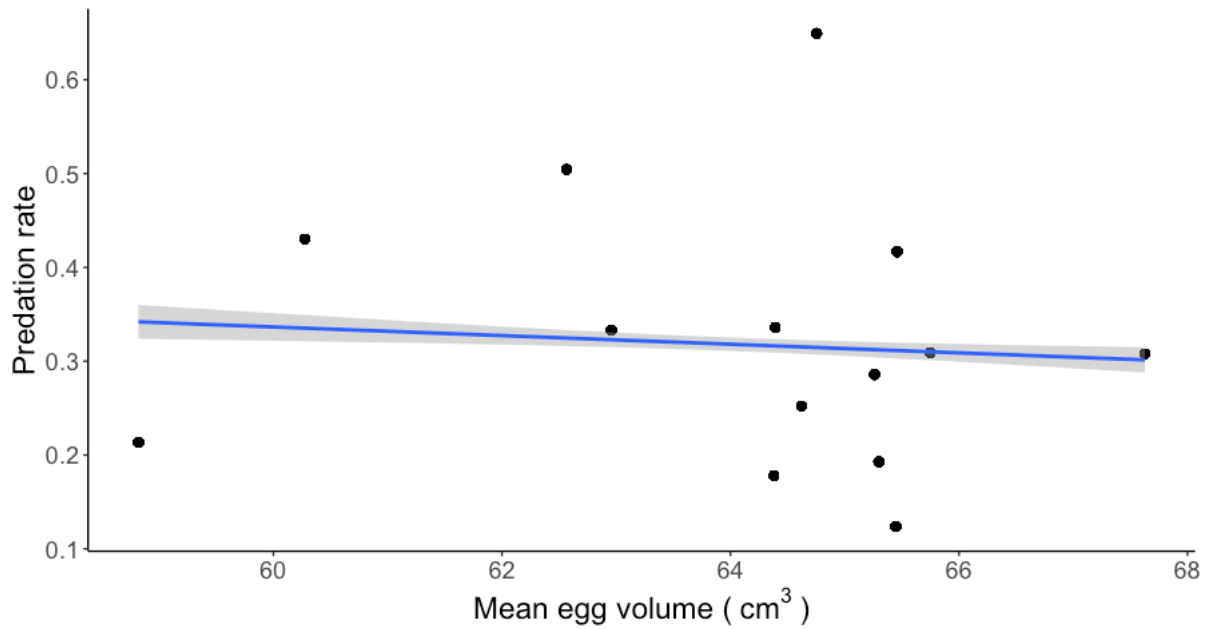


Figure 6: Regression line illustrating the relationship between the predation rate and mean egg volume of Atlantic puffin (*Fratercula arctica*) eggs at Hjelmsøya from 2007-2020. Each point represent a separate year.

Egg volume varied between years, although not significant ($P = 0.36$), where the highest variance was observed in years with low egg volume (Figure 7).

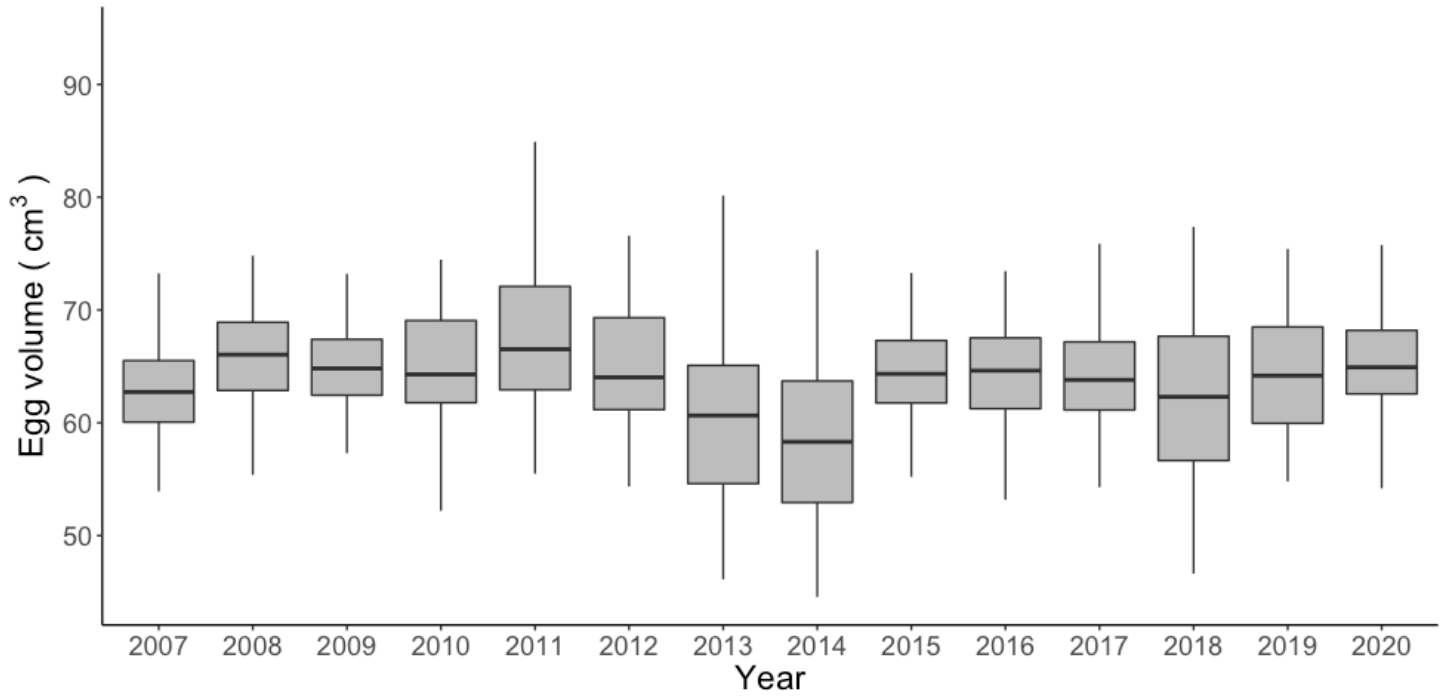


Figure 7: Volume for Atlantic puffin (*Fratercula arctica*) eggs at Hjelmsøya from 2007-2020. Each box represent the median and the the top (Q3) and bottom line (Q1) represents within-year variability (SD) in egg volume. .

The model selection based on AIC scores suggested that volume was significantly linked to mean SST prior to breeding, winter NAO (1 year lagged effect) and the abundance of 0-group herring, 0-group cod and capelin (Table 2).

Table 2: Comparison of AIC scores for the top ranking models in each step using forward selection. Δ AIC indicate the relative amount that separates the given model from the top ranking model.

Step	Model	AIC	Δ AIC
0	Intercept	7967.586	26.71
1	Volume~ 0-group herring	7962.303	21.42
2	Volume~ 0-group herring + Capelin_TSB	7962.303	21.42
3	Volume~ 0-group herring + Capelin_TSB + winternao_1lag	7951.129	10.25
4	Volume~ 0-group herring + Capelin_TSB + winternao_1lag + 0-group cod	7945.044	4.16
5	Volume~ 0-group herring + Capelin_TSB + winternao_1lag + 0-group cod + mean SST	7940.875	0.00

This model suggest significant effects ($P < 0.05$) of 0-group herring (Estimate = -0.0050 ± 0.00088 SE) and 0-group cod (Estimate = 0.0050 ± 0.0014 SE), mean SST (Estimate = -2.345 ± 0.94 SE), and winter NAO index (Estimate = 3.91 ± 0.88 SE). Capelin (Estimate = 0.00015 ± 0.00026 SE) was also included in the model, although not significant ($P = 0.56$). These factors had annual fluctuations affecting the variation in mean egg volume. Egg volume increased in years with a higher abundance of capelin, 0-group cod, and higher winter NAO indices as indicated by the positive estimates Egg volume decreased in years with a higher abundance of 0-group herring and higher mean SSTs prior to breeding as indicated by the negative estimates (Figure 8).

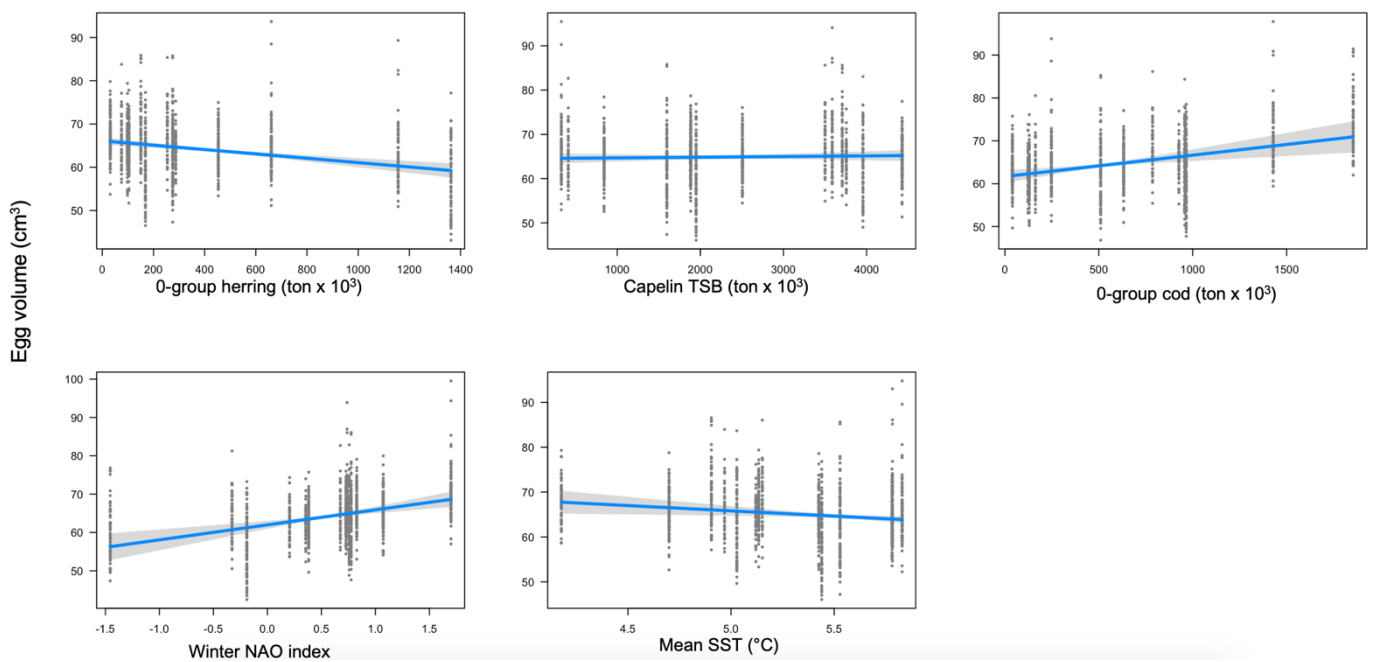


Figure 8: The blue regression line represent the trend of the relationship between egg volume and the selected environmental covariates: 0-group herring, capelin TSB (total stock biomass), 0-group cod, winter NAO index (1 year lagged effect) and mean SST (sea surface temperature). Each vertical line of points represent a different year, and each point within in the line represent the volume of individual eggs.

4 Discussion

In this study, I evaluate annual variation in nest predation of Atlantic puffins. Further, I examine whether this can be related to climatic variability and parental investment. Egg volume was used as a proxy to determine female condition and thus parental investment for Atlantic puffins at Hjelmsøya. I found that predation rate was significantly higher in years with lower egg volume. Different mechanisms may explain this result. Firstly, years with smaller eggs can be a consequence of poor female condition. They have overall low reproductive investment and offspring are more vulnerable to predation. Food availability are especially important when determining egg investment (Barrett et al., 2012). Studies have shown that the Atlantic puffin relies on a high trophic level diet prior to the breeding season to meet the nutritional demands of egg production (Kouwenberg et al., 2013). This suggest that egg size were limited by food shortage, leaving the female with less energy to invest in the egg (Barrett, Erikstad, & Reiertsen, 2017). This corresponds to the findings in Oro et al. (1999), where the average egg volume for the Audouin's gull (*Larus audouinii*) was significantly affected by variations in food supply. Years with lower volume might also have higher recruitments of that young and inexperienced females. Younger females tend to be less willing to make costly egg investments because they have high probabilities of surviving until the next breeding season and are likely to have more chances to reproduce compared to older females (Pilz et al., 2003).

In addition, smaller eggs are usually correlated with smaller hatchlings with slow growth rates (Kouwenberg et al., 2013; Krist, 2011). They require more feeding and stay in the nest longer before fledging, and predation risk increase during this time (Johnsen et al., 1994). When resources are scarce, parents struggle to feed their chicks enough during the rearing period. They are forced to spend considerably more time and energy foraging for prey away from their colony and nest, which leave eggs and chicks more unprotected and vulnerable to predation (Monaghan et al., 1994). In addition, chicks may respond to this nutritional stress by venturing towards the nest opening, and the risk of predation increase further. At Hjelmsøya, this makes them prone to predation not only from terrestrial predators such as mink, but it also makes them more accessible for avian predators such as seagulls and eagles (SEAPOPOP, n.d.).

Birds have the ability to respond to different levels of predation to themselves and their offspring over ecological time (Lima, 2009). This might explain why eggs are smaller in years with higher predation rates. Studies have shown that in years with increased risk of nest predation, parents decrease reproductive investment because the reproductive value of the current offspring is low (Chalfoun & Martin, 2010). The probability of chick survival is lower in years with higher predation rates, and parents might decide to reduce their investment or completely abandon their chick to increase their own survival and maximize their reproductive fitness (Erikstad et al., 1997; Fitzsimmons et al., 2018).

Even though the relationship between predation and egg size was statistically significant, the estimated effect was small and one might argue that it's not biologically significant. However, considering this puffin population has suffered great losses to predation, higher predation rates is likely to cause additional negative effects on their breeding success during low-quality years with less parental investment.

The variation in egg size for Atlantic puffins at Hjelmsøya can be directly related to biological covariates such as the abundance of early life stages of herring and cod. The abundance of 0-group herring had a negative effect on egg size, whereas the abundance of 0-group cod had positive effects. All age classes of capelin were also included in the best model, although the effect on egg size seem to be insignificant. These are all essential prey to the Atlantic puffin pre-breeding, and the recruitment of these species in the Barents Sea can vary greatly between years (Barrett, 2002; Barrett & Erikstad, 2013; Bogstad et al., 2013; Joë M. Durant et al., 2003). Therefore, this result was somewhat expected. Barrett et al. (2012) found that declines in egg size in two separate Atlantic puffin colonies were related to interannual changes in abundance of important prey, including capelin and early life stages of herring. However, the early life stages of cod seemed to be of equal importance in this study. Hamre (1994) states that juvenile herring and capelin suffer from high predation rates from juvenile cod, which might explain why there was a positive relationship between cod abundance and egg size. The negative estimates for 0-group herring and positive estimates for 0-group cod suggest that herring is more available in years with higher SST, whereas 0-group cod is more available in years with lower SST.

Both the climatic covariates chosen for this study were included in the best model, suggesting that egg size is strongly correlated with large scale- and local scale conditions prior to egg-laying. The winter NAO index was included as a proxy for large scale climatic conditions, and eggs were larger in years with higher NAO indices. This index has previously been connected with climatic variability in the Barents Sea, and environmental conditions in north-western Europe are closely linked to this index (Gordo, Barriocanal, & Robson, 2011). Several studies have found that it can be connected to the success of seabird populations in various ways. Thompson & Ollason (2001) found that the annual variation in the breeding performance of the northern fulmar (*Fulmarus glacialis*) was related to the NAO index through lagged effects, and Sandvik et al. (2005) found that the NAO index could be related to the adult survival in five different species of Atlantic seabirds. Even though I found no studies examining the relationship between this index and egg size, it seemed to have profound effects on egg size in this colony. Further more, lagged effects of the NAO index have been related to the abundance of 0-group cod and herring in the Barents Sea, which coincides with the result of this study (Hjermann, Stenseth, & Ottersen, 2004) and might explain how it connects to egg size.

Sea surface temperature was used as a proxy for local climatic conditions, and eggs were smaller in years with higher temperatures. SST is the oceanographic parameter that is commonly associated with seabird biology (Furness, 2016). Several studies have found that the recent increase in ocean temperatures has had detrimental effects on the success of seabirds (Hansen et al., 2021; Sandvik et al., 2014). Temperature is highly correlated with prey abundance (Diamond & Devlin, 2003), and marine organisms are especially sensitive to temperatures changes (Jenouvrier et al., 2018). As the climate in the northern hemisphere is getting warmer, spring conditions occur earlier in the season, which also means that seasonal patterns and events are being pushed back to match these conditions.

Temperature has profound effects on seabirds' phenology, especially when it comes to the timing of reproduction (Stenseth & Mysterud, 2002). Therefore, warmer oceans can cause shifts in the annual timing of peak food availability, which is likely to be the cause of a potential mismatch between the seasonal peak of prey abundance and the rearing period for the puffins (Durant et al., 2004; Barrett & Erikstad, 2013). This might explain why eggs were smaller in years with a higher abundance of 0-group herring and larger in years with a

higher abundance of 0-group cod. The hatching of fish larvae coincides with primary production which again determines the peak timing of zooplankton abundance. The variation in egg size at Hjelmsøya might therefore be driven by the match or mismatch between plankton production and the abundance of herring and cod (Durant, Anker-Nilssen, & Stenseth, 2003).

As predicted, the variation in egg size is most likely due to the indirect effects of climatic variables on prey abundance. SST and the NAO index are both variables known to affect the distribution and abundance of prey in the North Atlantic (Barrett & Erikstad, 2013; Thompson & Ollason, 2001). The environmental covariates included in this study are likely to interact with each other in addition to the effect they pose on egg volume at Hjelmsøya. This is most apparent for the abundance of prey species, where one species might deplete the other through predation or competition for resources (Hamre, 1988). This can be seen in Barrett et al. (2012), which found that the increase of strong year classes of herring might deplete the capelin stocks at Hornøya. This study shows how interactions between different prey species can result in complex dynamics, which in turn can have profound effects on top marine predators like seabirds.

5 Conclusion

Several studies have documented the effect of predation on prey communities, and there has been extensive research on how seabird populations are affected by climate fluctuations. In this study, I aimed to assess annual variation in nest predation and evaluate whether it could be related to climatic variability and parental investment. Nest predation was higher in years with smaller eggs, which may profoundly affect the Atlantic puffin colony at Hjelmsøya. Two mechanisms may explain this result: 1) Unfavourable seasons with low food availability lead to smaller eggs because females in poor condition invest more in themselves and less in their current offspring. This makes eggs and chicks more vulnerable to predation. 2) Females invest less in their eggs if the perception of local predation is high and survival prospects of current offspring are low. Further, the variation in egg size seemed best explained by indirect effects of climatic variables through the abundance of important prey. The environmental covariates included used in study most likely interact and affect each other in addition to the effect they have on egg size. The results of this study can provide new information on how predation, parental investment and environmental fluctuations correlate and affect the puffin population at Hjelmsøya, and therefore be a valuable asset for future conservation initiatives for the species.

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