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Effects of a fluctuating climate on the body condition of Atlantic Puffins *Fratercula Arctica* at Røst, Norway

Effektene av et varierende klima på
kroppskondisjonen til Lundefugl *Fratercula
Arctica* på Røst, Norge

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PREFACE

This thesis marks the end of my Master's degree in natural resource management at the Norwegian University of Life Sciences (NMBU), Ås, spring 2017. The process of writing this thesis has given me valuable insight into the field of ecological research. First, I would like to thank my supervisor and Senior Research Scientist at the Norwegian Institute for Nature Research (NINA) Tycho Anker-Nilssen. He provided me the opportunity to write a master thesis with fieldwork stationed at Hernyken in the spectacular surroundings at Røst. Thank you for all your support, guidance and patience during the entire process of working on this thesis. I would also like to give special thanks to my supervisors at NMBU Svein Dale, Ole Wiggo Røstad and Ronny Steen. Ole Wiggo Røstad introduced me to the opportunity of studying the life of the Atlantic Puffin and other fascinating seabirds, especially on such close range. His support and knowledge has been essential during this whole writing process. Moreover, I will also thank Ronny Steen for his statistical guidance. His support during the spring of 2017 has been invaluable and I am incredibly grateful for this learning experience and his patience.

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ABSTRACT

The Atlantic puffin *fratercula arctica* population is declining in the North Sea- and the Norwegian Sea region. Puffin colonies located in the Røst archipelago at the outermost tip of the Lofoten Islands, experienced almost complete reproductive failures every year from 2006 until 2016. The present situation in the puffin colonies at Røst is closely related to the life history of a puffin. Puffins are considered a “K-selected” species and are therefore recognized for having long generation times, low reproductive rates, and a delayed onset of reproduction. According to life history theory, adult puffins evaluate their chances of survival and reproduction during all stages of the breeding season in order to maximize their total reproductive success. In this trade-off between reproduction and survival, the body condition of puffins may influence the allocation of resources. The aim of this study was to examine whether and how the body condition of breeding puffins is influenced by climatic conditions, both within the breeding season and between years. To that objective, the relationship between *body condition* of adult puffins and environmental variables such as *sea surface temperature (SST)*, *breeding success*, and *0-group herring abundance* was tested in two separated periods of the breeding season. These periods included (1) the pre-laying period (before 15th of May), and (2) the period after the mean hatching date (in late June/July). I also used *gender* as an interactive covariate to test for sex-specific responses in explanatory variables. The residuals from a body size versus body mass regression was used as an index of body condition. A discriminant analysis showed that *head+bill* and *wing length* distinguished the sexes most precisely. The relationship between environmental variables and the body condition of adult puffins was analyzed in linear mixed effects models (LMM) using restricted maximum likelihood (REML). Akaike’s information criterion (AIC) was used in the model selection. The results suggested that the SST in March had a positive and significant impact on the body condition of adult puffins during all stages of the breeding season. Fledging success was found to be positively correlated with body condition in the pre-laying period. However, the effect turned in the period after mean hatching date. I could not detect a significant difference in the body condition responses of female and male puffins. Moreover, 0-group herring abundance had no effect on body condition in the pre-laying period, whereas a minor negative, but significant impact could be found in the later stages of the breeding season. The body condition of adult puffins was found to be lower in the pre-laying period than in the period after mean hatching date. This study contributes to the understanding of the physiological responses of puffins to fluctuating environmental conditions by exploring variations in their body condition, as well as inter-sexual differences in these responses.

SAMMENDRAG

Populasjonen av lundefugl *fratercula arctica* i Norskehavet og Nordsjøen minker. For lundekoloniene på øygruppene i Røst kommune i Lofoten har det vært nær total hekkedekollaps hvert år mellom 2006 og 2016. Den nåværende situasjonen for lundekoloniene på Røst er sannsynligvis nært knyttet til livshistorien til lunden. Lundefuglen har lang levetid, lav reprodutiv rate og blir sent fruktbar. Den er derfor å regne som en «K-selektert» art. I følge livshistorieteori, vil en voksen lunde vurdere sine sjanser til å overleve og reprodusere seg gjennom hele hekkesesongen, for å kunne maksimere sin reprodutive suksess. På grunn av lundens livshistoriestrategi og et habitat som er preget av stor usikkerhet med hensyn til mattilgang, vil lunden lettere prioritere egen overlevelse fremfor reproduksjon. I denne avveilingen av reproduksjon og overlevelse, spiller kroppskondisjonen hos lunde en viktig rolle. Målet med denne studien var å undersøke hvilke og hvordan kroppskondisjonen hos lundefugl er påvirket av klimaforhold, både innenfor hekkesesongen og mellom år. Korrelasjoner mellom kroppskondisjon for voksne lundefugl og miljøvariablene *havoverflatetemperatur*, *hekkesuksess* og *årsklassestyrke for 0-gruppe sild* ble derfor testet i to separate perioder av hekkesesongen. Periodene omfattet, (1) perioden før egglegging (før 15. mai) og (2) perioden etter gjennomsnittlig klekketidspunkt (sent i juni/juli). Jeg testet også for kjønnseffekter ved å bruke kjønn som en interaktiv kovariabel. Residualene fra en regresjon som inkluderte kroppsstørrelse og kroppsmasse ble brukt som en indeks på kroppskondisjon, og en diskriminantanalyse viste at de morfometriske variablene hode+nebb og vingelengde best forklarte forskjellen mellom kjønn. Korrelasjoner mellom miljøvariablene og kroppskondisjon for voksen lundefugl ble analysert ved bruk av linear mixed effect models (LMM) og restricted maximum likelihood (REML). Akaike's information criterion (AIC) ble brukt til modell utvelgelse. Resultatene tydet på at havoverflatetemperaturen i mars hadde en positiv og signifikant påvirkning på kroppskondisjon hos voksen lundefugl gjennom hele hekkesesongen. Hekkesuksess var positivt korrelert med kroppskondisjon i perioden før egglegging, men modellene viste omvendt effekt i perioden etter gjennomsnittlig klekketidspunkt. Jeg kunne ikke finne en signifikant forskjell i responsene på kroppskondisjon mellom hannkjønn og hunkjønn. Årsklassestyrke for 0-gruppe sild hadde ingen effekt på kroppskondisjon i perioden før egglegging, men den hadde en signifikant, svakt negativ påvirkning i perioden sent i hekkesesongen. Vi fant at kroppskondisjonen til voksen lundefugl var lavere i perioden før egglegging enn i perioden etter gjennomsnittlig klekkedato. Denne studien bidrar til forståelsen av lundefuglens fysiologiske responser på et varierende miljø ved å utforske variasjoner i deres kroppskondisjon, i tillegg til kjønnsforskjeller i disse responsene.

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1. INTRODUCTION

The ultimate choices made by different species in situations of distress, depends primarily on their life history traits. Bird species can be separated in two fairly distinct groups based on their life history character (Stearns 1992). At one extremity, the species may produce a large number of offspring in a short period of time, but with a lower risk of adult survival. In this selection of species, also called “r-selected” species, biological traits such as a high fecundity, early maturity onset, small body size, short generation time and the ability to disperse offspring widely is considered characteristic (MacArthur & Wilson 2015). At the other end of the scale are species that have evolved a life history character of producing few offspring in a successful breeding season, often as few as one single progeny (Stearns 1976). These “K-selected” species are characterized by high adult survival rates, long generation times, a long period until sexual maturity and, due to the production of few offspring, extensive parental care until maturation (Stearns 1992). The majority of organisms do not follow this pattern of selection and it is important to notice the species-specific differences in regards to the different biological traits (Pianka 1970). For instance, the production of 20 eggs for the salmon species Salmonidae would be considered of low fecundity, whilst it would be characterized as abnormally productive for a large mammal such as the whale Cetacea. Because “K-selected” species have a higher adult survival rate and a longer life expectancy, they are granted with the opportunity of choosing between their own survival and reproduction. Thus, a trade-off between reproduction and survival exist that refers to the terminology “cost of reproduction” (Williams et al. 2007; Williams 1966). MacArthur and Wilson (1967) were the first to coin the term “K-selected” and “r-selected” species in order to describe two completely different strategies in achieving optimal individual fitness (Pianka 1970). However, no species are considered completely r-selected or K-selected. Usually the different species are adapted to make compromises between the two selections.

The allocation of resources between reproduction and survival in long-lived species is of extraordinary importance because a minor reduction in adult survival may impose a large negative effect on lifetime reproduction (Stearns 1982). Most seabirds, such as the Atlantic Puffin *Fratercula arctica* (hereafter referred to as puffin), have long generation times, low reproductive rates and a delayed onset of reproduction (Erikstad et al. 1997; Øyan & Anker-Nilssen 1996). Procellariiformes and some Alcidae species, such as the puffin, are possibly some of the clearest examples of life history strategy at its extreme, as they produce only a single egg in each breeding event (Erikstad et al. 1997). According to current life-history

theory (Stearns 1992), seabirds should therefore balance their investment in the next generation against their chances of adult survival and reproduction in the future in order to maximize their overall individual fitness (Erikstad et al. 1997; Erikstad et al. 1998). Because pelagic seabirds are situated in an environment of considerable uncertainty with regards to food availability, they have developed a strategy in which survival is prioritized over reproduction. Survival is crucial for puffins because an early death involves a much higher cost of reproduction than a failed breeding attempt, considering that they have many opportunities of reproduction during a lifetime. Life history theory suggest that adult puffins evaluate their chances of survival and reproduction during all stages of the breeding season in order to maximize their total reproductive success or optimal individual fitness (Johnsen et al. 1994). The definition of fitness is often described as equivalent to “a measure of reproductive success” or the actual number of offspring which are produced by an individual relative to its reproductive propensity (Dobzhansky 1970; Waddington 1968). However, fitness cannot be measured based on the productivity of a single individual and the terminology refers to a propensity rather than the actual number of offspring produced. Thus, fitness should be viewed as a property of a group of individuals, or more accurately the average contribution to the gene pool of the next generation from individuals with the same genotype or phenotype (Smith & Parker 1976; Sober 1994). In the trade-off between costs paid in survival and cost paid in reproduction, the body condition of adult puffins may play a vital role in determining breeding decisions. For instance, Erikstad et al. (1997) suggested that puffins have evolved a fixed effort in raising chicks dependent on their body condition at the time of breeding, but not affected by the chicks demands. This fixed level of effort may be a strategy to increase life expectancy and at the same time prevent too much investment in reproduction (Erikstad et al. 1998; Johnsen et al. 1994). Furthermore, studies have detected that body condition, particularly in the early stages of the breeding season, may have an effect on the willingness to invest in reproduction (Johnsen et al. 1994). Thus, it is reasonable to assume that the body condition of adult puffins is a key factor in their life history strategy.

Because most seabirds are K-selected species and their life history-strategy involves prioritizing survival, they are especially sensitive to fluctuating climatic conditions that reduces life expectancy. For instance, seabirds will easily choose to leave the colony or abandon their chicks if environmental conditions are poor during the breeding season (i.e., low food availability). Their actions can therefore give indications on both short- and long-term variations in oceanographic conditions and fish populations at an early stage (Barrett

2002; Boyd et al. 2006; Diamond & Devlin 2003; Montevecchi 1993). Thus, seabirds are well suited as bioindicators of change in the marine ecosystem (Furness & Camphuysen 1997; Parsons et al. 2008). Furthermore, the performance and population trends of seabirds are known to be dependent on a wide range of ecological factors (Boyd et al. 2006; Croxall 1987). Fluctuations in food availability can influence diet, reproductive success, adult survival rate and body condition (Barrett 2002; Cairns 1988; Cairns 1992; Montevecchi 2002; Williams et al. 2007). Previous studies have discussed how reduced prey availability can affect the body condition of breeding adult puffins, as well as food provisioning and adjustment in the adult body mass according to the availability of food (Cairns 1988; Williams et al. 2007). Puffins search for food within a limited area (<100 km) of the breeding colony. Therefore, they are dependent on the abundance of prey being at an optimum in the time of breeding, especially during the chick rearing (Boyd et al. 2006; Croxall 1987). Also, timing of breeding is of crucial importance to match the drift of the young herring from the main spawning grounds in south-west Norway northwards with the Norwegian Coastal Currents towards their nursery ground in the Barents Sea (Durant et al. 2004a). Norwegian spring-spawning herring spawns from late February to late March and starts to drift northwards at this time. Their growth and survival eventually depends on the phytoplankton bloom and climate conditions in spring. The temperatures in March may affect the growth and mortality of herring, and thereby, the quality and the quantity of food reaching the foraging areas of chick-feeding puffins at Røst (Durant et al. 2003). Furthermore, puffins are known to gradually lose their body mass during the breeding season (Barrett et al. 1985). This has been interpreted as being either a result of physiological stress or an adaption to reduce flight costs during the nestling period (Barrett & Rikardsen 1992). By monitoring individuals, particularly their physiological responses to fluctuating environmental conditions, it may be easier to predict the mechanisms of changes in the population structures.

1.1 Puffins

The puffin is a medium-sized auk Alcidae (350-600g) that feeds entirely on marine prey and breeds on isolated oceanic islands or exposed mainland cliffs throughout the North Atlantic. It is the only puffin native to the Atlantic Ocean (Harris & Wanless 2011). It breeds on both sides of the North Atlantic, from the north-eastern part of North America and Brittany in France to as far north and east as Spitsbergen and Novaya Zemlya and many other North Atlantic Islands (Strøm 2015). Figure two illustrates the global distribution of the puffin. The puffin spends the winter exclusively at sea and come ashore to remote areas or islands only during the summer to breed. The breeding colonies are in general densely populated, with the numbers of breeding pairs ranging from a few hundred to several hundred thousand. In the winter period, the puffin covers vast areas of the North Atlantic and the western Mediterranean (Icelandic Institute of Natural History (IINH) 2012; SEATRACK 2017).

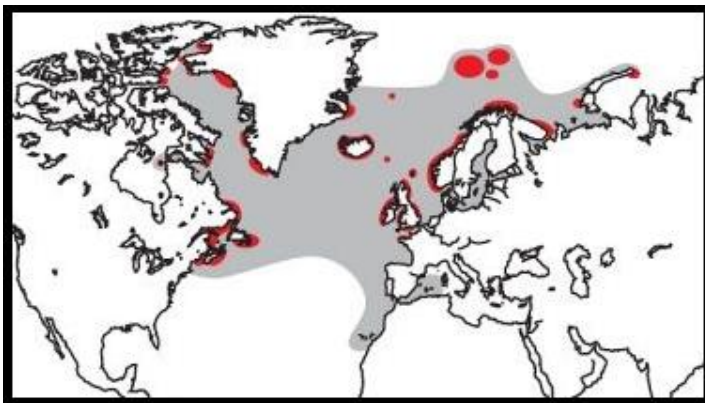


Figure 1: Global distribution of the Atlantic puffin, the grey area marks feeding and wintering areas and the red dots illustrate the distribution of breeding areas (Icelandic Institute of Natural History (IINH) 2012).

The puffin is the most numerous seabird species breeding in Norway (Anker-Nilssen et al. 2015; Fauchald et al. 2015), approximately 900 000 pairs breed on the Barent Sea coast from Senja to Vardø and more than 550 000 pairs are found breeding along the Norwegian Sea coast from Stad to Andøya (Anker-Nilssen et al. 2015; Fauchald et al. 2015). In 2004, the global population of puffins was estimated to 6,6 million pairs (Mitchell et al. 2004), of which 1,7 million pairs were breeding in Norway (Barrett et al. 2006). Although it has a large population and a vast distribution range, the species has declined rapidly across its European range and it is therefore considered endangered by the IUCN (BirdLife International 2015). In Norway, the decline is most apparent in the Norwegian Sea region, whilst the population in the Barents Sea is stable or even slightly increasing (Fauchald et al. 2015). At Røst, around 433 000 pairs (SE \pm 10 %) were breeding in 2005, which constituted about 25% of the total Norwegian population (Anker-Nilssen & Aarvak 2006). However, the estimate for 2005

actually represents a 70% decline since 1979, when 1,5 million pairs of puffins were breeding at Røst (Anker-Nilssen & Røstad 1993; Anker-Nilssen & Øyan 1995). The decline in the puffin population has continued steadily at Røst. In 2015 only 289 000 pairs of puffins remained and around 1,5 million pairs was breeding in all of Norway (Miljødirektoratet 2016a). Despite the huge reduction in breeding numbers at Røst, the adult survival rate of puffins has still remained high (> 90% p.a.), even though this have varied considerably between years (81-97 %) (Harris et al. 2005; SEAPOP 2017a). Because the puffin population at Røst experienced almost complete reproductive failures each year after 2006, the age structure in the breeding population is currently strongly skewed in favour of old and experienced breeders (Gimenez et al. 2012; Grosbois et al. 2009).

Puffins that survive to maturity have an average life expectancy of 25 years and they are expected to breed for the first time between 4-8 years old (Harris & Wanless 2011). They usually arrive at the breeding areas in late March/early April, and the subsequent breeding season lasts from May to July (Harris et al. 2005). The puffin is a highly colonial species and pairs are mainly found nesting in underground burrows that are dug in grass-covered soil or in rock crevices close to the sea. Also, puffins are a territorial species and the same nesting site can be used for generations. The incubation period usually lasts for about 38-44 days (Myrberget 1962), and the following nestling period takes from another 38-44 days and may be extended to up to 80 days under very unfavorable conditions (Harris & Wanless 2011; Johnsen et al. 1994). The parents work together to incubate the egg and raise the chick, which is independent from the time it leaves the nest. As a diving pelagic seabird they forage mainly in open water and the food loads they feed to the chick consist mostly of fish, occasionally supplemented by a few invertebrates (e.g., krill and squid). The main food items at Røst include the first-year transparent larvae and metamorphosed young of Norwegian spring-spawning (NSS) herring (*Clupea harengus*) (Anker-Nilssen & Aarvak 2006). In general, the prey of puffins varies in space and time, but small fish such as capelin *Mallotus villosus*, sandeels *Ammodytes spp.* and a variety of gadoids *Gadidae* can be considered important. In winter, crustaceans *Crustacea* and mollusks *Mollusca* also constitute important contributions to the diet (Falk et al. 1992).

1.2 Study aim and predictions

The aim of this master thesis was to examine whether and how the body condition of breeding puffins is influenced by climatic conditions, both within the breeding season and between years. The breeding performance of puffins have been monitored annually since 1964 in the Røst archipelago (Anker-Nilssen 1992; Anker-Nilssen & Aarvak 2004; SEAPOP 2017b) and this study is based on a data material collected from 1964 to 2016. Climate variables in this context refers to indices on breeding success (%), oceanic temperature (SST) and the abundance of first-year Norwegian spring spawning herring. The variable breeding success is used as a proxy for all factors capable of influencing breeding performance, mainly referring to extrinsic environmental factors. However, intrinsic factors such as behavioral mechanisms can also have an effect on breeding results. Additionally, I will investigate if there are any differences between the sexes in their body condition responses to fluctuating climate variables. Previous analyses of sex differences in reproductive behavior have revealed that adult puffins seems to respond differently to poor environmental conditions (Anker-Nilssen & Aarvak 2004). For instance, it is to be expected that males invest less in parental effort and more in mating effort than females. Also, previous research has shown that males more easily leave the colony if the breeding conditions are poor (Creelman & Storey 1991). Thus, determination of gender can be useful to assess the role played by gender during variable climatic conditions. In order to test whether the relationship between environmental variables changes in different stages of the breeding season, I separated the data in two periods; (1) before the 15th of May and (2) after the mean hatching date within the same year. The first period in May refers to the pre-laying period, while the second period involves the chick rearing-period in late June/July. It is to be expected that both the extrinsic and intrinsic behavioral aspects, as well as the environmental conditions, vary a lot in these two periods (Durant et al. 2003).

Based on the linkage between SST in March and the level of food abundance reaching the foraging areas of breeding puffins (Croxall 1987; Durant et al. 2003; Durant et al. 2004a), I hypothesize that climate conditions in spring will have a significant effect on the body condition of adult puffins. Moreover, because puffins are K-selected species and therefore tend to invest in survival rather than reproducing when the breeding conditions are poor (Erikstad et al. 1997; Stearns 1992; Øyan & Anker-Nilssen 1996), I propose that breeding success is negatively correlated with the body condition of adult puffins. Based on the findings of inter-sexual differences in reproductive behavior of puffins (Creelman & Storey

1991), I assume that males acquire a higher body condition than females during breeding. Also, because the Norwegian spring spawning herring is such an important component of the puffin's diet during the breeding season (Durant et al. 2005), it is reasonable to assume that an increase in 0-group herring abundance would positively affect the body condition of adult puffins. At last, I suggest that adult puffins will experience reduced body condition in the later stages of the breeding season. This assumption is based on the evidence of the gradually loss of body mass during breeding as a response to physiological stress or an adaptation to reduce flight cost (Barrett et al. 1985).

Predictions:

- P1)** The body condition of adult puffins will improve as SST increases in March (within the boundaries of natural variations in SST).
- P2)** Breeding success and body condition of adult puffins will be negatively correlated during the breeding season.
- P3)** Male adult puffins will have a higher body condition than females during the breeding season.
- P4)** The body condition of adult puffins is likely to increase with increasing abundance of 0-group Norwegian spring spawning herring.
- P5)** The body condition of adult puffins will be lower in the later stages of the breeding season.

2. MATERIALS AND METHOD

2.1 Study area and period

The data on puffins were sampled on a field station operated by The Norwegian Institute for Nature Research (NINA), located on the island of Herynken (67°26' N, 11°52' E) in the Røst archipelago, at the outermost tip of the Lofoten Islands ((Durant et al. 2003). Figure one shows a map of the area. Herynken is part of Nykan Nature Reserve, which was established in 2002 (LOVDATA 2002). Being situated >100 km off the mainland coast, the area is very exposed to open sea. Therefore the climate is both oceanic and humid with a mean average summer temperature of 8.6 °C (calculated in the period from 1900 to 2010) (Miljødirektoratet 2016b; Norwegian Meteorological Institute 2016). In addition, the mean summer temperature is close-range to the SST in the area, which demonstrates the strength of the oceanic influence on climate (Bjerknes 1969; Folland et al. 1986; Rodwell et al. 1999). Furthermore, the island is valued an A class natural area because of its importance for breeding seabirds (Miljødirektoratet 2016b). In total, nearly 300 bird species have been registered in the Røst archipelago and the area is especially known for its big population of puffins (Anker-Nilssen 2015).



Figure 2: Location of study area Herynken in the Norwegian Sea (Kartverket 2016).

Seabird research in Røst started already in the late 1950's and has continued on an yearly basis through a variety of projects (Anker-Nilssen 2015). The collection of data material from Herynken used in this master thesis has been conducted during both the incubation and chick-rearing period of the puffins since 1964. However, the duration of the field work has varied considerably between years and the fieldwork was less intensive in the 1960s and 1970s (see more details in 2.3 Data acquisition). My fieldwork took place at NINA's field station at Herynken and lasted for one month in June 2016.

2.2 Morphometric measurements

In order to measure morphometric characteristics of puffins, they need to be captured. Because puffins are sensitive to disturbance and may easily abandon the nest if captured inside the burrow, we used mist nets erected at the surface of the colony. Within a few minutes of capture, unmarked birds were ringed with a stainless-steel leg band, some also with one or more acrylic/darvic colour rings to identify them in the field. We measured body mass (hereafter *mass*) to the nearest 1.0 g using a ® Pesola spring balance, wing length (hereafter *wing*) to the nearest 1.0 mm using a stopped ruler of stainless steel, and culmen length, head+bill length and bill depth at gonys (hereafter *culmen*, *head+bill* and *gonys*, respectively) to the nearest 0.1 mm using a Vernier caliper (Anker-Nilssen & Lorentsen 2003). *Head+bill* (=head plus bill = total head length) equals the distance from the tip of the bill to the back of the head. *Gonys* (=bill depth at the gonys) was measured as the vertical depth of the bill at the gonys. *Culmen* (=bill length) is measured from the edge of the horny sheath of the upper mandible to the tip of the beak. Figure three illustrates the Atlantic puffin bill and wing measurements used in Norway. The wing length was measured by holding the wing close into the body and then inserting the ruler between wing and body. The wing was straightened by pushing the edge of the wing so that it lies along the edge of the ruler (Figure 3) (Anker-Nilssen & Lorentsen 2003). Adults and sub-adults were separated by counting bill grooves. If the number of bill grooves was less than two, the result indicated an immature/sub-adult individual (Harris & Wanless 2011). However, due to the subsequent and complete breeding failure at Røst in the period of 2006-2015 (Anker-Nilssen et al. 2017), no such birds were expected to be found during the last years of the study.

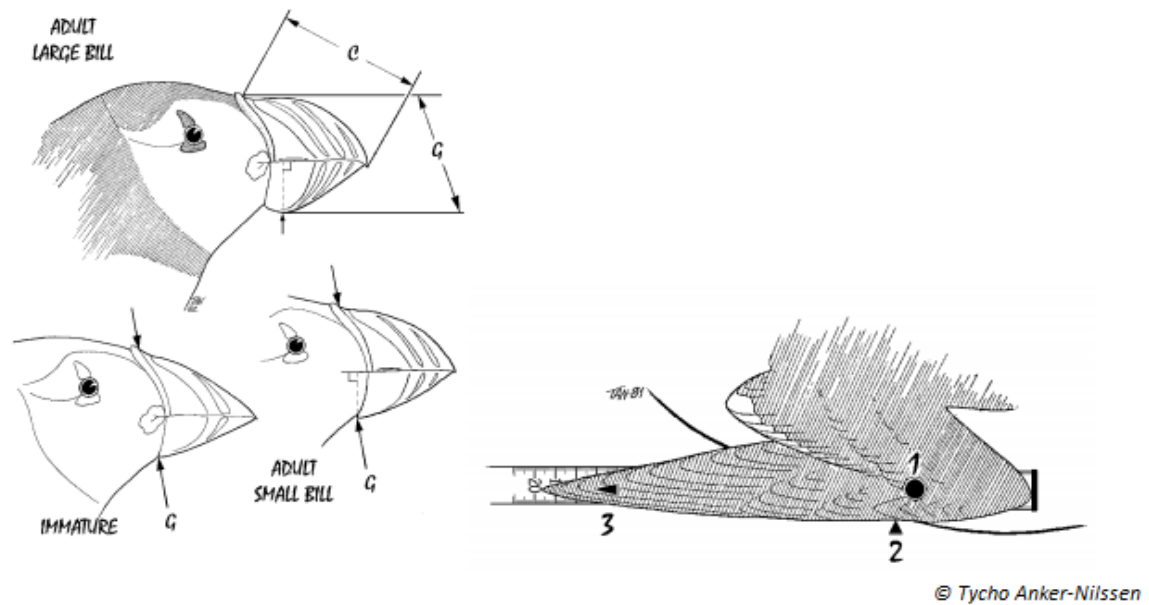


Figure 3: Atlantic puffin bill and wing measurements in Norway. The picture to the left illustrates culmen and gonys bill measurements (C =culmen, G =Gonys) in immature and adult (small and large bill) puffins. The illustration to the right depicts the procedure of wing measurement (=winglength – maximum flattened chord); 1. Press down, 2. Push in, 3. Stretch out (Anker-Nilssen & Lorentsen 2003).

2.3 Data acquisition

2.3.1. Sea surface temperature (SST)

The mean *Sea Surface Temperature (SST)* at Røst has increased steadily during the period from 1970 to 2016 (Figure 4). As SST was found to be a good predictor of breeding success, it was used as a proxy for environmental conditions experienced by the potential prey of puffins in the colony area during the breeding season (Durant et al. 2003). The Extended Reconstructed Sea Surface Temperature (ERSST) used in this thesis includes in situ global monthly SST derived from the International Comprehensive Ocean-Atmosphere Dataset (ICOADS) (Appendix 1, nb.1). The SST was collected from satellite data at a resolution of 2° longitude \times 2° latitude around the colony at Heryken (Huang et al. 2015; Huang et al. 2016; Liu et al. 2015). The satellite data are calibrated based on in situ ship and buoy measurements (Huang et al. 2015). From these data, I chose to use the monthly mean SST for March month, because this period coincides with the climate sensitive drifting period for young herring (Durant et al. 2003).

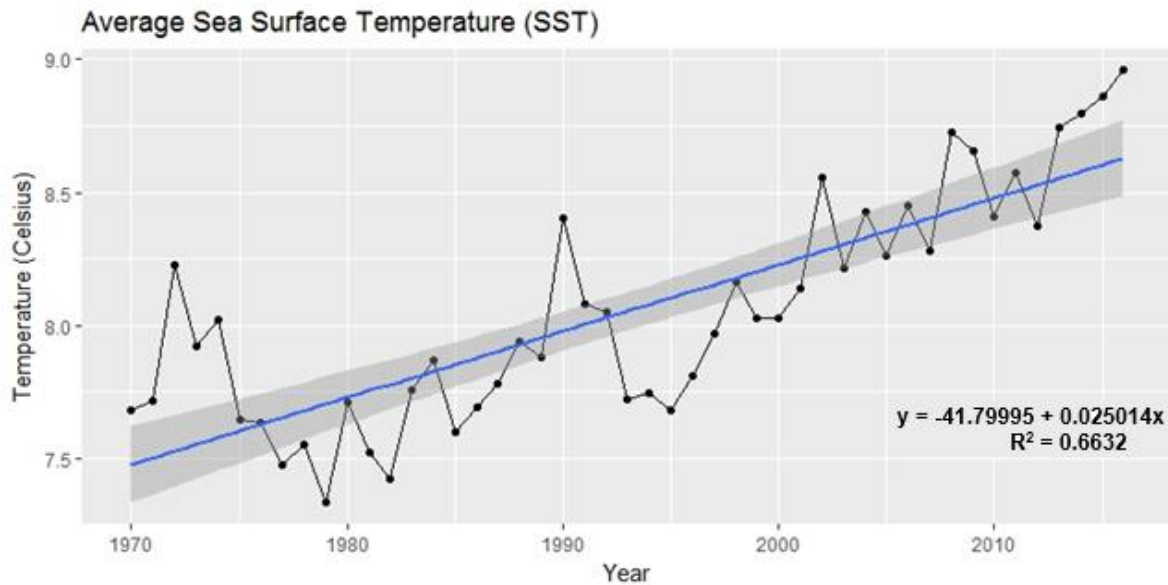


Figure 4: Annual mean Sea Surface Temperature (SST) at Herynken from 1970-2016, the figure is created in R Gui v.3.3.2 based on the ERSST dataset (Appendix 1, nb. 1).

2.3.2 Fledging success

The estimation of breeding success was based on regular inspections of nests (usually at 1-6 days' intervals) of a selection of control nests (usually > 100, range 10-304) from late in the incubation period in first half of June until the egg or chick was lost or the chick fledged (Appendix 1, nb. 2). The inspections were most frequent around hatching and periods of fledging or high chick mortality. In 1965-1977, breeding success was estimated less accurately, and primarily based on qualitative information and physical examination of chicks on their way to the sea (Lid 1981), see also Anker-Nilssen (1992). Because of the substantial inter-annual variation in how many pairs that skip breeding or choose to desert their egg, accurate data on breeding success of puffins is hard to obtain. Moreover, puffins are particularly sensitive to disturbance at the nest site, especially early in the breeding cycle (Rodway et al. 1996). The disturbance effect of visiting burrows also varies according to environmental conditions (Anker-Nilssen & Aarvak 2002). Consequently, the total breeding success (chicks fledged per breeding pair) is difficult to estimate, and fledging success, (i.e., the mean number of chicks fledged per egg hatched) was therefore used as a proxy for breeding success (see Durant et al. (2003) for more details on methods). Breeding success is hereafter referred to as fledging success.

2.3.3 Hatching date

Individual hatching dates were estimated by visual nest inspections at variable intervals during hatching or egg laying (Appendix 1, nb. 3). In case of observing an egg during a nest inspection and a chick in the same nest on the following visit, hatching date was determined as the midpoint in time of two visits. In some cases, more information from the nest inspections was also considered, such as observing eggshells in the burrow entrance, measurements of eggs density, the existence of hatching cracks (“stars”), and size measurements of the chick (see Durant et al. (2004a) for more details on method). Hatching dates with a poor precision level (± 6 d) were excluded from the analyses.

2.3.4 Herring data

Abundance estimates (in billions, 10^9) of 0-group NSS herring calculated by the International Council for the Exploration of the Sea (ICES) and Institute of Marine Research (IMR) were used as data input in the analyses (Appendix 1, nb. 4). The cohort data were derived from the reports of the ICES Working Group on Widely Distributed Stocks (WGWIDE) (ICES 2012; ICES 2016) and the Working Group on Northern Pelagic and Blue Whiting Fisheries (WGNPBW) from 2007 (ICES 2007). The estimates were based on a Virtual Population Analysis (VPA) (see the (ICES 2007; 2012; 2016) reports for more details on methods). As an estimate for 0-group abundance was not given for all years, this was back-calculated for all years from 1950 to 2014, by using numbers from the three separate ICES reports (2007, 2012, 2016). The abundance estimate of 0-group herring for the whole-time series was estimated based on the average reduction in cohort strength from 0-group to 2-group herring. Because the cohort strength of 0-group herring cannot be calculated before the young herring recruit to the spawning stock as three years old, the last three years of herring data were not available for analyses.

2.4 Analysis and Statistical test

The raw data (Appendix 1, nb. 5) used in this master thesis was recorded in Microsoft Office Excel 2016 version 1701 and then exported to the R Gui statistical computing software version 3.3.2 (R Core team 2016) for statistical analyses. The raw data consists of all datasets described in Appendix 1 and is therefore reduced according to the combined size of these datasets and depending on the objective of the analysis performed. A level of significance of 0.05 was used when assessing the validity of analytic results. All figures and tables were produced in R Gui and Excel.

2.4.1 Discriminant analysis

Because the external appearance of male and female puffins are identical, except that the male is slightly larger in size, it is impossible to determine the gender without measuring the morphometric traits or do a DNA analysis (Creelman & Storey 1991; Friars & Diamond 2011). By using morphometric measurements of birds sexed by gonadal inspection or DNA, it is possible to calculate a discriminant function that enables gender determination of other birds from similar measurements with reasonable accuracy. This was done by running a linear discriminant analysis (LDA) from the “Support Functions and Datasets for Venables and Ripley's MASS” package in the statistical computing software R Gui (Ripley 2002). Linear discriminant analysis are used in statistics to find linear combination of features which characterizes or separates two or more groups of objects or events (Bordens & Abbott 2002). The purpose of the linear discriminant analysis in this case was to find such combinations of size variables that gives the best possible separation between the groups “female” and “male”. This analysis produces i.a. linear discriminant coefficients which are regression coefficients used to construct discriminant functions based on combinations of explanatory variables. The six size variables *head+bill*, *wing*, *gonys*, *culmen*, *bill-grooves* and *weight* were separately tested for discriminant power by running the LDA. The explanatory variables *head+bill* and *wing* were identified with the highest discriminant power (LD coefficients of 0.052 and 0.057 respectively) and therefore used in further predictions. A discriminant function consisting of these explanatory variables can be used to classify new objects described by the same variables used in the LDA analysis. Hence, the LDA analysis was first run on 551 separate measurements of puffins (293 individuals) with previously confirmed gender through DNA testing (Appendix 1, nb.6). The resulting discriminant coefficients were then used to predict the grouping of “females” and “males” for the whole dataset (Appendix 1, nb.5). Thus, the result from the group of puffins with DNA samples will also facilitate a control of the discriminant function used on the remaining individuals based on morphometric measurements (Anker-Nilssen & Aarvak 2004). The MASS package did not include random variables in the LDA analysis, which made it difficult to consider repeated measurements for some individuals. Alternatively, I could have used the average value per individual in order to account for random variables.

2.4.2 Fitness index

The body mass of breeding puffins usually decreases during the chick-rearing period and their body condition might be affected by the external environment (Barrett et al. 1985; Erikstad et al. 1997). In order to test whether changes in body condition during breeding were influenced by environmental conditions, the residuals from a body size versus body mass regression were used as an index of body condition. Body condition is defined as a measurement of body mass relative to structural size (Johnsen et al. 1994). Hence, when considering variation in individual body mass, differences in structural size needs to be accounted for. In order to identify which of the following parameter's *wing*, *head+bill*, *culmen* and *gonys* best explained the variation in body weight, I executed a linear regression analysis in the R Gui software for linear mixed-effect models (lme) from the package "Linear and Nonlinear Mixed Effects Models (nlme)" (Jose Pinheiro et al. 2017). A log-log plot was chosen for all separate regressions in order to account for skewness in the dataset. To assess for gender biased differences, I based my analyses on a dataset which only included measurements of puffin's gender based by DNA samples (Appendix 1, nb.6) and I executed the regressions separately for a subset of each gender ($n = 832$, individuals = 293). In addition, the regression analyses were run separately for all the independent variables *wing*, *head+bill*, *gonys* and *culmen*, with response variable *weight*. We compared the coefficient of determination (r^2) for all regressions by running the command "r.squaredGLMM" from the package "Multi-Model Inference (MuMIn)". The morphometric variable *head+bill* was found to have the highest coefficient of determination ($r^2 = 0.6$ for females and $r^2 = 0.52$ for males) and was therefore chosen as the measure of individual variation on structural body size. The variable *fitness index* is used as a proxy for body condition in this thesis. Ultimately, I used the coefficients provided by the following *head+bill* regressions, in order to predict the *fitness index* for all remaining individuals in the dataset:

$$\text{female: } y = -1.77 + b * 1.52 \quad (n = 449 \text{ (167 individuals)})$$

$$\text{male: } y = -1.29 + b * 1.35 \quad (n = 382 \text{ (126 individuals)})$$

2.4.3 Linear mixed effects modelling

Linear mixed effects models (LMM) are extensions of linear regression that are considered useful when dealing with non-normally distributed data that includes random and fixed effects to realistic biological systems (Bolker et al. 2009; Grueber et al. 2011). In order to test for relationships between environmental variables and the body condition of adult puffins I used linear mixed effects models (lme) in the R Gui software from the package “nlme” (Jose Pinheiro et al. 2017), to assess for both fixed and random effects. The “dredge” function in the package “MuMIn” was performed in order to conduct an automated model selection with subset $2 > \Delta AIC$ of the supplied full model (Barton 2016). Every model tested was given an individual ID number by the dredge function in order to separate them. *Fledging success*, *SST* and *0-group herring abundance* were explanatory variables in the model, whilst *days from hatching* was used as a controlling covariable (Table 1). Covariable *days from hatching* involved the number of days before or after the mean hatching date of the puffin’s eggs calculated every year. This made it possible to adjust the results according to the period of time in the breeding season. Additionally, *gender* was used as an interactive covariate in order to account for sex-specific responses of an explanatory variable, (e.g., if an interaction was found to be significant this would mean that this explanatory variable had a different effect on the response variable depending on the sex of the puffin). Variable *ring number*, which is a unique number for every individual in the dataset, was used as a random effect in order to account for repeated measurements on the same individual (for more details on the estimation of explanatory variables, see section 2.3 Data acquisition and 2.4.1 Discriminant analysis). The response variable *fitness index* was log transformed before running the LMM in order to account for skewness in the dataset (for more details on estimation of response variable *fitness index* see 2.4.2 Fitness index).

Table 1: Summary of input variables in the full linear mixed effect model. Gender is expressed in bivariate numbers (1= male, 2= female). Interactions between variable “gender” and all explanatory variables were tested in the analyses in order to account for sex-specific responses ($n= 4621$, year= 1979-2015 (data from 1985-1987 are missing)).

Independent variables	Mean	Median	Range
Fledging success (%)	49.04	51.09	0.00 to 95.87
Herring abundance (individuals $\times 10^9$)	159.4	106.4	1.2 to 382.9
Sea Surface Temperature (SST)	5.6	5.6	5.0 to 6.4
Days from hatching	9.2	13	-74 to 53
Gender (1= male, 2= female)			
Response			
Fitness index (log)	-0.0057	-0.0056	-0.11 to 0.17

2.4.3.1. Accounting for gender and seasonal effects

Because the reproductive behaviour of male and female puffins are known to differ (Creelman & Storey 1991), *gender* was included in the full model as an interactive covariate and tested for all possible combinations of interactions with the explanatory variables. Additionally, I made two new subsets of the dataset: **1.** before 15th of May and **2.** after mean hatching date within years. The subsets were applied in order to investigate if the relationship between the environmental variables behaves differently in the pre-laying period of May compared to the chick-rearing period in late June/July. Because the explanatory variable *fledging success* and *0-group herring abundance* were strongly correlated ($r = -0.63$) I chose not to run them simultaneously in the full model.

2.4.3.2 Model selection

The fixed effects in a mixed model can be used to predict the value for the response variable if all covariates are measured or estimated (Bueno-López & Bevilacqua 2013). To compare different combinations of fixed effects from the global model I had to reduce the data set by removing observations with missing values. Akaike's Information Criterion (AIC) were used for model selection. As a rule of thumb, models within 2 AIC units ($\Delta AIC \leq 2$) of the top supported model can be considered substantially evident, whereas values between 3 and 7 suggest that the model has considerably less support and $\Delta AIC > 10$ demonstrates that the model is very unlikely (Burnham & Anderson 2004). Hence, all models within 2 AIC units ($\Delta AIC \leq 2$) of the top supported model were included in the subset. Akaike weights (w_i) also reflects a measure of the strength of evidence for each model, by presenting the ratio of delta (ΔAIC_i) values for each model in relation to the whole set of candidate models. The scale of akaike weights (w_i) range from 0 to 1 (i.e. the sum of w_i equals 1) and they indicate the probability that the model is most fitted among the whole set of candidate models. For more details, see Wagenmakers and Farrell (2004).

2.4.3.3. Parsimony

In order to identify a model structure that was as parsimonious as possible while still describing the data satisfactorily, we used the restricted maximum likelihood (REML) approach in the R Gui software. The REML approach uses a likelihood function to calculate which parameter values that make the data most likely and removes unnecessary parameters from the model (see Corbeil and Searle (1976) for more information on method). Moreover, the most parsimonious model can be identified from the AIC criterion table as being the

model closest in range to the top supported model as well as having the fewest parameters (Burnham & Anderson 2004)

2.4.3.4 Model averaging

Because the top supported models selected based on the AIC criterion $\Delta i < 2$ are reasonably close in their data fit, it may be hard to distinguish a single best model from the model set. Under these circumstances, it may be appropriate to employ a model averaging approach. The model averaging procedure accounts for model selection uncertainty by calculating a weighted average of parameter estimates. In this way, parameter estimates from models that give little information about the variance in the response variable are given little significance (Grueber et al. 2011). Moreover, model averaging allows to compare how well the model predictions coincide with the observed values per year. The model averaging approach was executed using the function “model.avg” implemented in the MuMIn package in the R Gui software.

3. RESULTS

3.1. Model selection and evaluation

3.1.1. Before 15th of May

The mixed effects models that were found to best fit the response variable *fitness index* for the period before 15th of May are displayed below (Tables 2 and 3). Because the sample size is finite (n=4621) (Grueber et al. 2011), I used the Akaike's second-order information criterion (AICc) and the Akaike weights (w_i) for model selection. All models within $\Delta AIC \leq 2$ of the top supported model were included in the model selection tables. Model selection analysis was run separately for the two variables *fledging success* and *0-group herring abundance* in both periods, due to a very high correlation coefficient ($r = -0.63$). Eventually, I compared the AIC values of the two model variations in order to find which of the two variables *fledging success* and *0-group herring abundance* had the highest explanatory power. All parameters presented in the model selection tables below are significant at the $\alpha=0.05$.

3.1.2.1. Fitness index – version I (model w/fledging success)

According to the AIC model selection criterion, model ID 10 was found to be the best fitted model for the response variable *fitness index* in the period before 15th of May (Table 2). Model ID 10 had the fewest parameters, only including *fledging success* and *SST*, whilst the lowest ranked model (model ID 12) included an additional *gender effect*, however not significant ($p= 0.37$). *Fledging success* and *SST* clearly exhibited a positive effect on fitness index of adult puffins in the period before 15th of May, but the impact of *SST* showed a more prominent increase.

Table 2: Parameter estimates and Akaike's second-order information criterion (AICc) of the two best fitted models (LMM plus fixed effects) from the period before 15th of May. The variable **0-group herring abundance** was excluded from this model selection analysis. All models within $\Delta AIC \leq 2$ of the top supported model are included in this model selection table. A total of 478 observations were retained for the analysis in the period before 15th of May.

Model ID	Intercept	Fledging success (FS (%))	Gender (G)	Sea surface temperature (SST)	Df	LogLIK	AICc	ΔAIC	Akaike weight (w)
10	-217.5	0.08		33.32	5	-2334.5	4679.2	0.00	0.65
12	-216.6	0.08	+	33.39	6	-2334.1	4680.4	1.24	0.35

3.1.2.2. Fitness index – version II (model w/0-group herring abundance)

Among the models which included variable *0-group herring abundance* in the model selection analysis before 15th of May, three models were suggested to best fit the data (Table 3). Model ID 9 was considered most parsimonious according to the AIC values and because it had fewer parameters, only including variable *SST*. Model ID 10 included a *gender effect* in addition to variable *SST*, however the *gender effect* was not significant (Appendix 2). The lowest ranked model (model ID 13) included both variables *0-group herring abundance* and *SST*, whereas *0-group herring abundance* was negatively correlated with response variable *fitness index*, but there was no significant effect (Appendix 2). The *fitness index* of adult puffins was expected to increase with variable *SST* according to all models presented in table three, and the effect was distinctly and significantly positive for all models.

Table 3: Parameter estimates and Akaike’s second-order information criterion (AICc) of the three best fitted models (LMM plus fixed effects) from the period before 15th of May. Variable **fledging success** was excluded from this model selection analysis. All models with $\Delta AIC \leq 2$ of the top supported model are included in this model selection table. A total of 478 observations were retained for the analysis in the period before 15th of May.

Model ID	Intercept	Herring abundance (individuals in 109)	Gender (G)	Sea surface temperature (SST)	Df	LogLIK	AICc	ΔAIC	Akaike weight (w)
9	-183.8			27.94	4	-2336.5	4681.2	0.00	0.50
10	-183.6		+	28.13	5	-2336.1	4682.2	1.06	0.29
13	-182.2	-0.005		27.76	5	-2336.5	4683.1	1.91	0.19

3.1.2. After mean hatching date

The mixed effects models that were found to best fit the response variable *fitness index* for the period after mean hatching date are displayed below (Tables 4 and 5).

3.1.2.1. Fitness index – version I (model w/fledging success)

Among the models which included *fledging success* in the period after mean hatching date, the most parsimonious model consisted of variables *fledging success*, *days from hatching* and *SST* (model ID 14). In addition, model ID 16 included a *gender effect*, whereas model ID 48 incorporated all the above-mentioned variables, as well as an interaction between *gender effect* and *days from hatching*. Variable *fledging success* showed a negative effect on the response variable *fitness index* for all models presented. Both variables *days from hatching* and *SST* were expected to have a positive effect on the *fitness index* of adult puffins according to all the top supported models. *SST* had the strongest effect on *fitness index* among all

variables in every model. Moreover, all variables presented had a significant effect, except from the interaction and the gender effects (Tables 7 and 8).

Table 4: Parameter estimates and Akaike's second-order information criterion (AICc) of the three best fitted models (LMM plus fixed effects) from the period after mean hatching date. Variable **0-group herring abundance** was excluded from this model selection analysis. All models with $\Delta AIC \leq 2$ of the top supported model are included in this model selection table. A total of 3455 observations were retained for the analysis after hatching date.

Model ID	Intercept	FS*	Gender (G)	DH*	SST*	G:DH*	df	LogLIK	AICc	ΔAIC	Akaike Weight (w)
14	-79.24	-0.05		0.46	12.36		6	-15916.15	31844.3	0.00	0.401
16	-78.62	-0.05	+	0.46	12.38		7	-15915.36	31844.8	0.43	0.323
48	-79.27	-0.05	+	0.50	12.36	+	8	-15914.52	31845.1	0.75	0.276

Abbreviations: FS* = Fledging success (%), DH* = Days from hatching, SST = Sea Surface Temperature

Interactions: G:DH* = Gender:Days from hatching

3.1.2.2. Fitness index – version II (model w/0-group herring abundance)

In the model selection analysis which included variable *0-group herring abundance* in the period after hatching, five models were considered to best fit the data (Table 5). The top supported model among these five models, included variables *days from hatching*, *0-group herring abundance* and *SST*. Model ID 16 which is closest in range from the top supported model according to the AIC values, included an additional *gender effect*. The remaining models had a *gender effect* in addition to interactions between *gender effect* and *days from hatching* or *gender effect* and *0-group herring abundance*. None of the gender effects or interactions included in the models were significant (Appendix 3). The two variables *days from hatching* and *SST* had a positive effect on *fitness index* for adult puffins in later stages of the breeding season, also these models reveal a strong effect from variable *SST*. Moreover, there was a weak, but significant, negative correlation between the variable *0-group herring abundance* and the response variable *fitness index*.

Table 5: Parameter estimates and Akaike's second-order information criterion (AICc) of the six best fitted models (LMM plus fixed effects) from the period after mean hatching date. Variable **0-group herring abundance** was excluded from this model selection analysis. All models with $\Delta AIC \leq 2$ of the top supported model are included in this model selection table. A total of 3455 observations were retained for the analysis after hatching date.

Model ID	Intercept	HA*	Gender (G)	DH*	SST*	G:DH	G:HA	df	LogLIK	AICc	ΔAIC	Akaike Weight (w)
15	-78.93	-0.01		0.45	12.23			6	-15921.09	31854.2	0.00	0.298
16	-78.34	-0.01	+	0.45	12.25			7	-15920.29	31854.6	0.40	0.243
32	-78.99	-0.01	+	0.50	12.23	+		8	-15919.45	31854.9	0.73	0.206
48	-79.02	-0.01	+	0.45	12.27		+	8	-15919.91	31855.9	1.64	0.131
64	-78.67	-0.01	+	0.50	12.25	+	+	9	-15918.97	31856.0	1.78	0.122

Abbreviations: HA* = 0-group herring abundance, DH* = Days from hatching, SST = Sea Surface Temperature

Interactions: G:DH* = Gender:Days from hatching, G:HA* = Gender:0-group herring abundance

3.2. Presenting the most parsimonious models

3.2.1. Before 15th of May

By comparing the AICc of the two best fitted models which included either variable *fledging success* or *0-group herring abundance*, I chose to use only one of these for further predictions. Model ID 10 (Table 2), which included variable *fledging success*, had a higher AICc value than model ID 13 (Table 3), which included variable *0-group herring abundance* (AIC (Δ) = 3.9). Thus, variable *fledging success* hold a greater explanatory power for response variable *fitness index* and model ID 10 (Table 2) was found to be the most parsimonious and highest ranked model in the period before 15th of May according to the AICc values. Parameter estimates of the highest ranked models (within Δ AIC \leq 2 of the top supported model), which included variable *0-group herring abundance* in the pre-laying period is given in Appendix 2. The results from the top supported model (Model ID 10, Table 2) before the 15th of May are presented in figure five, and the parameter estimates of the lower ranked model for the same period (Model ID 12, Table 2) are displayed in table six.

3.2.1.1 Model ID 10

According to the top supported model (Model ID 10, Table 2), the body condition of adult puffins in the pre-laying period was low (negative values). However, *SST* had a positive effect on the *fitness index* of adult puffins in this period and *fledging success* was also positively correlated with the response variable. While *SST* showed a very strong significant effect on the body condition of adult puffins ($\beta=33.3$ and $p<0.001$), the effect of *fledging success* on *fitness index* was weak and hardly significant ($\beta=0.08$ and $p=0.05$).

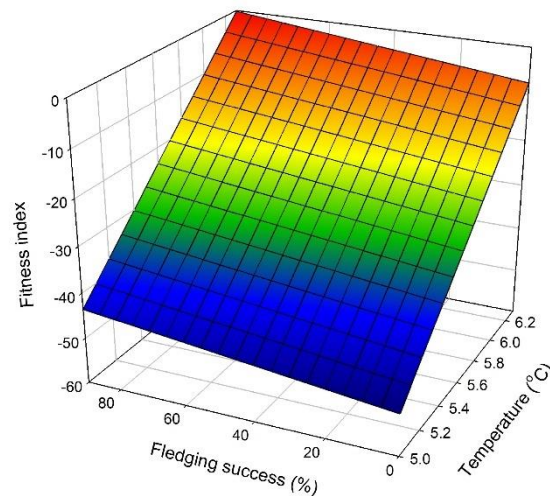


Figure 5: The top supported model in the period before 15th of May which displays the effects from fledging success (%) and SST ($^{\circ}$ C) on fitness index of adult puffins. The red and yellow area refers to the higher values of fitness index, while the blue area corresponds to lower fitness index values. According to the model, the fitness of adult puffins in the pre-laying period was low (negative values) and both SST and fledging success were positively correlated with fitness index. The effect of SST on fitness was significant and very distinct ($\beta=33.3$ and $p<0.001$), whereas the effect of fledging success on fitness was weak and not significant ($\beta=0.08$ and $p=0.05$). (Random effect ID= 380, $n= 478$, $R^2=0.40$) The figure is created in Microsoft Office Excel 2016 v. 1701.

3.2.1.2. Model ID 12

The lower ranked model (Model ID 12, Table 2) in the pre-laying period also showed a positive correlation between the response variable *fitness index* and *fledging success*, as well as a positive effect of *SST* on *fitness index* (Table 6). Increasing *SST* levels showed the same significant impact on *fitness index* as the top supported model, whereas *fledging success* still had a weak, non-significant correlation with the *fitness index* of adult puffins. In addition, the lower ranked model included a negative *gender effect*, which infers that female adult puffins had a lower body condition than males in the period before 15th of May, but the effect was not significant.

Table 6: Parameter estimates of the lowest ranked model ($\Delta AIC=1.24$) in the period before 15th of May (LME fitted by the restricted maximum likelihood (REML) (Random effect ID=380, n=478, R2=0.41)). Intercept presents male as the reference level.

	Estimate	SE	Df	t value	p value
Fixed effects/Coefficients:					
Intercept	-216.5	42.12	379	-5.13	0.00
Fledging success (FS) (%)	0.08	0.04	95	1.97	0.05
Sea Surface Temperature (SST)	33.37	7.15	95	4.67	0.00
Gender (female)	-2.93	3.23	95	-0.91	0.37

3.2.2. After mean hatching date

Also for the period after mean hatching date, the highest supported model was selected by comparing AICc values of the two best fitted models which included either variable *fledging success* or *0-group herring abundance*. Model ID 14 (Table 4) which included variable *fledging success* had a higher AICc value than model ID 15 (Table 5) which included variable *0-group herring abundance* (AIC (Δ) = 9.9). This result indicated that variable *fledging success* hold a greater explanatory power for response variable *fitness index*, also for the period after mean hatching date. Model ID 14 (Table 4) was therefore chosen as the top supported and most parsimonious model for my predictions in later stages of the breeding season. Parameter estimates of the highest ranked models (within $\Delta AIC \leq 2$ of the top supported model), which included variable *0-group herring abundance* in the period after mean hatching date is given in Appendix 3. The results from the top supported model are presented in figure six, and parameter estimates of the remaining models within 2 AICc steps of the top supported model are displayed in tables seven and eight.

3.2.2.1. Model ID 14

The top supported and most parsimonious model in the period after mean hatching date (Model ID 14, Table 4) included variables *fledging success*, *SST* and *days from hatching*. The effects from *SST* and *days from hatching* was significantly positive on the fitness index of adult puffins ($\beta=12.35$, $p<0.001$ and $\beta=0.5$ and $p<0.001$ respectively). *Fledging success* was negatively and significantly correlated with fitness index, even though the effect was weak ($\beta=-0.05$ and $p<0.001$). As for the previous results, *SST* had a more prominent effect on *fitness index* than the other variables included in the model. Moreover, the body condition of adult puffins was gradually increasing throughout the breeding season, as illustrated by figure six and the positive relationship between covariable *days from hatching* and response variable *fitness index*.

3.2.2.2. Model ID 16

The lower ranked model in the period after mean hatching date (Model ID 16, Table 4) included the same variables as model ID 14, but with an additional *gender effect* (Table 7). All results were significant expect from the *gender effect*. *SST* still showed a positive impact on the body condition of adult puffins and variable *days from hatching* was also positively correlated with *fitness index*. *Fledging success* was negatively associated with *fitness index* of adult puffins in this period. The strength of the effects was also similar to the results given in the top supported model. The *gender effect* was negative for females compared to males, which implies that the fitness index of females where somewhat lower than for males in the period after mean hatching date, however, the effect was far from significant.

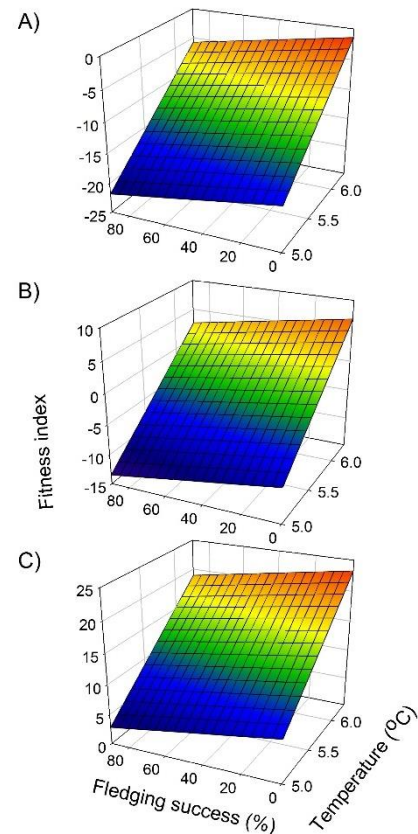


Figure 6: The top supported model in the period after mean hatching date of puffin's eggs, which displays the effects from fledging success (%), SST ($^{\circ}\text{C}$) and days from hatching on fitness index of adult puffins. The red and yellow area represents higher fitness values, whereas the blue area corresponds to low fitness values of adult puffins. Fledging success was significantly and negatively correlated with fitness index ($\beta=-0.05$, $p<0.001$), however, the effect was weak. Both variables SST and days from hatching showed a positive and significant effect on fitness index ($\beta=12.35$, $p<0.001$ and $\beta=0.5$, $p<0.001$ respectively). The variable days from hatching are presented in three different graphs: A) 0 days from mean hatching date (min. range), B) 18 days from mean hatching date (average time period since mean hatching date), C) 53 days from mean hatching date (max. range). Random effect ID=1872, $n=3455$, $R^2=0.57$). The figure is created in Microsoft Office Excel 2016 v. 1701.

Table 7: Parameter estimates of the lower ranked model ID 16 ($\Delta AIC=0.43$) in the period after mean hatching date (LME fitted by the restricted maximum likelihood (REML) (Random effect ID=1872, $n=3455$, $R^2=0.57$)). Intercept presents male as the reference level.

	Estimate	SE	Df	t value	p value
Fixed effects/Coefficients:					
Intercept	-78.62	8.56	1871	-9.18	0.00
Fledging success (%)	-0.04	0.01	1579	-4.48	0.00
Days from hatching	0.47	0.03	1579	14.42	0.00
Sea Surface Temperature (SST)	12.37	1.55	1579	7.99	0.00
Gender (female)	-1.40	1.12	1579	-1.26	0.21

3.2.2.3 Model ID 48

As for the previous presented models in the period after mean hatching date, the same effects from variables *fledging success*, *days from hatching* and *SST* were apparent in the lowest ranked model (Model ID 48, Table 4). The strength of the effects and significance level was also similar to the results presented in the two better supported models in the same period (Table 8). Moreover, the *gender effect* was included in the lowest ranked model, however, according to this model, female puffins had a higher *fitness index* than males in the period after mean hatching date. This result contradicts the *gender effect* presented in the previous model ID 16 and can only be interpreted as a trend at best, due to a small effect size and low significance level. In addition, an interaction between a negative *gender effect* for females and variable *days from hatching* was included in the lowest ranked model. This interaction implies that the fitness index of female puffins was gradually reduced according to the number of days from mean hatching date. Consequently, the interaction and gender effect presented in the same model is contradictory and both results should not be considered as reliable effects, bearing in mind the low significance levels and small effect sizes.

Table 8: Parameter estimates of the lowest ranked model ID 48 ($\Delta AIC=0.75$) in the period after mean hatching date (LME fitted by the restricted maximum likelihood (REML) (Random effect ID=1872, $n=3455$, $R^2=0.57$)). Intercept presents male as the reference level.

	Estimate	SE	Df	t value	p value
Fixed effects/Coefficients:					
Intercept	-79.27	8.58	1871	-9.24	0.00
Fledging success (%)	-0.05	0.01	1578	-4.49	0.00
Days from hatching	0.5	0.05	1578	0.08	0.00
Sea Surface Temperature (SST)	12.35	1.55	1578	7.98	0.00
Gender (female)	0.14	1.63	1578	0.08	0.93
Interactions:					
Gender (female): Days from hatching	-0.08	0.06	1578	-1.3	0.2

3.2.3. Model precision

In order to visualize the dispersion of my predictions on adult puffins *fitness index*, I used estimates from model averaging and compared them to the distribution of the raw data. The pattern between the model predictions and variables in the raw data illustrated in figure seven indicated that the distribution of predicted *fitness index* for adult puffins was similar to observations in the raw data. Because my predictions consists of much fewer environmental variables than the raw data, the pattern of distribution within the datasets are similar, but the degree of dispersal is evidently much larger in reality as presented by the raw data.

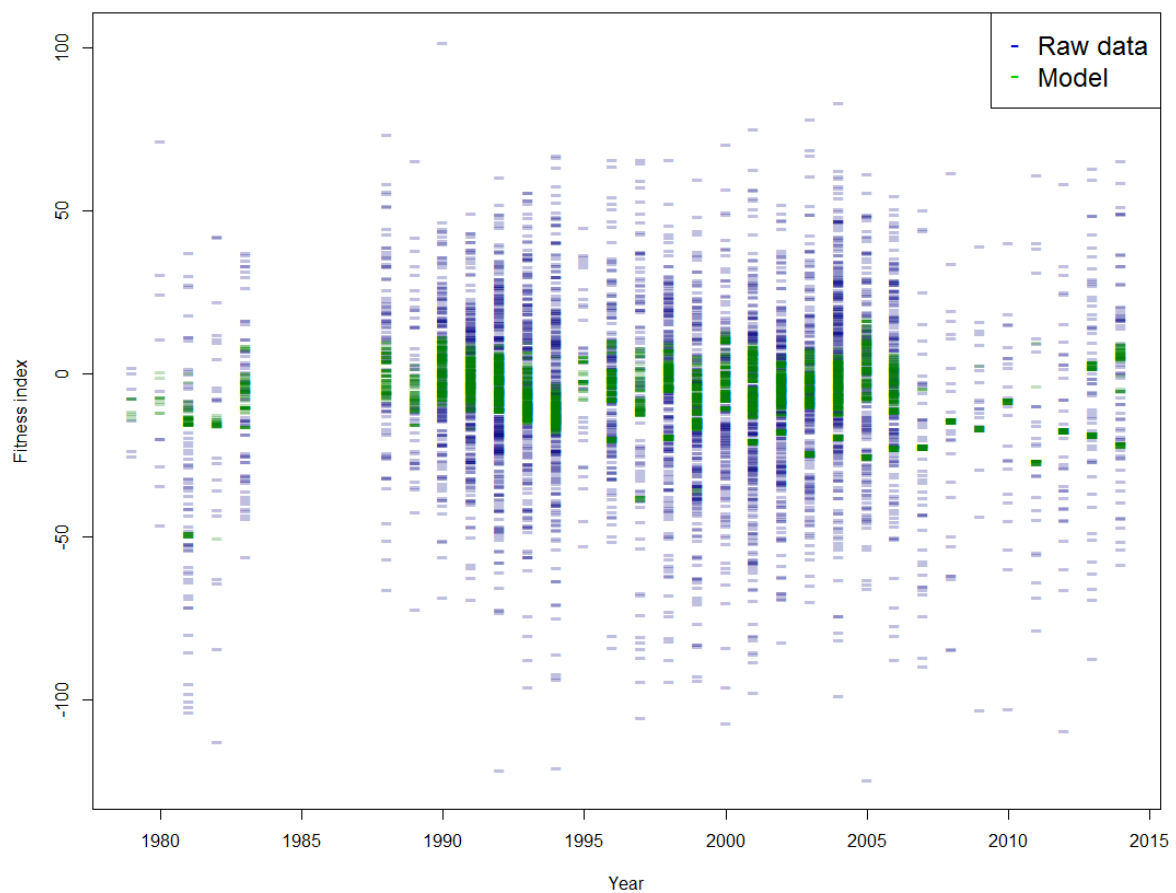


Figure 7: Raw data on the annual average fitness index of adult puffins (blue dots) plotted against model averaging predictions (green dots). The scatterplot illustrates large variations in the distribution of fitness index in the raw data per year for the time period 1980-2015. The dispersal of predicted fitness index of adult puffins per year are similar to the distribution of fitness index observed, illustrated by the raw data.

3.2.4. Model averaging

The model fit of my predictions presented in the most parsimonious model was tested by comparing an estimated average *fitness index* of adult puffins per year with actual recordings in the raw data (Figure 8). Hence, figure eight illustrates how well the model predictions, presented as model average estimates, fits the data. The predictions presented in figure eight are calculated from parameter estimates given in the functions below:

Before 15th May

$$\text{Male: } f(x) = -217.2 + 0.08x^1 + 33.35x^2$$

$$\text{Female: } f(x) = -219.2 + 0.08x^1 + 33.35x^2$$

$$x^1 = \text{Breeding success (\%)}$$

$$x^2 = \text{SST}$$

After hatching date

$$\text{Male: } f(x) = -79.0 + (-0.05)x^1 + 12.37x^2 + 0.05x^3 + (-0.02)x^4$$

$$\text{Female: } f(x) = -79.5 + (-0.05)x^1 + 12.37x^2 + 0.05x^3 + (-0.02)x^4$$

$$x^1 = \text{Breeding success (\%)}$$

$$x^2 = \text{SST}$$

$$x^3 = \text{Days from hatching (+/-)}$$

$$x^4 = \text{Gender effect: Days from hatching (+/-) (Interaction)}$$

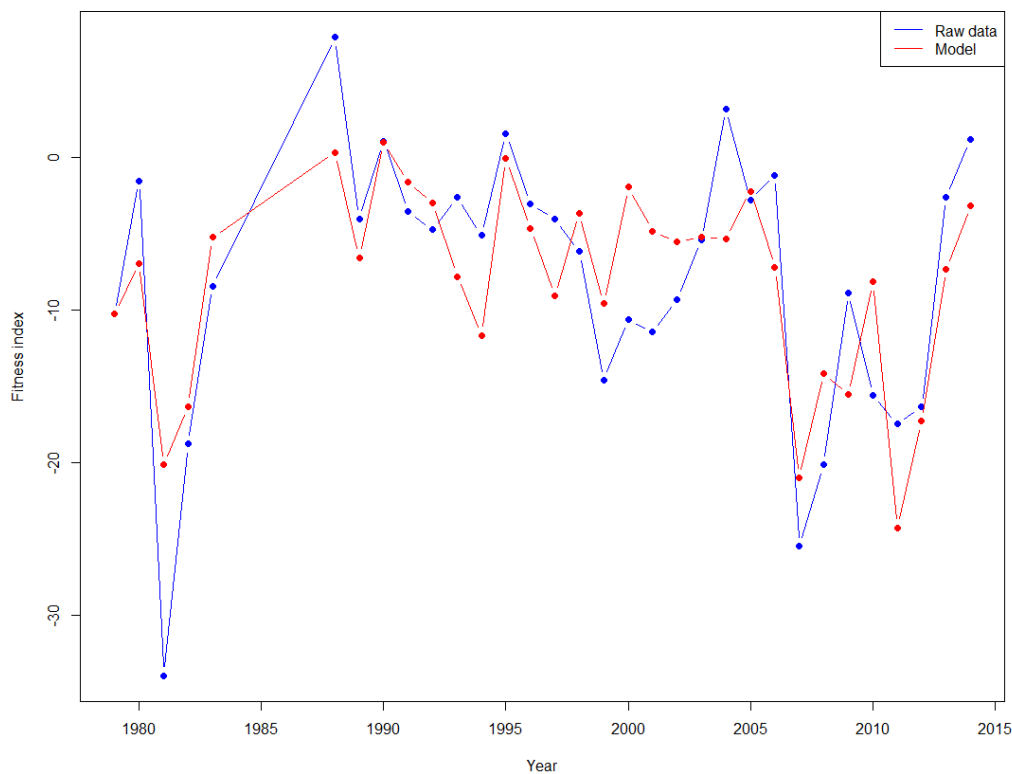


Figure 8: Annual mean fitness index of adult puffins for the raw data (blue line) and model average predictions (red line), in the time period 1980- 2015. The graph illustrates the degree of cohesion between model predictions and the raw data.

4. DISCUSSION

The cost of reproduction is a notion of central importance in life-history theory (Stearns 1989). The concept involves a trade-off between costs paid in survival and costs paid in reproduction. These trade-offs are exchanged in the currency of fitness in a situation where the benefit from altering one trait implies a detrimental change in another (Stearns 1989). Fitness therefore plays an important role in the trade-off equation and is likely to be a matter of careful consideration during all stages of the breeding season. According to Levins (1963), the fitness of a species is composed of different adaptive systems which depends on the pattern of heterogeneity of the environment in space and time. In other words, the tolerance for non-optimal conditions inhabited by an organism can vary a lot between species and even between populations or individuals, and this tolerance depends on the stability of the environment. Thus, the fitness of an organism is not static, and may change both during developmental stages and between environments (Levins 1963).

4.1. Before 15th of May

4.1.1 Sea Surface Temperature (SST)

In the period before egg laying, I found that the body condition of adult puffins increased with an increase in the oceanic temperature. This result support my prediction (P1) that *SST* should have a positive effect on the body condition of adult puffins. The results indicate that variations in *SST* in March had a significant impact on environmental conditions experienced by adult puffins during breeding. The linkage between average *SST* in March and reproductive output in the subsequent nestling period for puffins at Røst has previously been examined by Durant et al. (2006). Durant et al. (2006) found that low sea temperature and high salinity in March had a negative impact on chick survival due to its pronounced effect on prey availability. Climatic conditions such as water streams and oceanic temperature directly affect the transport and growth of fish larvae along the Norwegian coastline (Durant et al. 2003; Durant et al. 2006). Indirectly, oceanic temperature thereby affects the reproductive success of seabirds through the abundance of prey in the time of breeding, with following consequences for the fitness of the year classes (i.e., the cohort effect) (Durant et al. 2004b; Stenseth 2004). Puffins are known to adjust their breeding decisions according to prey availability during rearing, which makes them vulnerable to climatic fluctuations. In general, even small changes in oceanographic conditions are found to have profound effects on the reproductive success and survival of seabird populations (Montevecchi & Myers 1997;

Stenseth 2004). Typically, rising oceanic temperatures at Røst have been associated with increased food availability and improved breeding conditions for adult puffins (Durant et al. 2003). Lower *SST* levels have been found to negatively affect the population size of the puffin's main prey item, the young herring. Thus, it is reasonable to suggest that high *sea surface temperatures* in March has a positive impact on the *fitness index* of adult puffins at the study site. However, increased oceanic temperatures can potentially have a negative impact on body condition should the temperatures exceed a certain limit (Stenseth 2004). As an example, Kress et al. (2016) found that a decline in the body weight of puffin chicks in the Gulf of Maine was consistent with a trend for increasing *SST*. Moreover, the effects from changes in *SST* also depend on location and may affect different species in different ways (Diamond & Devlin 2003; Stenseth 2004) .

4.1.2 Fledging success

According to the results, the body condition of adult puffins is likely to increase with *fledging success* in the period before egg laying, contradicting my second prediction (P2). This finding highlights the importance of taking into account different periods throughout the breeding season as ecological and climatic very different as experienced by breeding puffins. The increase in *fitness index* during the pre-laying period as determined by *fledging success* was significant, however, the effect was not very strong. This finding might be explained by the relationship between environmental conditions and *fledging success*. It is to be expected that years with high reproductive success are recognized by favourable breeding conditions (Anker-Nilssen 1992; Durant et al. 2003; Erikstad et al. 1998). Hence, it is reasonable to assume that the observed positive relationship between the *fitness index* of adult puffins and *fledging success* in May is driven by climatic conditions. In other words, an increase in body condition experienced by adult puffins in early periods of the breeding season seems to be associated with years of higher *fledging success* due to favourable breeding conditions. The expected influence of environmental conditions on breeding success might also explain why variables *0-group herring abundance* and *fledging success* were found to be highly correlated.

4.1.3 Gender effect

The lowest ranked model among the two AIC selected models in the period before the 15th of May (Table 6) included the variable *gender*. Females were negatively correlated with the *fitness index* of adult puffins in the egg laying period, which implies that females had a lower body condition than males during this period. The result corresponds with my prediction (P3),

however, the effect was statistically insignificant. Even though the gender effect in the pre-laying period was non-significant, this type of negative association has previously been detected in research. For instance, Barrett et al. (1985) found that males tended to gain weight, while females lost weight from the pre-laying period into the second half of May. After incubation, both sexes lost weight until late July. Moreover, female puffins are likely to spend significantly more time than males incubating eggs and feeding chicks (Creelman & Storey 1991). As a result, males are much more conspicuous in the colony than females during the pre-laying period, especially in years of favourable breeding conditions. Even though females do leave the nest in order to search for food, males spend more time sitting out on the ledge than inside the burrow. This behaviour is most likely related to mate guarding and territorial defence (Creelman & Storey 1991). The energetic costs throughout the breeding season are similar for both sexes, due to a higher investment in territorial defence and mating effort by males. It is possible that differences in reproductive behaviour during the pre-laying period, such as males investing more energy in burrow-maintenance activities, whereas females are preparing for egg laying, support reasons for inter-sexual differences in body condition. Moreover, because there is no significant difference in time spent away from the colony during the pre-laying period (Creelman & Storey 1991), the additional energy cost experienced by females might be associated with the development and laying of the egg (Barrett et al. 1985). In general, inter-sexual differences in reproductive strategies throughout the breeding season are evident. However, underlying factors controlling some of these differences remain unclear (Williams et al. 2007).

4.1.4 Herring abundance

The models that included *0-group herring abundance* had a lower AIC value than the models that included *fledging success* in both periods of the breeding season. Parameter estimates of these models were therefore not presented in the results. However, the estimates on these models are described in Appendix 2 and 3. In the pre-laying period, only the lowest ranked model included *0-group herring abundance*. The direction of the effect was negative, but the effect size was small and non-significant (Appendix 2). The direction of the non-significant effect contradicts my prediction (P4). The weak effect size is reasonable considering that the analysis was run in the pre-laying period. The arrival of young herring in the foraging areas outside the colony at Røst is expected to be closer to hatching date (Durant et al. 2004a). Thus, the effect from *0-group herring abundance* on the body condition of adult puffins is likely to be more prominent in later stages of the breeding season.

4.2. After mean hatching date

4.2.1 Sea Surface Temperature (SST)

In the period after mean hatching date the *SST* had a significant and positive impact on *fitness index* for all models selected by the AIC. Hence, the relationship between ocean temperature and the body condition of adult puffins before the 15th of May and after mean hatching date in June/July was positive for both periods. However, the strength of the relationship was clearly more prominent in the pre-laying period in May compared to after mean hatching date, ($\beta=33.32$, $p<0.001$ and $\beta=12.36$, $p<0.001$ respectively for the highest ranked model in both periods). Because the growth and survival of spring-spawning herring depends on climatic conditions in spring, the *SST* in March is a suitable predictor of food availability during the breeding season (Durant et al. 2003). The sea temperature in March also affects the body condition of puffins in later stages of the breeding season through its effect on lower trophic levels, which eventually influence prey production. Consequently, the effect of *SST* on the body condition of puffins was also demonstrated by the correlation between *0-group herring abundance* and *fitness index* (see section 4.2.4 *herring abundance*).

4.2.2 Fledging success

Contrary to the pre-laying period, the *fledging success* was negatively associated with the body condition of adult puffins in the period after mean hatching date. The effect was significant, although not very strong. This result support my prediction (P2). Based on the cost of reproduction theory, seabirds are supposed to balance their investment in young against their own chances of survival during all stages of the breeding season (Williams 1966). The underlying elements that might influence the seabird's decision of either leaving the colony or continue rearing the chick are not fully understood. However, some studies suggest that long-lived seabirds are willing to increase their breeding effort, even at the expense of their own survival (Erikstad et al. 1997; Jacobsen et al. 1995; Johnsen et al. 1994). Moreover, this adjustment in parental investment is likely regulated by the body condition (Erikstad et al. 1997). Especially during chick-rearing, adult puffins are expected to lose body mass. Puffins needs to consider how much body mass they are able to lose in order to reduce flight costs and be more efficient feeders at any time (Barrett et al. 1985). These mechanisms of adjusting their own body condition in accordance with the needs of the chicks might be controlled by the breeding conditions, especially concerning food availability (Durant et al. 2003; Frederiksen et al. 2006). Conclusively, the negative relationship between *fledging*

success and *fitness index* in the period after mean hatching date is reasonable. However, the effect size in this study was small, which implies that there were unidentified factors that contribute to this understanding.

4.2.3 Gender effect

The two lowest ranked models among the three AIC selected models in the period after mean hatching date included variable *gender* (Tables 7 and 8). However, the effects were not significant and the highest ranked model did not include the *gender* variable. The two lowest ranked models showed contradictory gender effects and both effect sizes were small. The second ranked model had the most prominent gender effect that involved a negative correlation between females and the *fitness index* of puffins in the period after mean hatching date. Conversely, the lowest ranked model showed a positive relationship between females and the *fitness index* of puffins in the same period. Moreover, the lowest ranked model included a negative, but non-significant interaction between the variables *gender* and *days from hatching*. A significant interaction would imply that the body condition of males increases slightly faster than for females after the mean hatching date. Considering the intersexual differences in reproductive behaviour, the negative association between *gender* and *fitness index* in the period after the mean hatching date could be reasonable (Creelman & Storey 1991). As mentioned previously, it is to be expected that total investment in biparental care is close to similar for both sexes, although they may differ in the degree to which they engage in specific activities (Creelman & Storey 1991; Wright & Cuthill 1989). For instance, females have been found to invest more in direct care of the young (parental effort), whereas males invest more in territorial defence and mating effort (Creelman & Storey 1991). This close to equilibrium investment in reproduction, despite distinct differences in behavioural activities, may explain why the variable *gender* was included in several of the models even though the effects were non-significant.

4.2.4 Herring abundance

Regarding the highest ranked models that included the variable *0-group herring abundance* in the LMM analysis (Appendix 3), an effect from *0-group herring abundance* was found in all five models within ΔAIC 2 of the top supported model. Contrary to the pre-laying period, these effects were significant, but the effect size was low. Additionally, the direction of the effect was negative, which contradicts my prediction (P4). The abundance of Norwegian spring spawning herring is well known to play a major part in the breeding success of puffins

(Anker-Nilssen 1992; Durant et al. 2003; Durant et al. 2005). Hence, one can infer that *0-group herring abundance* is important also in regards to variations in the body condition of adult puffins. Despite the very low effect size, the negative relationship between herring abundance and the body condition of adult puffins is not necessarily clear. However, it is to be expected that breeding effort will increase in accordance with increased food availability, which may lead to increased energy consumption (Boyd et al. 2006; Cairns 1988). Evidently, the body condition of puffins may be adjusted dependent on the investment made in reproduction. Also, the risk associated with a reduction in the body condition for breeding puffins is dependent on the stability of food abundance (Anker-Nilssen, T. 2017, personal communication, 2nd May), and the risk is reduced if the breeding conditions are considered stable. Thus, a stable environment may stimulate increased breeding effort due to better opportunities of reproductive success. This may lead to an observed reduction in the body condition of breeding puffins. Moreover, the longer time spent in the colony, the greater is the risk of predation. Eventually, breeding puffins are continuously evaluating the cost and benefits associated with reproduction in order to achieve optimal fitness.

4.2.5 Changes in body condition

Despite the negative association between the *fitness index* and the *fledging success* in the period after mean hatching date, I found that the body condition of adult puffins increased in accordance with variable *days from hatching*. This result contradicts my last prediction (P5). The reasons for this relationship is not straightforward. However, in years of variable breeding conditions most puffins readily desert their nest and are likely to recover in body mass. Nevertheless, puffins that abandon their chicks due to unfavourable breeding conditions will most likely leave the colony and feed at sea (Harris et al. 2010), or they might choose to stay in order to defend their nest-site. Particularly, in high-density colonies, the competition for nest sites might induce adult puffins to stay longer in the colony (Hunt Jr et al. 1986), even though staying behind in the colony can inflict a cost on body condition. However, accurate data on breeding or fledging success can be difficult to obtain (Rodway et al. 1996). More specifically, to distinguish the number of birds that are present in the colony from the number of birds that are actually breeding can be difficult. Moreover, the positive relationship between *fitness index* and *fledging success* can be caused by confounding factors such as social interactions within the colony and climatic or biotic parameters not controlled in this study. For instance, the preparation for winter may have already started in later stages of the breeding season and the question remains how much breeding puffins are willing to invest in

chick rearing, at the expense of their own survival. Most importantly, reliable food abundance is the primary factor controlling the establishment and persistence of a colony, but also individual decisions on when to abandon the brood and leave the colony might be controlled by food availability (Sandvik et al. 2016). Furthermore, life history trade-offs have been found to differ between colonies for the same species, which is most likely related to the stability of the local environment (Frederiksen et al. 2005). In other words, unpredictable food availability and inter-population differences in life histories as defined by local climate conditions, may also be underlying factors that influence breeding decisions and thereby body condition. Again, the positive correlations between the variables *fitness index* and *days from hatching* may be caused by covariation from factors not included in the models. It is important to mention that the data used in this study lacked detailed information regarding individual differences between puffins such as age, which may influence reproductive behaviour or climate responses (Pinaud & Weimerskirch 2002). Additionally, the data does not distinguish between breeding individuals and puffins that have chosen to abandon their brood. This may also have implications for observed differences in the body condition of adult puffins. No relationship was found between the variables *fitness index* and *days from hatching* in the pre-laying period before the 15th of May.

5. CONCLUSION

This study indicates that the effect of fluctuating environmental conditions occurs both in the early and the late stages of the breeding season for breeding puffins. I have found that the *sea surface temperature (SST)* in March has a substantial positive effect on the body condition of puffins in both periods examined in this study. Researchers have previously investigated the effect of fluctuating climate on the reproductive success and adult survival of puffins. The direct and strong linkage between *SST* and *fitness index* for puffins found in this study contributes to the assumption that *SST* in March has strong implications for trophic interactions in the marine environment. Moreover, the relationship between the *fledging success* and the *fitness index* of puffins was found to be contradictory for the pre-laying period and the period after mean hatching date. The strong positive effect of *SST* in March on *fitness index*, as well as the positive correlation between *fledging success* and *fitness index* found in the pre-laying period suggest that environmental conditions are particularly important in the early stages of the breeding season. In the period after mean hatching date, the *fitness index* of puffins is negatively correlated with *fledging success*, which is to be expected considering the cost associated with reproduction. However, it is important to notice that this effect is proximate and that the ability of adjusting their body condition in accordance with the needs of their chick is ultimately controlled by fluctuations in the environment such as food availability. The variable *gender* was included in all the lower ranked models (within $\Delta AIC \leq 2$ of the top supported model) for both periods tested, but none of the effects were significant. This finding is consistent with the assumption that both sexes equally share the investment made in parental care, even though males and females may differ in the extent to which they engage in particular activities. At last, the variable *0-group herring abundance* was found to have a significant impact on the body condition of adult puffins in the period after mean hatching date. I could not detect any effect from *0-group herring abundance* on *fitness index* in the pre-laying period. However, *0-group herring abundance* was found to have a significant impact on *fitness index* in the chick rearing period, which indicates that first-year herring abundance directly affects the body condition of puffins in the period after mean hatching date. This finding is consistent with a strong correlation between puffin breeding success and the abundance of Norwegian spring spawning herring found in previous research. The results further suggest that the body condition of adult puffins increases in later stages of the breeding season. Throughout the breeding season it might be difficult to distinguish observed number of puffins from breeding pairs. Hence, the assumed increase in body

condition during the breeding season may be a result of confounding factors not controlled in this study, such as individual differences between puffins in regards to age and breeding status. Moreover, social interactions, inter-population differences in responses to a fluctuating climate and other biotic or climatic parameters not controlled in this study might contribute to this understanding.

Conclusively, the most prominent effect among all variables discussed in this study for both periods, was the climate variable *SST*. This result, as well as the significant effect of *0-group herring abundance* found in the period after mean hatching date, emphasizes the importance of climate variations as an ultimate factor controlling the breeding decisions of adult puffins. Moreover, the significant relationship between variables *fitness index* and *fledging success* indicates that the body condition of adult puffins is a crucial element in their life-history trade-off, such as regulating breeding investment. The absence of any significant *gender effect* suggests that the total reproductive investment, despite inter-sexual differences in reproductive behaviour, is close to similar for both sexes. My results contribute to previous documentation on the regulating mechanisms of environmental variables on the puffin population at Røst. In particular, this study examines the responses in the body condition of adult puffins to environmental conditions during the breeding season, including inter-sexual differences. Additional insight into the physiological responses of puffins to fluctuating environmental conditions is important in order to predict possible changes in population dynamics.

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Appendixes

Appendix 1: Summary of all datasets used in this thesis. The actual datasets are not included in appendix because the content is assembled and produced by established research institutions (NINA, HI and NMI) and thereby confidential. All datasets listed are merged in the raw data (nb.5). The total amount of data available for analyses performed in this thesis depended on which dataset was in use and the objective of each analysis.

Dataset	N (measurements)	N (individuals)	Range (min-max)	Year	NA	Description of measurement
<i>Nb. 1 ERSST</i>	563		5.01 – 13.5	1970-2016		Mean value of SST(°C) per month
<i>Nb. 2 Breeding success</i>	53		0.00% – 100%	1964-2016		Breeding success (%), based on mean value of all nest inspections per year
<i>Nb. 3 Hatching date</i>	35		10.6 – 51.5	1978-2015	1987, 1995, 2008, 2012-13	Mean hatching date (June), based on mean value of all nest inspections per year
<i>Nb. 4 Herring data</i>	66		0.00 – 758.5	1950-2014		Herring abundance (individuals in 10 ⁹) estimated per year
<i>Nb. 5 Raw data</i>	4621	2429		1979-2015	1985-1987	Morphometric measurements. All datasets + estimated fitness index included.
<i>Nb. 6 True sex</i>	881	293		1979-2015	1986-1987	Individuals gender based by DNA samples

Appendix 2: Parameter estimates of the three best fitted models in the pre-laying period before 15th of May which included variable *0-group herring abundance* in the global model. All models within Δ AIC 2 of the top supported model are included.

Parameter estimates of the best supported model in the pre-laying period (model ID 9) which included variable 0-group herring abundance in the global model. SST showed a significant, positive effect on the fitness index of adult puffins.

	Estimate	SE	Df	t value	p value
Fixed effects/Coefficients:					
Intercept	-183.78	38.83	379	-4.73	<0.001
Sea Surface Temperature (SST)	27.93	6.66	97	4.19	<0.001

Parameter estimates of the lower supported model in the pre-laying period (model ID 10) which included variable 0-group herring abundance in the global model. SST had a significant, positive impact on the fitness index of adult puffins. Female puffins seemed to be negatively correlated with the fitness of adult puffins, but the effect was not significant.

	Estimate	SE	Df	t value	p value
Fixed effects/Coefficients:					
Intercept	-183.48	38.8	379	-4.73	<0.001
Sea Surface Temperature (SST)	28.11	6.66	96	4.22	<0.001
Gender (female)	-3.23	3.24	96	-0.99	0.32

Parameter estimates of the lowest supported model in the pre-laying period (model ID 13) which included variable 0-group herring abundance in the global model. Once again, SST showed a significant, positive impact on the fitness index of adult puffins. A negative correspondence between 0-group herring abundance and fitness index was also included in this model, however, the effect was not significant.

	Estimate	SE	Df	t value	p value
Fixed effects/Coefficients:					
Intercept	-182.2	39.11	379	-4.66	<0.001
0-group herring abundance	-0.005	0.014	96	-0.37	0.72
Sea Surface Temperature (SST)	27.75	6.68	96	4.15	<0.001

Appendix 3: Parameter estimates of the five best fitted models in the period after mean hatching date which included variable *0-group herring abundance* in the global model. All models within Δ AIC 2 of the top supported model are included.

Parameter estimates of the best supported model in the period after mean hatching date (**model ID 15**) which included variable *0-group herring abundance* in the global model. Variable days from hatching were significantly and positively correlated with fitness index, while SST had a significant and positive impact on the fitness index of adult puffins. A negative correlation between *0-group herring abundance* and fitness index was also detected in the model, however, the effect was not significant.

	Estimate	SE	Df	t value	p value
Fixed effects/Coefficients:					
Intercept	-78.93	8.93	1871	-8.84	<0.001
0-group herring abundance	-0.01	0.003	1580	-3.18	0.0015
Days from hatching	0.45	0.03	1580	14	<0.001
Sea Surface Temperature (SST)	12.22	1.63	1580	7.5	<0.001

Parameter estimates of the lower supported model in the period after mean hatching date (**model ID 16**) which included variable *0-group herring abundance* in the global model. A significant and positive correlation between variable days from hatching and fitness index was found. Moreover, SST had a significant and positive impact on the fitness index of adult puffins. A negative correlation between *0-group herring abundance* and fitness index was also detected in this model, however, the effect was not significant. Additionally, a non-significant gender effect was also included in the model, implying that females had a lower fitness than males in the late part of the breeding season.

	Estimate	SE	Df	t value	p value
Fixed effects/Coefficients:					
Intercept	-78.34	8.94	1871	-8.76	<0.001
0-group herring abundance	-0.01	0.003	1579	-3.19	0.0014
Days from hatching	0.45	0.03	1579	14.01	<0.001
Sea Surface Temperature (SST)	12.25	1.63	1579	7.52	<0.001
Gender (female)	-1.42	1.12	1579	-1.26	0.21

Parameter estimates of the lower supported model in the period after mean hatching date (**model ID 32**) which included variable *0-group herring abundance* in the global model. Once again, variables days from hatching and SST had a significant, positive impact on the fitness index of adult puffins. A negative correlation between *0-group herring abundance* and fitness index was detected in the model, however, the effect was not significant. Additionally, a significant, positive correlation between gender (female) and fitness index was detected, which implies that females had a higher fitness than males in this period, but the effect was far from significant. Also, a negative interaction between gender (female) and days from hatching was found, which means that the fitness of males are likely to recover faster than for females in the period after mean hatching date, however, this result was also non-significant.

	Estimate	SE	df	t value	p value
Fixed effects/Coefficients:					
Intercept	-78.99	8.96	1871	-8.82	<0.001
0-group herring abundance	-0.01	0.003	1578	-3.2	0.0014
Days from hatching	0.5	0.05	1578	10.7	<0.001
Sea Surface Temperature (SST)	12.23	1.63	1578	7.51	<0.001
Gender (female)	0.12	1.63	1578	0.07	0.94
Interactions:					
Gender (female):Days from hatching	-0.08	0.06	1578	-1.3	0.2

Parameter estimates of the lower supported model in the period after mean hatching date (**model ID 48**) which included variable 0-group herring abundance in the global model. Variables days from hatching and SST had a significant, positive impact on the fitness index of adult puffins, similar to the previous models in the same period. 0-group herring abundance and fitness index was once again found to be negatively correlated, however, the effect was not significant. In this model gender (female) and fitness index was negatively correlated, which implies that females had a lower fitness than males in this period, however the effect was far from significant. Also, a positive interaction between gender (female) and 0-group herring abundance was found, which implies that the fitness of female puffins was increasing faster than for males depending on herring abundance, however, the result cannot even be considered a trend due to its low significance level.

	Estimate	SE	df	t value	p value
Fixed effects/Coefficients:					
Intercept	-78.02	8.95	1871	-8.72	<0.001
0-group herring abundance	-0.01	0.005	1578	-2.95	0.0032
Days from hatching	0.45	0.03	1578	14.02	<0.001
Sea Surface Temperature (SST)	12.23	1.63	1578	7.53	<0.001
Gender (female)	-2.29	1.5	1578	-1.53	0.13
Interactions:					
Gender (female):0-group herring abundance	0.005	0.006	1578	0.88	0.38

Parameter estimates of the lowest supported model in the period after mean hatching date (**model ID 64**) which included variable 0-group herring abundance in the global model. Variables days from hatching and SST had a significant, positive impact on the fitness index of adult puffins, similar to the all the models presented in the same period. 0-group herring abundance and fitness index was once again found to be non-significantly and negatively correlated. Gender (female) and fitness index was negatively correlated also in this model, which implies that females had a lower fitness than males in this period, however the effect was far from significant. The same interactions as presented in model ID 48. was found in the lowest supported model, again, their effects cannot be accepted due to the low significance level.

	Estimate	SE	df	t value	p value
Fixed effects/Coefficients:					
Intercept	-78.67	8.96	1871	-8.77	<0.001
0-group herring abundance	-0.01	0.005	1577	-3.02	0.026
Days from hatching	0.49	0.05	1577	10.75	<0.001
Sea Surface Temperature (SST)	12.25	1.63	1577	7.52	<0.001
Gender (female)	-0.77	1.87	1577	-0.42	0.68
Interactions:					
Gender (female):0-group herring abundance	0.006	0.006	1577	0.98	0.33
Gender (female):Days from hatching	-0.08	0.06	1577	-1.37	0.17



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