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## Abstract

The Polar Regions are warming twice as fast as the rest of the world, and one of the biggest concerns related to global warming is the melting of the polar ice caps. Seabird numbers all over the world are declining, and a large number of seabird species are associated with sea ice in various levels. The Common Eider breeding in Svalbard is mainly restricted by sea ice in spring at the start of breeding season. Eiders prefer breeding on islands to avoid the Arctic fox, and will not start nesting until there is no ice connection to the mainland. In this study, Common Eider distribution in Kongsfjorden was investigated as a response to less sea ice on the north-west coast of Spitsbergen and inside Kongsfjorden in the time period 1981 - 2017. The results show that the proportion of nests in the newly ice-free islands in Kongsfjorden has increased during the study period, and that there is a strong relationship between distribution of nests and amount of sea ice. Clutch size had changed over time, and had increased in the newly ice-free area. The effect of area on average clutch size was significant. There are numerous factors that could influence the breeding dynamics of the eider population in Kongsfjorden, and sea ice may no longer be the driving factor. Further research on predator effects from gulls, skuas and polar bears is recommended.

## Sammendrag

Jordas polare strøk varmes opp dobbelt så raskt som resten av kloden, og en av de største truslene knyttet til global oppvarming er nedsmelting av isen i polområdene. Verdens sjøfuglbestander synker i antall, og et stort antall sjøfuglarter er tilknyttet sjøis i varierende grad. Ærfuglene som hekker på Svalbard er hovedsakelig begrenset av sjøis rundt hekkestart på våren. Ærfuglene foretrekker å hekke på øyer for å unngå polarreven, og starter ikke hekking før isforbindelsen til fastlandet er brutt. Denne studien har undersøkt om hekkeutbredelsen til ærfuglene i Kongsfjorden har blitt påvirket av mindre sjøis utenfor nordvestkysten av Spitsbergen og inne i Kongsfjorden, i tidsperioden 1981 – 2017. Resultatene viser at andelen reir i de nylig isfrie øyene i Kongsfjorden har økt, og at det har vært en sterk sammenheng mellom fordeling av reir og mengde sjøis. Kullstørrelse har endret seg over tid, og økte i det nylig isfrie området, og område hadde en signifikant effekt på gjennomsnittlig kullstørrelse. Det er mange faktorer som kan påvirke hekkedynamikken i ærfuglpopulasjonen i Kongsfjorden, og sjøis er kanskje ikke lenger den mest avgjørende. Det er anbefalt å forske mer på predatoreffekter, både fra måker, joer og isbjørn.

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# 1. Introduction

Over the past 139 years, Earth's global temperature has increased by 0.8 degrees, with an increase of two thirds occurring in the latter four decades (Hansen et al., 2010, GISTEMPTeam, 2019). The polar regions are warming twice as fast as the rest of the world (Blunden, 2013), and it is widely recognized that there is a link between anthropogenic CO<sub>2</sub>-emissions, global warming and increased melting of sea ice in the Arctic (IPCC, 2018). One of the biggest concerns related to global warming is the melting of the polar ice caps. With less multi-year ice and a thinning of the Arctic ice cap (Mioduszewski et al., 2019), one ice-free summer in the Arctic Ocean is expected for every century with a global temperature increase of 1.5°C (IPCC, 2018).

Seabird numbers all over the world are currently declining (Paleczny et al., 2015, CAFF, 2013), and palaeontologists have recorded at least five major mass extinction events throughout Earth's history where more than 75% of biodiversity was lost (Ceballos et al., 2015, Barnosky et al., 2011). Since 1970, world biodiversity has already declined by 60% (WWF, 2018), and of all phylogenetic groups in the avifauna, seabirds are the group that struggles most (Grémillet et al., 2018). There are numerous biological consequences of global warming that could contribute to this declining trend, but mechanisms may vary across each species range.

A great number of seabird species are found the Arctic and sub-Arctic areas (Humphries and Huettmann, 2014), and many of them are directly or indirectly associated with sea ice. For instance, Ivory gulls (*Pagophila eburnea*) use sea ice extensively to scavenge upon seal carcasses after Polar bear meals, and the species is now threatened because of less sea ice (Gilg et al., 2016). A more indirect relationship is seen in the most abundant sea bird species in the Arctic, the Little Auk (*Alle alle*) (Keslinka et al., 2019), that depends entirely on the sea ice associated zooplankton *Calanus hyperboreus* and *Calanus glacialis* for raising their young (Pedersen and Falk, 2001). As the ice edge melts northwards, the Little Auk's sustenance disappears from their breeding range (Amélineau et al., 2019, Karnovsky et al., 2010, Welcker et al., 2009). Warmer water leads to serious consequences, as it 'Atlantificates' the Arctic Ocean, shifting temperate systems northwards (Vihtakari et al., 2018, Mackas et al., 2007). This results in some keystone species changing their distribution range, for example zooplankton and fish larvae (e.g. (Monaghan, 1992, Wanless et al., 2005, Montevecchi and A. Myers, 1997), while their consumers may not be as flexible in space. Trophic mismatch as a consequence of overfishing or climate factors are well described in literature, for instance the delayed timing

of Sandeel larvae hatching in Scotland as a consequence of warmer water, creating a mismatch with timing of chick rearing for Kittiwakes (*Rissa tridactyla*) (MacDonald et al., 2019). Similar problems are apparent in Newfoundland, where entire Common Guillemot (*Uria aalge*) breeding colonies suffer from temporal mismatch between chick rearing and arrival of Capelin (*Mallotus villosus*) (Regular et al., 2014).

As seabirds often have high site fidelity in their breeding range (Braby et al., 2012) they are especially vulnerable to change. A system's or a species' ability to adapt to or resist outer influence is measured as a combination of the rate of exposure and its intrinsic sensitivity to the impact. Together, this equals the capacity the system or species has to buffer the climatic changes through various adaptations, either through plastic in situ adaptations or genetic modifications (Moritz and Agudo, 2013). Nevertheless, if the impact is local and the system is mobile, migration is often the fastest short-term solution, and for mobile organisms, it opens up the possibility to find new habitats. In Finland's Atlas' survey of 2012, it is shown that a spectrum of bird species across the European range, has shifted their breeding distribution poleward as the climate is warming (Brommer et al., 2012). A similar trend is found for bats in a study from the UK, where the small *Pipistrellus nathusii* was found to expand its distribution with higher minimum temperature, which suggests that warmer climate can evidently influence a species range (Lundy et al., 2010). Site fidelity can be a beneficial trait for seabirds, since it gives high predictability with regard to mates, food and nest sites. But it also comes with a constraint, and studies have shown that high site fidelity can slow down population growth, and limit the population in occupation of potential available new habitats (Matthiopoulos et al., 2005). One seabird species, the Northern Gannet (*Morus bassanus*), has utilized its potential to alter its breeding distribution, most probably due to changes in the marine food chain. Several small populations of Gannets have been established along the north Norwegian coast during the latter seven decades, and in 2011 a colony was found as far north as in Bjørnøya, Svalbard (Barrett et al., 2017). For Arctic seabird species, it is believed that with increasing climate change, the southern nesting areas will become less suitable and the total breeding area considerably smaller (Jakubas et al., 2017). At the same time, increased melting of snow and ice in both terrestrial and coastal systems, opens up new available area for both foraging and breeding (Jensen et al., 2008). Therefore, there is high uncertainty of how bird colonies will distribute in the Arctic in the future.

One colonial ground breeding seabird that could be affected by the changing sea ice in the Arctic is the Common Eider *Somateria mollissima* (hereby 'eider'). Eiders have a circumpolar distribution ranging from the Boreal and Arctic zones of Europe, North America, Greenland and Siberia (Waltho and Coulson, 2015). Common eider numbers are currently declining in their distribution range (Suydam et al., 2000, Robertson and Gilchrist, 1998, Merkel, 2004, Iles et al., 2013), but the reasons are not very well known. With regard to eiders' life history traits such as late maturation, low annual reproduction and high adult survival (Waltho and Coulson, 2015), it is likely that colonies depend largely on adult survival. Nevertheless, annual production secures the future population viability, and in some areas, poor recruitment and fledging success is suggested as the main driver for population decline (Hario et al., 2009). It is debated whether eiders are pure capital or partly capital breeders (Stephens et al., 2009, Meijer and Drent, 1999) but eiders will indeed build up parts of their energy reserves needed for reproduction through foraging at the wintering site before migrating in spring (Christensen, 2000). Poor recruitment might thus be a result of insufficient food quality or availability in the wintering area, and studies confirm that eiders will in some areas follow the annual variation in food abundance in winter (Jesper and Magella, 2000).

One of the warmest high Arctic islands is the Norwegian archipelago Svalbard, located between 74 and 81 degrees north. Svalbard has a relatively mild climate due to the warm North Atlantic Current running northwards on its western side, and breeding eiders are found all along the west coast in addition to a few sites on the east coast. The total breeding population of eiders in Svalbard is estimated at 13 000 pairs (Stiansen et al., 2009), of which the majority breeds on the western part of Spitsbergen (Prestrud and Mehlum, 1991) on small islands along the coast to avoid the predatory Arctic fox (*Vulpes lagopus*) (Ahlén and Andersson, 1970). The largest eider population is located in Kongsfjorden (79 °N, 12 °E) with about 1 500 – 3 500 breeding pairs, but also here are large year-to-year variations due to fluctuations in climate (Prestrud and Mehlum, 1991, Mehlum, 2012). Kongsfjorden is a relatively large fjord that contains > 14 small islands. To protect the geese and ducks breeding here, it became prohibited to hunt for birds and collect eggs and down in 1963 and 15 bird sanctuaries were established in 1973. In Kongsfjorden there are two bird sanctuaries, that include 12 of the 14 islands inhabited by ground breeding birds.



Kongsfjorden has historically contained a variable fast ice cover that has sustained until spring and sometimes even until late summer, while the eiders arrive to Svalbard during the last half of April (Parker and Mehlum, 1991, Hanssen et al., 2016). During the past ten years, a change in fjord ice cover has been observed in Kongsfjorden. 2006 was the first year since the monitoring of eider ducks started that Kongsfjorden was completely ice-free first of June, on average the time eiders start their breeding. Of the following years, only in 2009, 2011, 2013 and 2015, ice was still present in the fjord on the first of June, but broke up shortly after (Norwegian Polar Institute, unpubl. data).

Literature describes the relationship between eiders and sea ice in context of an array of life history traits, and it is shown that timing of ice retreat could affect clutch size. A series of studies reports larger clutches in years where ice retreated early (Jean-Gagnon et al., 2018, Chaulk and Mahoney, 2012, Mehlum, 2012), as a consequence of a longer breeding season. A typical clutch consists of 4 to 6 eggs (Coulson and C., 2015), but the average clutch size can vary across the breeding range. If the winter prior to breeding had severe weather, females may not be able to allocate enough resources to produce a high number of eggs, or it affects the health of the ducklings (Lehikoinen et al., 2006).

The change from earlier ice conditions with substantial spring ice, to the present almost absent ice cover, could give common eiders in Kongsfjorden the possibility to spread and colonize new breeding habitat. Therefore we would expect to see an increase in breeding numbers as the total area available for nesting is larger. However, not only physical size of the area determines the carrying capacity of a habitat, and avian predators may in larger degree influence the density of nests, and also clutch size. A denser population is expected where there are high numbers of avian predators, as chances of being predated upon diminishes with more congeners (Stearns 1992). In years with little ice we would expect to see a larger clutch size, as breeding could be initiated earlier and chances for a successful breeding season are higher, although the effect might be diluted if predator numbers are high enough. As ice conditions have changed dramatically since the 1980's, we might still see a different pattern for the present situation that is yet to be demonstrated.

In light of ongoing climate change and the near future predictions of species extinctions, continuous research and uncovering potential responses and mitigation strategies are important in order to fully understand, manage and protect endangered species. It is important to document these ecosystem changes in order to understand the consequences of climate change, and to better predict accurate responses in the Arctic.

In this master thesis I consider sea ice as a physical factor behind potential changes in breeding distribution of common eiders, and will first describe how the sea ice cover and the total breeding population has developed during the study period 1981 – 2017. By using data on population size and clutch size from each island in Kongsfjorden, my main goals are to:

- 1) Investigate if Common eiders in Kongsfjorden have changed their breeding distribution, and if this has happened as a response to change in sea ice conditions.
- 2) Investigate if clutch size has changed during the study period, and if this has any relation to the diminishing sea ice and opening of new breeding habitats.

## 2. Method

### 2.1 Study site

The data used in this thesis is collected in Kongsfjorden, Svalbard (78°55' N, 12°00'E) during the years 1981 – 2017. The Common eider monitoring has been conducted by the Norwegian Polar Institute for all the years that data is used in this thesis. Kongsfjorden has an area of 231 km<sup>2</sup> (Hop et al., 2002) and contains >14 small islands and islets that serve as breeding grounds for Common eiders during the summer. Data is collected from Prins Heinrichøya, Dietrichholmen, Mietheholmen, Storholmen, Juttaholmen, Observasjonsholmen, Sigriddholmen, Midtholmen, Innerholmen, Leirholmen, Eskjæret, Gerdøya, Indre- og Ytre



Figure 1. Map over Kongsfjorden with all the islands included in the study (Norsk Polarinstitutt, 2019)

breholmen (Figure 1). The islands are spread out in the fjord, where Storholmen, Juttaholmen, Sigriddholmen, Observasjonsholmen, Midtholmen, Sigriddholmen and Leirholmen are clustered together as Lovénøyane. The islands vary in size from 0,01 to 30 ha, with an altitude varying between 0 and 35 m. asl. The total area of all the islands is 131 ha (Hanssen et al., 2013). Vegetation is fairly similar among all islands and consists mostly of moss, lichen and arctic

forbs and grasses, normally not exceeding 5 cm in height (Mehlum, 2012). Some islands vary more in topography than others, and the eiders are found to breed openly in various microhabitats, ranging from the shoreline to the highest points.

During the breeding season the weather conditions in Kongsfjorden are characterized by 24h daylight and an average summer temperature of 3.8 °C (Førland et al., 2011). Svalbard has a dry polar climate, but rain- or snowfalls occasionally happen during the field season.

## 2.2 Sea ice data

Data on local sea ice cover in Kongsfjorden has been obtained by the Norwegian Polar Institute for the years 1981 – 1987 and 2003 - 2017. These are based on hand-drawn maps and photographs from the research station at the top of the Zeppelin mountain, which provides a good view of the fjord. The islands Indre- and Ytre breholmen are located behind Blomstrandhalvøya and are not seen from the Zeppelin mountain. Therefore the ice condition around these two islands is not included in the local hand drawn maps.

Large scale data on sea ice concentrations outside North-West Spitsbergen is available as satellite data from the University of Colorado for the entire study period, and consists of measured ice concentration (%) in four adjacent areas of 25 x 25 km between 78 °N and 79 °N outside NW Spitsbergen (Supplement 1-Figure S3 Prop et al., 2015). Daily measurements of ice concentration for April and May are reduced to monthly means, and subsequently the mean of April + May is calculated, as this is the period when eiders return to Svalbard in spring (Hanssen et al., 2016).

Local ice data from Kongsfjorden would be preferred to use as climate variable, as this is valuable information that could describe the situation around each island in the fjord in more detail. However, local data is missing for a substantial part of the study period. The relationship between the large scale ice concentrations outside NW Spitsbergen and the local ice conditions in Kongsfjorden is therefore investigated to justify the use of large scale ice data as main climate variable in this study. This is done by checking for correlation between the large scale sea ice concentration (the monthly mean of April and May) with the local ice data for the years that exists. The local sea ice data variable has the value of ‘day of the year’ (day after 1<sup>st</sup> of January when sea ice has retreated behind Lovénøyane), for every year that there exists data. This

method is described for parts of the time series in a previous study from Kongsfjorden, but it will be tested in this thesis using data that corresponds for the entire study period.

## 2.3 Data categorization

In Kongsfjorden there are physical factors such as currents and exposure from the north-westerly winds and swell entering the fjord from the west. This results in some of the islands being free of ice earlier compared to the more sheltered islands, and thus have been more frequent breeding grounds for the eiders. The local sea ice data was used to categorize the islands into two categories, ‘early ice-free’ or ‘late ice-free’, depending on when the ice historically has been retreating from the islands in spring. This is done to aid the statistical analysis testing whether sea ice has influenced the distribution of breeding common eiders.

Figure 2 shows an example of how the ice retreats inwards the fjord during the melting in spring. This figure is made based on the hand drawn maps of Kongsfjorden for 2009. This year was typical in the pattern of ice retreat, and dates for the different observations show when the ice retreated from the different islands. Maps like this can show where the ice has been at the timing of breeding for common eiders, and thus explain why the ducks choose some islands over others in a given year. Historically, the outermost islands in the fjord have mainly been used as breeding sites for the eiders. These islands consist of Mietholmen, Eskjæret, Storholmen, Prinsheinrichøya and Ytre Breholmen, and will be placed in category “early ice-free”. The innermost islands are more sheltered, and here the ice retreats later. These islands consist of Juttaholmen, Observasjonsholmen, Midtholmen, Sigridholmen, Innerholmen, Leirholmen, Gerdøya and Indre breøya (Figure 2), and will be placed in category “late ice-free”.

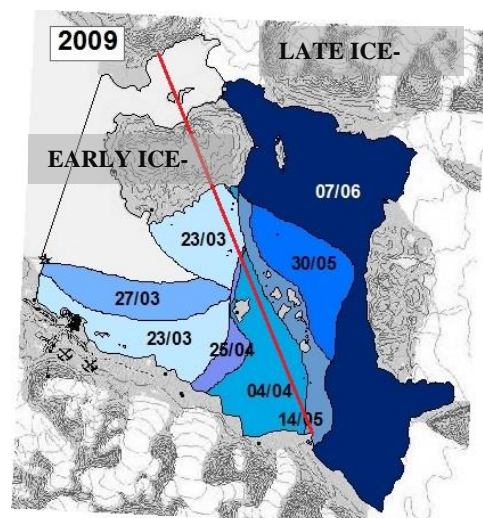


Figure 2. Map of Kongsfjorden with measured dates for ice retreat in spring 2009. Each line represent the ice edge at the given date, and 2009 is chosen as an example due to this year’s typical ice retreat pattern in the fjord. The red line separates the islands into two categories, early ice free and late ice free. (Norwegian Polar Institute)

The hand drawn maps do not include Indre- and Ytre breholmen behind Blomstrandhalvøya. Based on the ice conditions in the rest of Kongsfjorden, a discretionary assessment of which category these are to be placed in is necessary. Ytre Breholmen is the outermost of these two islands, and receive most swell from the fjord, thus being ice free earlier. Indre Breholmen is situated more sheltered, having protection from Ytre breholmen. As a similar pattern is visible for other islands in the fjord, with the same type of placement (e.g. Storholmen vs. Lovénøyane), it is assumed that Ytre breholmen can be placed in category ‘early ice-free’ and Indre breholmen in ‘late ice-free’.

Prins Heinrichøya is an island somewhat inbetween early and late due to the fact that there for some years is a small ice bridge between the island and mainland quite late in the season. Still, Prins Heinrich is placed quite far out and openly in the fjord, and it is therefore categorized as ‘early ice-free’. There is large variability in the amount of ice in the fjord, but the retreat of the ice usually follows the same pattern from the outermost to the innermost parts of the fjord, usually leaving Gerdøya as the last island to be ice free (Figure 4).

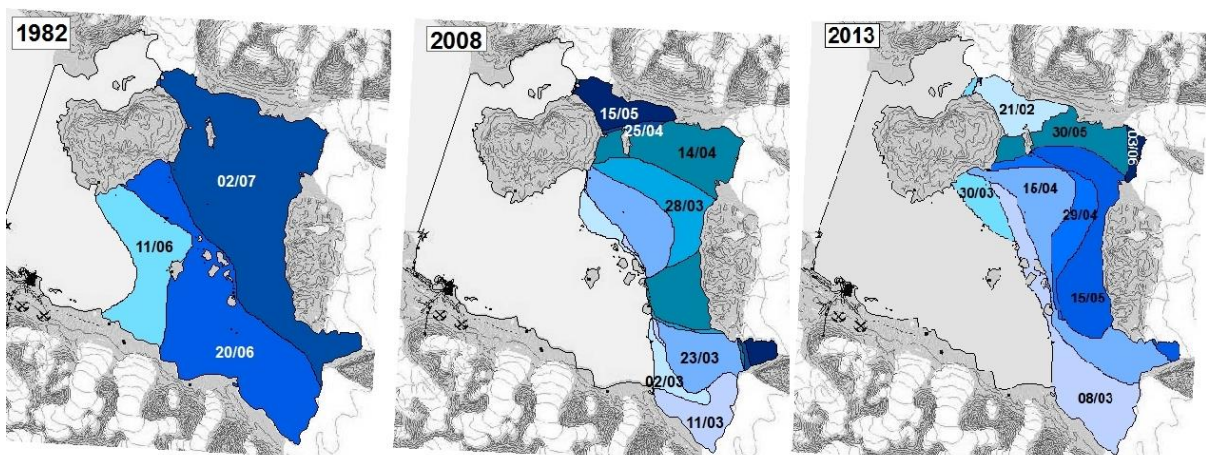


Figure 4. Example of the great variability in fjord ice retreat in Kongsfjorden. In 1982, ice was still present around the ‘late ice-free’ islands in late June, while 26 years later, almost all the islands were ice free by the time eiders start breeding. 2013 was again a cold year, where there was still ice present in the fjord at 1<sup>st</sup> of June.

## 2.4 Field procedures and recorded variables

The data on Common Eiders has been collected annually since the project started in 1981 (except 1988, 1992 and 1994). The counting was from the beginning conducted in the monthly shift between June and July, but in the later years, it has shifted towards mid to late June. In a long time series study it is important to maintain a uniform method, but if adjustments had not



been taken with regard on count date, the results would be skewed because the timing of breeding expedited with an earlier spring. The counting time aims to be as close to when egg laying is finished, but before hatching, to give an image of annual production of nests and eggs. What is to be considered is the possibility of depredation on the colony before counting occurred, and thus will clutch size not be an accurate measure of investment in this context. The recorded variables are count data of number of nests on each island and numbers of eggs in each nest on the 14 different island in Kongsfjorden. The clutch size ranges from 1 to 12 eggs, with >8 eggs being extremely rare. Number of nests is used as a measure of the size of the breeding population.

The field workers were usually a team of 2-4 people, and approached the islands by boat. Counting started at the point of disembarkation. Depending on the shape and size of the island, it was usually divided in two halves, counting one half on the way to the other end and the other half on the way back (figure 5). The counters always stayed in contact with each other to avoid counting the same nests. At the end of each day, tally notes were compared and gathered into one datasheet. Avian predators were also registered at a certain degree when collecting the common eider data, but without more detailed description than the approximate number of present birds and nests. If Arctic



Figure 5. Example of counting method. Numbers represent fieldworkers, red lines represents approximate walking routes, black markers represent each persons counting limit, to avoid overlap.

foxes or polar bears were seen, this would also be noted down. Some years predated nests (nest scrapes where down had been moved around, eggshells etc.) have been registered as count data, as well as hatched nests where chicks and female already had left at the moment of counting time. The procedure of registering predators and hatched nests was not in use before 2002, and due to the low consistency it will be left out of the analysis.

The wildlife in Svalbard generally shows little fear against humans (Gabrielsen et al., 1985, Ø. and Øystein Overrein, 2005, Reimers et al., 2011), and this also applies for the eiders breeding in Kongsfjorden. It can be costly for a female eider to leave her nest in the incubation period

with numerous avian predators present. When a nest is being counted, the female will in most cases leave her nest for a few meters away, and then return when the fieldworker has moved away. If in some cases she flees to the water, the eggs are covered with down by the counters to minimize heat loss and predation risk. In days with heavy rain or snow, counting did not occur with regard to the wellbeing of the eiders.

## 2.5 Statistical analyses

All statistical analyses were conducted using R software v. 1.1.383 (R Core Team 2017). The packages used in R were AICcmodavg for the model selection and XLConnect for importing excel files into R.

### 2.5.1 Candidate models and model selection

The following set of three candidate models was created as a foundation for all the statistical analyses. Mod 1 represents a model where the response does not vary as a function of x. Mod 2 represents a linear change and Mod 3 allows a relationship with curvature. These three models represent different biological hypotheses in the analyses that are evaluated against each other, and the data determines which hypothesis there is support for.

- Mod 1 - intercept only ( $y = a$ )
- Mod 2 - linear ( $y = ax + b$ )
- Mod 3 - quadratic ( $y = ax^2 + bx + c$ )

Depending on the analysis, not all of the models were included in all cases. Akaike's Information Criteria with correction for small sample size (AICc) was used to select the most parsimonious model from the candidate models (Akaike, 1978, Bedrick and Tsai, 1994, Burnham and Anderson, 1998, Anderson and Burnham, 2002). When models are compared, the model with the lowest AICc value is preferred.

## 2.5.2 Sea ice

To test the hypotheses regarding how sea ice has influenced Common eider breeding distribution, it was first necessary to describe how the ice condition has developed during the study period. Using the LM function in R, the three candidate models were applied in the following analyses:

- Large-scale sea ice concentration over time. In this analysis the ice concentration (%) outside NW Spitsbergen (See 2.2 for details on sea ice data) was entered as the response variable and year (1981-2017) as predictor variable
- Timing of ice cover retreat behind Lovénøyane over time in Kongsfjorden, where ‘day of the year’ was used as a response variable and year (1981 – 2017) as predictor variable.
- Timing of ice retreat behind Lovénøyane as a function of percentage ice concentration (%) outside NW Spitsbergen. This analysis was done to test if there was a strong enough correlation to justify the use of large scale data in further analysis. ‘Days of the year’ was used as a response variable, and ice concentration (%) was used as a predictor variable.

## 2.5.3 Number of nests on the islands in Kongsfjorden

The total number of nests in Kongsfjorden was plotted as a function of year (1981-2017), to give a descriptive overview of the total breeding population of eiders in Kongsfjorden through the entire study period.

The number of nests on each island in Kongsfjorden was subjected to more detailed analysis. Number of nests is count data, and the three candidate models described in section 2.5.1 were applied in generalized linear models (GLM in R) with Poisson distribution and log-link to investigate the number of nests on each island, and in the two island groups (see 2.3 for details on data categorization). Number of nests (N=0-2000) was entered as a response variable and year (1981 – 2017) as a predictor variable.



#### 2.5.4 Distribution of nests in the fjord

One of the two main goals of this thesis was to reveal if a change in distribution of breeding eiders has occurred in Kongsfjorden. To do so, I tested whether the proportion of nests in ‘late ice-free’ islands has changed over the study period, and in relation to sea ice concentration. This was done using generalized linear models with binomial distribution (link=logit). The response variable consisted of two columns; each containing the sum of nests in the groups of islands. Year (1981-2017) and ice concentration (%) was used as predictor variables in two individual analyses. I did not include year and sea ice concentration in the same analysis, as these two variables correlate.

#### 2.5.5 Clutch size

The second main objective was to investigate if the average clutch size was different in the two areas, and if the average clutch size had *changed differently* in the two areas during the study period.

Using the set of candidate models described in section 2.5.1 and the LM function in R, the average clutch size was analyzed and plotted as a function of time for all the islands and the two island groups. Average clutch size was entered as a response variable, while year (1981 - 2017) was entered as predictor variable.

Furthermore, a multiple regression model was used to estimate the effect of year and area and an interaction between year and area, on the average clutch size. The estimates from the analysis were extracted, and p-values were used to determine the significance of the different variables on the average clutch size.

### 3. Results

#### 3.1 Sea ice

The sea ice concentration (%) outside NW Spitsbergen has declined from >30 % in the beginning of the 1980's to 0 % in 2017 (Figure 5a). Ice concentration shows a steep drop in the start of the study period, and after a peak of relatively high ice concentration of >15% in the late 1990's, it decreases further with variations of what seems to be a peak every 3-4 years. There was from 2012 and onwards almost no sea ice present outside NW Spitsbergen in April and May. Mod 3 was selected and used for inference in this analysis (table 1a).

The timing of ice retreat behind Lovénøyane has expedited throughout the study period (Figure 5b). Data is missing for a large part of the study period (1989 – 2002), but in the first half (1981 – 1988) the timing of ice retreat is in late May or later, meaning that Lovénøyane is not ice free by the time the Common eiders are starting to breed. In the second period of the dataset (2003 – 2017), the timing of ice retreat is highly variable, but shows a negative trend. Of all the three linear candidate models, Mod 3 was selected based on Akaike's Information Criteria with correction for small sample sizes (AICc) (table 1b).

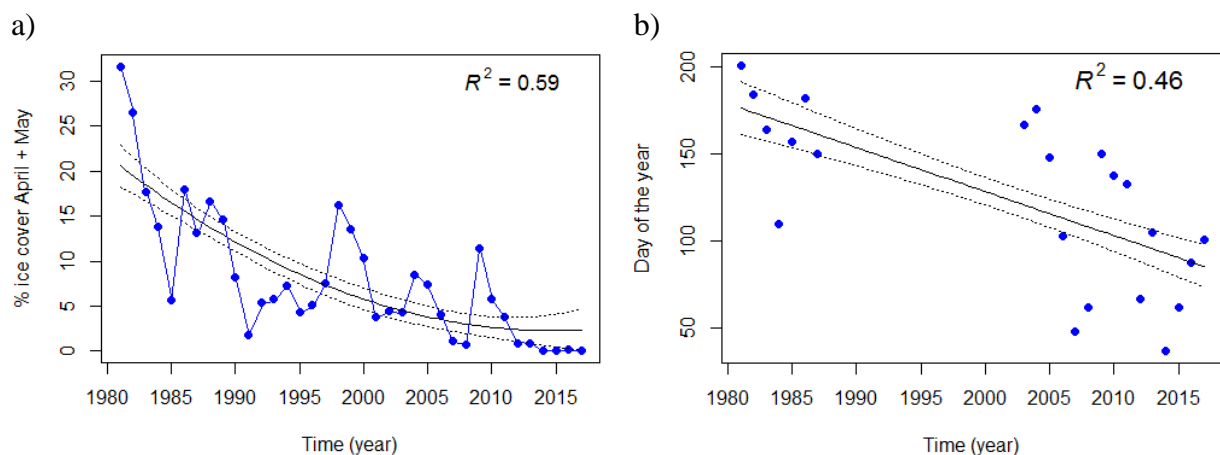


Figure 5 a) % ice cover outside NW Spitsbergen as a function of time in years. Each data point represents the mean ice concentration (%) of April and May in the given year. b) Timing of ice retreat behind Lovénøyane as a function of time in year. Each data point represents the number of days after 1<sup>st</sup> of January in the given year.

To investigate the possibility to use large-scale satellite data from outside NW Spitsbergen in substitute for local-scale ice data from Kongsfjorden, I tested how local-scale ice data was explained by large-scale data on sea ice concentration (Figure 6). From the analysis, Mod 3 was selected using AICc (table 1c). The association is strong between the two different types of ice data, indicating that the sea ice outside NW Spitsbergen is well reflected in the sea ice present inside Kongsfjorden in spring. In years where sea ice % was low (<4%) outside west-Spitsbergen, the fjord ice in Kongsfjorden had retreated before mid April. If the sea ice cover outside NW Spitsbergen was >5%, the fjord ice in Kongsfjorden has sustained until early May to early June. Based on these findings, it is therefore assumed that large-scale data on sea ice is appropriate for use in further analyses.

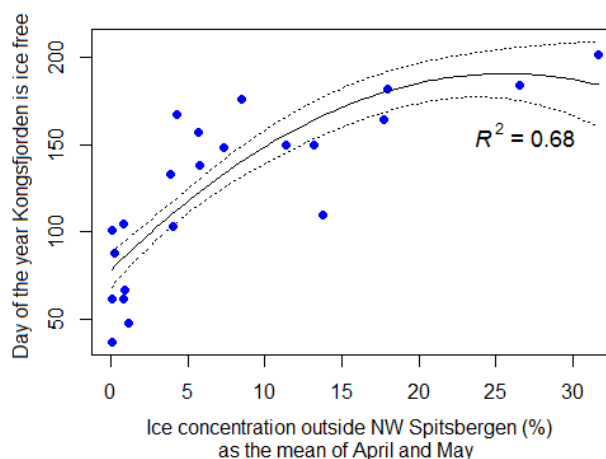


Figure 6. Correlation plot of timing of ice retreat behind Lovénøyane in Kongsfjorden as a function of % sea ice concentration outside NW Spitsbergen. Timing of ice retreat is measured as days after 1<sup>st</sup> of January, and % ice concentration is the mean of ice concentration in April and May for each year that there exists data for timing of ice retreat.

Table 1 AIC values from model selection using AICc for a) % sea ice concentration as a function of time, b) timing of ice retreat as a function of time and c) timing of ice retreat as a function of % ice concentration

	<b>K</b>	<b>AICC</b>	<b>DELTA AICC</b>	<b>AIC WT</b>
<b>A) % SEA ICE ~TIME (YEAR)</b>				
<b>MOD 3 POLYNOMIAL</b>	4	228.90	0.00	0.7
<b>MOD 2 LINEAR</b>	3	230.56	1.66	0.3
<b>MOD 1 INTERCEPT</b>	2	256.98	28.08	0.0
<b>B) ICE RETREAT~TIME(YEAR)</b>				
<b>MOD 2 LINEAR</b>	3	226.18	0.00	0.73
<b>MOD 3 POLYNOMIAL</b>	4	228.21	2.03	0.27
<b>MOD 1 INTERCEPT</b>	2	236.85	10.67	0.00
<b>C) ICE RETREAT~% SEA ICE</b>				
<b>MOD 3 POLYNOMIAL</b>	4	217.67	0.00	0.76
<b>MOD 2 LINEAR</b>	3	220.02	2.35	0.24
<b>MOD 1 INTERCEPT</b>	2	236.85	19.18	0.00

### 3.2 Total population data

The total population of breeding eiders is highly dynamic and shows great variation ( $\pm 100 - 2000$  nests) during the study period (Figure 7), and ranges from 843 - 4712 nests for years where data exists. The plotted development suggests an increase in number of nests in the first half of the study period (1981 ~ 1996), followed by a steep drop in the population in the late 1990's. The population shows a slight decrease from 1997 and onwards, despite large yearly variation in the last two decades.

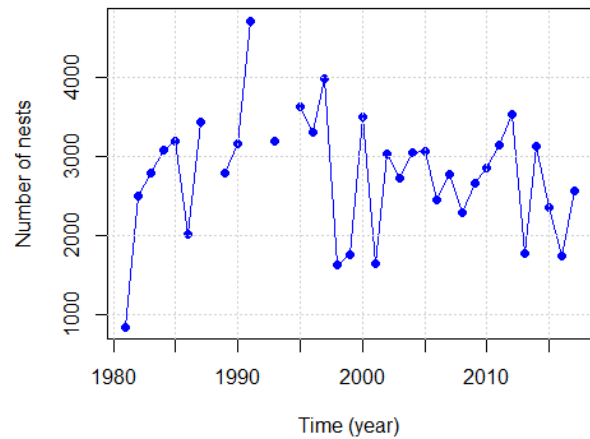


Figure 7 Total number of active nests in Kongsfjorden ( $N < 1000 - 4900$ ) plotted for all the years in the study period (1981 – 2017), except 1988, 1992 and 1994.

### 3.3 Distribution of the common eider population

The plotted number of active nests in the two island groups shows that there is a different development in the two groups (Figure 8). The early ice-free islands had a positive trend until the early 1990's, while the population declined to  $< 500$  nests in the end of the study period. The late ice-free islands show an opposite trend, where there has been a strong increase throughout the entire study period, starting from almost no nests in the early 1980's to almost 2000 nests in 2014. From the analysis using general linear models with Poisson distribution, Mod 3 was selected as the most parsimonious for both island groups using AICc (Table 2). Plots for the nest development on all the islands in Kongsfjorden can be found in Appendix A 1 and AIC values in Appendix B 1.

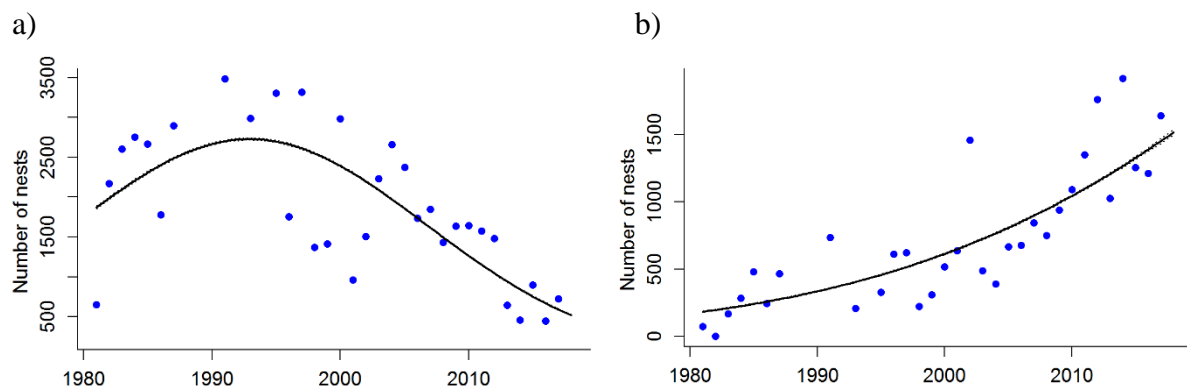


Figure 8. Number of active nests as a function of time for both a) early ice-free islands and b) late ice-free islands.

Table 2. AIC values from model selection using AICc for number of nests as a function of time for a) early ice-free islands and b) late ice-free islands.

	<b>K</b>	<b>AICc</b>	<b>DELTA AICc</b>	<b>AIC WT</b>
<b>A) EARLY ICE-FREE</b>				
<b>MOD 3 POLYNOMIAL</b>	3	6402.162	0.000	1
<b>MOD 2 LINEAR</b>	2	10291.075	3888.912	0
<b>MOD 1 INTERCEPT</b>	1	14832.707	8430.544	0
<b>B) LATE ICE-FREE</b>				
<b>MOD 3 POLYNOMIAL</b>	3	6604.130	0.00000	1.000000e+00
<b>MOD 2 LINEAR</b>	2	6648.642	44.51268	2.158714e-10
<b>MOD 1 INTERCEPT</b>	1	18521.050	11916.91979	0.000000e+00

To demonstrate that the breeding distribution has changed as a consequence of less sea ice in the fjord, the proportion of nests in the late ice-free area in relation to the early ice-free area was analysed as a function of both time and ice concentration outside NW Spitsbergen. The results shows that the proportion of nests in the late ice-free area has increased during the entire study period (Figure 9a), indicating that a change in breeding distribution has occurred. Even more importantly, it appears that the proportion of nests in late ice-free area was related to sea ice concentration outside NW Spitsbergen (Figure 9b). The proportion of nests in the late ice-free area is highest when the ice concentration is low, and for years with >15% ice, there were almost no nests in this area. For both analyses, Mod 2 was selected using AICc (Table 3).

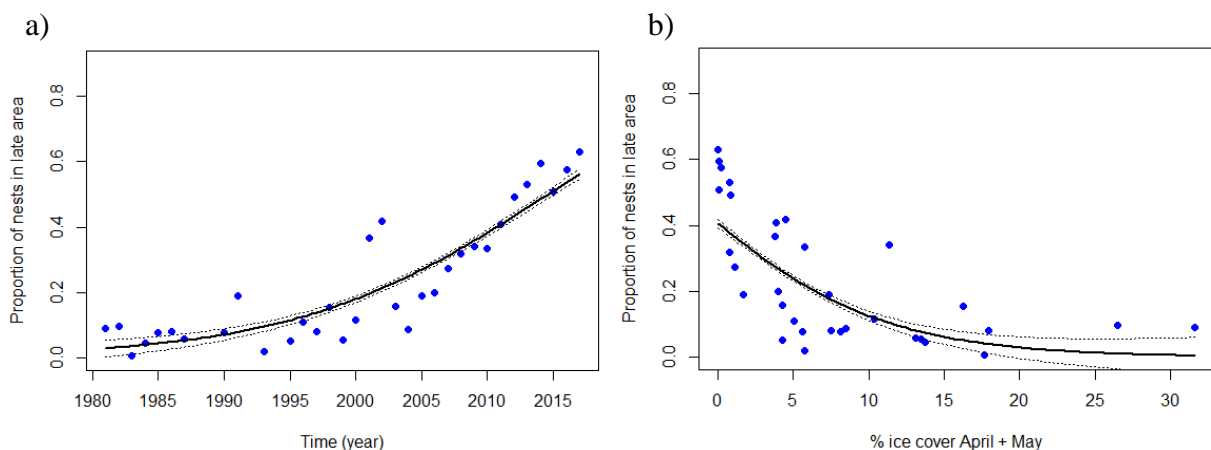


Figure 9. Proportion of nests in late ice-free area as a function of a) year (1981-2017) and b) % ice concentration outside NW Spitsbergen.

Table 3. AIC values from model selection using AICc for proportion of nests in late ice-free areas as a function of a) time (year) and b) sea ice concentration (%) outside NW Spitsbergen.

	<b>K</b>	<b>AICc</b>	<b>DELTA AICc</b>	<b>AIC WT</b>
<b>A) PROPORTION ~ TIME</b>				
<b>MOD 2 LINEAR</b>	2	4355.23	0.00	1
<b>MOD 1 INTERCEPT</b>	1	18278.12	13922.89	0
<b>B) PROPORTION ~ ICE</b>				
<b>MOD 2 LINEAR</b>	2	9907.92	0.0	1
<b>MOD 1 INTERCEPT</b>	1	18278.12	8370.2	0

### 3.4 Clutch size

The average clutch size was plotted as a function of year (1981 – 2017) for all islands and the two island areas. The results shows that there was a difference in the average clutch size in the two areas over time (Figure 10a). The average clutch size has a declining trend in the early late-free area over the entire study period. In the late ice-free area, average clutch size showed a different temporal trend and seemed to increase over time (table 4). More importantly, the correlation analysis between the two models shows that the average clutch size has changed differently in the two areas, indicating that island group and time combined have an effect on average clutch size (table 5). Plots for the nest development on all the islands in Kongsfjorden can be found in Appendix A 2, and AIC values in Appendix B 2.

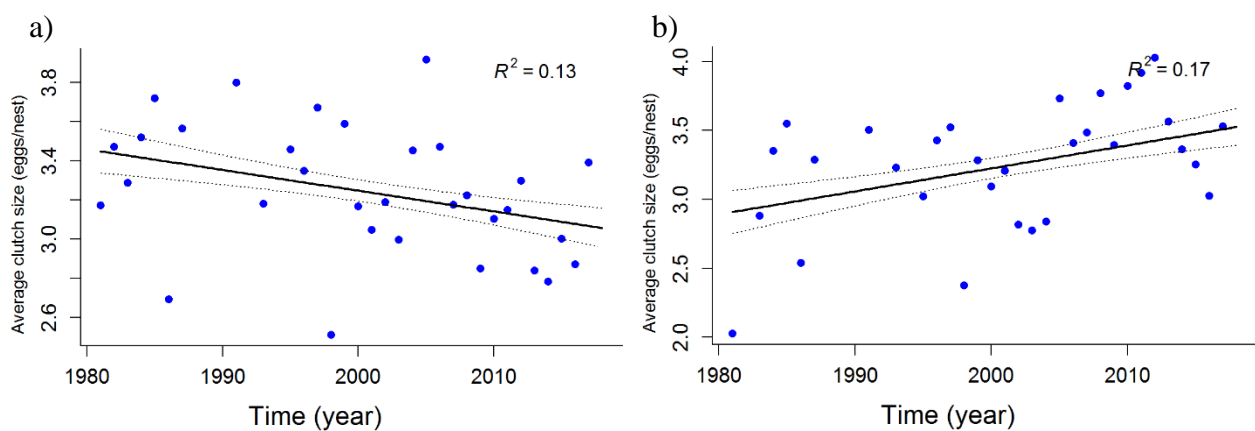


Figure 10 Average clutch size as a function of time in a) early ice-free area and b) late ice-free area.

Table 4. AIC values from model selection using AICc for average clutch size as a function of time for a) early ice-free islands and b) late ice-free islands.

	<b>K</b>	<b>AICc</b>	<b>DELTA AICc</b>	<b>AIC WT</b>
<b>A) EARLY ICE-FREE</b>				
<b>MOD 2 LINEAR</b>	3	22.02087	0.000000	0.5640007
<b>MOD 3 POLYNOMIAL</b>	4	23.67218	1.651307	0.2470034
<b>MOD 1 INTERCEPT</b>	2	24.20754	2.186661	0.1889958
<b>B) LATE ICE-FREE</b>				
<b>MOD 2 LINEAR</b>	3	39.07878	0.000000	0.6268018
<b>MOD 3 POLYNOMIAL</b>	4	40.82847	1.749692	0.2613301
<b>MOD 1 INTERCEPT</b>	2	42.52540	3.446619	0.1118681

Table 5. Estimates from the multiple regression model for average clutch size. Intercept represents the early ice-free area, year represents 1981-2017, area represents the late ice-free area and year\*area represents the correlation between year and area.

	<b>ESTIMATE</b>	<b>STD.ERROR</b>	<b>T VALUE</b>	<b>PR(&gt; T )</b>
<b>INTERCEPT (EARLY ICE-FREE)</b>	24.446173	11.463837	2.132	0.03700 *
<b>YEAR</b>	-0.010599	0.005729	-1.850	0.06916 .
<b>AREA (LATE ICE-FREE)</b>	-54.585763	16.608833	-3.287	0.00168 **
<b>YEAR * AREA (LATE ICE-FREE)</b>	0.027282	0.008299	3.287	0.00168 **

Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

## 4. Discussion

### 4.1 Summary of findings

The breeding distribution of Common Eiders in Kongsfjorden has changed during the years 1981 – 2017. Ice concentration outside NW Spitsbergen has declined substantially during the study period, and there is a strong relationship between the ice concentration outside NW Spitsbergen and the timing of ice retreat inside Kongsfjorden. Timing of ice retreat in spring has expedited, resulting in a larger area and more islands available for eiders to breed on. The results of this thesis show that the eiders in Kongsfjorden have shifted their breeding distribution from the early ice-free islands to the new available late ice-free islands as a response to a decrease in sea ice. Average clutch size has decreased in the early ice-free islands, while it has increased in the late ice-free islands over the entire study period. The results show that both area and a correlation between area and time have a significant effect on average clutch size, which implies that there are different conditions on the islands that play a role in adjusting the average clutch size.

### 4.2 Sea ice and population size

With new land available, we would expect the total population to increase in numbers. This is not the case for the eiders in Kongsfjorden. On the contrary, there seems to be a slight decline in population size. As the sea ice conditions have developed in the years 1981 - 2017, it appears that the population has to a certain degree followed the ice fluctuations (Figure 5a and 7). In years with extreme amounts of ice, for instance 1981 or a cold year like 2013, the eider population had low nest numbers ( $N_{\text{nest}} < 2000$ ). In such years, ice may have sustained in the fjord for so long that breeding could not be initiated in time. In general the growth of natural populations can eventually be constrained by an array of factors such as space, competition, resource availability, diseases, predation and so forth (Sæther et al., 2002). Sea ice may historically have been the most important factor constraining the expansion of the eiders, but today the eider population is probably controlled mainly by other mechanisms.



### 4.3 Change in distribution of nests

It is interesting to reflect upon which part of the population colonizes the newly available islands, in addition to why this happens. Our data can not answer these questions directly, but it could aid in the discussion. More female than male ducklings of common eider return to their natal breeding site (Mallory, 2015), and for eiders, newly matured individuals could be the first to colonize the newly ice free islands. The eider studies from the 1980s report that eiders arriving to Svalbard in spring spend the time foraging outside the NW coast of Spitsbergen while waiting for the ice to break up. Birds are frequently observed visiting the inner fjord to check the ice conditions, while they wait for the islands to be surrounded by open water (Mehlum, 1991). Young inexperienced individuals that have not previously bred, probably choose breeding sites based on surrounding cues. Since the fittest females often take the best nest sites (Bolduc et al., 2005, Öst et al., 2008), newcomers may be forced to choose the least inhabited islands despite the potential for protection in sites with high eider density.

Individuals that have previously failed breeding, may be likely to seek other breeding grounds. Adult individuals in Kongsfjorden are observed changing islands between breeding seasons. Yet unpublished data has found that marked females have moved as far as from Storholmen to Indre breholmen, which means that the bird has moved from her 'native' island to an island she could not even see from her original spot (Moe, B., pers.comm). Common Eiders very often show high natal philopatry that will ensure a return to the same area as previously used when it is time to breed (Swennen, 1990, Prestrud and Mehlum, 1991, Bustnes and Erikstad, 1993), but it is not well known how prone eiders are to switching between nest sites. How successful a breeding eiders' neighbours are, may give valuable information that affects the decision of where to breed (Danchin et al., 1998, Valone and Sociobiology, 2007). A study from Iceland found that the probability of switching islands decreased with increased density (Jónsson and Lúðvíksson, 2012), since this increases the social facilitation. However, this depends on successful breeding, and in the early ice-free islands in Kongsfjorden, predation may have become too severe to sustain a high breeding density. The presence of researchers on Prins Heinrich period (Bjorn and Erikstad, 1994, Gabrielsen et al., 1991) and Storholmen (Criscuolo et al., 2002, Bourgeon et al., 2006, Fenstad et al., 2016) could maybe also influence the breeding behaviour of the eiders, as these are the two islands in Kongsfjorden with most extensive research.

## 4.4 Predation and competition

The decline of eiders in the early ice-free islands has been strong since the mid '90s. At the same time, the Glaucous gull (*Larus hyperboreus*) population in Kongsfjorden has increased dramatically (Anker-Nilssen et al., 2018). Predators follow their prey, and the change in breeding distribution now observed for eiders in Kongsfjorden, might be a result of a constant search for the habitat with the lowest predator pressure. If an island becomes inhabited due to low predation, increased breeding success will after a period of time increase the density of eiders. This will consequently attract a higher density of predators. For most colonial breeding birds, a high density is beneficial against avian predators, as it dilutes the individual predation effect (Stearns, 1992). In long lived birds with a low reproduction rate, population size is often dependent on adult survival. In addition to Glaucous gulls, there are Great skuas (*Stercorarius skua*) breeding in Kongsfjorden that mainly predate upon adult eiders. It is very costly for the colony to breed among Great skuas, because as losing an adult individual removes the possibility for future reproduction.

On the contrary, a low breeding density is beneficial if the predator is an Arctic fox or a Polar bear (*Ursus maritimus*). These predators are attracted by higher densities since they will have access to more food in less time and space. In recent years, an increase in Polar bear visits has been observed in Kongsfjorden during summertime. Most probably due to less prey availability for the bears because of loss of the amount of fjord ice (Prop et al., 2015). Previous studies have shown that Polar bears can eradicate breeding populations of common eiders (Iversen, S. A, et al. 2014). Observations made by field workers in Kongsfjorden state that a bear with cubs could destroy almost all the nests on an island in one go, much because of the playfulness of polar bear cubs. The bears that have visited Kongsfjorden often had cubs with them. This probably increases the chances for returning bears in the future, since the cubs learn where there is available food. In an area with frequent visits of Polar bears we would expect a more scattered population, to minimize loss to predation. However, it is important to mention that Polar bears not only eat eider eggs, but also the eggs of Glaucous gulls. This can result in two different scenarios; either it decreases the number of predators at the island, or it increases the food for the Glaucous gulls that survive the Polar bear raids. The surviving or the non-breeding Glaucous gulls may thus be tempted to return to the island.

The Barnacle goose (*Branta leucopsis*) is another ground breeding bird in Kongsfjorden, and this species has exploded in numbers since it became illegal to hunt for in 1950 (Trinder, 2014). The barnacle goose is a somewhat more aggressive and dominant species, and it might outcompete the eider at the breeding site (Stahl et al., 2001). “Stolen nests” are observed on the islands in Kongsfjorden, where a Barnacle goose nest contains one, or in rare cases two eider eggs (Dørum, H. personal observation). This could be evidence for Barnacle geese occupying newly begun eider nests. Increased Barnacle geese numbers may yield protection against predators, but the intraspecific competition for nest sites is more likely to be in favour of the Barnacle geese if these continues to increase in numbers.

#### 4.5 Clutch size

The increase in average clutch size in the late ice-free islands is an indication that reproduction success was higher here. A change in breeding distribution therefore seems beneficial for the Common eiders in Kongsfjorden. Many of the islands in the late ice-free area were colonized around early 2000, and showed a high clutch size in the beginning followed by a decrease after some years. Observations from field workers suggest that there is a lag from when an island becomes ice-free until the first eiders start utilizing it. In addition, an even longer lag is observed until when predators also start inhabiting the island (Gabrielsen, G. W. pers comm). The increase in clutch size the late ice-free islands may be a result of higher success related to lower predator numbers in the beginning. Although clutch size will stabilize after a time in the new habitat, the first years with a higher clutch is still valuable for the individual eider.

Generally, average clutch size shows a large variation for almost all of the islands. In the early ice-free islands, only Eskjæret and Mietholmen shows a clear decline around the turn of the century, but these are also the two most dense islands in the early ice-free area. When density has decreased in the early ice-free areas, protection against predators have also gone down, and could in turn lead to a lower clutch size. Dietrichholmen always had low numbers, as it is a very small islet.

As ice retreats earlier in spring, eiders have the possibility to start breeding earlier and produce a larger clutch (Lehikoinen et al., 2006). Previous results from Kongsfjorden shows that an earlier timing of ice retreat could result in a larger clutch (Mehlum, 2012). If high success in breeding result in the female eider continues to breed on the same place in the future, it should

in theory decrease the breeding dispersal (Switzer, 1993, Öst et al., 2011). However, if predator numbers gets too high, investment may become lower because chances of getting predated upon increases (Travers et al., 2010). Predator numbers and density of nests must therefore affect the clutch size together.

How much resources are put into reproduction depends on the females body condition prior to breeding (Houston et al., 1983). A shorter incubation period is found for female eiders in good condition (Erikstad et al., 1993), and together with a longer breeding season in Kongsfjorden, there is enhanced potential for producing a larger clutch. However, not much is known about the conditions in the wintering area for Common eiders breeding in Svalbard, which is fundamental for the female eiders ability to build up reserves prior to breeding. Approximately 77 % of the Svalbard breeding eiders winter in Iceland, while the rest migrates to Northern Norway (Hanssen et al., 2016). Although warmer climate could improve breeding conditions in Kongsfjorden, the viability of the population might be negatively influenced if food availability in the wintering area decreases (Bustnes, 1998, Jones et al., 2010).

## 4.6 Conclusion and implications for conservation and further research

In conclusion, the change in distribution of Common Eiders in Kongsfjorden is indeed related to a warmer climate and the diminishing sea ice in the Arctic. New islands are utilized as breeding habitat, and together with a longer season, it opens up possibilities for an increased reproductive success. Still, it is likely that predation also plays a major role in regulating the density and reproduction for the eiders. It is not known which part of the population colonizes the new areas first, but the increased average clutch size on the new islands indicates that the eiders that moved here are more successful compared to the old islands.

To fully understand the dynamics that drive the changes in the Common Eider population in Kongsfjorden, further research is recommended. Particularly on the relationship between both egg-eating and adult-eating avian predators and eiders, as well as how the increasing Barnacle goose numbers will further affect the eider population.

It is likely that we will see an increase in Polar bear visits in Kongsfjorden in the future. Therefore it is important to continue the monitoring of eiders in order to follow the development of the population as it will interact more with different types of predators in the future.

For most islands today, there is no longer any limitation of timing of breeding start from sea ice, as the fjord is ice free all year round. Gerdøya is the only islands which is still partly affected by ice. In cold years, there is still an ice bridge connecting the island to the mainland and birds choose to breed on the other islands. In years with little or no ice, there are relatively high numbers of breeding birds in Gerdøya ( $N_{\text{nest}}=1490$ ). Gerdøya is a large island situated sheltered in the innermost parts of the fjord, with similar topography as for instance Juttaholmen, and has big potential for becoming an important habitat for future eiders. This island, in addition to Indre Breholmen, is presently not included in the bird sanctuary. This study provides evidence of high numbers and breeding consistency on Indre Breholmen since 2000 and Gerdøya since 2010. This study suggests that conservation measures are to be considered with regard to implementing these two islands in the bird sanctuary.

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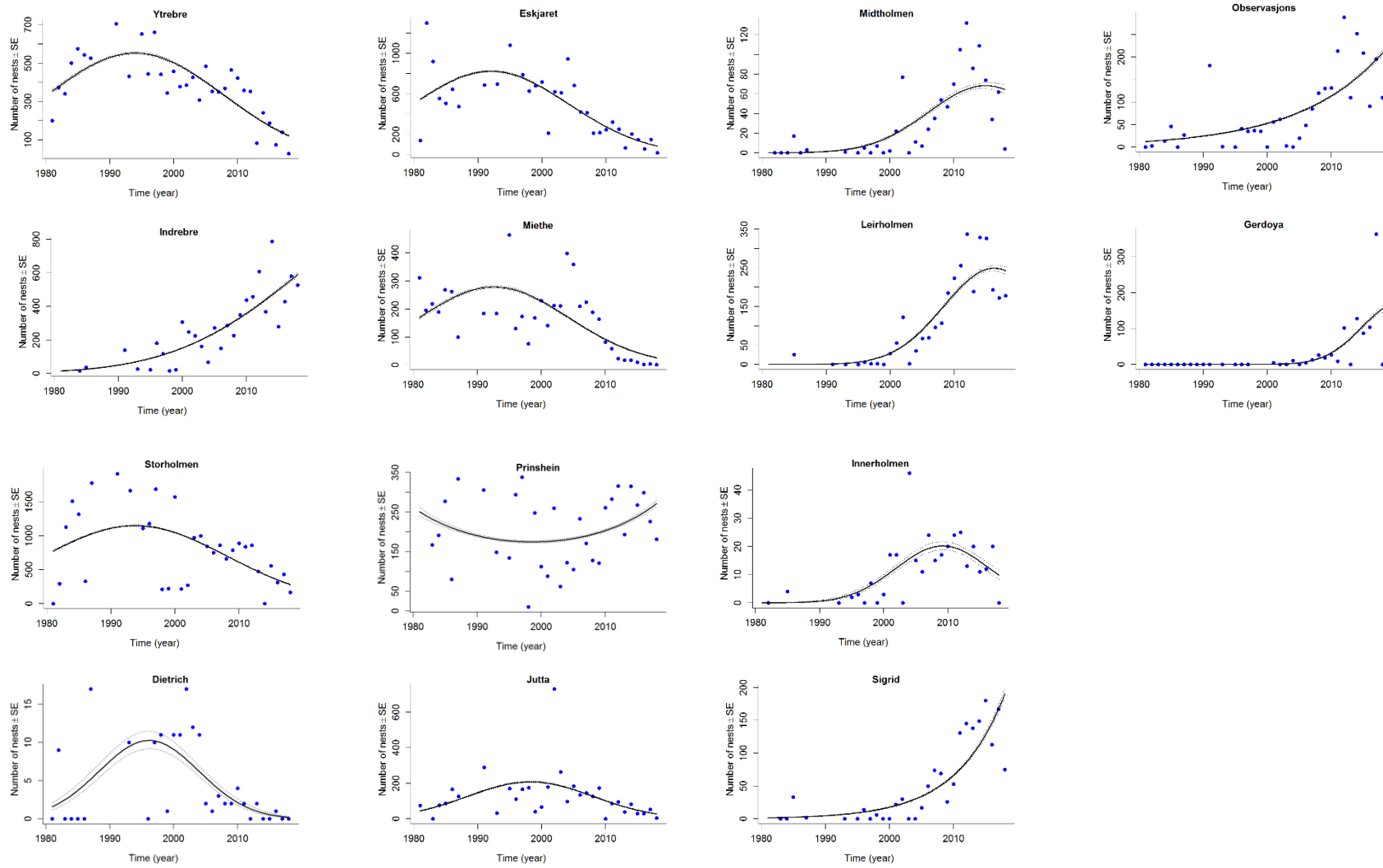
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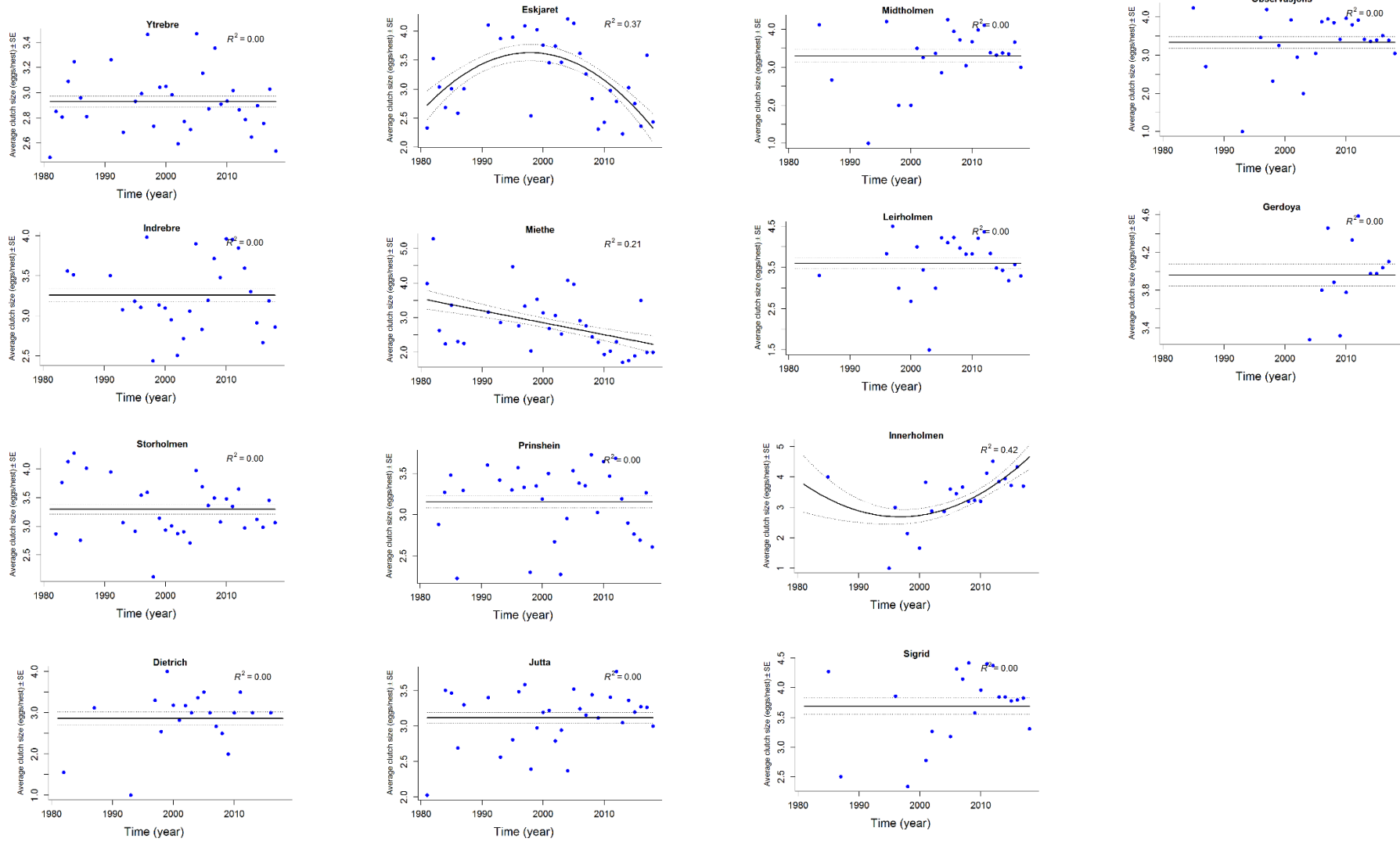
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# Appendix A 1 Population size of all individual islands in the study



# Appendix A 2

# Clutch size of all individual islands in the study



## Appendix B 1 AIC values from model selection Population size of individual islands

### DIETRICHHOLMEN

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	Dietrich	modPoT	3	134.5081	0.00000	1.000000e+00	1.000000e+00	-63.73230	1
2	Dietrich	modLmT	2	170.4095	35.90143	1.599941e-08	1.599941e-08	-82.95475	1
1	Dietrich	modInt	1	249.9180	115.40993	8.690628e-26	8.690628e-26	-123.87900	1

### ESKJÆRET

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	Eskjaret	modPoT	3	4105.151	0.000	1	1	-2049.188	1
2	Eskjaret	modLmT	2	6575.104	2469.954	0	0	-3285.365	1
1	Eskjaret	modInt	1	10265.473	6160.322	0	0	-5131.676	1

### GERDØYA

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	Gerdoya	modPoT	3	913.8723	0.00000	1.000000e+00	1.000000e+00	-453.3907	1
2	Gerdoya	modLmT	2	963.7871	49.91485	1.449199e-11	1.449199e-11	-479.6327	1
1	Gerdoya	modInt	1	2558.4281	1644.55587	0.000000e+00	0.000000e+00	-1278.1307	1

### INDRE BREHOLMEN

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	Indrebre	modPoT	3	1605.723	0.00000	1.000000e+00	1.000000e+00	-799.3614	1
2	Indrebre	modLmT	2	1650.139	44.41588	2.265762e-10	2.265762e-10	-822.8293	1
1	Indrebre	modInt	1	4799.079	3193.35664	0.000000e+00	0.000000e+00	-2398.4628	1

### INNERHOLMEN

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	Innerholmen	modPoT	3	346.1697	0.00000	1.000000e+00	9.999285e-01	-169.6563	0.9999285
2	Innerholmen	modLmT	2	365.2617	19.09197	7.148769e-05	7.148258e-05	-180.4240	1.0000000
1	Innerholmen	modInt	1	482.0917	135.92194	3.054392e-30	3.054173e-30	-239.9792	1.0000000

### JUTTA

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	Jutta	modPoT	3	2660.645	0.0000	1.000000e+00	1.000000e+00	-1326.922	1
2	Jutta	modLmT	2	3399.842	739.1974	3.057205e-161	3.057205e-161	-1697.728	1
1	Jutta	modInt	1	3534.006	873.3613	2.249120e-190	2.249120e-190	-1765.941	1

**LEIRHOLMEN**

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	Leirholmen	modPoT	3	1298.740	0.000000	1.00000000	0.91599782	-645.9255	0.9159978
2	Leirholmen	modLmT	2	1303.518	4.778342	0.09170565	0.08400218	-649.5448	1.0000000
1	Leirholmen	modInt	1	3724.044	2425.304555	0.00000000	0.00000000	-1860.9532	1.0000000

**MIDTHOLMEN**

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
2	Midtholmen	modLmT	2	1216.096	0.000000	1.000000e+00	7.606317e-01	-605.8409	0.7606317
3	Midtholmen	modPoT	3	1218.408	2.312291	3.146968e-01	2.393683e-01	-605.7754	1.0000000
1	Midtholmen	modInt	1	1596.499	380.403544	2.491266e-83	1.894935e-83	-797.1829	1.0000000

**MIETHEHOLMEN**

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	Miethe	modPoT	3	1901.129	0.0000	1.000000e+00	1.000000e+00	-947.1775	1
2	Miethe	modLmT	2	2651.496	750.3666	1.148065e-163	1.148065e-163	-1323.5604	1
1	Miethe	modInt	1	3593.441	1692.3118	0.000000e+00	0.000000e+00	-1795.6599	1

**EARLY ICE-FREE**

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	NG1	modPoT	3	6402.162	0.000	1	1	-3197.694	1
2	NG1	modLmT	2	10291.075	3888.912	0	0	-5143.350	1
1	NG1	modInt	1	14832.707	8430.544	0	0	-7415.293	1

**LATE ICE-FREE**

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	NG2	modPoT	3	6604.130	0.00000	1.000000e+00	1.000000e+00	-3298.712	1
2	NG2	modLmT	2	6648.642	44.51268	2.158714e-10	2.158714e-10	-3322.150	1
1	NG2	modInt	1	18521.050	11916.91979	0.000000e+00	0.000000e+00	-9259.469	1

**PRINS HEINRICH**

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	Prinshein	modPoT	3	2547.840	0.000000	1.00000000	0.90602816	-1270.520	0.9060282
2	Prinshein	modLmT	2	2552.635	4.795305	0.09093116	0.08238620	-1274.124	0.9884144
1	Prinshein	modInt	1	2556.558	8.718606	0.01278729	0.01158565	-1277.217	1.0000000

**SIGRIDHOLMEN**

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	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	Sigrid	modPoT	3	928.3112	0.000000	1.0000000	0.8730071	-460.7418	0.8730071
2	Sigrid	modLmT	2	932.1668	3.855625	0.1454661	0.1269929	-463.8834	1.0000000
1	Sigrid	modInt	1	2431.2268	1502.915636	0.0000000	0.0000000	-1214.5489	1.0000000

**STORHOLMEN**

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	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	Storholmen	modPoT	3	9371.644	0.000	1.000000e+00	1.000000e+00	-4682.422	1
2	Storholmen	modLmT	2	10833.627	1461.983	3.422921e-318	3.422921e-318	-5414.620	1
1	Storholmen	modInt	1	12214.057	2842.413	0.000000e+00	0.000000e+00	-6105.966	1

**YTRE BREHOLMEN**

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	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	Ytrebre	modPoT	3	5755.638	0.0000	1.000000e+00	1.000000e+00	-2874.466	1
2	Ytrebre	modLmT	2	6279.589	523.9509	1.680746e-114	1.680746e-114	-3137.623	1
1	Ytrebre	modInt	1	6471.591	715.9530	3.410264e-156	3.410264e-156	-3234.740	1

## Appendix B 2 AIC values from model selection Average clutch size of individual islands

### DIETRICHHOLMEN

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
1	Dietrich	modInt	2	45.71989	0.0000000	1.0000000	0.4149874	-20.50701	0.4149874
2	Dietrich	modLmT	3	45.90779	0.1879001	0.9103282	0.3777747	-19.20390	0.7927621
3	Dietrich	modPoT	4	47.10865	1.3887613	0.4993836	0.2072379	-18.22099	1.0000000

### ESKJÆRET

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	Eskjaret	modPoT	4	55.50113	0.0000000	1.000000000	0.987735811	-23.00982	0.9877358
1	Eskjaret	modInt	2	65.03374	9.532613	0.008511759	0.008407369	-30.30998	0.9961432
2	Eskjaret	modLmT	3	66.59227	11.091145	0.003904708	0.003856819	-29.86757	1.0000000

### GERDØYA

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
1	Gerdoya	modInt	2	16.38733	0.0000000	1.0000000	0.64638406	-5.527000	0.6463841
2	Gerdoya	modLmT	3	17.97384	1.586502	0.4523718	0.29240590	-4.486918	0.9387900
3	Gerdoya	modPoT	4	21.10150	4.714165	0.0946961	0.06121005	-3.693607	1.0000000

### INDRE BREHOLMEN

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
1	Indrebre	modInt	2	38.11519	0.0000000	1.000000000	0.72836184	-16.81759	0.7283618
2	Indrebre	modLmT	3	40.60610	2.490913	0.28780949	0.20962945	-16.80305	0.9379913
3	Indrebre	modPoT	4	43.04224	4.927046	0.08513449	0.06200872	-16.65155	1.0000000

### INNERHOLMEN

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
3	Inner	modPoT	4	51.57198	0.0000000	1.000000000	0.72723739	-20.53599	3 0.7272374
2	Inner	modLmT	3	53.86594	2.293959	0.31759464	0.23096669	-23.22709	2 0.9582041
1	Inner	modInt	2	57.28489	5.712909	0.05747218	0.04179592	-26.30911	1 1.0000000

### JUTTAHOLMEN

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
1	Jutta	modInt	2	34.01313	0.0000000	1.0000000	0.4658661	-14.78434	0.4658661
2	Jutta	modLmT	3	34.21193	0.1988003	0.9053803	0.4217860	-13.64443	0.8876522
3	Jutta	modPoT	4	36.85773	2.8445970	0.2411591	0.1123478	-13.62886	1.0000000

**LEIRHOLMEN**

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
1	Leirholmen	modInt	2	50.04965	0.000000	1.00000000	0.72390098	-22.72482	0.7239010
2	Leirholmen	modLmT	3	52.42073	2.371087	0.30558008	0.22120972	-22.57879	0.9451107
3	Leirholmen	modPoT	4	55.20832	5.158673	0.07582431	0.05488929	-22.49305	1.0000000

**MIDTHOLMEN**

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
1	Midtholmen	modInt	2	58.18783	0.0000000	1.00000000	0.52993565	-26.79391	0.5299357
2	Midtholmen	modLmT	3	58.86325	0.6754229	0.7134011	0.37805668	-25.80005	0.9079923
3	Midtholmen	modPoT	4	61.68960	3.5017673	0.1736205	0.09200767	-25.73369	1.0000000

**MIETHEHOLMEN**

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
2	Miethe	modLmT	3	80.93311	0.000000	1.00000000	0.68621546	-37.05276	0.6862155
3	Miethe	modPoT	4	82.80609	1.872986	0.39200012	0.26899655	-36.68876	0.9552120
1	Miethe	modInt	2	86.39161	5.458503	0.06526812	0.04478799	-40.99580	1.0000000

**EARLY ICE-FREE**

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
2	NG1	modLmT	3	22.02087	0.000000	1.00000000	0.5640007	-7.596644	0.5640007
3	NG1	modPoT	4	23.67218	1.651307	0.4379488	0.2470034	-7.121805	0.8110042
1	NG1	modInt	2	24.20754	2.186661	0.3350986	0.1889958	-9.903768	1.0000000

**LATE ICE-FREE**

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
2	NG2	modLmT	3	39.07878	0.000000	1.00000000	0.6268018	-16.11082	0.6268018
3	NG2	modPoT	4	40.82847	1.749692	0.4169262	0.2613301	-15.67350	0.8881319
1	NG2	modInt	2	42.52540	3.446619	0.1784745	0.1118681	-19.05580	1.0000000

**OBSERVASJONSHOLMEN**

	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
1	Observasjons	modInt	2	57.71184	0.000000	1.00000000	0.61015676	-26.57021	1 0.6101568
2	Observasjons	modLmT	3	59.03964	1.327793	0.5148414	0.31413395	-25.91982	2 0.9242907
3	Observasjons	modPoT	4	61.88547	4.173630	0.1240817	0.07570929	-25.89010	3 1.0000000



**PRINS HEINRICH**

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	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
1	Prinshein	modInt	2	38.53809	0.000000	1.0000000	0.6912826	-17.05476	0.6912826
2	Prinshein	modLmT	3	40.97117	2.433075	0.2962542	0.2047953	-17.04114	0.8960779
3	Prinshein	modPoT	4	42.32791	3.789814	0.1503323	0.1039221	-16.39472	1.0000000

**SIGRIDHOLMEN**

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	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
1	Sigrid	modInt	2	41.45757	0.0000000	1.0000000	0.48793884	-18.37585	0.4879388
2	Sigrid	modLmT	3	41.74656	0.2889877	0.8654603	0.42229167	-17.12328	0.9102305
3	Sigrid	modPoT	4	44.84346	3.3858898	0.1839769	0.08976949	-17.08840	1.0000000

**STORHOLMEN**

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	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
1	Storholmen	modInt	2	46.88958	0.0000000	1.0000000	0.4737731	-21.23051	0.4737731
2	Storholmen	modLmT	3	47.57089	0.6813085	0.7113048	0.3369971	-20.34100	0.8107703
3	Storholmen	modPoT	4	48.72512	1.8355334	0.3994100	0.1892297	-19.59333	1.0000000

**YTRE BREHOLMEN**

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	Area	Modnames	K	AICc	Delta_AICc	ModelLik	AICcwt	LL	Cum.Wt
1	Ytrebre	modInt	2	4.028434	0.0000000	1.0000000	0.5030170	0.1857829	0.5030170
3	Ytrebre	modPoT	4	4.848851	0.8204167	0.6635120	0.3337578	2.2898602	0.8367748
2	Ytrebre	modLmT	3	6.279421	2.2509867	0.3244923	0.1632252	0.2740826	1.0000000