UNIVERSITY
OF OSLO

Master thesis

Right place, right time: Influences on breeding start in three Norwegian kittiwake (Rissa tridactyla) colonies

Using GLS data to investigate timing of breeding in a colonial seabird

Mari Dønnum Klaussen

Ecology and Evolution
60 credits

Centre for Ecological and Evolutionary Synthesis (CEES)
Faculty of Mathematics and Natural sciences

Right place, right time: Influences on breeding start in three Norwegian kittiwake (*Rissa tridactyla*) colonies

Using GLS data to investigate timing of breeding in a colonial seabird

Mari Dønnum Klaussen

Mari Dønnum Klaussen

Mari.dklaussen@gmail.com

Supervisors

Joel M. Durant

Department of Biosciences, UiO

Joel.durant@ibv.uio.no

Per Fauchald

NINA Tromsø

Per.fauchald@nina.no

Arnaud Tarroux

NINA Tromsø

Arnaud.Tarroux@nina.no

Acknowledgements

First off, I would like to thank my two main supervisors Joel Durant and Per Fauchald for providing me with a challenging but rewarding project for my master's thesis. I would also like to thank my co-supervisor Arnaud Tarroux for the valuable help and insight with GLS data, and for helping me with all my problems in R. Thank you all for your invaluable knowledge and for answering all my questions about kittiwakes, and for the helpful feedback on my research and writing.
I would also like to thank Signe Christensen-Dalsgaard and Nina Dehnhard for providing me with lots of information about my study colonies and wonderful pictures of kittiwakes, and for sharing your knowledge and enthusiasm about kittiwakes with me. Thank you also to Håvard Frøysa at HI for doing the drift modelling for me, and for answering my questions about how drift modelling works.

A huge thank you to all my friends and fellow master students for supporting me and cheering on me, even though you don't know anything about seabirds. An especially huge thank you to you Jackie, for being such an amazing friend during these two years and for sharing so many experiences, both good and bad, both in Norway and in France.
I would also like to thank my boyfriend, Audun. Thank you for all your love and support, and for lifting me up when I felt like nothing was going the way I wanted them to. You have listened to so many of my rambling monologues about seabirds, never failing to be interested, and for that I am very grateful.
Lastly, I would like to thank my family. To mom and dad, thank you for introducing me to the field of biology from the very beginning, for taking me along on fieldwork and for showing such enthusiasm and passion for your field. Thank you, Thomas, for being the most wonderful brother and for being supportive, even though I know the rest of us in the family sometimes talk about biology too much.

Abstract

The North Atlantic is a highly seasonal environment where species need to be able to time their breeding to optimal conditions in order to successfully breed. One such species is the black-lagged kittiwake (*Rissa tridactyla*), a colonial seabird nesting along the Norwegian coast.
Several aspects of the kittiwake breeding cycle, such as egg laying, hatching timing, brooding, and breeding outcome, have been extensively studied in both the North-Atlantic and the North-Pacific. Timing of breeding or breeding start, however is a less studied event in the kittiwake breeding cycle, but it has been indicated that this event is of importance to other aspects of the breeding cycle (Goutte et al. 2014; Shultz et al. 2009). The North Atlantic is expected to undergo drastic changes under climate change in the coming decade. Understanding how the phenology of seabirds such as the kittiwake is affected by the environment is important, as it provides insight into how this species will be able to cope with the coming changes in the environment.

Several studies have indicated that large-scale and local environmental variables can have an effect on the breeding cycle of seabirds (Frederiksen, Harris, et al. 2004; Frederiksen et al. 2013; Moe et al. 2009; Lauria et al. 2012). This is thought to be partially due to the environmental effects on prey populations within the foraging range of seabird colonies. Sizes of the breeding population has also been found to effect both arrival at the colony and egg laying in seabirds (Votier et al. 2009; Merkel et al. 2019; Kokko, Harris, and Wanless 2004).
This study investigated how the factors in the environment, such as NAO and local SST, and size of the breeding population influences the breeding start in three Norwegian kittiwake colonies, using conductivity data collected by GLS. In this study breeding start was defined as the time when individuals start to guard their nest and prepare for egg laying.

It has also been suggested in previous studies that advection of prey with the currents along the Norwegian coast could be an important factor during the breeding season of colonial seabirds, as they are dependent on food being supplied within the foraging range as food availability depletes through the season (Sandvik et al. 2016; Burr et al. 2016). Differences in breeding start between colonies as a result of prey advection between colony locations was therefore also investigated.

Results indicated that spring SST and population sizes advanced breeding start for the study colonies, with higher SST values and larger populations leading to earlier breeding start, while no effect was observed for NAO. This has potential implications for the future, as temperatures are expected to increase, shifting species northwards. It was not possible to fit a model to investigate the effect of prey advection, due to very small numbers of observations. And it was therefore not possible in this study to conclude anything about the potential effect of prey advection on synchrony in timing of breeding between colonies.

Small sample sizes were a prevailing problem throughout the statistical modelling of this project, and solutions and advice for the future is provided at the end of the thesis.

Contents

1 Introduction

Many of the worlds bird populations experience drastic declines both globally and locally (Dias et al. 2019). This is also the reality for the Norwegian populations of black-legged kittiwake (*Rissa tridactyla*) (hereafter referred to as kittiwake) (Fauchald et al. 2015). Globally the kittiwake is listed as vulnerable (VU) with declining numbers by the IUCN red list of endangered species (IUCN 2017). Declines have been linked to changes in the environment and human activities such as fishing (Fauchald et al. 2015), and the breeding season seems to be an especially vulnerable period, as both adults and chicks are affected (Christensen-Dalsgaard et al. 2018; Christensen-Dalsgaard, May, and Lorentsen 2018; Hamer et al. 2008; Bech et al. 2002)

Understanding how kittiwakes respond to their environment is therefore important in order to understand how this seabird will be affected by climate change in the future.

1.1 Kittiwake breeding cycle and foraging behaviour

To be able to understand how kittiwakes are affected by factors in their environment during a vulnerable period such as the breeding season, and how this might impact the start of breeding, it is important to understand the ecological adaptions and behaviour of the kittiwake during said period. Understanding the behaviour of individuals in the period leading up to the breeding season and during the breeding season is also important for interpretation of the time-series data used to extract estimates for breeding start in this study (outlined in section 2.3).

1.1.1 Kittiwake breeding cycle and behaviour

Kittiwakes return to the vicinity of the colony sometime between January and March (Figure 1-1 and Figure 1-2). Some individual variation exists, linked to sex, age, choice of wintering area, and breeding outcome of the previous breeding season (Bogdanova et al. 2011; Coulson 2011; Wooller and Coulson 1977).

The time of arrival at the colony site in the pre-breeding period can have both negative and positive impacts on the rest of the breeding season, depending on when the adults arrive (Rotics et al. 2018). Arriving early means having access to better nest-sites, sufficient time for partner-bonding, and sufficient time to forage before the egg laying. It is especially important for the females to the able to forage extensively in the pre-breeding period to have enough energy to develop healthy eggs (Gill, Hatch, and Lanctot 2002).

At the same time, arriving early means that the pair, especially the male, will use more energy to protect the nest site from competitors, and have less time to improve physical condition before the physically demanding breeding period (Coulson 2011; Chardine 1983).

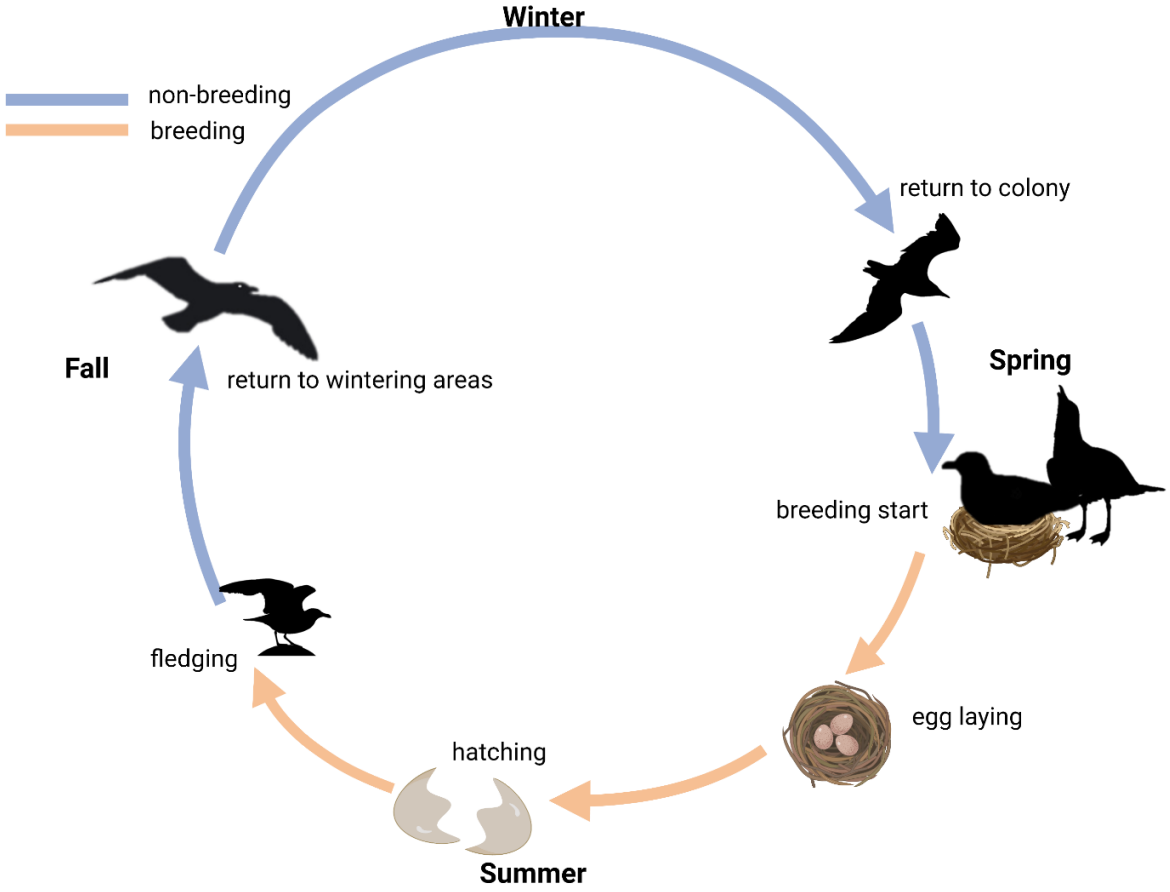

Figure 1-1: kittiwake breeding cycle. The breeding season starts in spring and ends in late summer when chicks fledge from the nest. After the breeding season, individuals return to their wintering areas. Most of the Norwegian kittiwake populations overwinter in the North-West Atlantic, with many colonies overlapping in wintering areas. Created using https://www.biorender.com/.

A variety of behaviours have been observed in kittiwakes when it comes to the arrival at the colony to begin a new breeding cycle. Some individuals return briefly early in the year, but this first visit to the colony is often not permanent. Many birds will leave and often travel far away from the colony after the initial visit to forage, before coming back months or weeks later to participate in the breeding season (Coulson 2011). Other individuals will return to the site of the colony early in spring, closer to the breeding season, and some very few individuals never leave the site of the colony after ending the previous breeding season (Coulson 2011). Some of this variation can be explained by age, with older, more experienced individuals tending to arrive earlier and use more time defending the nest site (Hamer et al. 2008; Coulson 2011; Chardine 1983).

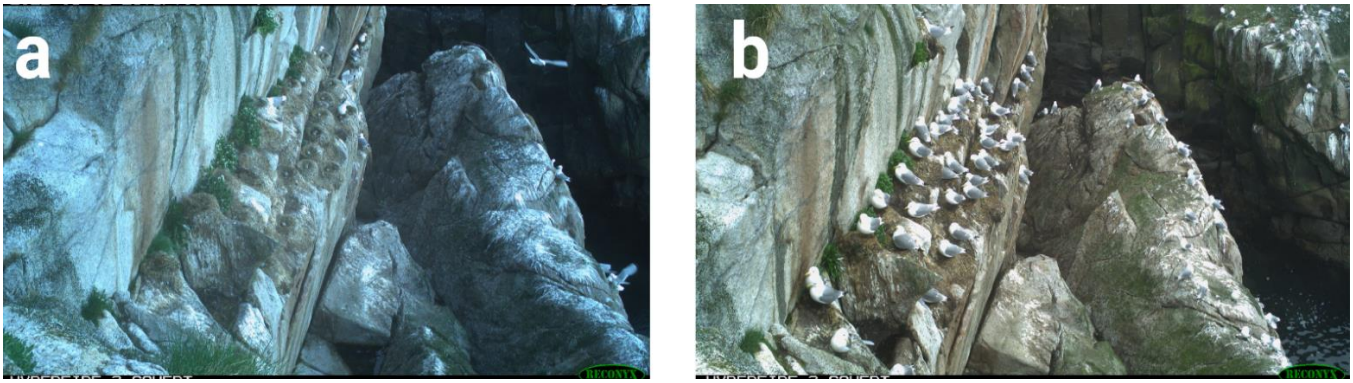

Figure 1-2: Reoccupation of Anda. Early in the year few birds occupy the colony (a). Later in the season more nests are occupied (b) and the activity in and around the colony rises. Pictures provided by Signe Christensen-Dalsgaard.

Differences between sexes have also been observed in kittiwakes. As mentioned previously, females need to have enough built-up energy to produce eggs, and often leave the site of the colony to forage, being gone for some time, and in the meantime the males defend the nest-site and can be observed closer to the colony (Coulson 2011; Gill, Hatch, and Lanctot 2002).

In spring the first pairs begin to form, and the level of activity in and around the colony rises (Figure 1-3). Kittiwakes tend to be monogamous, choosing the same partner every year, but unsuccessful breeders have a higher probability of choosing a different partner the following season (Mercier, Yoccoz, and Descamps 2021; Ens, Choudhury, and Black 1996).
Behavioural differences have been observed between newly formed pairs and more established pairs. New pairs use more time on partner bonding and have a higher nest attendance in the pre-breeding period (Angelier et al. 2007; Chardine 1983). Years of high breeding failure could therefore lead to a higher divorce rate and thus alter the population wide pre-breeding behaviour the following season.

Figure 1-3: Pairs occupying nest-site during the day during early stages of the breeding season. Pictures provided by Nina Dehnhard.

As the egg laying approaches, individuals visit the nest site more frequently, often occupying and tending to the nest more during the day, while spending the night at sea, resting and foraging (Roberts and Hatch 1993; Coulson 2011). A shift to a more complete diurnal nest attendance can be observed closer to the egg laying, as the number of hours per day spent at the nest increases as the date of egg laying approaches (Coulson 2011).

Intense nest building begins approximately 7-14 days before the egg laying. The male and female will take turns defending the nest and spending the time away from the nest-site to forage for food and materials for nest. The pair also participates in courtship feeding, where the male feeds the female a portion of his food. This shift system is a precursor to the patterns exhibited during the incubation period and early chick rearing (Figure 1-4) (Coulson 2011).

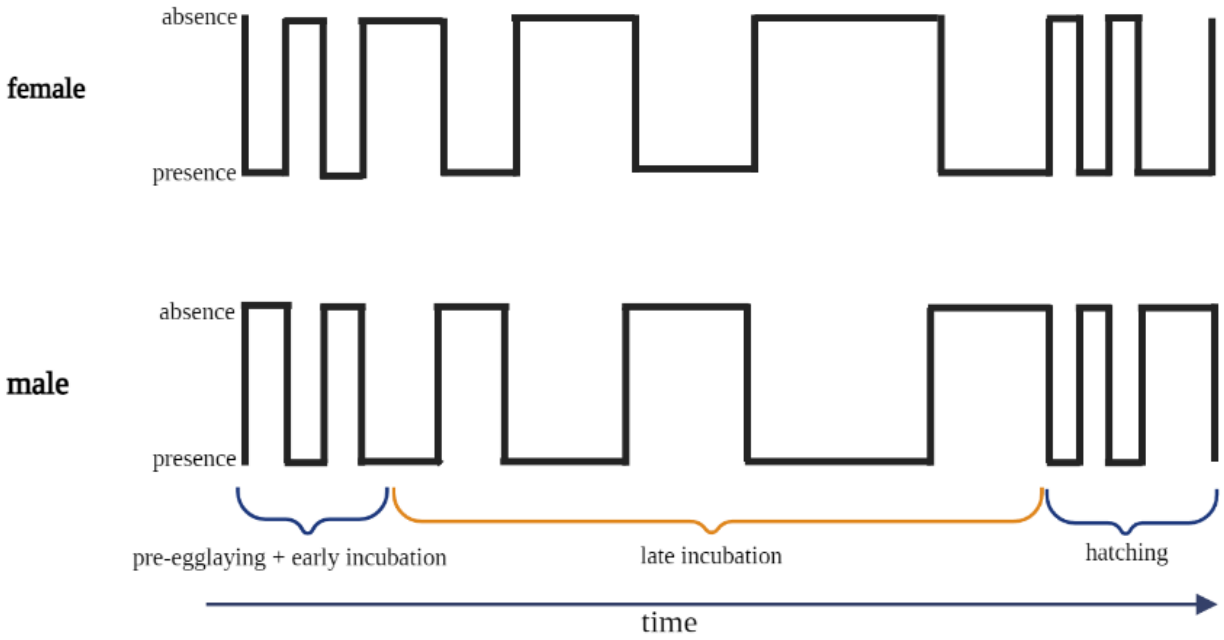

Figure 1-4: changeover patterns or stints in breeding kittiwake pair over time. In the period before and right after egg laying the change overs are rapid and become longer over time. In the first weeks after hatching the changeovers become rapid once again, until chicks can be left alone while both parents forage. Modified from (Coulson 2011). Created using https://www.biorender.com/.

The incubation period in kittiwakes lasts for approximately 28 days. The clutch size is usually 1-2 eggs, but clutch sizes of 3-4 eggs can occur (Coulson 2011). Eggs are often laid at 1-2 day intervals, extending the total incubation period depending on how may eggs are laid (Runde and Barrett 1981). Both parents participate in incubation, taking turns staying on the nest to incubate and self-maintaining by foraging and/or resting. The end of an incubation interval, or stint, is marked by a change-over from one partner to the other. The switch of incubating parent needs to happen quickly so that the egg(s) are not exposed to the cold air-temperatures for too long (Coulson 2011).

In the beginning of the incubation period the incubation stints are short, with many changeovers occurring in one day (Figure 1-4).
After approximately 10 days the intervals between incubation stints become longer and the number of changeovers per day decreases. The interval length is usually quite regular, except for overnight incubation. One individual will often stay on the nest throughout the night, and the changeover pattern resumes the following day (Coulson 2011; Chardine 1983).
This pattern of longer incubation intervals will continue until the eggs hatch in late summer (Figure 1-1). Once the chicks have hatched the changeovers become more frequent once again (Figure 1-4), as the chicks need food frequently to meet their caloric need in order to grow, and cannot be left unattended the first two to three weeks after hatching because of risk of predation and hypothermia (Coulson 2011). When the chicks reach a certain size, they can be left unattended for short periods, while both parents forage. This usually happens around 20 days after hatching but is more dependent on the size of the chick rather than the age (Coulson and Porter 2008). A steady supply of food has been found to be especially important in the early stage of chick rearing, with underfed chicks fledging later and at lower weights (Hamer et al. 2008; Gill, Hatch, and Lanctot 2002).

1.1.2 Foraging adaptions and behaviour during the breeding season

During the breeding season, kittiwakes are central place foragers, with the breeding site as the centre of their foraging ranges. The foraging trips are primarily determined by the maximum length between feeding intervals for the chicks or incubating partner, how long the chicks can be left unattended, food availability and quality in different foraging habitats, and the body condition of adults (Sandvik et al. 2016; Christensen-Dalsgaard, May, and Lorentsen 2018).
Predation pressure could also influence the foraging range of breeding kittiwakes. A higher number of predators means that parents cannot leave the chicks unattended for too long, as the risk of predation increases with the length of parental absence (Anker-Nilssen, Fayet, and Aarvak 2023).

The composition and size of available prey species also plays an important role in kittiwake foraging activity (Ropert-Coudert et al. 2009; Christensen-Dalsgaard, May, and Lorentsen 2018). The kittiwake is a relatively small seabird and can therefore not carry or digest prey of larger sizes, restricting them in regard to species of prey, but also year-class of prey species (Figure 1-5) (Monaghan 1996; Coulson 2011).

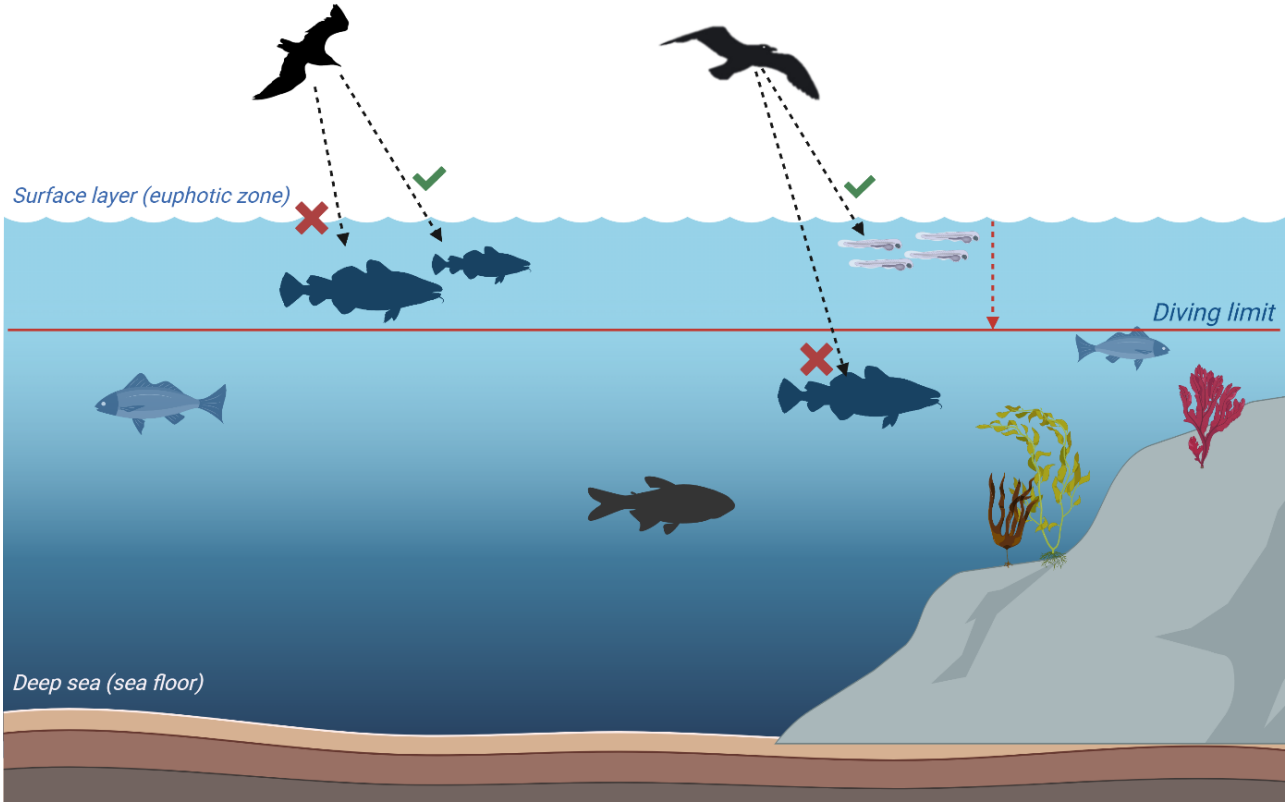

Figure 1-5: The kittiwake is limited to both the size and prey species when foraging. Species below the diving limit are unavailable for hunting (bird 2). Fish of larger sizes can be difficult for the kittiwake to handle and is therefore not an available food source (bird 1). Created using https://www.biorender.com/.

Kittiwakes are pelagic feeders; they are specialized for flying longer distances and forage in the upper parts of the water column, depending on what diving technique they use in a specific foraging attempt (Coulson 2011; Galbraith 1983). They are therefore restricted to prey available within their diving range but can cover a wide area of potential prey patches. Access to predictable foraging habitats with high food availability is therefore essential for breeding kittiwakes. Predictable feeding areas can arise in areas where prey is made available by biological forcing or vertical migration (Paredes et al. 2012; Kaartvedt 2000).

Along the Norwegian coast there are several productive upwelling zones linked to the continental shelf (Kostianoy, Nihoul, and Rodionov 2004). These upwelling zones are linked to the two main-currents off the coast of Norway, the Norwegian Coastal Current (NCC) and the North Atlantic Current (NAC) (R.T. Barrett, Lorentsen, and Anker-Nilssen 2006; Skjoldal, Dalpadado, and Dommasnes 2004) (Figure 1-6). The proximity of these upwelling-zones to the kittiwake colonies are however not evenly distributed. Off the coast of central Norway, the shelf is quite wide, putting the shelf break and productive up-welling zones more than 300km from the colonies. Further north

along the coast, near Lofoten, the shelf becomes narrower with the shelf break being as close as 10km from some of the kittiwake colonies (Christensen-Dalsgaard, May, and Lorentsen 2018). The shelf is also quite narrow close to Runde (Figure 1-6).

Despite these differences in travelling distance for the different colonies, the different foraging habitats are used to the same extent in colonies close to and far from the shelf break (Christensen-Dalsgaard, May, and Lorentsen 2018). To be able to compensate for longer trips, individuals in colonies far from the shelf break have to consume a larger amount of food in order to both cover the cost of making the trip and secure food for themselves or the chicks (Stephens and Krebs 1986). The fact that individuals from colonies far from the shelf utilize these foraging habitats suggests that these areas provide kittiwakes with a high and predictable food abundance and quality (Christensen-Dalsgaard, May, and Lorentsen 2018).

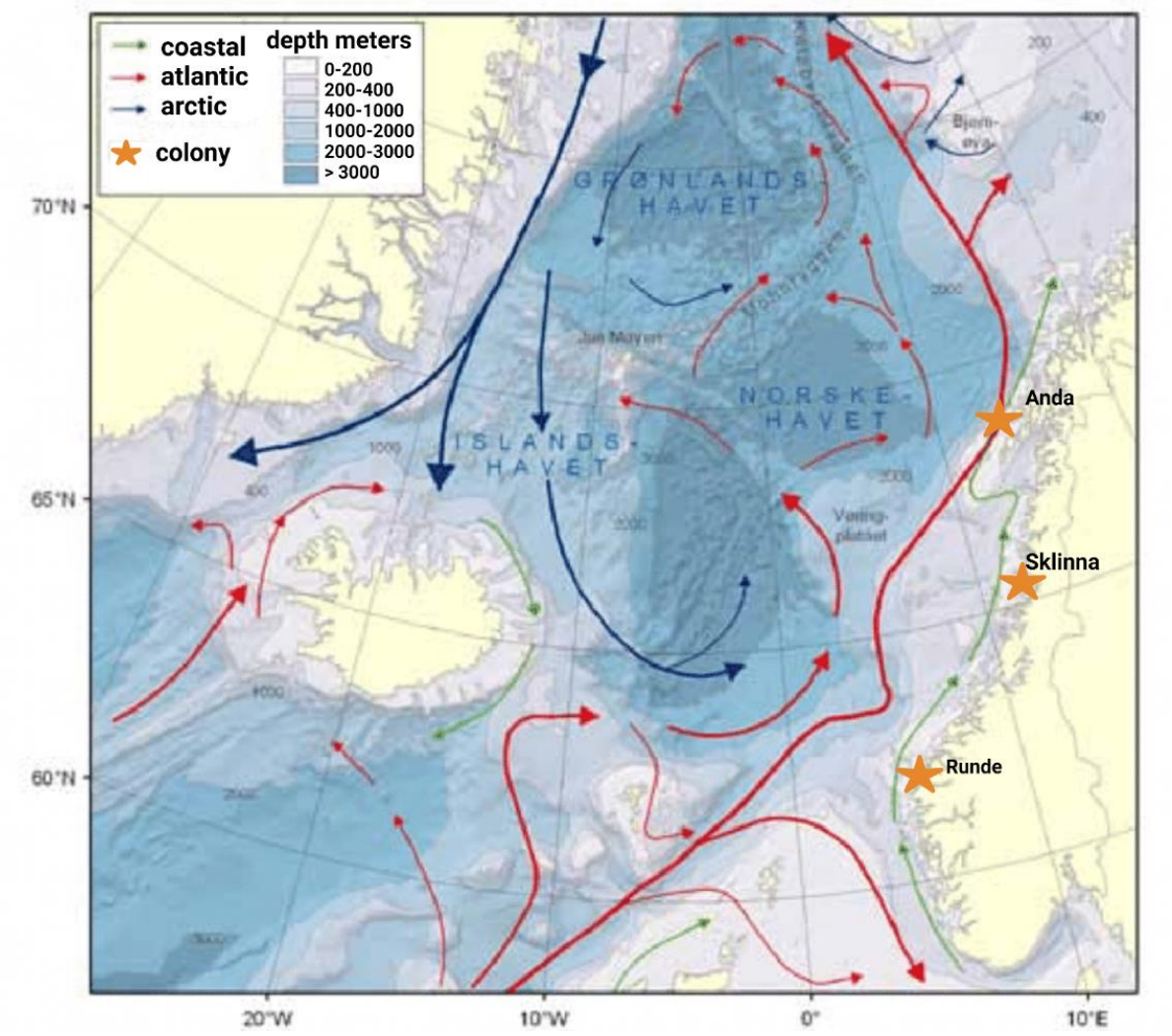

Figure 1-6: Map with major currents in the North-Atlantic and depth, modified from (Kålås et al. 2010). Sklinna has a considerably shallower coast compared to the two other colonies.

If prey availability becomes too low in proximity to the colony, different strategies can be applied to overcome the shortage of food.
One such strategy is to switch to other prey species, for example by switching from their favoured prey to a more available, but less favourable prey species. Intensifying the time spent foraging in the prey patches and extending the foraging trips to increase the chance of successfully discovering prey are also common strategies and are often employed simultaneously, and has been observed in breeding kittiwakes (Chivers et al. 2012; Christensen-Dalsgaard, May, and Lorentsen 2018).
Because of their foraging adaptions, prey switching might be limited for kittiwakes and can only be done when alternative food sources meeting the foraging criteria are available (Hamer et al. 2008; Robert T. Barrett and Furness 1990; Christensen-Dalsgaard, May, and Lorentsen 2018).

By employing one or more of these tactics, kittiwakes can adapt to the fluctuations in food availability during the pre-breeding period and breeding season. Some disadvantages are however observed in these scenarios.
Preferred prey species and year-classes often have a higher caloric density, meaning that kittiwakes have to spend less time and energy on obtaining enough food, both for themselves and the chicks, resulting in better outcome of the breeding season (Christensen-Dalsgaard et al. 2018; Hamer et al. 2008). Prey switching could therefore lead to breeding failure as unfavourable prey species do not meet the feeding requirements of chicks (Hamer et al. 2008; Christensen-Dalsgaard et al. 2018).

Extending the foraging range and foraging intensity can have a negative impact on the breeding season, both during incubation and chick rearing. When more time is allocated to foraging, the intervals between changeovers during incubation and early chick rearing become longer (Gill, Hatch, and Lanctot 2002). For the incubating partner this means longer periods without food and can result in the incubating partner leaving the nest to forage, leaving the eggs without protection from the weather or predators, or in worst case abandoning the nest completely (Hamer et al. 2008).
Chick growth during brooding is rapid, and correct growth to meet favourable weights in time for fledging depends on a constant food supply of food items meeting the caloric needs of chicks (Coulson 2011). When foraging trips increase in length during years of low prey availability, chicks are fed at more irregular intervals and the likelihood of the nest being left unguarded increases, ultimately increasing the risk of breeding failure (Hamer et al. 2008).

A built-up energy reserve, obtained during the early stages of the breeding season, might therefore be crucial since it can act as a buffer against low food availability in later phases of the breeding season, and thus prevent breeding failure.

Well-fed individuals with better body condition can take longer foraging trips with fewer rests, resulting in more time being allocated to foraging attempts and return to the nest at favourable times to feed and look after the chicks (Christensen-Dalsgaard et al. 2018). It has been suggested that low food availability in the early breeding period, resulting in adults with low body condition, could carry over to the chick rearing and result in breeding failure, even when food availability is high during brooding (Hamer et al. 2008).

Understanding what influences the breeding start for kittiwakes is therefore important, as some of the difficulties colonies face with respect to breeding outcome, might already arise early in the breeding season.

1.2 Factors influencing the onset of breeding in kittiwakes

It has been suggested that initiation of breeding depends on resource availability during the period between arrival and breeding (January-March) and/or the early breeding phase (April-May) (Frederiksen, Harris, et al. 2004; Shultz et al. 2009).

Sand eels (*Ammodytes ssp.*), a very important food item for many kittiwake colonies, for example is only available after emerging from the seafloor after lying dormant through the winter, and is therefore not available until spring in many regions (Frederiksen et al. 2007). Low food availability in the early stages of the breeding season might therefore affect when individuals initiate breeding, since birds with poorer body condition have to prolong the period of pre-breeding in order to reach good physiological condition (Goutte et al. 2014).

This might be especially important for females, since better physiological condition is linked to gonad development and healthy development of eggs (Gill, Hatch, and Lanctot 2002). In studies on fed vs. unfed individuals, fed individuals laid eggs earlier than their unfed counterparts, indicating that favourable food conditions before egg laying could influence the timing of breeding and egg laying (Gill, Hatch, and Lanctot 2002).

Many fish species, such as herring (*Clupea harengus)*, sand eel (*Ammodytes ssp.)*, capelin (*Mallotus villosus)*, saithe (*Pollachius virens*), and *Gadus* species, spawn along the Norwegian coast (Olsen et al. 2010). Fish larvae are an important food source for kittiwakes, as the larvae are small enough for the kittiwakes to forage on and have a high caloric density (Lewis et al. 2001). The importance of each fish species as a food item can vary between kittiwake colonies. At Anda, kittiwakes have been observed to forage mainly on sandeel in the coastal regions close to the colony, while foraging on mesopelagic fish in oceanic foraging habitats during the breeding season (Christensen-Dalsgaard et al. 2018).

After spawning, fish eggs and larvae are transported along the coast up to the Barents Sea with the NCC (Olsen et al. 2010). This food source is therefore not stationery and availability fluctuate with the drift, and high larval densities have been correlated with the distribution of sea bird colonies along the coast of Norway (Sandvik et al. 2016). Larval drift and fish spawning grounds therefore play important roles during the breeding season by supplying colonies with food inside the foraging range (Sandvik et al. 2016).

If dependency on the same prey species and prey populations for kittiwake colonies along the Norwegian coast is assumed, colonies closer to large spawning grounds might start the breeding

season earlier than colonies situated further away from spawning grounds, as these colonies must wait for the larval drift to transport prey into the colony foraging range to increase the food availability within the foraging range.
An inter-annual synchrony of breeding start between colonies, going from south to north with the transport of prey, with colonies to the south starting breeding earlier, might therefore arise along the Norwegian coast, and has been suggested in previous studies (Burr et al. 2016).

Spawning and development of fish species has been found to be dependent on environmental variables, both large-scale and local, such as the North Atlantic Oscillation (NAO) and sea surface temperatures (SST) respectively (Stige et al. 2006; Ottersen et al. 2001). Fluctuations and changes in these environmental variables could therefore influence the food availability of kittiwakes. In fact, studies have shown that the NAO has an effect on the breeding season and the breeding phenology of some arctic bird species (Frederiksen, Harris, et al. 2004; Lewis et al. 2009).
The connection between breeding phenology and SST has a larger spatial variation than that of breeding phenology and NAO indexes, with some kittiwake colonies having very weak relationships to local SST values (Lauria et al. 2012; Frederiksen et al. 2007). However, SST values have been linked to fish recruitment (Dippner 1997; Stige et al. 2006), and colder winter SST for example has being associated with better recruitment in sand eel in the North Sea, a very important prey species for many of the region's kittiwake colonies (Frederiksen, Wanless, et al. 2004). Similar patterns between local SST and kittiwake breeding phenology might be expected in the Norwegian Sea region as kittiwakes here have similar diets to that of colonies in the North Sea.

In addition to the environment, the size of the breeding population might also influence when individuals decide to breed. Larger populations mean a higher competition pressure for the best nest sites, and has been found to drive the reoccupation of the colony in different seabird species (Merkel et al. 2019; Kokko, Harris, and Wanless 2004). At the same time, larger populations can offer protection from predators during the early stages of the breeding season. Indeed, individuals have been observed to be more courageous when the number of occupied nests are larger (Coulson 2011).

1.3 Study aims

Kittiwake colonies are distributed over a large area and are possibly affected by both local and large-scale processes and events. Understanding what drives the decision to breed in kittiwakes and what drives local variation is important to be able to understand how climate change, changes in prey dynamics and population sizes might influence these kittiwake populations differently in the future.

The relationship between egg laying, breeding success and environment have been studied in many kittiwake colonies both in the Atlantic and the Pacific. The start of breeding activities and its relation to the environment, however, is a less studied part of the kittiwake breeding cycle.
Still, the timing of breeding activities has been found to affect both the egg laying and success of the breeding season in some colonies (Goutte et al. 2014; Shultz et al. 2009). Investigating what drives the timing of breeding could therefore provide useful insight about how kittiwakes interact with their environment in the early stages of the breeding season.

The aim of this study was therefore to investigate what drives the breeding start in Norwegian kittiwake colonies, in order to better understand how changes in the environment and fluctuations in population sizes might alter trends in kittiwake breeding phenology in the future.

Several research questions were developed to reach the aims of the study:

1. Can breeding start in Norwegian kittiwake colonies be explained by regional or local environmental factors?
2. Is breeding start in Norwegian kittiwake colonies influenced by the size of the breeding population?
3. Can inter-annual synchrony in breeding start between colonies be explained by the passive transport of prey between colonies?

1.4 Hypotheses

Three hypotheses were formulated as a motivation for investigating the chosen aims of the study. These hypotheses reflect what I expect the results of the thesis to show. Hypotheses and the reasoning behind them are given below.

H1: Changes in large-scale and/or local environmental variables advance or delay breeding start in kittiwake colonies.
Reasoning: Changes in the environment might affect zooplankton and fish populations in the Norwegian Sea, indirectly affecting the timing of breeding in kittiwakes through changes in food availability.

H2: Larger population sizes leads to earlier breeding start.
Reasoning: Larger population sizes of participating breeders would increase the competition for nest sites and food, potentially advancing the breeding start, as starting earlier would mean access to better nest sites and longer time to forage to achieve better body condition. Larger populations might also provide protection from potential predators.

H3: A time-lag between colony breeding start from south to north is created by the prey advection between colonies. Where colonies to the north starting breeding later than colonies to the south.
Reasoning: Currents travel from south to north along the coast of Norway, and fish larvae is therefore advected from spawning grounds further south, up towards the Barents Sea, transporting prey past kittiwake colonies on the way.

2 Methods

The project consisted of two main parts; obtaining estimates for timing of breeding, or breeding start, for the sampled individuals using data collected by GLS loggers fitted to the individuals (section 2.3), and statistical analysis of said estimated breeding start dates (section 2.4). The methods used in this project will be discussed in the order they were conducted, but before that I will provide some background of the data that was used to estimate breeding start (section 2.1-2.2).

2.1 Global Location Sensors

The data used in this study was collected using Global Location Sensors, or GLS loggers. The logger is fitted to the leg of the bird during fieldwork. Fieldwork is conducted during the breeding season when adults are present at the colony. Additional data on sex, partner, breeding status and breeding stage, as well as some measurements on chicks (if present), is also collected to a varying degree with respect to the colony and year the fieldwork was conducted.

The loggers are light-weight and have not been found to interfere with the behaviour or movement of tagged individuals (Ropert-Coudert et al. 2009; Nicoll et al. 2022). In order to access the data, the logger must be retrieved, and the data downloaded. Therefore, there might be missing data for specific years where an individual was not re-captured.

GLS loggers record ambient light (Figure 2-1) every three seconds, and every 10 minutes an average value is saved, each recorded value from the logger is therefore the average over the last 10-minute period. Multiple types of loggers were used to tag individuals in the study colonies. Different loggers have different scales of measuring variables of interest, and values from different loggers can therefore not be compared directly. Values are therefore standardized (ε) to make it possible to compare values between different loggers. The standardized values are calculated by dividing each value by the maximum value for the specific logger. Standardized values range between 0 and 1, where 0 is no recorded light and 1 is complete light exposure (Figure 2-3).

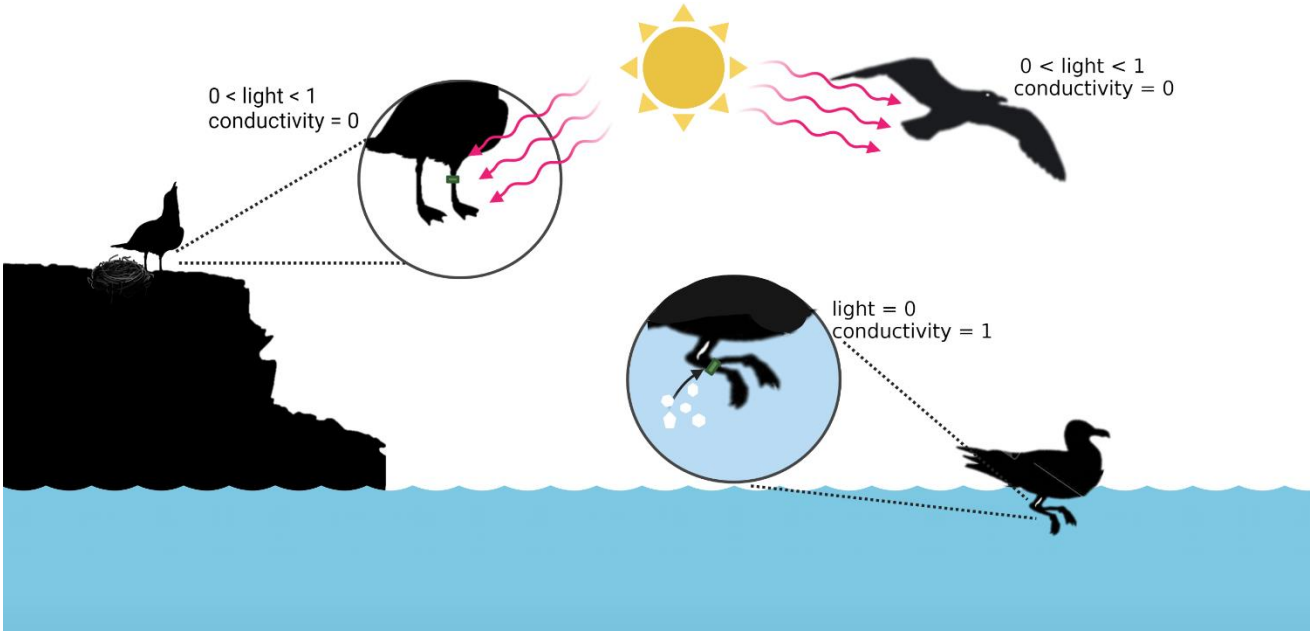

Figure 2-1: loggers record data both for ambient light and conductivity. High values indicate more exposure/contact with light/saltwater during 10-minute period. Low values indicate less exposure/contact with light/saltwater during 10-minute period. Created using https://www.biorender.com/.

The light data can be used to estimate geographical positions of the individuals carrying the logger. Latitude is derived from the day length, while longitude is derived from the local midday, with respect to the Greenwich Mean Time and Julian day (Lisovski et al. 2020).
However, for colonies north of the polar circle, position cannot be calculated during the summer months because of constant light exposure due to the midnight sun. The same, but opposite, applies during the polar nights. There will also be gaps in the data during the spring and autumn equinox (Figure 2-2). Because of this, there is a lack information about the movements of individuals for some of the study colonies in the time period of interest, and it was therefore decided that position data would not be used in this study.

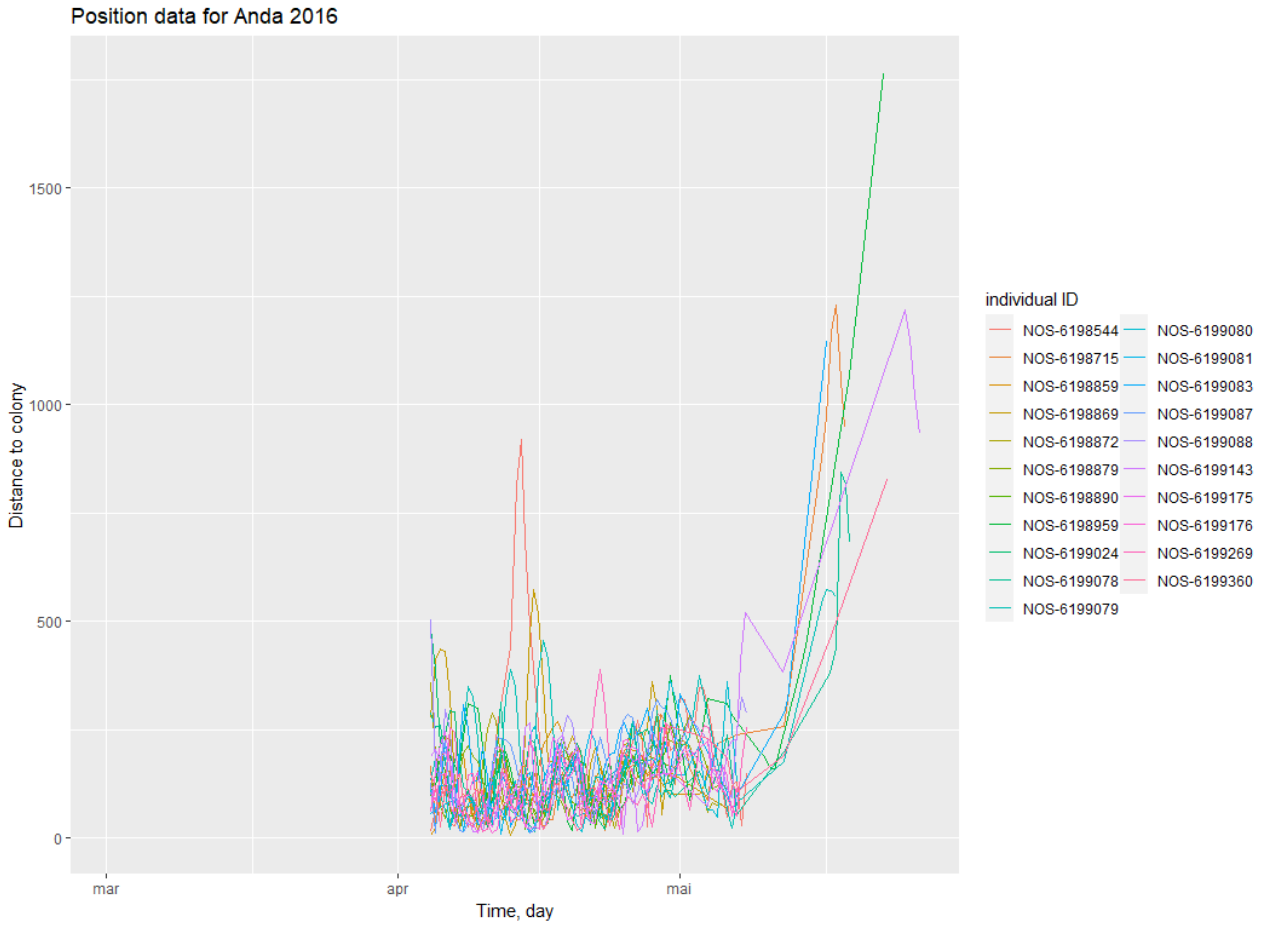

Figure 2-2: Position data from Anda year 2016 in the period of interest. Data is lacking from early April and from mid may. Position data could therefore not be used in this study. The lack of data is due to the midnight sun continuously exposing the logger to light.

The logger also contains a device for recording conductivity: suspension in saltwater (Figure 2-1 and Figure 2-3). Standardized measurements were used in order to be able to compare measurements from different loggers and are calculated using the same method as the standardization of light data (see above). A standardized value (ε) of 1 indicated that the individual spent the whole 10-minute period in contact with water, while a standardized value of 0 indicates no contact with water for the last 10-min period. Intermediate values suggests that parts of the 10-min interval was spent in contact with water (Figure 2-3).

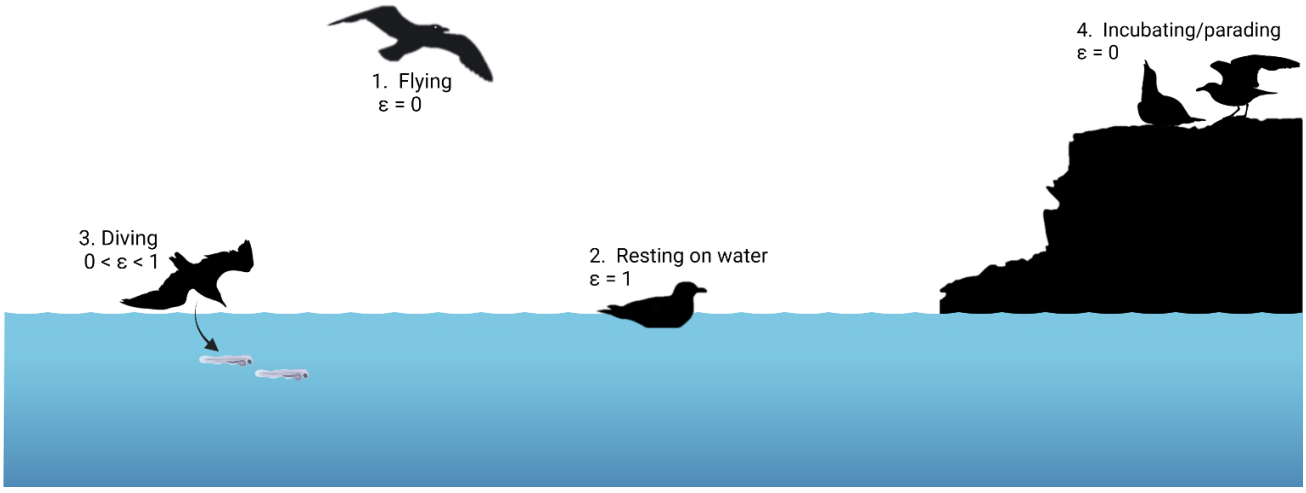

Figure 2-3: 1. Flying, 2. resting on water surface, 3. Diving/foraging, 4. Incubating or parading. ε indicates the measured conductivity for the given activities exhibited by breeding kittiwakes. Created using https://www.biorender.com/.

Four main activities have been observed in breeding seabirds (Figure 2-3) and can be related to the measurements in the conductivity data recorded by the loggers, and is often used as the standard interpretation of data from GLS loggers (Cherel et al. 2016; Grissot et al. 2023; Erikstad et al. 2018). When the bird is resting on the water surface (Figure 2-3) the logger will be completely submerged in saltwater and ε = 1. High conductivity values in the data can therefore be interpreted as the bird spending the whole ten-minute period on the water surface resting or waiting for foraging opportunities.

When the bird is more actively foraging and diving (Figure 2-3), the measurements are typically lower than what is observed when resting on the water surface, because of the short time spent actively in water when diving and fishing, and intermediate conductivity values, $0 < \varepsilon < 1$, can be interpreted as foraging. When incubating or defending the nest-site, the logger will be completely, or almost completely dry (Figure 2-3). This is also the case when the bird is flying for extended periods (Figure 2-3). Recorded conductivity values of ε = 0 can therefore be interpreted as the individual spending all its time out of contact with water, either incubating, spending time at the nest or flying.

2.2 Study-sites

Data between 2010-2021 was obtained for three colonies along the Norwegian coast. The initial plan was to use five colonies, but data from two of the colonies was not possible to access. The colonies used in this study was located at Runde (62.436°N x 05.874°E), Sklinna (64.740°N x 10.770°E), and Anda (69.065°N x 15.170°E) (Figure 2-4). All chosen colonies are well known breeding grounds for kittiwakes and are monitored to some extent every year. For Sklinna the population at Sør-Gjæslingan was used, as the colony at the Sklinna main archipelago has disappeared.
Fieldwork is conducted each year to both deploy new individuals with loggers and retrieve data from previously deployed loggers. New loggers are only fitted to breeding birds. Thus, we know that the individual was breeding the first year of the recorded data. The fieldwork is however often conducted in the middle of the breeding season, so data from the first half of the breeding season is almost always missing from the first year of recorded data when the logger was deployed to the individual.

All the data from the loggers are collected by and stored in the SEATRACK project (https://seapop.no/en/seatrack/). SEATRACK is an international project aiming to collect information about seabirds on the northern hemisphere.

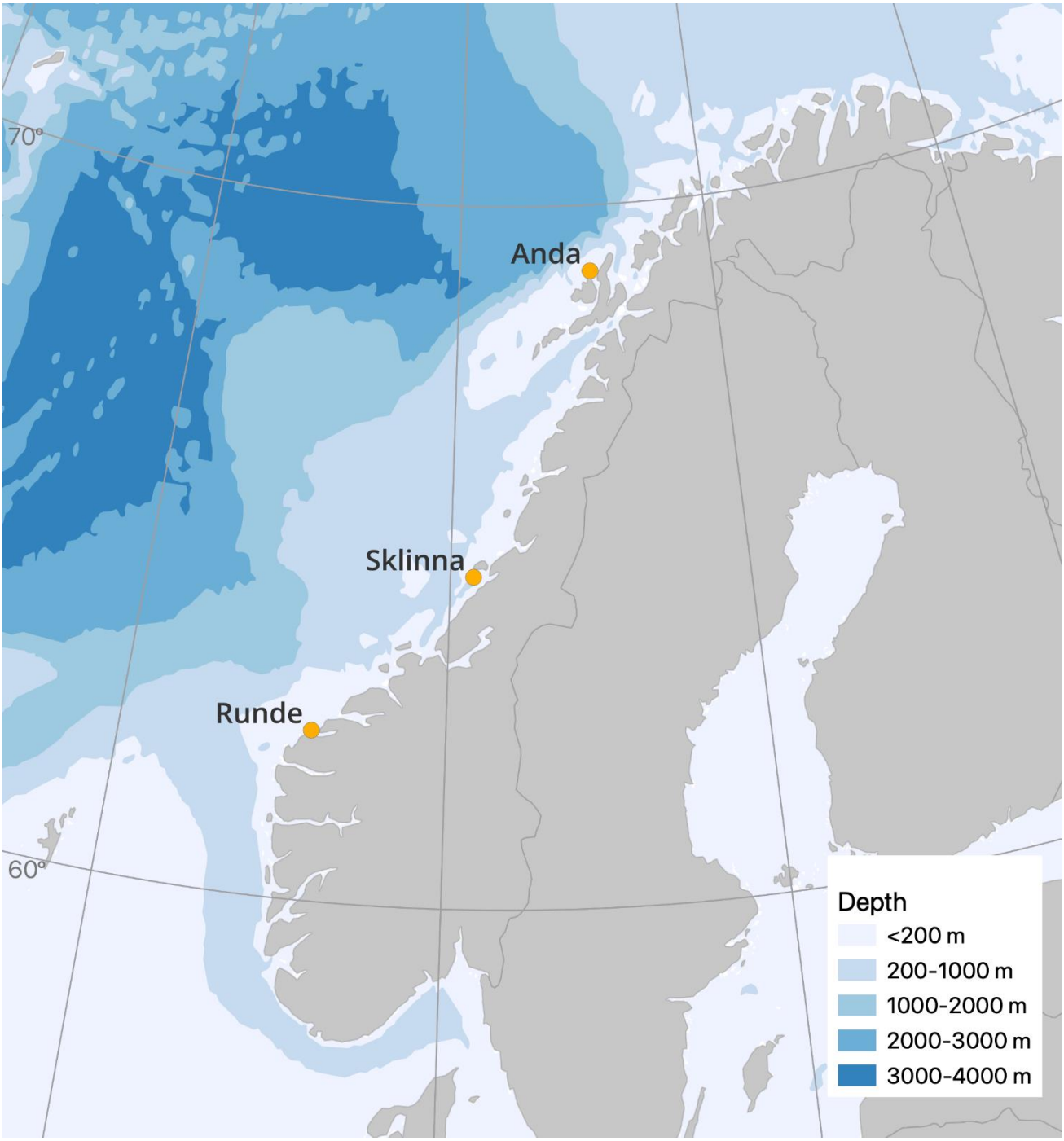

Figure 2-4: Map showing the locations of the study colonies. Colonies were chosen as they form a gradient along the Norwegian coast. Created using QGIS ('QGIS Geographic Information System.' 2023)

2.3 Working with the data

All data handling and analysis in this project was conducted in RStudio, running R version 4.1.3 (R Core Team 2022).

Two biological events related to the early breeding season in kittiwakes were considered estimated in this study: the first arrival at the colony and the timing of breeding, or breeding start.
Because many individuals return to the colony briefly early in the year before leaving, coming back months or weeks later, and some birds never leave the colony site after the breeding season, it is difficult to precisely define a return date.
These difficulties were exacerbated by the lack of position data during the period of return to the colony for many individuals the data analysis would also be difficult. There are no apparent changes in the conductivity data during this period that could indicate a return, without having to confirm this by looking at where the bird was with the help of the position data. Because of these issues, it was decided to not estimate the arrival date and only focus on estimating start of breeding.

2.3.1 Estimating breeding start

Breeding start, or timing of breeding, was in this study defined as the time when individuals spend more time at the nest than at sea. As the breeding season approaches, individuals will spend more time at the nest-site to defend it and bond with the partner to prepare for copulation and egg laying (Coulson 2011; Chardine 1983). A decrease in conductivity data over time is therefore expected in this period, and a strong decrease in conductivity value might indicate a behavioural shift from non-breeding to breeding. Analysing trends in conductivity data of individuals was therefore used to estimate the timing of breeding.

Light data has the potential of working in a similar way to the conductivity data. Low values in the light data suggests that the logger is being covered, depending on time of day, either when the bird is on the nest or laying on the water surface. Using the light data in unison with the conductivity could therefore give some more insight into the behaviour of the bird. There are however some limitations.

Kittiwakes tend to position their legs under their bodies when flying, limiting the logger's exposure to light. Distinguishing between flying and activities linked to the individual occupying the nest is therefore quite difficult, since both also have similar conductivity values (Figure 2-1). There were also no sources at the time when the study was conducted on how to interpret the behaviour of an individual based on the light data. Interpreting the trend in light data in an ecologically meaningful

way was difficult and would need more proofing than what was possible in terms of time and capacity in this project.

Using the light data would also have doubled the analysis effort of the project with the analysis method utilized in the project, and because of the strict time limit of the project it was decided to not use the light data to estimate breeding start. However, potential uses for light data in future studies is discussed in section 4.3.2.

No method on how to interpret changes in behaviour in kittiwakes from non-breeding to breeding, based on conductivity data existed at the time this project was carried out.

A method therefore had to be developed to obtain the estimates of interest. The work process of this part of the project can be divided into two main parts with several steps. Preparing the data for analysis (Part 1) and analysing the data of interest to get estimates related to the start of the breeding season (Part 2) (Figure 2-5).

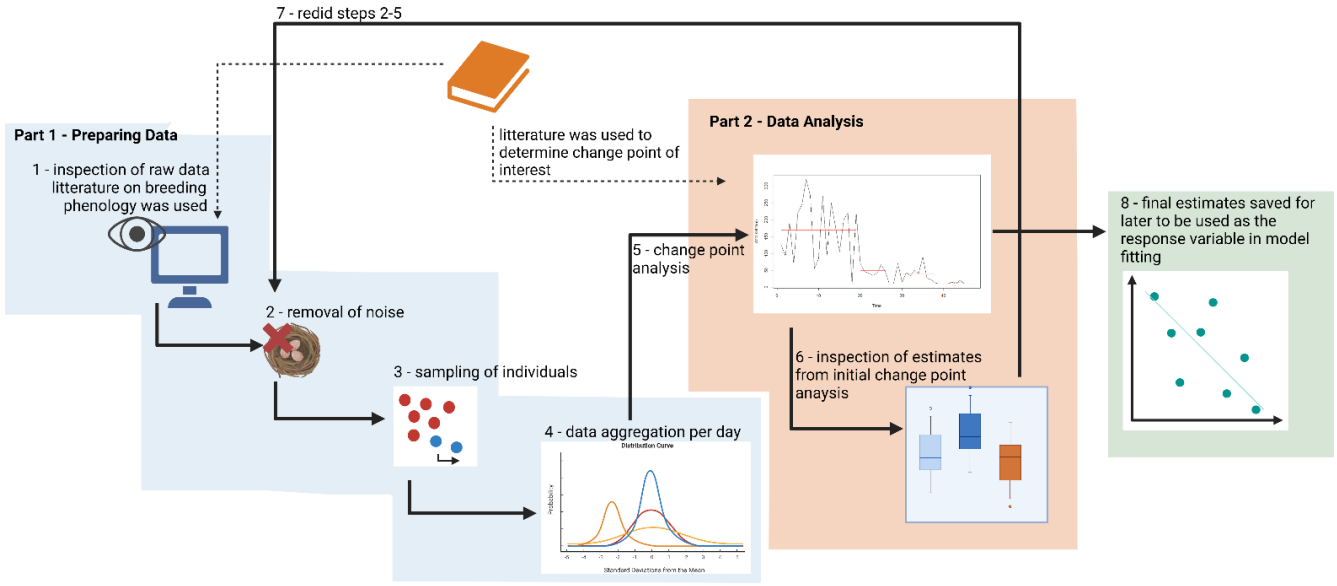

Figure 2-5: overview of the workflow. Step 1-3 was carried out to obtain a dataset with the least amount of noise possible. Conductivity data was aggregated per day (step 4). Existing literature was also used in step 5 to determine change point of interest. After inspection of results from the first round of change point analysis (step 6), it was evident that working on a narrower time frame could provide better estimates. The workflow was repeated on a narrower timeframe, producing better estimates (step 7). Improved estimates were used in further analysis and model fitting (step 8). Created using https://www.biorender.com/.

2.3.2 Preparing the Data

Preparing the data consisted of four main steps (Figure 2-5 step 1-4). Since the loggers record data continuously throughout the year, the amount of data collected per year is quite substantial, producing a lot of noise in the time series (the initial dataset contained > $2.2x10^7$ datapoints). To minimize the computation time and analysis effort, unnecessary data had to be identified and removed.

To be able to decide on what to include in the study, the raw data for each colony was inspected. Different literature (Figure 2-5 step 1) was used to decide on a suitable time interval to work with. For all colonies, breeding before April and egg laying and incubation after August is rare (Burr et al. 2016) (Coulson 2011), and will most likely end with breeding failure. An interval between the months April to June was therefore selected for initial inspection and analysis (Figure 2-5 step 2).

For most individuals, a lot of data was lacking from the first year of the logger deployment. This is due to fieldwork being conducted during the breeding season, meaning that there is no recorded data for the beginning of the season of the first year of logger data (Figure 2-6). Data might also be lacking if re-capture of individuals was not possible in some years.

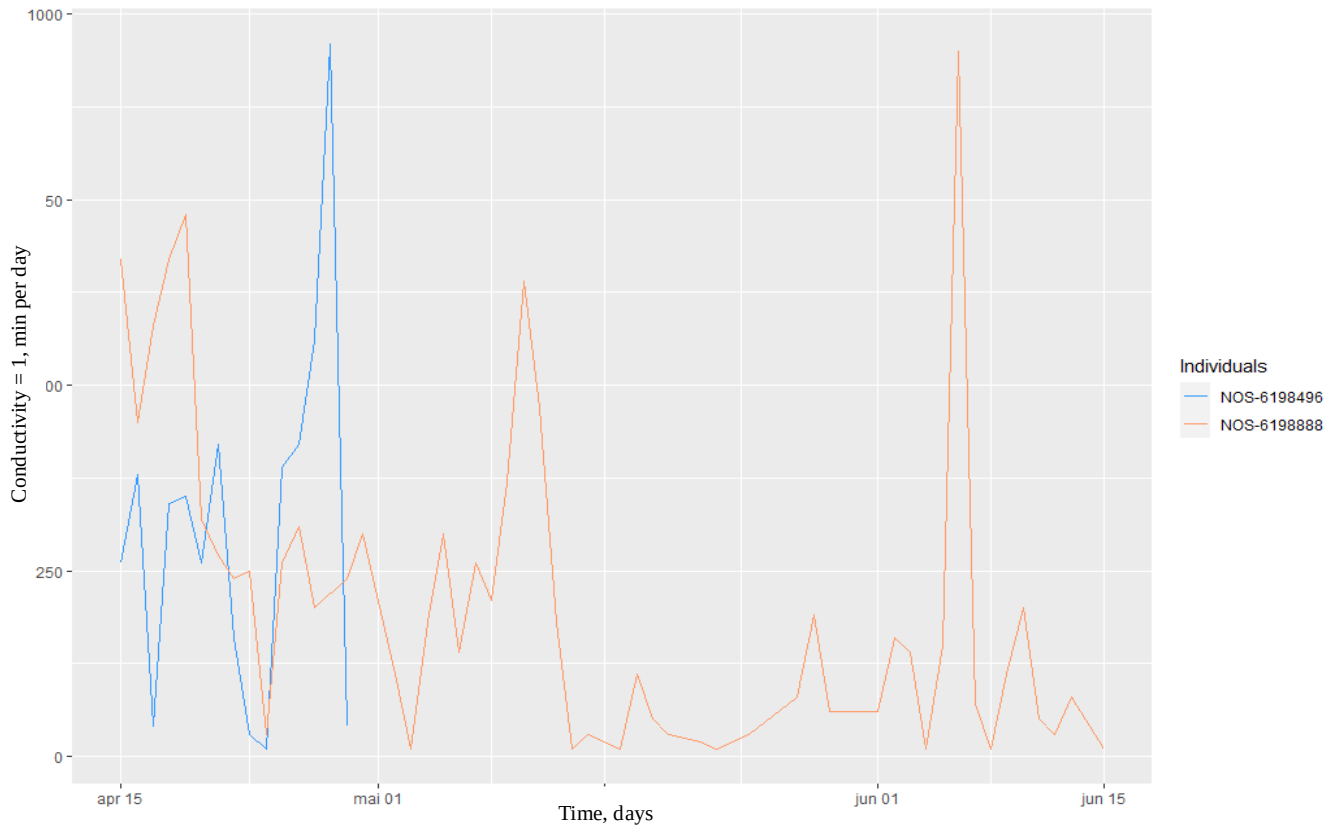

Figure 2-6: Individual with missing data (blue) vs individual with data in the whole breeding period (orange). Individuals with missing data was removed, as no interpretation of breeding start could be done for these birds.

Some information about the breeding status observed during fieldwork was available for some of the tagged individuals in each colony. Birds recorded as non-breeders were removed together with the individuals lacking substantial amounts of recorded data (<6000 data points) within the period to further reduce noise (Figure 2-5 step 2) (see Appendix B2).

The number of individuals each year varied between colonies (Table 2-1 and Table 2-2). For Anda data was extracted between the years 2012-2022, with the years 2014 and 2020 having especially few individuals to analyse. This might be due to the fact that few birds were tagged before 2014, meaning that there was less data to collect prior to 2015. For Sklinna data was obtained between the years 2014-2020. Runde lacked data for a considerable amount of the years, with data only available for the years 2016-2019 and 2021.

For each year of available data, 10 females and 10 males were randomly sampled, when possible, to investigate the differences in estimated breeding start between sexes (see section 2.4.2, see Appendix B2 for script).

This was not addressed as one of the main study questions in the study but was still relevant to investigate, especially as the sex of all individuals was not known (Figure 2-7), and therefore the sex-ratios of each year were unknown as well. As mentioned in section 1.1, males will often arrive first at the nest-site to defend it, so that he is ready to attract a partner when females begin to arrive (Coulson 2011; Chardine 1983). A shift in behaviour might therefore be expected to happen earlier in males, because of the intense nest defending and courtship.

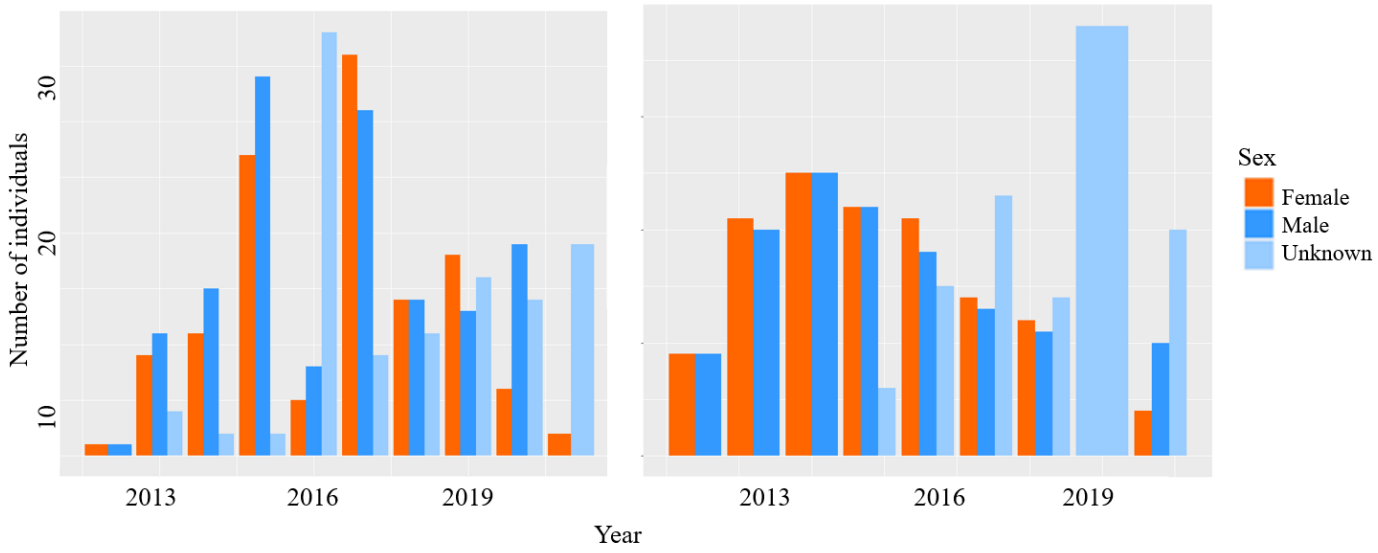

Figure 2-7: ratios of males, females and individuals of unknown sex for all years included in the study. To the left: ratios for Anda. To the right: ratios for Sklinna. Plots show the total number of individuals before noise removal.

For colonies or years where there was no information on the sex for all individuals, individuals were sampled with unknown sex to reach the sample size of at least 20 individuals per year (Figure 2-5 step 3) (see Appendix B2). It was however not possible to sample 20 individuals for all years, due to data not being available for all individuals for different reasons (Table 2-1 and Table 2-2).
In some years there was data on >30 individuals, but because of the time limitation of the project there was not time to analyse all individuals in those years.

2.3.3 Change point analysis of time series

Change point analysis was used to analyse the change in conductivity data over time (Figure 2-5 step 5). A total of 350 time series were analysed using change point analysis. Change point analysis has been used in previous studies on seabird behaviour with good results (Hestem 2019; Erikstad et al. 2018).

Change point analysis was chosen because of its efficiency and potential for constructing segmentations that represent the true changes in the time series, either by changes in mean, variance, or both. The change point analysis was carried out twice, once on the initial time frame (1st of April - 1st of July) (see Appendix B3), and a second time on an improved time frame (15th of April – 15th of June) (see Appendix B4), based on the results from the first change point analysis (Figure 2-5 step 6).

The cpt.meanvar function from the package changepoint (Rebecca Killick and Eckley 2014) using the PELT (Pruned Exact Linear Time) method with CROPS penalty (Change points for a Range of Penalties). The cpt.meanvar function was chosen because of the assumption that when there is a change in mean, there is often a change in the variance.

Many of the time-series in this study had more than one change point. Detecting the optimal change points in time series with multiple possible change points can be a slow process. PELT incorporates a pruning procedure, cutting down the computational cost without compromising the computation of the best change points for the time series (R. Killick, Fearnhead, and Eckley 2012). For many of the standard change point analyses the number of penalties must be set *a priori* to the analysis. Knowing the underlying properties of the data to decide on a suitable penalty value is not always straightforward. The CROPS penalty eliminates this problem by allowing for search of the best segmentation based on a range of penalty values (Haynes, Eckley, and Fearnhead 2014). In this study a range from 5-500 penalties was used for the penalty criteria of the function. There is however a need for visual inspection of each individual change point analysis to establish a suitable number of segments, which adds to the total time of analysis per time series. Since many of the time series had multiple segments, only one change point per time series was selected to be the estimate of interest.

2.3.3.1 Initial change point analysis

The first change point analysis was carried out for the years 2015-2020, with varying amounts of individuals sampled each year for each colony. Mean conductivity per day was calculated for each individual (Appendix B2) and was used to investigate changes in conductivity per day over time. To minimize the subjectiveness of interpretation, a drastic change in the conductivity pattern, going from a high daily average conductivity to lower mean conductivity levels was taken to be the change point of interest (Figure 2-8), since such a drastic change reflects a change in the daily behaviour of the individual and could point to the initiation of breeding.

Table 2-1: Sampled individuals after noise removal used in initial change point analysis

Colony	Year	Number of sampled individuals	Total number of individuals	Females	Males	Unknown sex
Anda	2015	20	33	10	10	0
	2016	20	42	10	8	2
	2017	20	40	10	10	0
	2018	20	36	8	10	2
	2019	21	21	8	10	2
	2020	9	9	0	0	9
	2021	10	10	0	0	10
Sklinna	2015	19	19	9	8	3
	2016	22	22	10	10	2
	2017	23	23	10	6	7
	2018	19	19	6	5	8
	2019	13	13	0	3	10
	2020	14	14	0	0	14
Runde	2016	17	17	6	0	11
	2017	17	17	4	0	13
	2018	15	15	3	0	12
	2019	15	15	0	0	15

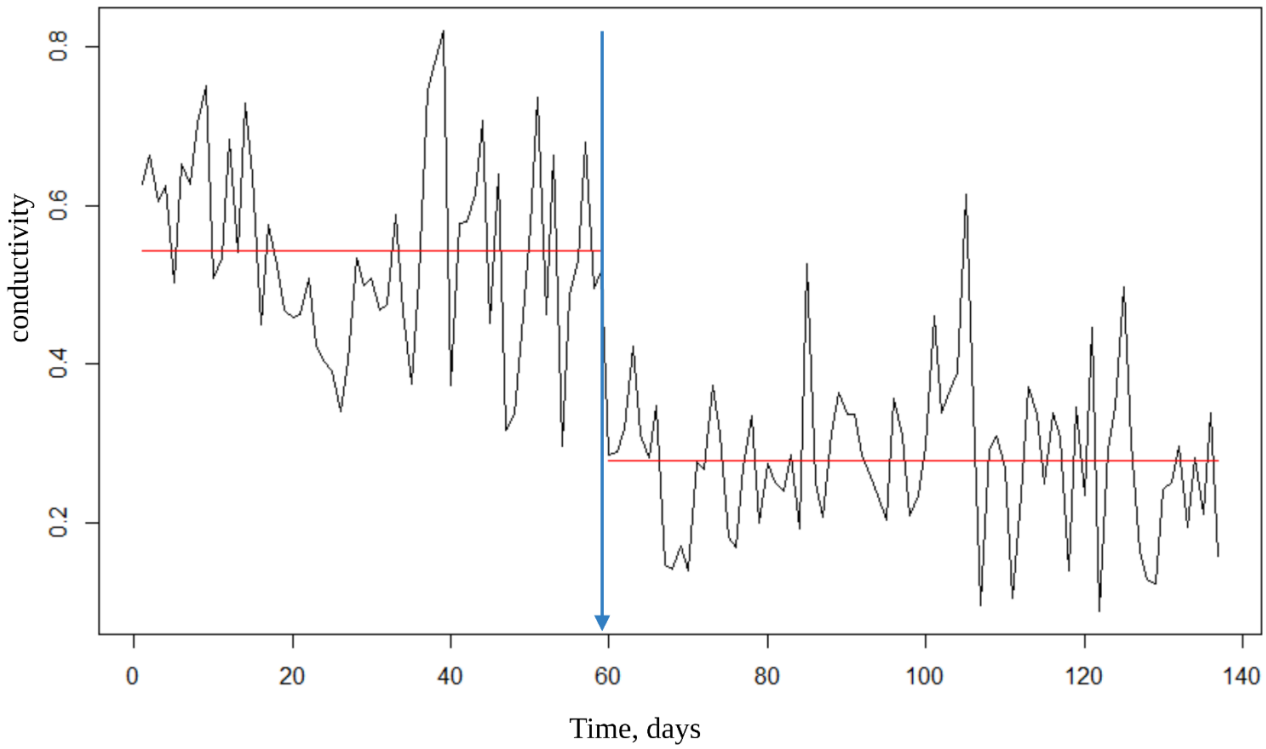

Figure 2-8: Change point analysis of one individual from the first round of change point analysis. Change point of interest is indicated by the blue arrow. Change points were calculated using the cpt.meanvar function. Time in days on x-axis. X-axis = 0 represents the first day of the time interval chosen. Y-axis represents the mean conductivity per day ranging from 0-1.

Results from the initial change point analysis suggested that more exact estimates could be obtained on a narrower time frame. For all colonies the interval 15.04-15.06 captured the variation in behavioural change detected by the time series analysis for all years (Figure 2-9).

This shorter interval was chosen for all colonies, and a second change point analysis was carried out (Figure 2-5 step 7). The same interval (15.04-15.06) was used for all colonies to minimize the risk of subjective interpretation of the results from the initial change point analysis. Results from the initial change point analysis were therefore only used to find the time interval where change was observed for all colonies in the years included and was therefore not used in any statistical analysis.

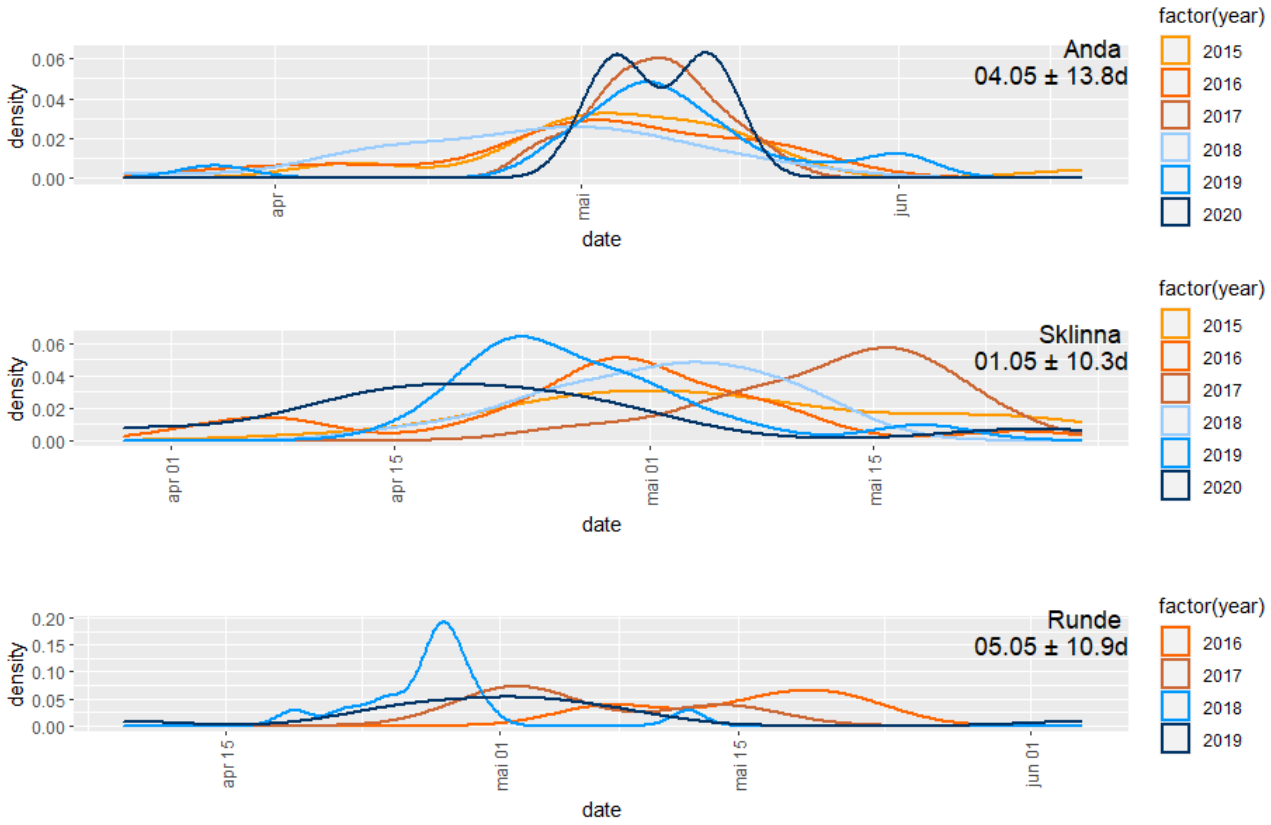

Figure 2-9: Distributions of breeding start for all colonies obtained from the first change point analysis, shown for the years 2015-2020. For all colonies, the interval between April-June captured the variation in mean breeding start in all years included. Note that density curves have differently scaled axes.

2.3.3.2 Final change point analysis on improved timeframe

The same approach as that of the initial change point analysis was followed with regards to removing noise and selecting individuals (see section 2.3.2) for the second change point analysis. For the final change point analysis more years were added, so that the final dataset consisted of data from the years 2012-2021. Note that not all years was sampled for all colonies, due to lack of data (Table 2-2).

To better visualize the patterns in conductivity over time, all conductivity values below 0.9 were removed from the data set, and the number of minutes of activity above 0.9 within the period (Figure 2-5 step 4) was calculated per day. This was done to be able to strictly look at the change in behaviour linked to high conductivity values (wet data), indicating spending time on water, without having the noise from intermediate and low values (see Appendix B4).

Table 2-2: Sampled individuals after noise removal used in final change point analysis

Colony	Year	Number of sampled individuals	Total number of individuals	Females	Males	Unknown sex
Anda	2012	11	11	0	0	11
	2013	11	11	0	0	11
	2014	5	5	0	0	5
	2015	20	33	10	10	0
	2016	20	42	10	8	2
	2017	20	40	10	10	0
	2018	19	36	8	10	2
	2019	21	21	8	10	2
	2020	9	9	0	0	9
	2021	10	10	0	0	10
Sklinna	2014	19	19	0	0	19
	2015	19	19	9	8	3
	2016	22	22	10	10	2
	2017	23	23	10	6	7
	2018	19	19	6	5	8
	2019	13	13	0	3	10
	2020	14	14	0	0	14
Runde	2016	17	17	6	0	11
	2017	17	17	4	0	13
	2018	15	15	3	0	12
	2019	15	15	0	0	15
	2020	NA	NA	0	0	0
	2021	11	11	0	0	11

The opposite approach, using dry data ($\varepsilon = 0$) to estimate breeding start was considered, but as mentioned in section 2.1, dry data can be associated with two types of behaviours, flying and spending time at the nest. This would therefore mean that it is quite difficult to separate flying from nest-activity without the help from position data or by looking at patterns in the activity data at a very fine scale, such as hourly activity. None of these approaches were possible, either because of lacking position data or time restrictions, and the use of dry data to estimate changes in behaviour linked to breeding was therefore not pursued further.

Values of $\varepsilon = 1$ for the conductivity data is usually used to signify that the bird spent time on water (Grissot et al. 2023; Cherel et al. 2016; Erikstad et al. 2018). In this study the threshold of $\varepsilon > 0.9$ was used to filter out data defined as "wet". This was done to make the signals in the time-series a bit stronger, since values > 0.9 are still very high, indicating that most of the 10-minute interval was spent in contact with water, and cannot be associated with the bird being on or around the nest.

There was a considerable amount of variation in time series between individuals. In order to be as consistent as possible with the analysis, the change in behaviour was determined either as the first change point where there was a clear break in the time series, going from spending more than 200 min per day on water to less than 200 min (Figure 2-10), or the start of a segment where there was a long period of very low values, typically less than 100 min spent on the water surface per day (Figure 2-11). For each individual change point analysis an estimated breeding start date, based on the segmentation of the time series, was recorded and saved for later statistical analysis outlined in section 2.4 (Figure 2-5 step 8).

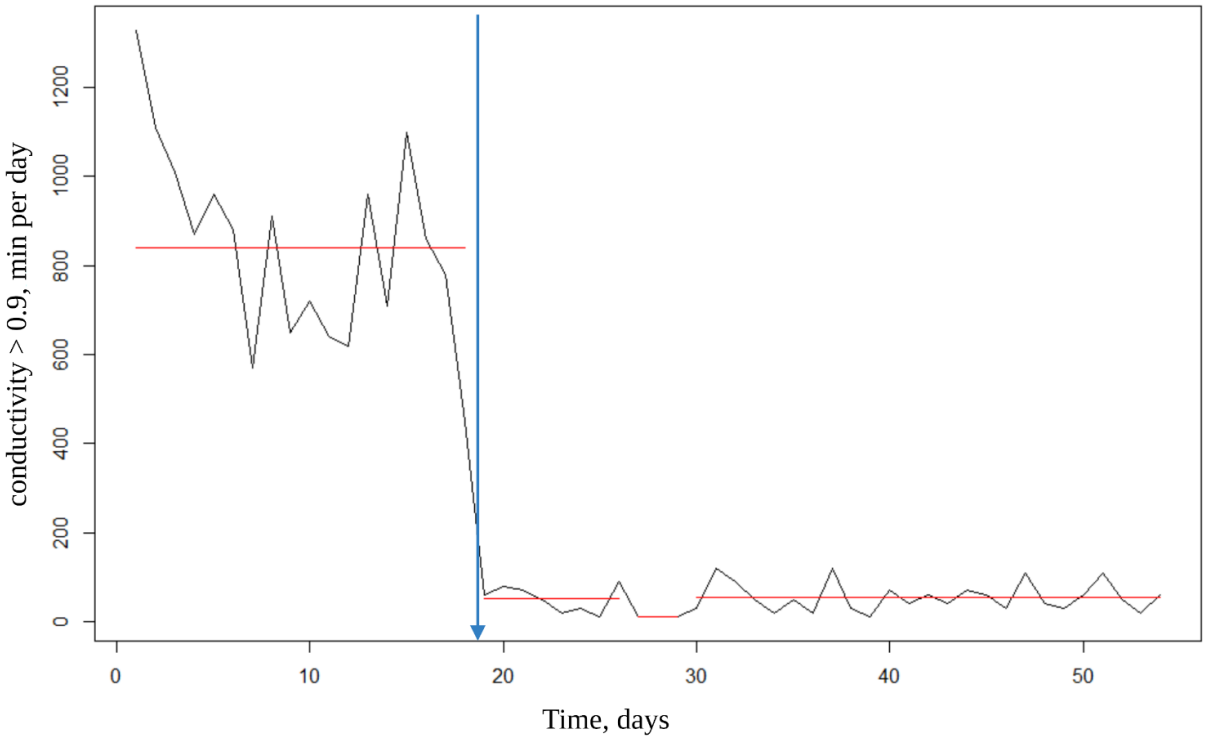

Figure 2-10: Change point analysis of one individual. X-axis shows time in days, with day 0 being the start date of the interval. Y-axis showing time spent on water (conductivity >0.9) in minutes per day. Change point of interest indicated with blue arrow.

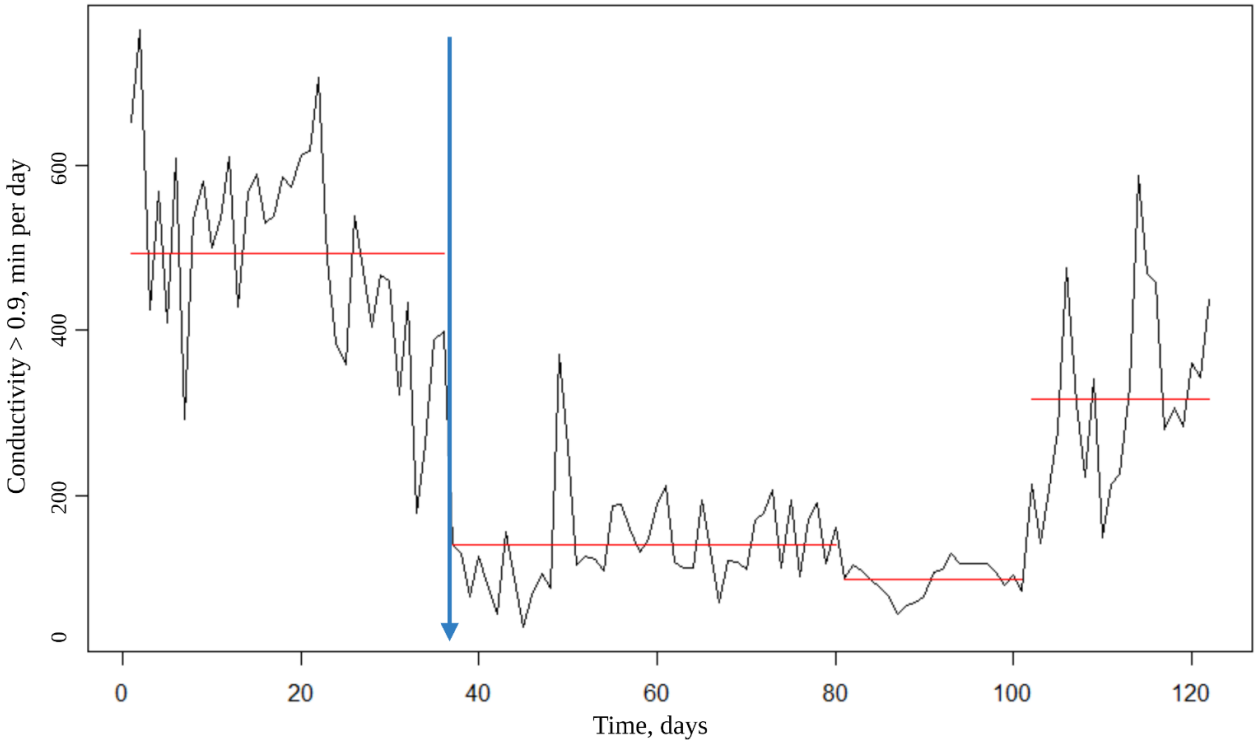

Figure 2-11: Change point analysis of one individual. X-axis shows time in days, with day 0 being the start date of the interval. Y-axis showing time spent on water (conductivity >0.9) in minutes per day. The time-series consists of multiple segments, and so the first drastic change from high to low average conductivity was taken to be the change point of interest (blue arrow).

2.4 Statistical Analysis

All statistical analysis in this project was conducted in RStudio, running R version 4.1.3 (R Core Team 2022). Statistical investigation and exploration of the data is described below in the order of which it was conducted.

2.4.1 Validation of estimates from change point analysis

Since the model fitting of the project relies on the estimates obtained from the change point analysis, it was important to make sure that the estimates detected by the change point analysis reflected the biologically meaningful event (breeding start in kittiwakes) the study was concerned with investigating.

To do this, estimated breeding start dates were checked against estimated hatching dates, to see if the two events in the kittiwake breeding cycle matched for each year of included data. If the estimated breeding start dates from the change point analysis match the observed hatching dates, there is a good indication that the estimates from the change point analysis are reliable and can be used in further statistical analysis. Data on hatching dates was obtained for Anda, for the two other colonies no data on hatching events was obtained, and this part of the analysis was therefore only carried out for one colony.

Hatching data is estimated from observations on already hatched chicks. Estimates for hatching dates for each chick is derived from measuring the beak length of the chick. For each year the average hatching date was calculated. The average breeding start date per year was also calculated, and for each year the two average dates were compared in order to see if the breeding start dates matched the hatching dates.
Intense nest defence and incubation last for approximately 35-40 days in kittiwakes, see section 1.1. A difference of 35-40 days is therefore expected between the estimated hatching dates and estimated breeding start dates from the change point analysis. Correlation between the two estimates were calculated using a weighted correlation approach, in order to account for the small sample sizes in some years.

2.4.2 Differences between sexes

As previously mentioned, investigating the difference between sexes was not one of the main parts of this study, but was important to investigate as proportions of sexes in the sampled populations might differ. A difference in breeding start between sexes could partially explain the estimated breeding starts for each colony.

The mean breeding start was estimated for each sex per year of data for the colonies Anda and Sklinna (Table 3-4). Runde was not included because of lack of data with known sex. Because of small sample sizes that were not normally distributed, a Wilcox signed rank test with significance level = 0.05 was used to check if there was a significant difference between estimated median breeding start dates for males and females. Since it is expected that males might start breeding activities earlier than females, a one-sided alternative was tested, where the alternative hypothesis was that males have a lower median than that of females.

2.4.3 Predictor variables

Reoccurring phenological events such as breeding are influenced by a multitude of different environmental factors. In this study several predictors were therefore included to investigate variations in breeding start (Table 2-3) and will be discussed below.

Table 2-3: Description of predictor variables used

	Variable name	Description	Obtained by
Random factor	Bird ID	Individual identification code	Extracted from raw data
	Year	Year that breeding start was estimated	Extracted from raw data
Environmental variables	Winter SST	Mean SST Dec-March	Website of NOAA
	Spring SST	Mean SST April-June	Website of NOAA
	Lagged SST	Mean SST Dec-March of previous year	Website of NOAA
	NAO	Mean NAO Dec-March	Website of NOAA
	Drift	Time of drift from one colony to the other	LADiM modelling
Colony variables	Population size	Number of occupied nests	Counting data from fieldwork
	Colony	Location of breeding population	Extracted from raw data

For some colonial birds, the timing of breeding activities are linked, to some degree, to social behaviour (Votier et al. 2009). A larger number of breeding pairs means a higher competition pressure for nest sites and food and can result in earlier onset of breeding specific behaviours (Merkel et al. 2019). Pairs also tend to match their own breeding cycle to other pairs, so when breeding starts for a proportion of the population the rest often follow (Chardine 1983; Coulson 2011).

A larger breeding population size also provides a higher protection from predators, both for individuals and chicks (Coulson 2011). Breeding population sizes for all the study colonies fluctuated between years (Table 2-4). To investigate the potential effect of fluctuations in breeding population sizes on breeding start in the study colonies, population sizes were included as a predictor in the models.

Population sizes of breeding pairs for all colonies was retrieved from fieldwork data from all the years of interest (see Appendix B5). The population size was measured by number of occupied nests, so the numbers only reflect the breeding population for each colony (Table 2-4).

In the North-Atlantic large-scale variables such as NAO (North Atlantic Oscillation) and local variables such as SST (Sea Surface Temperature) can have an impact on the life cycle of different species and effects of these variables can carry over to other parts of the ecosystem (Ottersen et al. 2001; Stige et al. 2006). To try and explain the variation in the start of kittiwake breeding behaviour, NAO and SST was used as proxies for food availability.

Data for the winter NAO index was collected from the website of NOAA – National Oceanic and Atmospheric Administration (https://www.ncei.noaa.gov/access/monitoring/nao/). Data for the years 2012-2021 was retrieved from the file, and a mean NAO index was calculated for the months December (of the previous year) to March to represent the average winter NAO index for each year of interest. Since the NAO is a large-scale environmental variable, there is no local variation and colonies are affected by the same NAO indexes (see Appendix B5).

Table 2-4: Size of breeding population for all study colonies

Colony	Year	Number of occupied nests
Anda	2012	941
	2013	906
	2014	788
	2015	795
	2016	765
	2017	785
	2018	865
	2019	917
	2020	941
	2021	875
Sklinna (Sør-Gjæslingan)	2014	226
	2015	155
	2016	32
	2017	96
	2018	83
	2019	94
	2020	125
Runde	2016	641
	2017	657
	2018	615
	2019	633
	2020	694
	2021	691

SST values were retrieved from the website of NOAA – National Oceanic and Atmospheric Administration (https://www1.ncdc.noaa.gov/pub/data/cmb/ersst/v5/netcdf/) as cdf-files. For each colony, longitude and latitude (Table 2-5) was used to extract monthly estimated SST temperatures in grid-cells surrounding the location of the colony, and a mean SST value for the selected grid cells was computed per month of interest (January-June) for all years (2012-2021).
SST values retrieved from measurements from field stations close to the colonies would have been preferred, but field stations in close proximity to all colonies did not exist. Estimated values based on modelling prediction from NOAA was therefore used, so that all SST data used as predictors originated from the same method of extracting SST values.

Table 2-5: Longitudes and latitudes used for extracting SST values per colony

Colony	Latitude N	Latitude S	Longitude W	Longitude E
Anda	70	68	14	16
Sklinna	66	64	9	11
Runde	63	61	4	6

Three SST values were calculated in R based on the values extracted from the cdf-files. One for the period before the breeding season (Jan-March) called SST_winter in the R script, one during pre-breeding and the breeding season (April-June), called SST_spring in the R script, and one representing winter SST from the previous year called SST_lagged in the R script (see Appendix B5).
The three different SST values were used in order to investigate how SST values before (winter SST) and during the early stages of the breeding season (spring SST) might affect the onset of breeding in Norwegian kittiwake colonies differently (Moe et al. 2009; Frederiksen et al. 2007). Lagged SST was included as studies have indicated that winter SST values of the previous year might affect breeding in kittiwakes through the influence on prey recruitment (Frederiksen et al. 2007; Frederiksen, Wanless, et al. 2004).

How fast the currents can transport prey along the coast might explain the breeding synchrony between colonies. If spawning happens close to one colony, and prey is transported from this location towards more northern colonies, colonies further north might be expected to start breeding later.

Drift was modelled by Postdoctoral Fellow Håvard Frøysa at the Norwegian Institute of Marine research, using the LADiM model (Ådlandsvik 2022). To model the physical environment of the Norwegian coastal zone the NorKyst800 model was used together with LADiM. For the years 2014-2016 the archive Hindcast was used, while Lus was used for the years 2017-2020 (Albertsen et al. 2022).

For each area 1000 particles were released at three different depths, 10m, 20m and 30m, and were held constantly at these depths thorugh the whole simulation. Particles were released from Runde on the west side of the island (5°33' to 5°34'30'') from 04.05-18.04, and from Sklinna on the east side of the island (10°59' to 11°00'30'') between the 23rd of April to 14th of May. Particles were moved horizontally using Runge Kutta 4 and a horizontal diffusion at 0.1m^2/s.

The mean and median number of days of transport between two colonies was determined by the number of days it took for particles to drift from one colony site to another (Table 2-6 and Table 2-7).

For the purposes of this study, it only made sense to use the mean number of days as a predictor in the fitted models, since the median number of days were not ecologically meaningful for breeding kittiwakes. The median number of days are substantially higher because the drift model used to make predictions assumes that some of the particles are lost or stuck and therefore take a long time to passively drift to the final destination.

Table 2-6: Mean drift in days Runde - Sklinna

Year	Depth 10m	Depth 20m	Depth 30m
2014	28.5	50	56
2015	18.5	20	20.5
2016	24.5	43	42.5
2017	19.5	37.5	38
2018	23	26	19.5
2019	30.5	36	36.5

Table 2-7: Mean drift in days Sklinna - Anda

Year	Depth 10m	Depth 20m	Depth 30m
2014	25	32.5	35.5
2015	27.5	25.5	31
2016	30.5	28.5	32
2017	31	41	39
2018	36.5	22	20
2019	39.5	36	46
2020	22	21	21.5

2.4.4 Model specification

To be able to answer the research questions (see section 1.3) two response variables were investigated (Table 2-8):

1. Breeding start for individuals (per year), used to answer study question 1 and 2.
2. Interannual difference in mean breeding start between colonies, used to answer study question 3.

Table 2-8: overview of response variables and belonging predictors used to answer study questions

Response	Unit	Observations	Predictor	Type of model
Breeding start	Breeding start per individual	333	Winter SST Spring SST Lagged SST NAO Colony	GAMM LMER
Δbreeding start	mean breeding start$_{\text{colony 1}}$ − mean breeding start$_{\text{colony 2}}$	11	Drift at 10m Drift at 20m Drift at 30m	GAMM

Model fitting for the two different response variables is discussed separately in section 2.4.4.1 and 2.4.4.2. Because of the small sample size for both data sets, only simple models with additive effects were fitted. Before model fitting was done, outliers in the dataset were identified and removed. Outliers were identified by being higher than 1.5 times the inter quantile range, or lower than 1.5 than the inter quantile range. Outliers were removed, resulting in a dataset with 335 observations. In two cases the change point analysis was not able to detect any change points and no breeding start date was noted for these two individuals. The final dataset therefore contained 333 estimated breeding start dates distributed among the colonies and years of data.

Generalized Additive Mixed Models (GAMM) were used for both datasets and fitted using the gamm4 function from the gamm4 package in R (Wood and Scheipl 2020) using the REML method, with number of basis functions (k) set to 3. The number of basis functions was chosen based on the small sample size of the dataset.

$$g\big(E(Y)\big) = \beta_0 + \sum_1 f_i x_i + Zb$$

Where β_0 is the parametric intercept, $\sum_1 f_i x_i$ is the additive terms, and Zb is the random-effects part. GAMM models can be a useful exploratory tool when using time-series data since the relationship between response and covariates is not known *a priori*. Linear models assume a fixed linear fit between variables, but since time-series data do not always follow a linear relationship, using GAMMs provides more freedom when fitting models.

The REML method was used for penalizing smooth terms because of the mixed model structure in our models, and because default penalizing methods are prone to under smoothing.

A shrinkage effect, (bs="ts") was added to all predictor variables (see Appendix B7). This was done to penalize the degrees of smoothness, effectively shrinking terms towards zero, and remove terms that do not explain any variation in the data. The shrinkage used however does not remove the unsuitable terms from the model directly but indicate what terms should be removed, signified by the edf (effective degrees of freedom) values for each term, as edf values can be used as a proxy for the degree of non-linearity of a term.

An edf close to 1 indicates a linear fit, an edf between 1 and 2 indicates a weak non-linear relationship, while edf > 2 indicates a highly non-linear relationship. Edf values close to 0 indicate that no smoothing was done for the term, and that the term should be removed from the model. However, visualization of each term is necessary to investigate the relationship between response and predictor. To make sure predictor variables were not dependent, collinearity was checked for all predictor variables using the Variance Inflation Factor (VIF) criteria using a specified VIF function (Appendix B6). AICc scores were used to compare models and decide on the best model.

2.4.4.1 Modelling potential effects on breeding start

To be able to answer study questions 1 and 2, a response variable with individual breeding start per year for each colony was used. All colonies were included in the same models creating models with 333 observations. For this dataset both GAMM models and Linear Mixed Effects models were fitted (Table 2-8).

GAMM models were fitted first. Year and individuals were included as random effects in the models, to account for the autocorrelation between years and pseudo-replication, as some of the individuals have been sampled for several years. SST values, NAO indexes, colony and population size were used as predictors in the models (Table 3-1).

Linear Mixed Effect models were fitted using the lmer function from the "lme4" package in R (Bates et al. 2015) (Appendix B7). LME models were used to investigate the effects of predictors on the response variable, since the terms in GAMM models cannot say anything about the strength or direction of significant effects.

$$y = X\beta + Zu + \varepsilon$$

Where $X\beta$ is the fixed effects term, Zu is the random effects term, and ε being the random errors with mean $E(u) = 0$.

Year and individuals were included as random effects in the LME model as well, for the same reasons as given for the GAMMs (see above).

To make interpretation easier, all SST variables, as well as NAO indexes and population sizes, were standardized by centring and scaling. The intercept is therefore interpreted as the expected value of the response when all centred predictors are at their mean.

Model assumptions of homogeneity of variance and normally distributed residuals were checked both by checking diagnostics plots (qq-plot of residuals, residuals vs. fitted values plot, response vs. fitted values plot) and using the Shapiro-Wilk normality test.

P-values cannot be obtained for linear mixed models, due to the difficulty in determining degrees of freedom. Confidence intervals was therefore used to investigate if there was a significant effect of predictor variables on the response. The confidence intervals also include a bit more information than just p-values, as the confidence intervals also report on the uncertainty and precision of an effect, not just if there is a significant effect or not.

2.4.4.2 Modelling the effect of drift on synchrony between colonies

To answer research question 3, a new response variable was calculated, since we are not interested in the breeding start per colony but the difference in breeding start between pairs of colonies in this part of the study.

For each colony a mean start date was calculated per year and converted into day of year to make model fitting smoother, based on the estimates from the change point analysis. This was done because comparison between colonies could not be done on the individual level. The number of observations is therefore considerably smaller for this dataset.

For each year the difference in mean breeding day between pairs of colonies, Runde-Sklinna and Sklinna-Anda, was calculated, resulting in 11 observations. A negative sign indicates that the southernmost colony in the pair had an earlier mean breeding start that year compared to the northernmost colony. The colony pair Runde-Anda was not used in this study as it was assumed that the passive transport of prey with the currents would transport prey past Sklinna before transporting prey further north, and so the time-intervals between Runde and Sklinna and Sklinna and Anda captures the temporal gradient of interest.

A Dunn test, using the dunn.test function from the R package “dunn.test” (Dinno 2017), was carried out on the data to check if there was a difference in mean breeding start between colonies (Table 2-9). The Dunn test indicated that only the colony pair Anda-Sklinna had significantly different median breeding start ($p\text{-value} < 0.05$). Modelling the difference between Sklinna and Runde was therefore unnecessary. However, the small sample sizes should be noted. Having more data would improve the power of our statistics test, supporting or rejecting our present findings.

Removing this colony pair from the dataset reduced the number of observations to 7. There were already too few observations to begin with, and therefore this part of the modelling was not pursued any further. However, this part of the study is discussed in section 4.3.1.1, especially advice for improvement in the future to properly address this study question.

Table 2-9: Difference in mean breeding date between pairs of colonies

Year	Colony 1	Colony 2	Difference (days)
2016	Runde	Sklinna	0
2017	Runde	Sklinna	5
2018	Runde	Sklinna	8
2019	Runde	Sklinna	-5
2014	Sklinna	Anda	16
2015	Sklinna	Anda	3
2016	Sklinna	Anda	-3
2017	Sklinna	Anda	4
2018	Sklinna	Anda	1
2019	Sklinna	Anda	25
2020	Sklinna	Anda	13

3 Results

Results of the study are presented with the results from model fitting first, as these were the main results of the study. Results from investigating the correlation between breeding start and hatching, and differences between sexes are presented last.

3.1 Results from model fitting

3.1.1 GAMM models

The results from the VIF tests suggested that the predictor variables winter SST, spring SST and lagged SST should not be included in the same model (VIF score >3), because the effect of one can be explained by one of the other SST variables. For all the terms with significant values ($p < 0.05$) the edf values suggested a linear fit (edf ~1) (Table 3-1). This was confirmed by inspecting plots of all terms. The AICc scores suggested that the model with spring SST had the best fit, as the ΔAICc was > 2 (Table 3-2). An LME model was therefore fitted for this model structure in order to compute predictions for the fixed effects of the model.

Table 3-1: Model structures and summaries for fitted GAMM models

Response	Family	Model structure	Explanatory variable	Random effects	df	edf	p-value
Estimated breeding start	identity	Est_start ~	Intercept				<<0.05
		s(SST_winter) +	SST_winter		2	~0	1
		s(NAO) +	NAO		2	~0	0.19
		s(colony)	colony		2	~0	0.1
		s(pop_size)	population size		2	~1	<0.05
				Year			
				individuals			
Estimated breeding start	Identity	Est_start ~	Intercept				<<0.05
		s(SST_spring) +	SST_spring		2	~1	<<0.05
		s(NAO) +	NAO		2	~0	0.31
		s(colony)	Colony		2	~0	1
		+ s(pop_size)	Pop_size		2	~0	0.39
				Year			
				individuals			
Estimated breeding start	Identity	Est_start ~	Intercept				<<0.05
		s(SST_lagged) +	SST_lagged		2	~0	0.85
		s(NAO)	NAO		2	~0	0.19
		+ s(colony)	Colony		2	~0	0.10
		+ s(pop_size)	Pop_size		2	~1	<<0.05
				Year			
				individuals			

Table 3-2: AICc for GAMM models

Model	AICc	ΔAICc
Spring SST	2325.19	0
Winter SST	2327.47	2.28
Lagged SST	2329.19	4.00

3.1.2 LME model

An LME model was only fitted for the GAMM model with the lowest AICc score, which was the model with spring SST. Results from the LME fitting is reported below. For spring SST, population size and NAO centred and scaled variables were used. The intercepts are therefore interpreted as the value of the response when predictors are at their mean.

Table 3-3: Summary and confidence intervals for model predictors

Response	Model structure	Fixed Effects	Random effects	Estimate	Variance	2.5%	97.5%
Estimated breeding start	Est_start ~ SST_spring + colony + pop_size + NAO	Intercept		131		124.17	138.10
		SST_spring		-9.54		-14.38	-4.69
		Runde		12.33		1.27	23.26
		Sklinna		-7.78		-22.46	6.17
		Pop_size		-8.161		-15.02	-1.52
		NAO		0.685		-0.53	1.89
			Individual		8.93	1.32	4.15
			Year		3.66	0.66	3.30
			Residual		50.1	6.42	7.79

3.2 Estimates from change point analysis

3.2.1 Estimates of changes in behaviour

The number of years sampled varied between the colonies in our study. Anda had a sample size of 10 years, Sklinna a sample size of 7 years and Runde a sample size of 5 years, see Appendix A for plots of distribution of breeding start per year. Number of years sampled are however, similar to that of some of the colonies included in the study by Burr et al. 2016.

There was a lot of variation in estimated start dates from the change point analysis for all colonies (Figure 3-1), with the estimated breeding start of Anda ranging from day 128-139 of the year, breeding start for Sklinna ranging from day 124-136 of the year, and breeding start for Runde ranging from day 131-137 of the year (Figure 3-1) (see Appendix A Table 6-1).
The overall mean breeding start date was very close for all colonies, with Anda having a mean breeding start of day 134 (14th of May), Sklinna a mean breeding start of day 128 (8th of May), and Runde a mean breeding start of day 128 (8th of May), suggesting that on average the breeding start at Anda is 6 days later than that of the two other colonies. Additional plots are provided in Appendix A. The Dunn test suggested that there was a significant difference between mean breeding start date for Anda and Sklinna (p-value < 0.05), but not between Anda and Runde or Sklinna and Runde, the last one is not surprising as the two colonies have the same breeding start date on average.

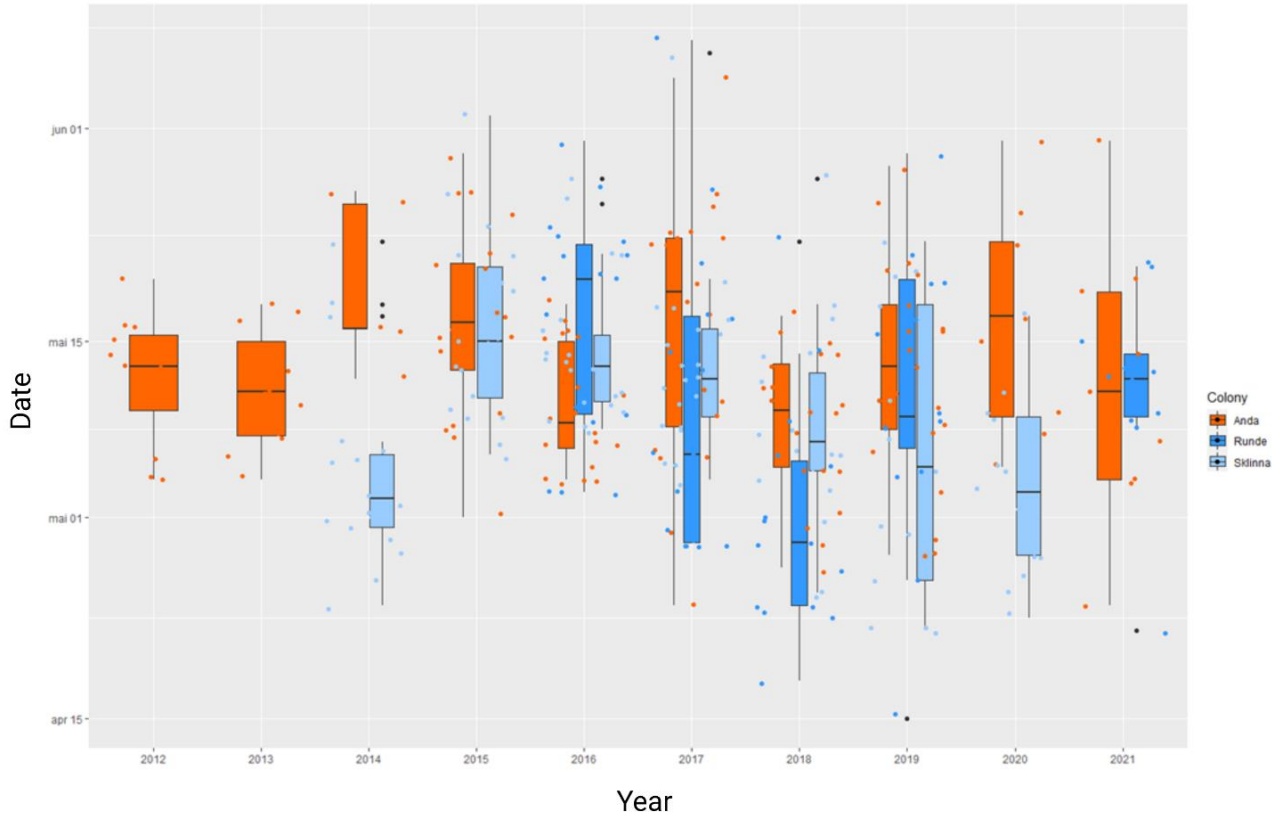

Figure 3-1: boxplots of distribution of estimates per year for all colonies in the study. Median is shown as black line through each box plot. Anda tends to have the latest median breeding start date, expect for the years 2016 and 2021.

3.2.1.1 Correlation between estimated breeding start and hatching dates

Synchrony between estimated hatching dates and estimated start dates was investigated only for Anda. This was due to hatching data not being available for the two other colonies.

The mean hatching date was estimated to occur around 22nd of June (day 173 of the year) for the selected years (Figure 3-2) at Anda.

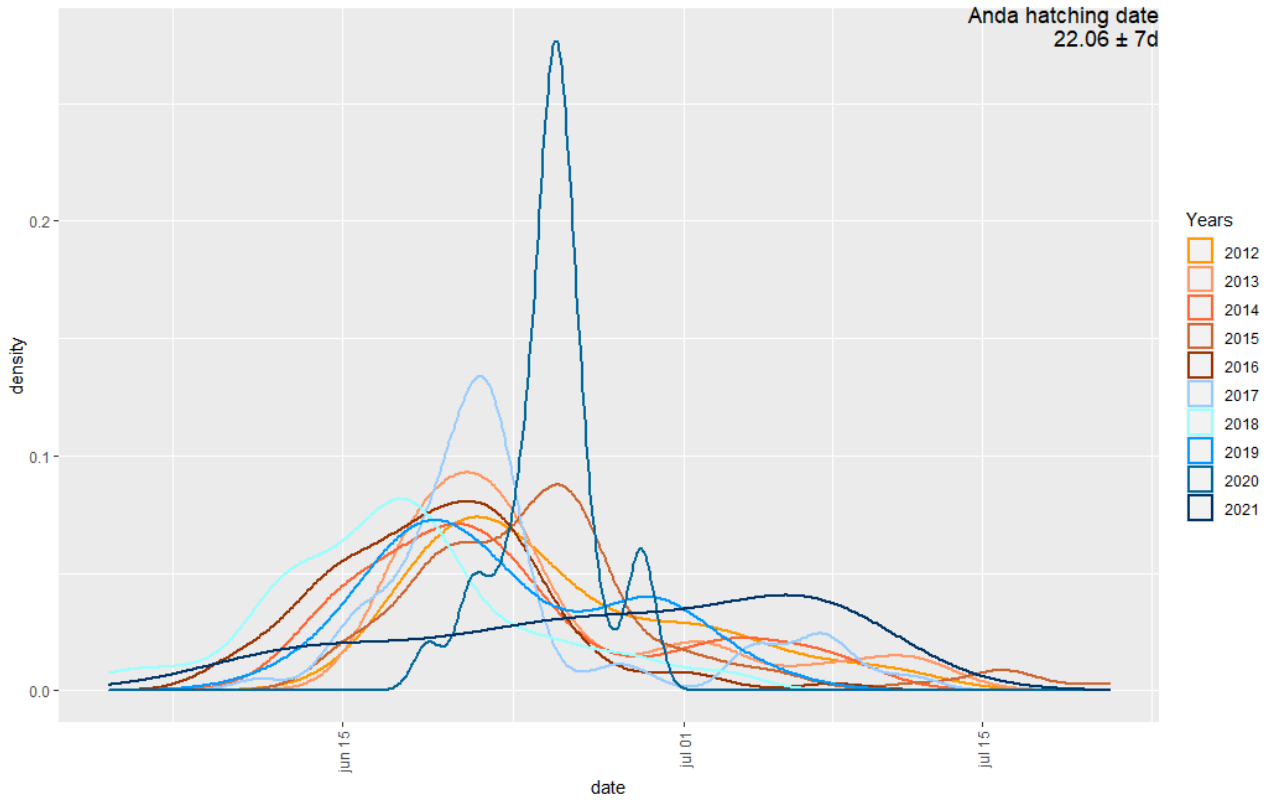

Figure 3-2: distribution of hatching dates for the years 2012-2021 at Anda. The mean hatching date for all years was estimated to happen around 22.06 (day 173).

A mean difference of 41 days, with a standard deviation of 4 days, between estimated hatching dates and start dates was calculated (Figure 3-3, see Appendix Table 6-2).

Most of the estimated differences between estimated breeding start dates and hatching dates fell within the interval of 35-45 days, with the only exception being year 2021 with a difference of 47 days. Year 2014 had a difference of 35 days, which was the lowest observed difference between the estimates.

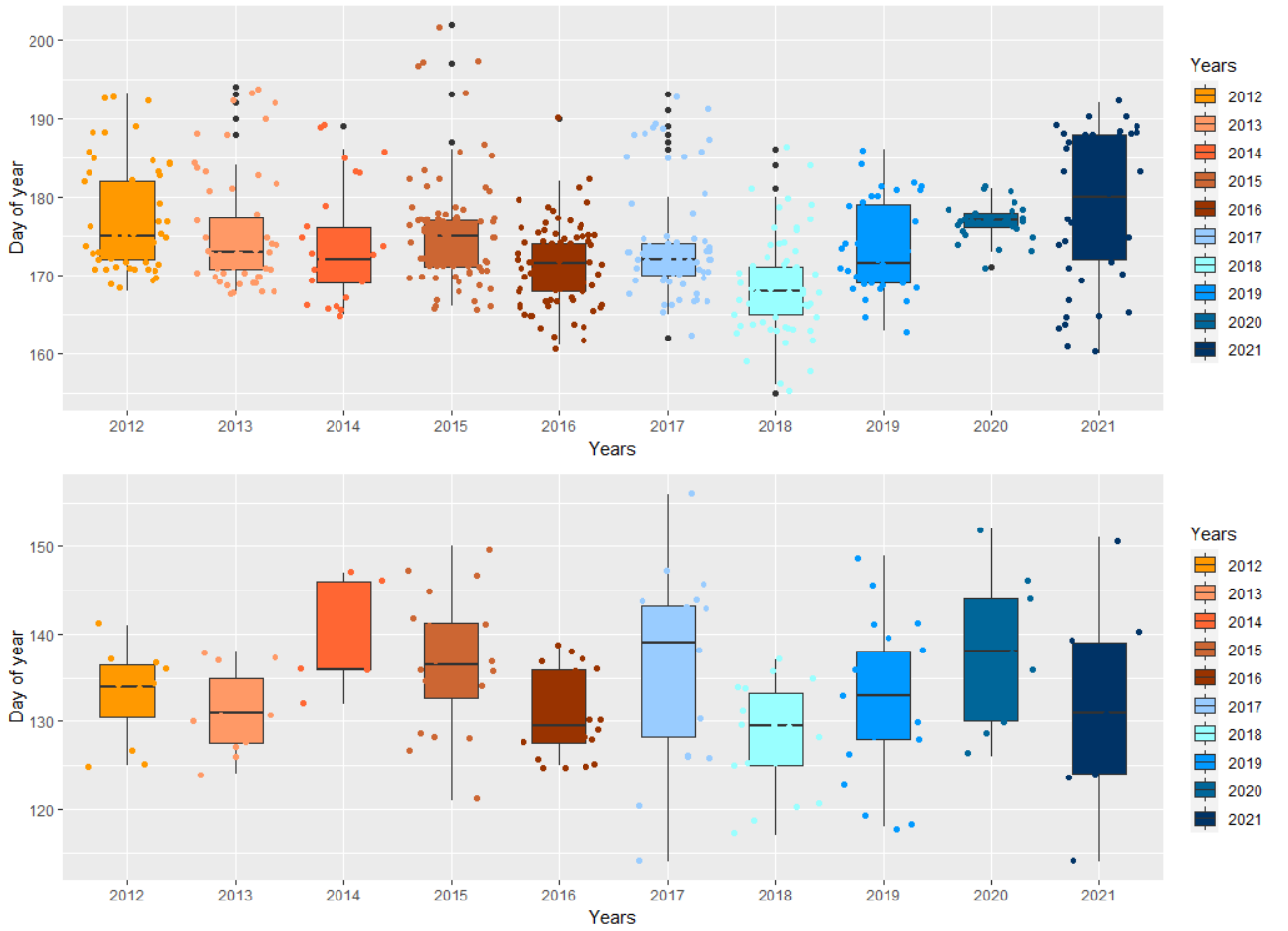

Figure 3-3: boxplots per year for estimated hatching dates (above) and start dates (below) for Anda. Median is shown as black line through box. Whiskers indicate the 25 and 75 percentiles.

The estimated R^2 between estimated hatching dates and estimated start dates when all years were included equalled to 0.38, indicating a moderate correlation between the two estimates (Figure 3-4).

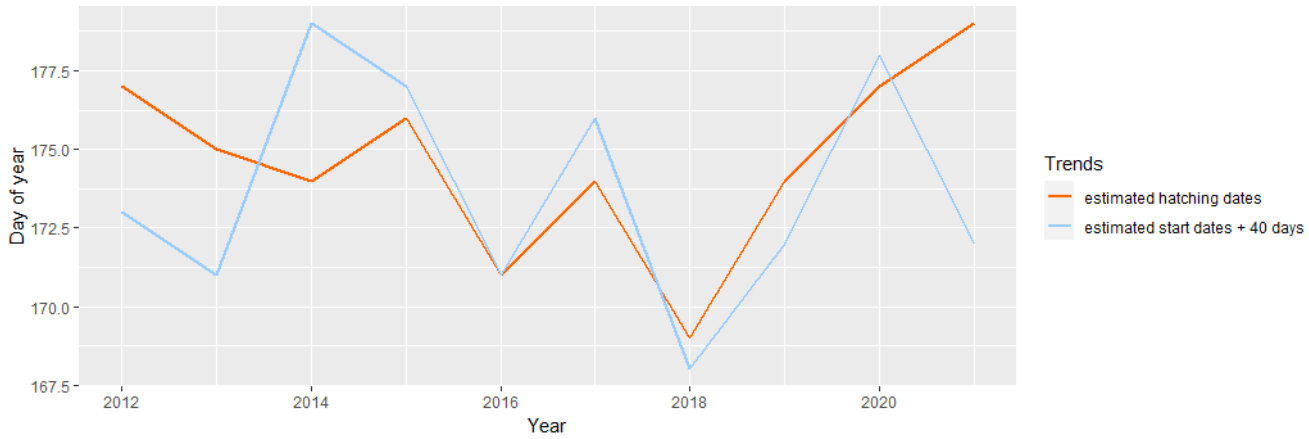

Figure 3-4: trend lines in mean hatching and breeding start date between years. Deviations between trends can be found for the years 2014 and 2021.

3.2.1.2 Differences between sexes

Estimated start dates varied between individuals for both sexes in both colonies (Table 3-4), with females from Anda having an average estimated breeding start date ranging from day 129-137 of the year, and females at Sklinna having an average estimated start date ranging from day 131-136 of the year. Males at Anda had an average breeding start date ranging between 127-136, while males at Sklinna ranged from day 122-134 of the year in their estimates (Table 3-4). Additional figures are provided in Appendix A.

The sample size was quite small (n = 9) and might therefore not represent the true difference between sexes in the populations. The estimated mean breeding start date per year for both sexes are quite close, with females having a mean breeding start date 2-3 days later compared to males (Figure 3-5) in both colonies.

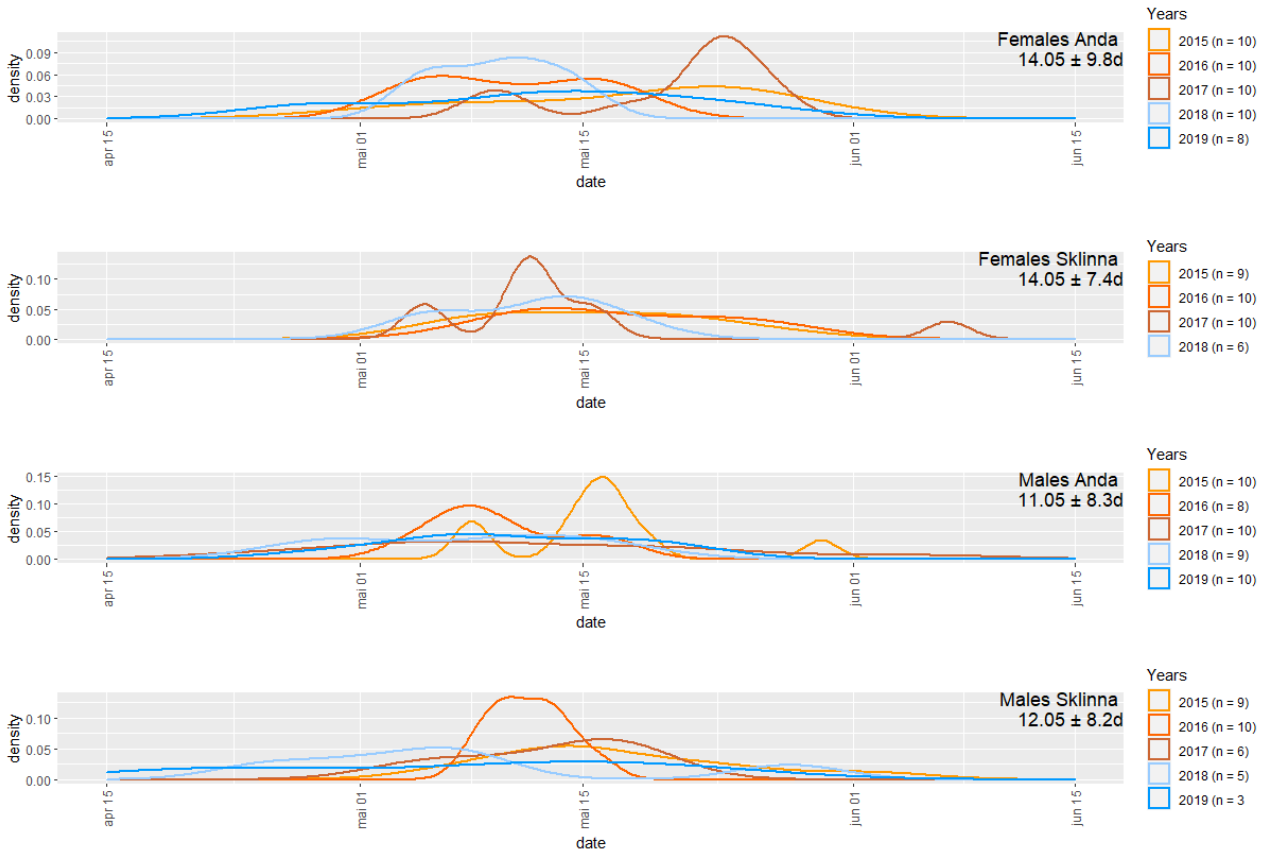

Figure 3-5 distributions of mean start date for both sexes in the colonies Anda and Sklinna. Sklinna only had 4 years of available data for both sexes. For Anda 5 years of available data for both sexes were obtained. Note that the density function is not the same for all y-axes.

Table 3-4: Estimated start dates for both males and females in both colonies

Colony	Year	$Median_F$	SD_F	N_F	$Median_M$	SD_M	N_M
Anda	2015	137	9.1	10	136	6.1	10
	2016	131	5.4	10	130	4.3	8
	2017	140	6.3	10	131	12.3	10
	2018	129	3.8	8	127	7.5	10
	2019	132	9.9	8	130	7.5	10
Sklinna	2015	134	6.7	9	134	7.9	3
	2016	136	6.7	10	132	2.4	2
	2017	131	9.3	10	132	5.7	7
	2018	131	5.0	6	122	12.5	8
	2019	NA	0	0	127	14.2	10

The result from the one-sided Wilcox signed rank test suggested a significant difference between males and females in our study (p-value = 0.02), indicating that males do have a median estimated breeding start slightly earlier than that of females (see Appendix Figure 6-4 and Figure 6-5). However, the estimated median breeding start per year for each sex has a considerable overlap, especially if we take into account the standard deviations.

4 Discussion

The aim of this study was to gain insight into the effects on breeding start in Norwegian kittiwake colonies, focusing on environmental variables (both local and regional) as well as intrinsic variables such as the population size. My findings support those of similar studies, namely that warmer SST and larger population sizes tend to advance the breeding start in this colonial seabird.

4.1 The effect of environmental variables and population size on breeding start in Norwegian kittiwake colonies

From the model comparison, the model with both spring SST, NAO and population size had the best fit according to the AICc criterion of the GAMM models (Table 3-2) and an LME model was only fitted for this model structure. In this section only the LME model will be discussed, as it contains information about the parameters and their effect on the response.

The residual variance in the model was quite high (Table 3-3), suggesting that there is a lot of variance that could not be explained by the fixed effects of the model. This suggests that there is some unknown variable, or variables, that could better explain the variation in the breeding start for the data used in this study. The random effects did not explain a lot of the total variation in the data, indicating that there is little difference in the variation between the individuals and years of the colonies in the study, suggesting that the start of breeding was not completely random.

4.1.1 The effect of the environmental variables on breeding start

The LME model suggested that the effect of spring SST on breeding start was negative, with an increase in spring SST resulting in an earlier breeding start (Table 3-3). The confidence interval of the predictor did not include zero indicating that the effect of the predictor was significant for the years and colonies included in this study (Table 3-3). Increasing spring SST by one unit would advance breeding start by 9.54 ± 4.8 days.

NAO had a positive effect, but with a confidence interval including zero, indicating that NAO did not have a significant effect on breeding start in our study (Table 3-3). However, the confidence

interval of this predictor is quite narrow suggesting a more precise estimate. A one unit increase in NAO delay breeding start by 0.68 ± 0.68 days.
It could be that a large-scale variable such as NAO is less important for breeding start in the study colonies, and that local variation in the environment is of higher importance when individuals stay in the same are for longer periods, e.g. the breeding season (Frederiksen, Harris, et al. 2004). However, previous studies have found that NAO is of importance to breeding seabirds, especially if latitude was included in the model, where the effect of NAO got progressively negative with increasing latitude, suggesting differences in effect of NAO between regions (Sandvik, Coulson, and Sæther 2008). Including latitude as a predictor in our model could therefore have been useful to fully investigate the potential effect of NAO on the spatial scale.

A potential explanation for the effect of spring SST on breeding start in the study colonies could be due to the relationship between zooplankton spring spawning events and food availability for fish species such as herring, sand eel and mesopelagic fish (Kaartvedt 2000; Deurs et al. 2009). Copepods, especially the species *Calanus finmarchicus*, is an important prey item for many fish species in the North-Atlantic, both for juvenile and larval stages (Kaartvedt 2000; Frederiksen et al. 2013). *C. finmarchicus* overwinters in the deep-water basin in the Norwegian Sea, and migrates towards the surface to spawn in early spring (Dale, Rey, and Heimdal 1999). The spring spawning of copepods in the oceanic habitats outside the shelf-break in the Norwegian Sea provides favourable feeding conditions for planktivorous fish species (Kaartvedt 2000; Utne et al. 2012) (Figure 4-1) and could explain why these habitats are favoured by foraging kittiwakes during the breeding season, even when colonies are situated far from the shelf-break as observed by Christensen-Dalsgaard et al. 2018. Advection of copepods into coastal areas in spring also ensures increased feeding availability for fish larvae in these areas, providing kittiwake colonies with higher food availability closer to the colony (Figure 4-1).

With the rising sea temperatures caused by climate change, the distribution of *C. finmarchicus* is expected to shift north-east (Reygondeau and Beaugrand 2010). It has also been suggested that *C. finmarchicus* spawning events and peak in abundance happens earlier in years of warmer water, especially SST temperatures above 6°C, but lower than 11°C (Weydmann et al. 2018; E. F. Møller et al. 2012). Trends toward earlier peak abundancy of *C. finmarchicus* has also been observed in the Norwegian Sea (Dupont, Bagøien, and Melle 2017).

Earlier peak abundance of copepods might result in fish species reaching higher abundancies earlier in spring, advancing the breeding start of kittiwake colonies as a result.
Earlier breeding, caused by a warmer climate, has been observed in other kittiwake populations, as well as other seabird species (Moe et al. 2009; A. P. Møller, Flensted-Jensen, and Mardal 2006; Descamps et al. 2019; Frederiksen, Harris, et al. 2004).

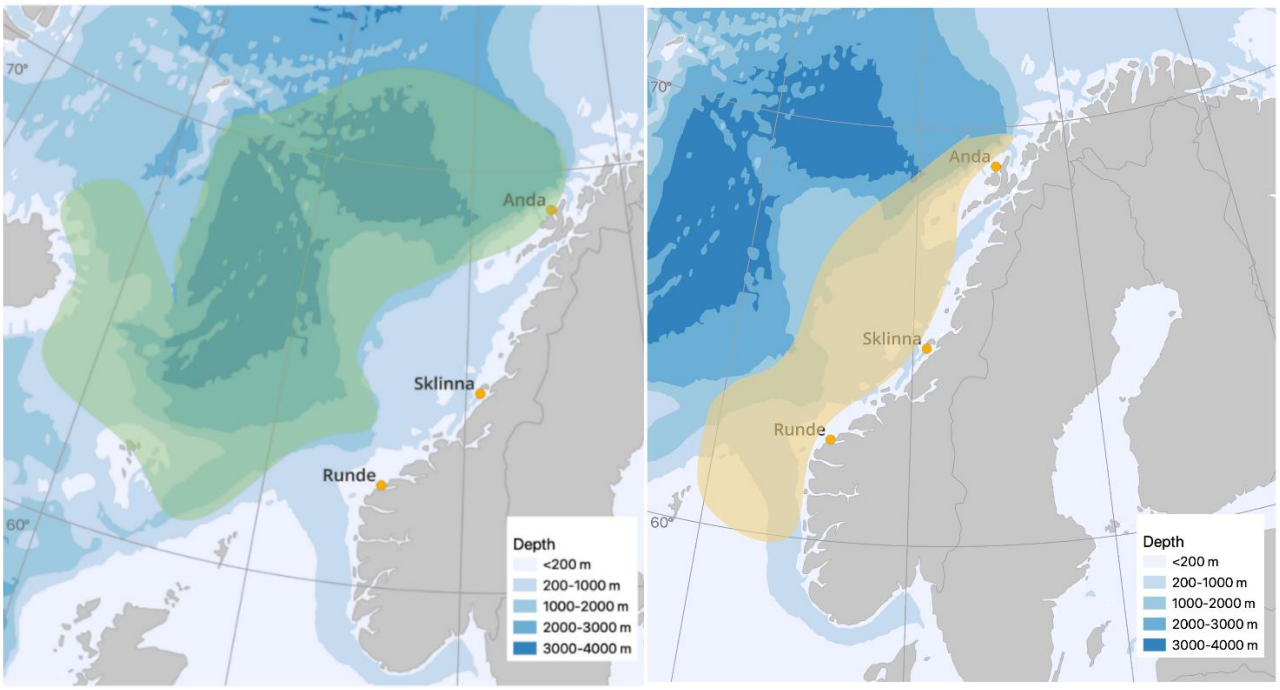

Figure 4-1: Left: Approximate distribution of C. finmarchicus in winter in the Norwegian Sea marked by green area. Kittiwake study colonies marked in orange. Distribution of copepods are concentrated in deep water areas following the shelf along the Norwegian coast. Right: approximate distribution of C. finmarchicus in spring in the Norwegian Sea marked by yellow area. After overwintering in the deep-water basin, copepods ascend to the upper layers and are advected into the coastal waters. Created using QGIS ('QGIS Geographic Information System.' 2023).

I think that there are two potential explanations for how warmer spring SST affects the breeding start in kittiwakes on the Norwegian coast, with respect to the prey abundancy and copepod spring spawning.
Firstly, breeding start might be mediated by the body condition of the breeding adults (Goutte et al. 2014; 2010). It has been suggested that factors such as temperature and food availability in early stages of breeding are of importance to parental health during the breeding season (Monaghan 2007). If fish larvae availability has an earlier peak in warmer years, as a result of earlier copepod spawning, kittiwake adults could reach higher body conditions earlier, potentially advancing the start of breeding. This is in accordance with previous findings, where a high food abundancy prior to egg laying resulted in individuals laying earlier (Shultz et al. 2009).

Another explanation for this relationship might be that breeding kittiwakes time their breeding to higher abundancies of prey. Since kittiwakes do not feed directly on copepods, but on their predators, a time-lag exists between copepod spring bloom and kittiwake breeding start, caused by the time it takes for fish larvae to grow (Durant et al. 2007). The decision to breed in kittiwakes might therefore be motivated by the increase in prey abundancy in the foraging habitats, signified by the copepod spring bloom. If fish availability is advanced in years with earlier copepod spawning, kittiwakes might start breeding earlier in order to time their reproduction to peak prey availability.
Earlier kittiwake breeding start could therefore potentially be explained by individuals timing the breeding to match that of peak abundancy in prey and/or by the body condition of breeding adults.

However, from a life-history theory perspective, prioritizing one's own physical condition over a current reproductive attempt is more favourable for a long-lived species such as the kittiwake, as new breeding attempts can be carried out in the future if the individual survives (Erikstad et al. 1998). I think it is therefore likely that body condition of the adults is of high importance for making the decision to breed, and high food availability on its own is not enough to induce breeding if individuals are of significantly poor physical condition. This is however only a suggestion and would have to be further tested in future studies.

Unfortunately, it is difficult to say anything about the strength of the effect of spring SST on kittiwake breeding start, as the confidence interval of the spring SST estimate was quite wide (Table 3-3), resulting in a high uncertainty and an unprecise estimate, probably caused by small sample sizes. The effect of SST have been shown to disappear when longer time-series on breeding phenology in kittiwakes were analysed (Frederiksen, Harris, et al. 2004; Wanless et al. 2009).
Local SST has also been found to have varying effect on kittiwake breeding success. In the North Sea some kittiwake colonies showed no relationship to local STT values (Frederiksen, Harris, et al. 2004; Frederiksen et al. 2007; Eerkes-Medrano et al. 2017; Carroll et al. 2015).
Similar variation in the effect size of SST on breeding start at a local scale might be present in kittiwake colonies in the Norwegian Sea, and SST as a proxy for food availability might therefore be somewhat simplified due to the complexity of the food-web in the North-Atlantic.

For example, increased abundancy of fish species does not only rely on food availability through copepod spawning but has also been found to be affected by the presence of other fish species. It has for example been shown that the environment has an indirect effect on capelin stocks through the effect on cod and herring reproduction, with positive effects on cod and herring resulting in negative

effects on capelin in the Barents Sea, as cod and herring are two of the main predators on caplin larvae (Hjermann, Stenseth, and Ottersen 2004). Fluctuations in the climate has also been found to affect different age-classes of copepods differently, with C5 stages of copepods increasing with warmer temperatures, potentially leading to earlier spawning, while C1 and C2 stages having higher abundancies in colder years (Weydmann et al. 2018).

However, I do believe that the findings in this study point towards the potential relevance of environmental variables when it comes to kittiwake breeding start in Norwegian colonies, and further investigation is of importance.
Studies from the North Sea region has shown that the abundancy of many of the kittiwakes' important prey species, such as sandeel and herring, have declined, and the decline has been linked to the simultaneous decline in *C. finmarchicus* in the region (Frederiksen et al. 2013; Régnier, Gibb, and Wright 2017). Fish and copepod species, like *C. finmarchicus*, are closer to their upper temperature limit in southern regions of the Atlantic (Montero et al. 2021). The rising sea temperatures are expected to bring regions such as the North Sea above the threshold of temperature tolerance of many marine species, and as a result, many species will shift their distribution northwards, and this trend is expected to continuously shift northwards as temperatures rise (Beaugrand 2003). Regime shifts in copepod populations have also been observed in the North Sea (Montero et al. 2021; E. F. Møller et al. 2012), which could have an effect on higher trophic levels.

All the included kittiwake colonies in our study had mean spring SST temperatures within the optimal range for *C. finmarchicus* (E. F. Møller et al. 2012), with SST values ranging from ~7-9 °C, favouring earlier spawning and peak abundance. This could explain why more seabird colonies in the North Sea are failing compared to colonies on the Norwegian coast and the Barents Sea at present. Indeed, studies indicate that the rising temperatures in the North Sea drive the distribution of fish stocks northwards, leaving seabird colonies situated in the North Sea with a low food availability, negatively impacting the breeding productivity and success of these colonies (Frederiksen et al. 2013; Burthe et al. 2012; Harris and Wanless 1997). Studies have also suggested that breeding in North Sea colonies happen later, resulting in decreased breeding success (Wanless et al. 2009). This made it hard to compare the effects of the trends in the environment observed in studies of regions such as the North Sea and observations made in our study on kittiwakes in the Norwegian see, since effects of a changing climate might differ due to the differences in for example temperature ranges at different latitudes.

However, the trends observed in the North Sea are likely to emerge in the Norwegian Sea and Barents Sea in the future, and the present status of southern kittiwake colonies might give us some insight into the future of northern kittiwake colonies.

4.1.2 The effect of the breeding population size on breeding start

The LME model also suggested that there is a negative relationship between the breeding start and the size of the breeding population, with larger population sizes advancing the breeding start for the study colonies (Table 3-3). Again, the confidence interval was very wide, signifying a lot of uncertainty and an unprecise estimate of the predictor. Of what importance the size of the breeding population has when it comes to explaining the start of breeding related behaviour in the three study populations is therefore difficult to say.

Larger populations would contribute to a higher competition pressure for the best nest sites, and it is therefore possible that this might contribute to an earlier breeding start, as individuals would have to secure the best nest-site earlier in the season.

Similar trends to that observed in this study, have been found in other seabird species, with larger colonies starting the breeding season earlier than that of smaller colonies or smaller population sizes of the same colony, often resulting in a lot of variability of pre-hatching durations between years (Merkel et al. 2019; Kokko, Harris, and Wanless 2004; Hatchwell 1988).

Larger populations also provide greater protection from potential predators (Anker-Nilssen, Fayet, and Aarvak 2023). Frederiksen et al 2004. did report that later egg laying in a North Sea kittiwake colony was linked to the population density, with lower population density leading to later egg laying, suggesting that predator pressure might be of importance. Early in the season kittiwakes visiting nest-sites are reported as being nervous when few individuals occupy the area around the colony (Coulson 2011). This could suggest that individual kittiwakes rely on the population size to some extent for protection against predators. As a result, it could be that individuals start the breeding season earlier when the population is larger.

This has potential management implications as kittiwake populations have continued to decrease the last decades (Fauchald et al. 2015). As mentioned previously, later breeding start has been linked to lower breeding success (Goutte et al. 2014; Burthe et al. 2012; Harris and Wanless 1997; Moe et al. 2009) and decreasing population sizes could therefore accelerate the failure of the colony through the influence on breeding start and breeding outcome, together with low food availability.

In two of the study populations, population sizes fluctuated between the years included in the study, with the population size of breeding individuals being as low as 32 individuals in Sklinna one year (Table 2-4). Breeding failure has been observed for this colonies in years with similar population sizes (Christensen-Dalsgaard, May, and Lorentsen 2018), so it is not unreasonable to assume that the colony had a low breeding success in the years with small population sizes of this study as well.

4.2 From non-breeding to breeding

Comparison between the estimated breeding start dates and estimated hatching dates was only possible for Anda, because of lacking data on hatching dates for the two other colonies. The optimal solution would have been to investigate the differences for all colonies to see how well the method worked on different colony data, but a proper investigation of one colony gave at least an indication of how well the change point method worked for estimating breeding start in kittiwakes.

The estimated correlation between breeding start and hatching was 0.38, suggesting that the breeding start somewhat fit the hatching dates in the years included when the mean difference of 40 days was applied (Figure 3-4). No information about the sampled individuals was available for the hatching data, so from what individuals the data came from was not known. This could explain the relatively large amount of unexplained variation in the correlation, and comparing the estimates of breeding start and hatching on the individual level would have been useful, as it would indicate how precise the estimation was for different individuals, and not on the colony mean. It would also have provided more insight into variation in pre-hatching duration on the individual level.
As mentioned in section 1.1 and 2.4.1, the number of days spent on the early breeding and incubation period for kittiwakes is approximately 35-45 days (Coulson 2011). Most of the individual variation is probably due to the length of the early breeding period, where activities like nest building, pair formation, partner bonding, and copulation takes place. Strategies for inducing breeding behaviours vary between pairs and factors such as age, length of relationship with partner, physiological condition, and food availability seems to be the main factors driving the length of this period (see section 1.1 and 1.2 for more), with more experienced birds starting nest-building and defending earlier while also laying earlier than their young and inexperienced counterparts (Goutte et al. 2014). Younger and more inexperienced birds do however spend more time overall at the nest to be able to synchronize and bond with their partner (Chardine 1983).

Breeding-failure the previous season could also influence the length of the period between breeding start and hatching, as the likelihood of choosing a new partner increases after a failed breeding season and newly established pairs spend more time bonding and tending to their nest (Chardine 1983; Mercier, Yoccoz, and Descamps 2021; Ens, Choudhury, and Black 1996). It could be that as a result, these pairs take longer to produce and lay eggs and therefore have longer intervals between breeding start and hatching.

All of these factors contribute to the variation in the duration of the pre-hatching period. I think it is therefore reasonable to assume that the estimated dates in this study do reflect a change in behaviour from non-breeding to breeding in kittiwakes, and that the estimates presented in this study represent the breeding start dates for the individuals sampled, even though the correlation between breeding start and hatching on the colony level was not particularly high. Similar variation between years have been observed in other studies on breeding kittiwakes (Goutte et al. 2014; Burr et al. 2016; Kokko, Harris, and Wanless 2004), and there is no apparent reason suggesting that our results should not follow the same patterns.

Only few of the individuals were sampled for all years of data, and the sampled population might therefore have different structures each year, with some years having more individuals of older age with more experience, or vice versa. If the proportion of new pairs in the sampled population change between years as a result of poor breeding success the previous season, the colony average interval between breeding start and hatching might be expected to change accordingly.
A higher proportion of well-established pairs could also influence the colony average breeding start, as these birds tend to start nest defending and breeding earlier, shifting the colony average towards an earlier breeding start.
Accounting for factors such as age, previous breeding success and if the pair is newly established or not, could be worth looking into in order to understand how the interval between breeding start and hatching fluctuate between years, and how this influences the colony average breeding start and variation.

There is also a possibility that some of the individuals that were analysed were not participating breeders. From previous studies it has been indicated that early stages of nest defence and pair bonding happen before the pair, or one of the individuals in a pair, decide not to breed (Goutte et al. 2014). There is therefore a possibility that data was retrieved from unknown non-breeders during fieldwork in some years.
When choosing individuals to analyse, known non-breeders were removed (see section 2.3.1). However, the breeding status of all individuals was not known. Unknown non-breeders might contribute to noise in the mean estimated breeding start for each year, but since the potential presence of non-breeders was not known, it was not possible to say if this had an effect on the estimated breeding start dates, and thus the difference between breeding start and hatching.

4.2.1.1 Change point as a method for detecting breeding start in kittiwakes

In this study it was shown that change point analysis did provide estimates for the breeding start of kittiwakes in the study colonies.

In addition to the hatching data for Anda, researchers from the two other colonies confirmed that the estimated dates of breeding start fit relatively well with observations from fieldwork. In particular, hatching had been observed to start early at Runde in the year 2018 (Christensen-Dalsgaard, pers. Comm). The estimated mean breeding start date for this year was considerably earlier than that of the other years (Figure 3-1). The additional information from researchers working with the colonies, in combination with the comparison with hatching dates, suggests that the estimates from the change point analysis approach do fit the breeding phenology of the study colonies.

However, the individuals in this study were not monitored using cameras or other equipment during the time interval of interest, so it was not possible to check if what we interpreted as breeding start actually matched what the individuals were doing in the colony at that time. It could be that the estimated dates in this study was something other than breeding start, and this would have been confirmed by monitoring data from cameras (Figure 4-2).

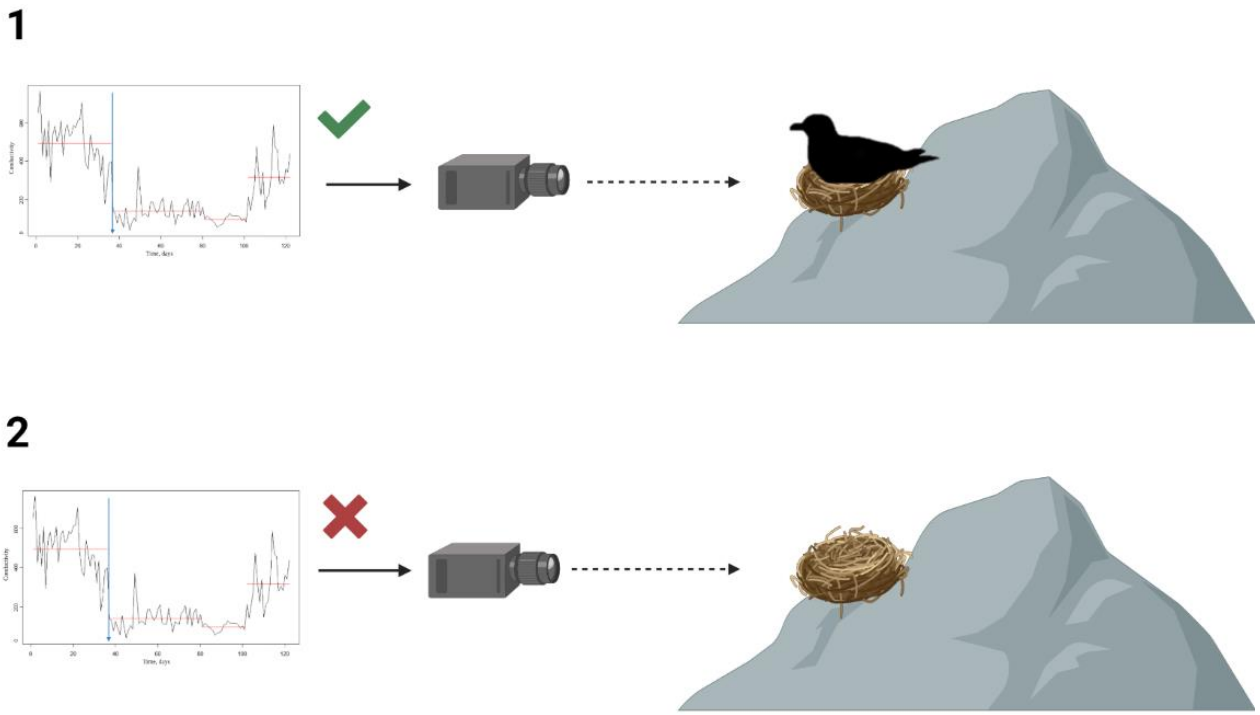

Figure 4-2: Example of how monitoring data can be used as a reference for the data analysis. Monitoring data suggesting that suggested change point matches behaviour of individual (1). Monitoring data contradicting the suggested change point (2). Created using https://www.biorender.com/.

Just as age and breeding experience might influence the breeding start date, they might also influence the proportion of wet and dry data in the time-series. As discussed above, younger and inexperienced birds tend to spend more time at the nest to bond with their partner. This might lead to differences in the conductivity data, with younger and inexperienced birds having lower overall conductivity values during the period and having a later change in the mean conductivity compared to the older and more experienced breeders. Investigating how age and breeding experience, as well as pair status, affect the data collected by the GLS loggers could be worth looking into to understand how differences in conductivity data arise.

As mentioned in section 2.3.2, change point analysis of time series with potentially multiple change points needs to be visualized in order to determine what change point in the time series is the one of interest. In this study 154 different individuals from three different study sites over multiple years were analysed, resulting in 350 unique time-series. Since the analysis was carried out multiple times in order to get the best possible estimates, more than 700 plots were analysed. This is an extremely inefficient method of extracting estimates for breeding start. A possible solution would be to have more people do the analysis of time-series.
However, this would increase the risk of variation in interpretation. In this study, only one person conducted the change point analysis, so faults in the interpretation would be consistent for the whole study. It is therefore recommended that the results of the change point analysis, if conducted by multiple people to reduce time use, should be compared between analysts in order to get an idea of how interpretations of change points of interest vary between analysts. This also opens for calibration between analysts, so that major interpretation differences can be corrected.
However, this does not necessarily improve the efficiency of the change point approach, as having multiple people to conduct such analyses is not always possible. An alternative approach to the change point method is to automize the procedure by constructing an algorithm that can analyse the data without the need for visual inspection of each individual time series.
Using machine learning has proven to be successful in describing different behaviours of nesting little auks (*Alle alle*) (Grissot et al. 2023). The method utilized both conductivity and light data from GLS loggers to make a framework for deciding on type of behaviour of logger bearing individuals during the breeding season. The method of Grissot et al. was tested, and proven effective, on incubation and early chick rearing data, but was not tried on early breeding behaviour data. It is therefore difficult to say if this exact approach would work on data used in this study on kittiwakes, since the method was developed for a different species and timeframe. Potential use of machine learning as an alternative to change point analysis will be discussed further in section 4.4.2.

4.2.1.2 Differences between sexes

The difference between sexes was significant (p = 0.002), indicating that there is a difference in the mean estimated breeding start dates for males and females in the study population. Even though the results indicated that there was a significant difference in estimated breeding start dates for the sexes, it is worth noting that the sample size was quite small (n = 9), and it is therefore possible that our sample does not reflect the reality of the study populations.

This difference however, does indicate that males on average start their breeding related behaviour slightly earlier than females. This slighly earlier change in conductivity data could reflect that males begin the intensive nest defending a few days prior to females arriving at the colony site to find a partner. Differences in attendance and nest-defence has been observed between sexes in kittiwakes in colonies in Great Britain (Coulson 2011), but also in other seabird species (Hatchwell 1988).
It is important to be aware of this difference since the sex of all individuals was not known in this study (Figure 2-7). Accounting for variation between males and females could therefore not be assessed properly in the models. As a result it is not possible to know if the observed difference in the breeding start between colonies is due to the sex ratio of the sampled population.
It could be that for some of the sampled colonies the majority of the sampled individuals are of one sex. This would potentially skew the mean breeding start in one direction, depending on the sex that is in majority. If more females were sampled, the overall breeding start would be expected to be later for the study population, and opposite if the majority of the study population consited of males (Figure 4-3).
Since the difference between mean breeding start for the colonies was so small in this study, it is not unlikely that the sex of the sampled individuals could contribute to this difference in mean breeding start if the ratios of males and females were not similar for the different colonies.

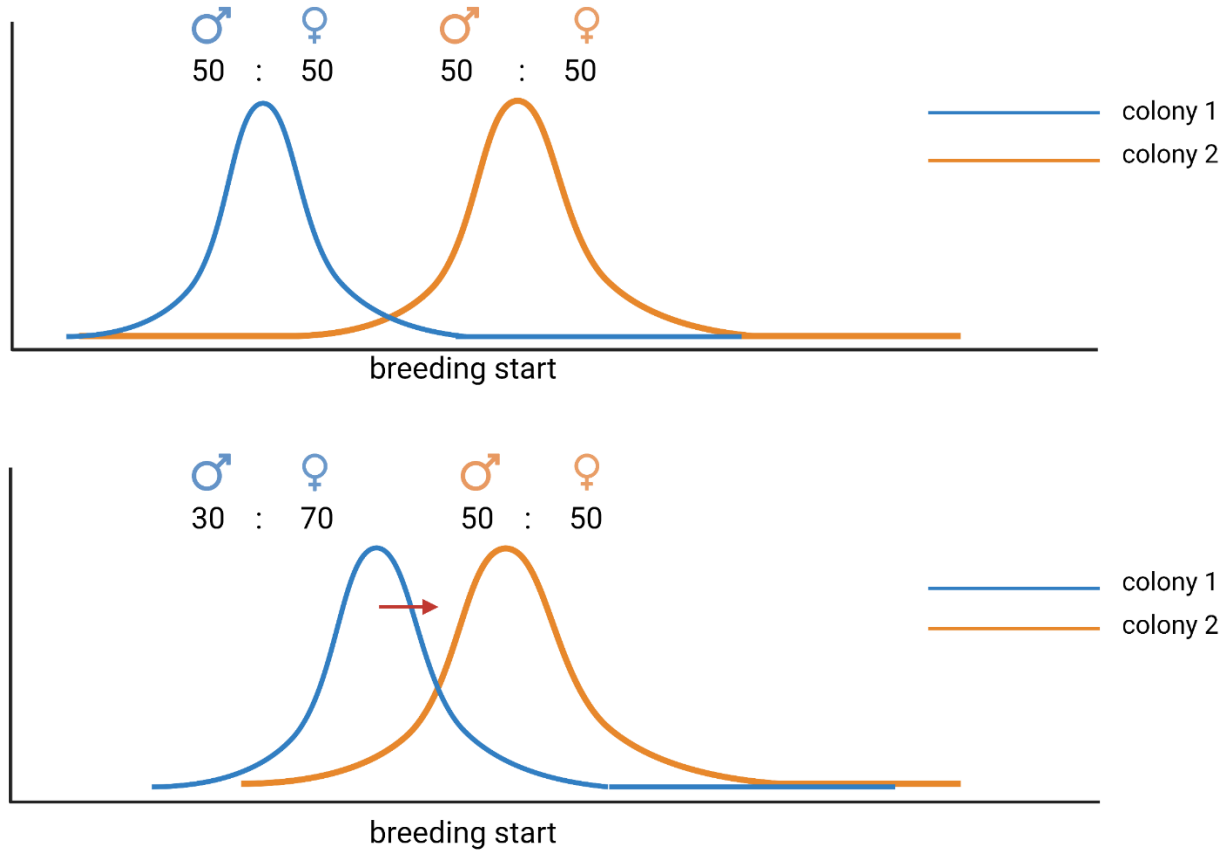

Figure 4-3: change in estimated breeding start if sex-ratio of sampled individuals changes, red arrow indicates a shift in mean breeding start for colony one to a later date, bringing the two colony means closer together. More sampled females would mean a later mean breeding start for the colony. Differences in sex-ratios of sampled individuals might therefore explain the differences in mean breeding date between colonies. Created using https://www.biorender.com/.

4.3 Suggestions for future studies

Some advice for the improving the study has been mentioned in previous sections of the discussion, but I will here sum them up and elaborate on some of them.

4.3.1 Increasing amount of data used

An aspect that was present in all parts of this study was the limitations created by the lack of data, highlighting the need for large quantities of data in order to make inferences in ecology.
The data used in this study spanned a very short timescale, covering only 10 years of breeding seasons and with varying amounts of contributing data from each of the included colonies. Lack of data within each colony was also apparent with regards to sampled individuals and information about individuals (sex, partner, breeding status). The spatial scale of the study was also not optimal, since it only covered the southern part of the spatial gradient of kittiwake colonies in the Norwegian Sea and Barents Sea (Figure 4-4).

Including more data in the study opens up for creating models of higher complexity than those explored here. In this study, only models with additive effects could be investigated, as more complex models had increased uncertainty and were even more unreliable than the models presented here, with regards to predictions and confidence intervals.
Complex models might pick up on complex structures and effects in the data. One such effect might be that of colony size. For the simple model used in this study, population size was assumed to have the same effect for all colonies (Table 3-3). The studied colony at Sklinna has a much smaller breeding population size compared to Anda especially (Table 2-4). The effect of population size on breeding start might therefore not be as large at Sklinna, since the competition for nest sites and food is expected to be smaller for colonies with smaller population sizes, and the slope of the colonies, with respect to the population size, might therefore differ. This is also potentially the case for SST, as the effect size of SST might vary between colonies, as observed in several other studies (Lauria et al. 2012; Frederiksen et al. 2007; Eerkes-Medrano et al. 2017).
Having more data on the spatial scale would make it possible to use colony as an interaction effect or random effect, making it possible to investigate both specific effects on breeding start in different colonies and effects on breeding start in general irrespective of what colony the data originated from.

More data would also make it possible to construct models separately for each colony, so that the effects on colonies, rather than breeding phenology in general, can be studied. At Sklinna for example there is another kittiwake colony in close proximity. The presence of this colony might

increase the competition pressure at Sklinna for food since birds from the two colonies forage within the same range. There might also be some exchange of individuals each season between the two colony sites, creating some competition for nest-sites. Including the population size of this nearby colony in a model could be useful to investigate how colonies in close proximity influence the breeding start of the study colony. This is however only possible if models are fitted for each colony.

Additional data on the population structure could also be valuable to use as intrinsic factors during model fitting to try and explain variation in breeding start. In this study, only the population size of breeding adults was used as an intrinsic factor to explain breeding start, but as previously discussed, the age and breeding experience structure of the population might explain some of the variation between years. As mentioned previously, older, more experienced birds tend to start the breeding season earlier (Chardine 1983; Coulson 2011), and a population structure consisting of many older pairs might explain some of the variation in breeding start. Controlling for population structures might therefore be useful in future model fitting.

In my opinion, the best ways to improve the study, with respect to the data limitation, would be to collect data in the coming years to construct longer time series, as well as deploying more individuals with loggers to increase the study population. This would also minimize the risk of only retrieving data from a few numbers of individuals, since the probability of re-capturing tagged individuals increases with the size of the tagged population. There is, however, potentially economic aspects to this side of the project, both in regard to expenses for equipment and conducting fieldwork, but this will not be discussed in this thesis.
The study would also greatly improve by including additional colonies, to complete the spatial gradient of kittiwake colony distribution along the Norwegian coast (Figure 4-4). Using additional colonies would also open for comparisons with other studies, such as Burr et al. 2016 and Sandvik et al. 2016.

Figure 4-4: all kittiwake colonies on the Norwegian coast. Study colonies are marked in orange, colonies not included in the study marked in black. Created using QGIS ('QGIS Geographic Information System.' 2023).

There is also potential for improvement in the understanding of how breeding behaviours vary between individuals and how this relates to the data collected by the loggers.
As outlined in section 1.1, nest attendance has been observed to be higher for younger and more inexperienced individuals in the pre-breeding period, since they need more time to bond with the partner (Chardine 1983). This is also the case for newly established pairs of previously unsuccessful breeders (Angelier et al. 2007; Chardine 1983). Patterns in the conductivity data, and potentially also light data, might differ from that of older, more established pairs.
A more in-depth analysis of failed or non-breeders, different age classes, and pairs would be needed to look into how these factors influence the data and our interpretation of the time-series. It would be especially interesting to investigate how time-series data differ between non-breeders and breeders.

In order to obtain this type of dataset, I suggest monitoring specific pairs for a number of years, preferably successful and unsuccessful breeders, and of different ages, to see how the patterns in conductivity and light data differ between inexperienced and experienced breeders, but also how an unsuccessful breeding season potentially influences next year's season.
This is also the case for investigating behavioural differences between sexes. In this study males and females were compared, but there was no information about what individuals formed specific pairs. Having more data from specific pairs over a number of breeding seasons would also provide more detailed information about the differences in behaviour between the males and females.

4.3.1.1 Investigating the effect of prey advection between colonies

Lack of data was also evident when attempting to investigate the effect of prey advection on differences in breeding start between colonies. There were not enough observations to fit a model on the response variable of interest.

In similar studies on colony synchrony more than 30 years of data was used to construct the time-series, with data being collected from 22 colonies in Great Britain (Olin et al. 2020). This results in a dataset that covers both a spatial and temporal scale that was sufficient in order to infer about the synchrony between colonies in relation to the main prey.
Including more data in our study, both spatial (additional colonies) and temporal (additional years), would be necessary to be able to construct a longer time-series and complete the spatial gradient needed in order to fully investigate the potential effect of prey drift between the study sites.
Some interesting dynamics between kittiwakes and prey might be present in colonies north of Anda, and comparison of these northern colonies with the colonies Runde and Sklinna, two of the colonies situated furthest south on the Norwegian coast (Figure 4-4), could shed light on how kittiwakes at different latitudes interact with their prey during the breeding season. It has already been shown that depending on the location of the colony and the distance to different foraging areas, kittiwakes from the colonies Anda (close to shelf-break) and Sklinna (long distance to shelf-break) utilize different foraging strategies in order to optimize the foraging outcome (Christensen-Dalsgaard, May, and Lorentsen 2018).

It should also be mentioned that the drift model used in this study was too coarse. In the model, only the transport of particles between the colony locations was simulated. This particle model might therefore reflect the egg stage in the fish life cycle rather than larval stages of fish. Since kittiwakes rely on fish larvae as a food source it might be better to use models representing larval fish, or a combination of larvae and eggs, to investigate the influence of prey advection on breeding start.
The drift model assumed fixed advection for each depth, however, larval fish are able to swim and can therefore move up and down in the water column to avoid predators and find food. This fixed transport at certain depths might therefore not be ecologically meaningful for kittiwakes, as the fish larvae would be inaccessible to foraging kittiwakes at the depths used in this model.
Implementing units (fish larvae) in the drift model that are not fixed at certain depths to represent vertical migration or biological forcing should therefore be considered.

The drift model was also not made with any particular fish species in mind, it only simulated general advection of particles between locations. Distribution of spawning areas and larvae of different fish species is not uniform along the Norwegian coast (Olsen et al. 2010; Sandvik et al. 2016), and kittiwake diet might therefore vary between colonies. If spawning of some prey species is important for the onset of breeding in some kittiwake colonies, using these specific fish species and spawning locations in the drift model, as opposed to the colony locations and general advection of particles, might be a better approach for understanding how prey transport influences the timing of breeding in kittiwakes. This is especially relevant if colonies rely on different prey species or populations, as the transport time between colony locations would be irrelevant.

Investigating the kittiwake diet of different colonies to obtain information about the main prey species of each colony might be necessary to be able to simulate drift of relevant prey for different colonies.

As mentioned in section 1.2, the distribution of seabird colonies is correlated with larval fish densities (Sandvik et al. 2016) and as a result, colonies might rely on both local prey populations and the advection of prey between colonies during the breeding season.

For at least two of the colonies included in the study, sand eel has been reported as being an important source of food during the breeding season (Christensen-Dalsgaard et al. 2018) (Dehnhard N, pers. Comm.). Unfortunately, little is known about the spawning grounds of these species. This could potentially make drift modelling of these species difficult, as the starting point of advection would not be known. How reliant the colonies are on the transportation of the same sandeel populations would also be difficult to assess since the origins of the sand eel around the colonies relies on knowing where the sand eel spawns. It might also be that sand eel are more stationary, and thus modelling drift of this species would not be relevant.

Further investigation of sand eel phenology and spawning ecology might therefore be quite useful when it comes to understanding how breeding start in kittiwake colonies rely on local sand eel populations and the potential transport of sand eel from distant spawning locations to the colony site.

4.3.2 Improvements of the data analysis for determining breeding events

It was not possible to separate the early breeding behaviour and egg laying with the approach used in this study, because the behaviour during early breeding and incubation is quite similar (see section 1.1). It was therefore not possible to extract estimates for egg laying, only when the individuals switched to a behaviour that was different from the assumed non-breeding behaviour, and it was therefore not possible to say anything about the effect on egg laying directly. Egg laying might be a more ecologically interesting event to investigate in the kittiwake breeding cycle, since it reflects more on the physiological condition of the individual, and hereby the food availability around the colony.

Timing of egg laying is more closely related to the hatching event than breeding start because incubation under normal circumstances is relatively fixed, meaning that the variation in interval length between egg laying and hatching is lower compared to the interval between breeding start and hatching.
Some variation can exist when it comes to the length of the incubation period, where the total incubation period depends on the number of eggs the pair lays, since eggs do not often hatch at the same time and can extend the incubation time by 1-3 days (Coulson 2011; Runde and Barrett 1981). There might also be an effect of temperature on embryotic development, with lower temperatures prolonging the incubation period, but this has not been studied in kittiwakes to my knowledge.

However, none of these factors are expected to create the level of difference between individuals as that of the decision to start breeding. Egg laying is also a more closely studied event in other kittiwake colonies, making it a better candidate for comparison with similar studies on breeding phenology in kittiwakes.
However, since the intense nest-defence and egg laying behaviour are so similar it was impossible to differentiate the two based on conductivity data alone. An approach incorporating light data, and potentially position data (when available) might be a way forward in order to obtain these estimates.

As previously discussed in section 4.3.1.1, change point analysis is an option for determining changes in the behaviour of kittiwakes, but the method have some downsides when it comes to efficiency and subjectiveness. It is also worth mentioning that including light and position data would only further increase these problems. For example, with the change point approached used,

the number of plots investigated would be doubled if light data was included, and three-doubled if all types of data were to be included.

Using the machine learning approach developed by Grissot et al. 2018 as a starting point to develop a framework for inferring breeding start and potentially also egg laying in kittiwakes could be an alternative approach to the manual change point analysis utilized in this project. Such an approach would cut down workload and time-use considerably, opening for analysis of larger quantities of data.

The framework would however need to be modified, especially for the light data, because of the difference between nesting in little auks and kittiwakes. Little auks use cervices when nesting, and values for both light and conductivity data would therefore be equal to 0 when the individual is at the nest (Grissot et al. 2023). Kittiwakes however nest on open cliffs and buildings (Figure 4-5). Some shadowing, from ledges and other structures, is expected, but few nests would be completely shadowed. Using a strict argument of light data = 0 when occupying the nest might therefore not be representative for breeding kittiwakes, especially prior to incubation where it is common for nest-occupants to stand up or work on the nest, exposing the logger to some degree of light.

Figure 4-5: Different nesting habitats used by breeding kittiwakes at Sør-Gjæslingan (Sklinna). Both natural structures (b) and human constructions (a) such as buildings are used. This can create some shadowing of nests, but not to the same extent as that of a nest hidden in a crevice. Pictures provided by Nina Dehnhard.

I propose using intermediate ($0 < \varepsilon < 1$) and low ($\varepsilon = 0$) value light data together with low conductivity data ($\varepsilon = 0$) to signify time spent at the nest, for a more accurate representation of kittiwakes occupying their nest-site prior to incubation (Figure 4-6 1).

Because of how efficient such frameworks can be, there is a possibility to use the raw data instead of computing daily averages in the time-series. My suggestion would be to look for patterns in how much of the hours of the night is spent in the colony during the period of interest (Figure 4-6 2).
As previously discussed in section 1.1 breeding kittiwakes will spend more and more time at the nest during the night as the timing of breeding and egg laying approaches, while spending less time resting and foraging at sea (Coulson 2011). A change in the data indicating a shift from spending most of the time at night at sea to spending most of the night at the nest could be a better way to represent when individuals decide to start breeding.
Grissot et al. 2023 monitored the studied pairs as a way of validating how well the method described different behaviours in breeding little auks. I think this type of monitoring could be useful in the investigation of kittiwake breeding behaviour in relation to logger data as well. Monitoring provides information about what individuals were doing at specific time points and can thus be compared with data from the loggers to see how the interpreted behaviour from the data analysis matches the actual behaviour of the individual at that time.

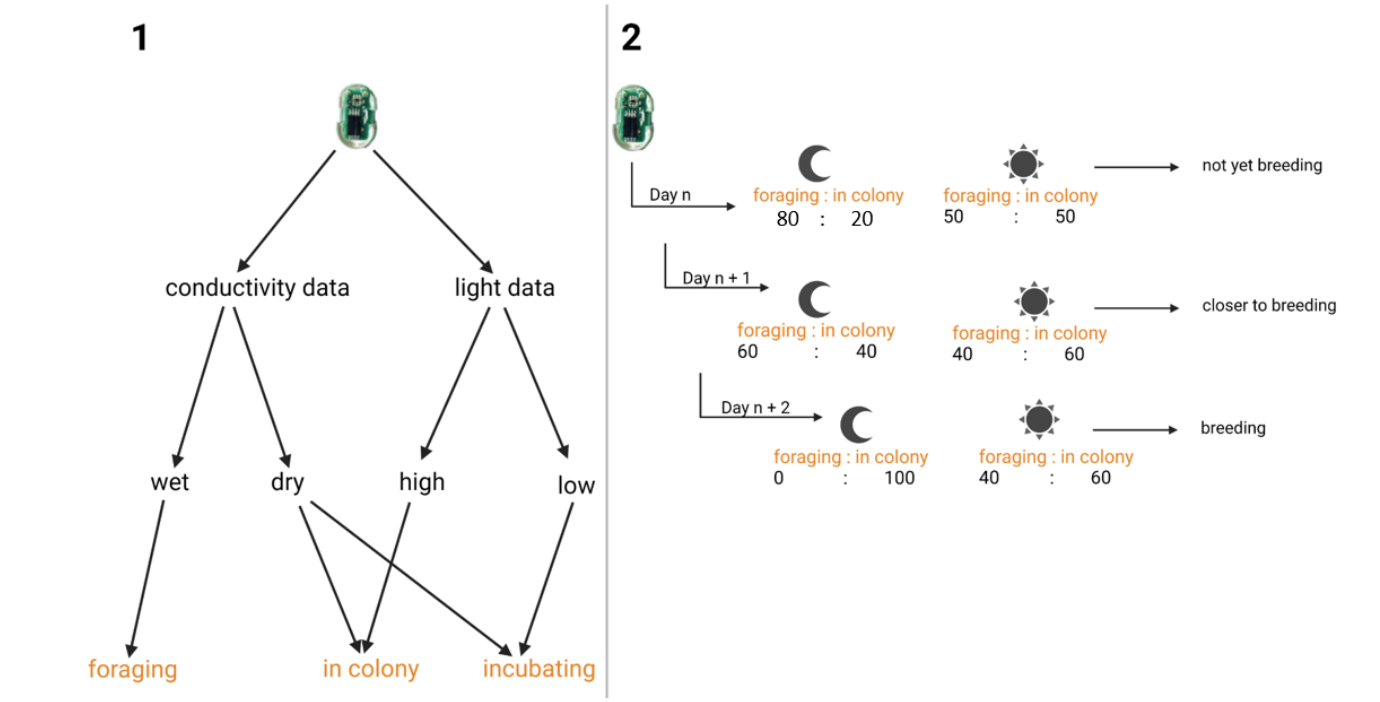

Figure 4-6: 1. Framework for determining different behaviours during early breeding season. 2. Suggestion for how behaviours determined by method can be used to investigate how the proportion of time spent away from the nest site at night changes over time. Closer to breeding the pair takes turns occupying the nest site, similar to that observed during incubation, and the nest will be occupied more during the night. Note that numbers here are only suggestions for proportions spent on different activities, and actual thresholds would have to be properly investigated. Modified from (Grissot et al. 2023). Created using https://www.biorender.com/.

4.3.3 Investigating other aspects of the kittiwake breeding season

The ecology of natural populations is often complex, with different aspects of the life cycle depending on and influencing each other, while also being subject to influences from the environment. In this study one event in the breeding cycle was investigated, with several different variables being included in order to explain the variance.
However, I think that there are several other variables worth considering when studying the kittiwake breeding cycle in the future. Below I will discuss other potentially useful variables, as well as the potential of investigating several aspects of the breeding cycle simultaneously to better understand the kittiwake breeding cycle as a whole.

The potential effects of competition with other breeding seabirds, predation and weather were not examined in this study since information about the variables were not obtained or available. However, all the colonies included in this study are well known breeding grounds for other seabirds. This would increase the competition, both for nest sites and food. It is therefore reasonable to assume that inter-specific competition could have some effect on breeding start, especially if the seabird species overlap in diet and preferred nesting habitat (Durant et al. 2012).

Risk of predation might also influence the timing of breeding, as colonial species such as the kittiwake rely on the size of the population to protect against predators (Hernández-Matías, Jover, and Ruiz 2003; Anderson and Hodum 1993). This would contribute to how population size affects breeding start, as individuals would potentially wait until the breeding population is large enough before they start to defend nest-sites and breed, to minimize the risk of being targeted by predators.

Weather conditions during the early stages of breeding season is also a factor that is worth considering. In studies on adult and chick survival, harsh weather conditions such as increased wind speed, has been linked to lower chick survival, partially due to the increased work effort of the parents leading to longer intervals between feeding for the chicks (Christensen-Dalsgaard et al. 2018). With higher windspeed, the cost of flying increases, leading to less time being spent on foraging attempts (Christensen-Dalsgaard et al. 2018). Prevailing weather conditions could affect the breeding start as well. If wind speeds during the pre-breeding and early breeding phase are higher, reaching favourable body condition would take longer to achieve, as more energy would be spent compensating for the increased energy loss from flying in stronger wind (Christensen-Dalsgaard et al. 2018; Collins et al. 2020), and the start of breeding might be postponed as a result.

In this study we examined only one event in the breeding cycle and how it was influenced by certain variables, but not the relationship between breeding start and other events or outcome in the kittiwake breeding cycle, such as egg laying or breeding success. As previously discussed, egg laying might be a better event to investigate in the breeding cycle, as it reflects more on the body conditions of individuals (females) and the variation in incubation lengths is quite low.
However, studies have shown that the timing of breeding has an effect on the outcome of the breeding season, with later breeding often resulting in breeding failure (Goutte et al. 2014; Moe et al. 2009). Environmental variables such as SST could therefore influence multiple parts of the breeding season in kittiwakes, where the effect on one event (like the breeding start) carries over to factors such as the outcome of the breeding season.

Winter SST and lagged SST has been found to negatively affect the breeding productivity and outcome in North Sea kittiwake colonies (Frederiksen et al. 2007), but how these environmental variables are related to the timing of breeding to my knowledge, not known.
In my study on Norwegian kittiwake populations, no effect of lagged SST or winter SST was observed on the breeding start, but we do not know how they may affect the breeding outcome, as breeding outcome was not included in the study. Comparison between my study and studies of other aspects of the breeding season was therefore not always straightforward, as the link between the different aspects of the breeding cycle is not often included in the same studies.
It might therefore be valuable to not look at just one event of the breeding season in isolation, as done in this study, but investigate how environmental variables affect multiple aspects of the breeding season and how events in the breeding season affect each other.

4.4 Returning to the hypotheses

Three hypotheses were formulated at the beginning of the thesis. In this section I will readdress each hypothesis and discuss whether any support was found in the results for each of them.

H1: Changes in large-scale and/or local environmental variables advance or delay breeding start in kittiwake colonies.

The result of the statistical modelling supported this hypothesis. Fluctuations in the local environmental factor spring SST did influence when breeding started for the study colonies, increased spring SST advanced the breeding start. No support however was found for effects of the large-scale environmental variable NAO. It would therefore seem that local variation is of higher importance to kittiwake breeding start in the colonies than that of large-scale interannual variation. However, to fully support this hypothesis I think more data would be needed (as discussed in section 4.4.1) to capture long-time trends in kittiwake breeding start in relation to the environment.

It should also be noted that environmental variables here was used as proxies for food availability. I was not able to directly test the effect of environmental variables on fish recruitment or stock biomass, and I can therefore not make any conclusions on how these environmental variables actually influenced the food availability around the study colonies in the years included. Only existing literature on the matter was used to make inferences about why spring SST could have an effect on the breeding start.
I did observe an effect of spring SST, but what caused the effect of spring SST (influence on prey availability or something else) could not be concluded in this study.

H2: Larger population sizes leads to earlier breeding start in kittiwakes.

This hypothesis was supported by the results of the statistical modelling. In years with a larger breeding population breeding start was advanced. Similar studies on the effect of population sizes have concluded that the effect is probably due to increased competition in larger colonies (Merkel et al. 2019; Kokko, Harris, and Wanless 2004).

However, I do think that there is a need for investigating how predator pressure, inter-specific competition and population structure plays a part in this. As explained in section 4.4.3, larger

populations might provide protection from predators, especially if the predation pressure is high. Increased protection from predators might therefore also partially explain the advanced breeding start observed in larger colonies. This might also be the case if competition is increased by the presence of other seabird species with overlapping niches.

As previously discussed, the population structure might change between years, effectively influencing when breeding start happens. Taking into consideration how age and experience structures in the breeding population might affect breeding start, as well as predator pressure and competition is therefore worth considering in order to properly test this hypothesis.

H3: A time-lag between colony breeding start from south to north is created by the prey advection between colonies. Where colonies to the north starting breeding later than colonies to the south.

Unfortunately, there was not enough data to construct a model in order to investigate this hypothesis. Further development of this part of the study is therefore, in my opinion, highly recommended, as some interesting patterns in breeding start might be present between kittiwake colonies along the Norwegian coast. In fact, it has been indicated that the predictability and availability of fish larvae explain the distribution of seabird colonies on the Norwegian coast (Sandvik et al. 2016).

5 Conclusion

In this study it was indicated that spring SST had a negative effect on breeding start, with warmer temperatures leading to an earlier breeding start in the studied colonies. An effect of breeding population size was also observed, with a larger colony size leading to earlier mean breeding start for the study colonies. Similar relationships have been observed in other kittiwake colonies, as well as other seabird species so it is not unreasonable to assume that the population size of the studied colonies and local SST values during spring could have an effect on the breeding start in the study colonies.

No effect of prey drift was observed for the years and colonies included in this study. More data, both from including more study sites and years of data would be needed to properly assess this part of the study. Utilizing a more complex drift model, both with regards to fish species, their behaviour and spawning grounds, is also worth considering to fully investigate the effect of prey advection on breeding start at different kittiwake colonies on the Norwegian coast.

Lack of data was evident throughout the project, making it difficult to properly investigate effects on breeding start in kittiwakes breeding on the Norwegian coast. However, I do believe that the findings of this study contributed some knowledge about the kittiwake breeding start and how data from GLS loggers can be used to estimate events in the breeding cycle of this seabird. I also believe that this study can serve as a starting point for future studies on the early stages of the breeding season in kittiwakes and be used for comparison with future findings on kittiwake breeding phenology.

Appendix

A. Supplementary plots and tables

Table 6-1: Mean and median start of breeding for all colonies in the study

$Mean_{Anda}$	$Median_{Anda}$	N_{Anda}	$Mean_{Sklinna}$	$Median_{Sklinna}$	$N_{Sklinna}$	$Mean_{Runde}$	$Median_{Runde}$	N_{Runde}
133	134	11	-	-	-	-	-	-
131	131	11	-	-	-	-	-	-
139	136	5	124	123	18	-	-	-
137	137	20	136	135	19	-	-	-
128	130	20	135	134	22	137	141	18
136	139	20	133	132	23	130	126	17
128	130	22	128	127	20	121	119	15
132	133	19	126	125	13	131	129	15
137	138	9	124	124	14	-	-	-
132	131	10	-	-	-	131	132	11

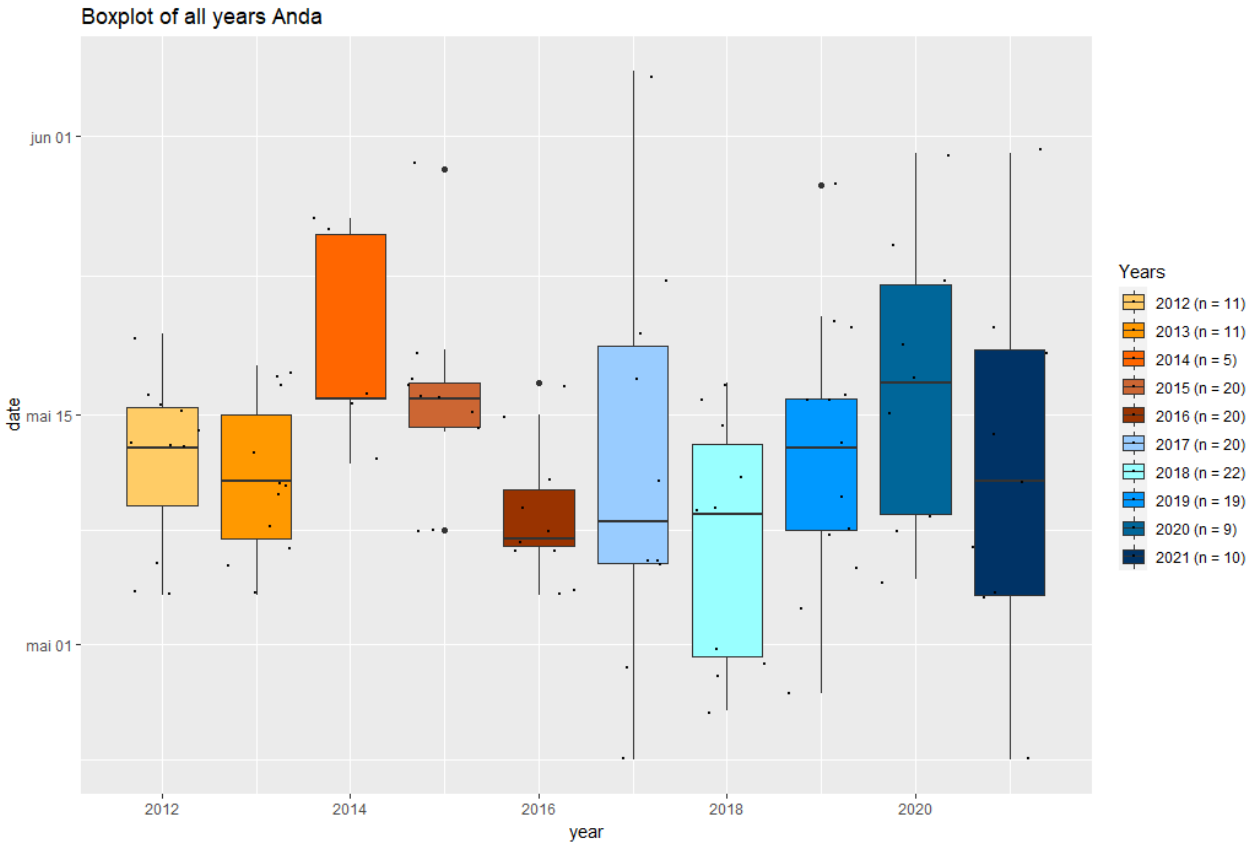

Figure A1: estimated breeding start for Anda. Black line thorugh box indicates median. Whiskers represent the 25% and 75% percentile.

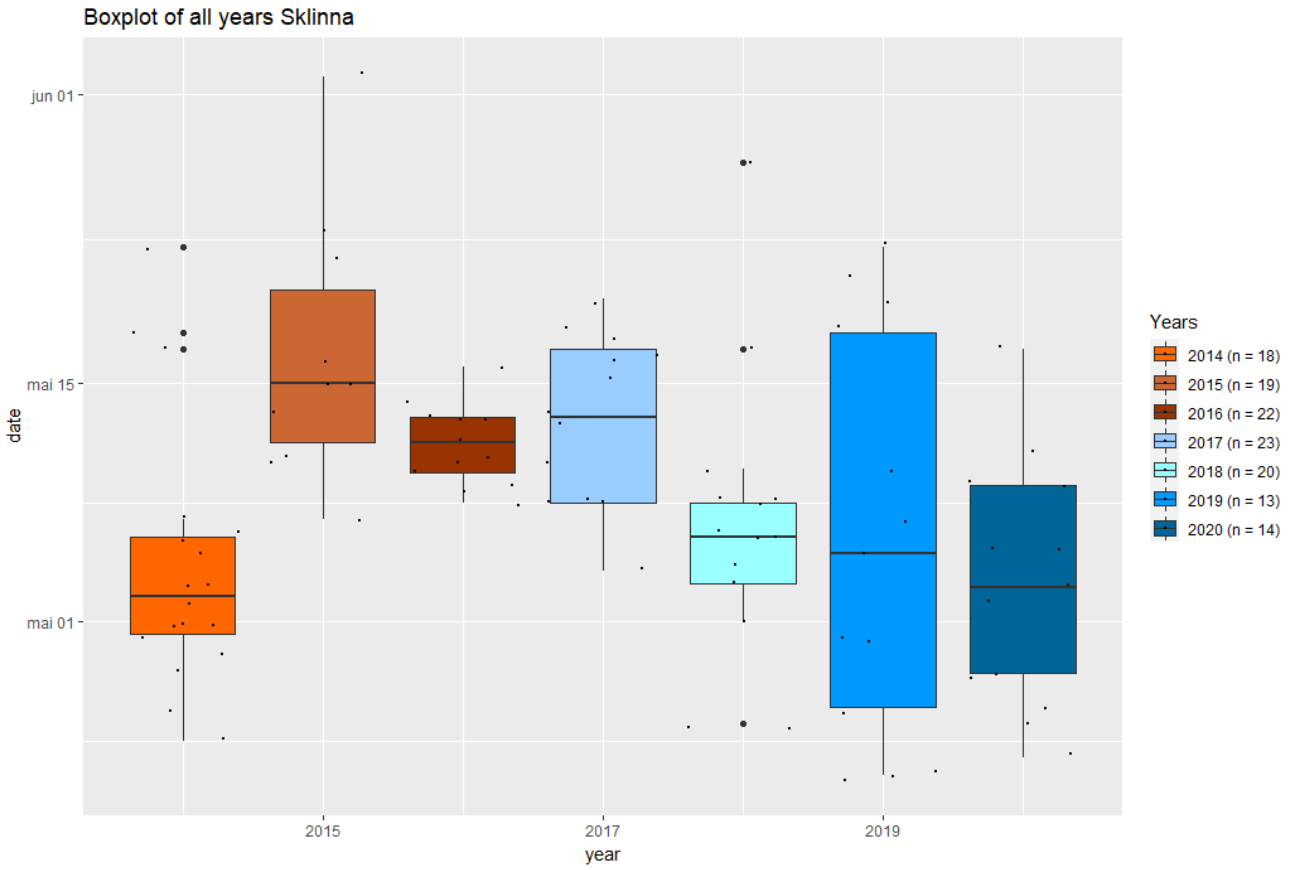

Figure A2: estimated breeding start for Sklinna. Black line thorugh box indicates median. Whiskers represent the 25% and 75% percentile.

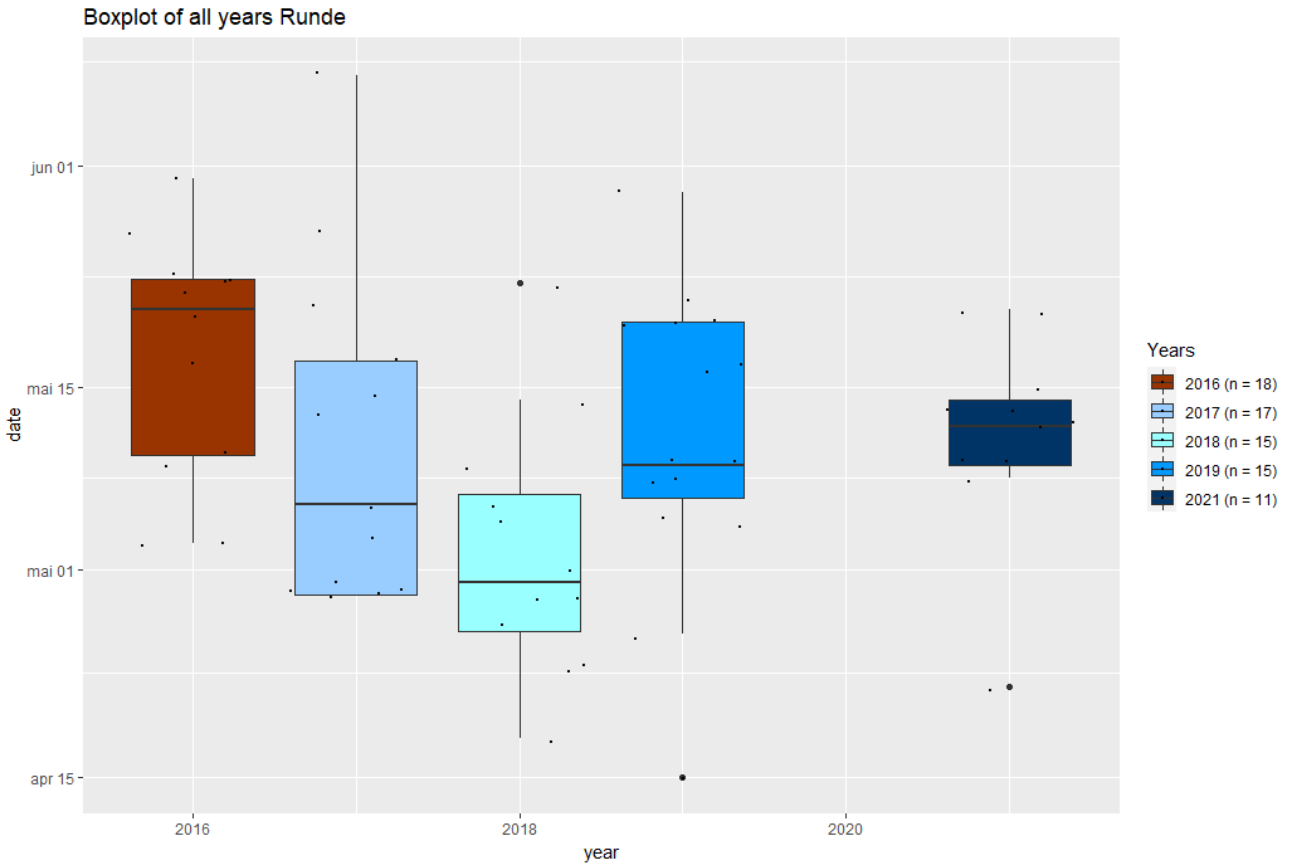

Figure A3: estimated breeding start for Runde. Black line thorugh box indicates median. Whiskers represent the 25% and 75% percentile.

Table 6-2: Estimated hatching and start dates for the years 2012-2021 at Anda

$Mean_{breeding\ start}$	$Median_{breeding\ start}$	$N_{breeding\ start}$	$Mean_{hatching}$	$Median_{hatching}$	$N_{hatching}$	Δmeans
133	134	11	177	175	36	44
131	131	11	175	173	39	44
139	136	5	174	172	18	35
137	136	20	176	175	58	39
131	129	20	171	172	51	40
136	139	20	174	172	49	38
128	130	22	169	168	41	41
132	133	19	174	172	28	42
138	138	9	177	177	17	39
132	131	10	179	180	30	47

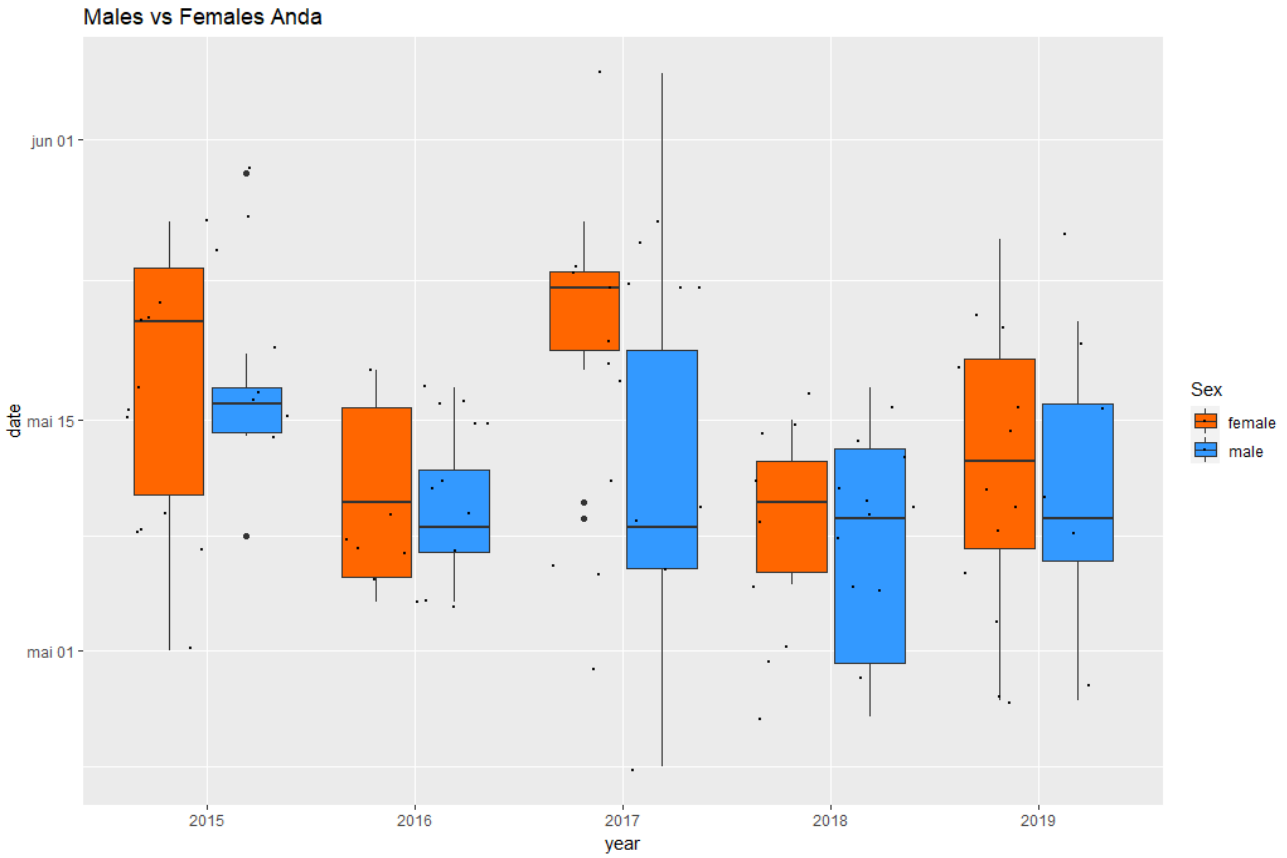

Figure A4: Boxplots of estimated start dates for males and females per year in Anda. Black line through each box plot signifies the median, whiskers indicate the 25th and 75th percentile.

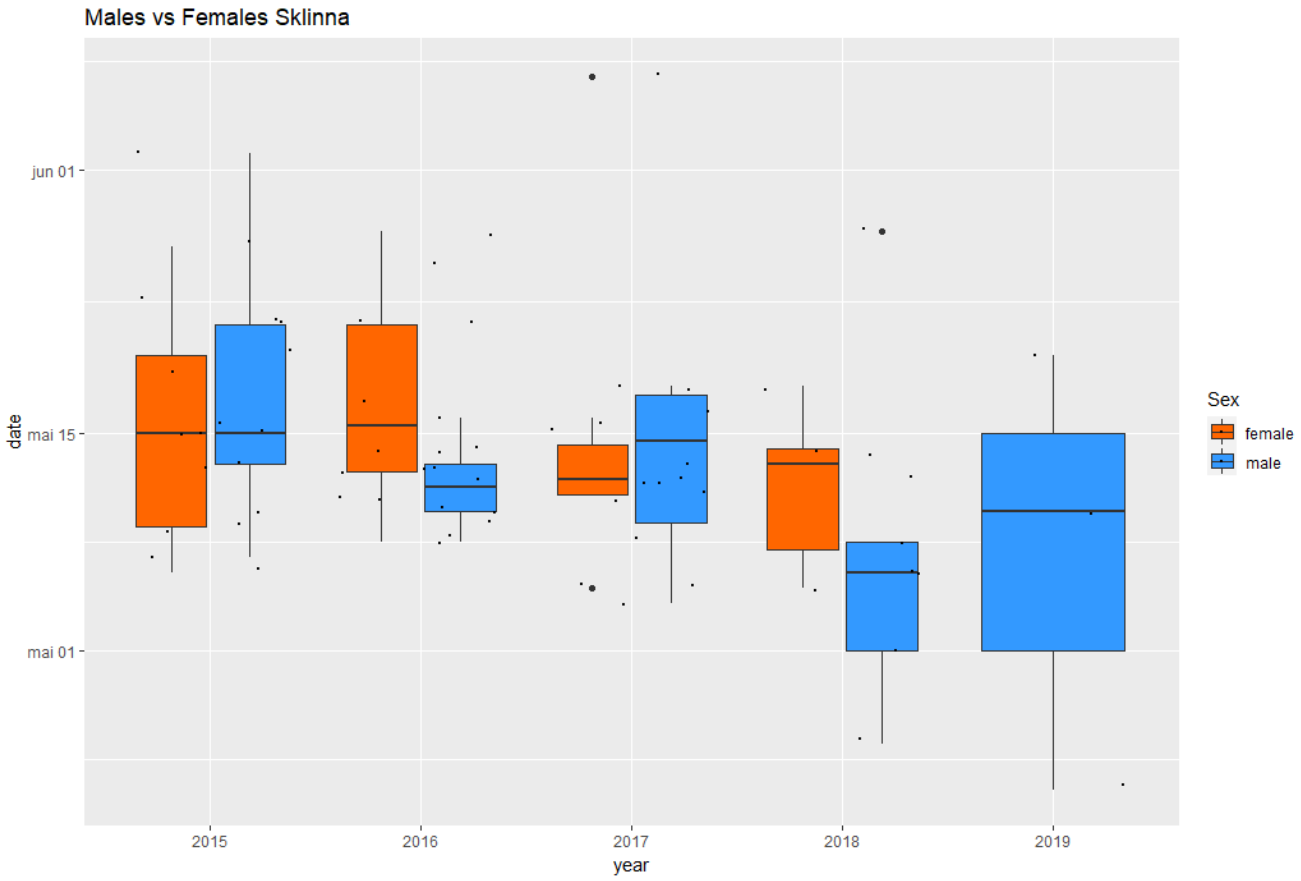

Figure A5: Boxplots of estimated start dates for males and females per year in Sklinna. Black line through each box plot signifies the median, whiskers indicate the 25th and 75th percentile. In 2019 only males were available, and this year was therefore not included in the analysis of difference.

B. Selected scripts

Script B1. Importing files with data needed to perform change point analysis.

```
#loading summaries ####
#used to left-join to colony data sets later
load("Seatrack_export_20220307_summaryTables_Msc_Mari.r")

#status data set
status <- readRDS("BLKW_indStatus_Msc_Mari.rds")
names(status)[1] <- "timestamp"
status$individ_id <- gsub("_", "-", status$individ_id) #replace _ with -
status$sex <- status$sex %>% replace_na("NA")
status$breeding_stage <- status$breeding_stage %>% replace_na("NA")



# create data frame with only ID and colony
individ.summary <- subset(individ.summary, select = -c(ring,
                                                        species,
                                                        timestamp_min,
                                                        timestamp_max,
                                                        n.total))



#function for reading rds and finding IDs
my_read_rds <- function(x) {
  out <- read_rds(x)
  site <- str_extract(x, "[A-Z]{3}-[0-9]{7}") #pattern for individ ID from file name
  cbind(individ_id=site, out)
}

filenames <- list.files(pattern = ".rds") #NB! set working directory to the folder with the files
act.dat.all <- lapply(filenames, my_read_rds) %>% bind_rows() #df with all data for all colonies
```

Script B2. Workflow for data preparation for initial change point analysis described in section 2.3.1. Shown for Anda, but the same approach was used for all colonies.

```
#Removing noise

anda <- act.dat.all %>%  #extracting all data belonging to Anda from main dataset
  left_join(individ.summary, by = "individ_id") %>% #extract the correct individuals
  filter(colony == "Anda")


#find breeding status per year for each individual, using status data set
anda <- status %>%
  select(individ_id, breeding_stage, breeding_success) %>%
  left_join(anda, by="individ_id")

#
#remove duplicated dates
anda <- anda %>%
  group_by(year(timestamp), individ_id) %>%
  distinct(timestamp, .keep_all = T)


#
#vector with breeding status of interest
activity <- c("incubating", "rearing chicks", "prebreeding", "breeding/stage_unknown", "NA")

#extract only individuals observed breeding or with unknown breeding status
bp.a <- anda %>%       #bp.a = breeding period anda
  filter(breeding_stage %in% activity)


#extract time-series of interest between 1st of April and 1st of July
#create date column
bp.a <- bp.a %>%
  filter(month(timestamp) %in% c(3:7))


#
#remove individuals with > 6000 data points
bp.a <- bp.a %>%
  group_by(year(timestamp), individ_id) %>%
  filter(!n() < 6000)

#
#
#
```

```r
#Random sampling of 10 individuals of each sex

#females
females <- status %>%
  filter(location == "Anda", sex == "female")

#filter out females in 2016
f.16 <- f %>%
  filter(year(timestamp) == 2016 & individ_id %in% females)

#random sampling
sample <- sample(unique(f.16$individ_id), size = 10)
f.16 <- f.16 %>%
  filter(individ_id %in% sample)

#
#s
#males
males <- status %>%
  filter(location == "Anda", sex == "male")

#filter out males in 2016
f.16 <- f %>%
  filter(year(timestamp) == 2016 & individ_id %in% females)

#random sampling
sample <- sample(unique(m.16$individ_id), size = 8) #only 8 males available
m.16 <- m.16 %>%
  filter(individ_id %in% sample)

#
#If no information of sex was available, up to 20 individuals was randomly sampled.
#find individuals of unknown sex
individuals <- status %>%
  filter(location == "Anda", sex %in% c("unknown", "NA"))

target <- 2016
ind <- bp.a %>%
  filter(individ_id %in% individuals & year(timestamp) %in% target)
```

Script B3. Initial change point was done on time-series with mean conductivity per day.

```
#Mean conductivity per day

avg_act <- aggregate(data = f.16, std_conductivity ~ individ_id + date(timestamp),
                     FUN = mean) #mean per day

#function for computing SE of the mean
standard_error <- function(x) sd(x) / sqrt(length(x))
avg_act$se <- aggregate(data = f.16, std_conductivity ~ date(timestamp),
                        FUN = standard_error)$std_conductivity #compute SE

#
#
#Change point

#empty df to store all estimates from Change point analysis
anda.f <- data.frame(year = rep("NA", 48)) #anda.f = df females anda
#add rest of the columns
anda.f$ID <- "NA" #individuals ID
anda.f$est_start <- "NA" #estimated breeding start
anda.f$colony <- "Anda" #colony of origin


#filtering out individual of interest
act.1 <- filter(avg_act, individ_id == "NOS-6198715")

#find optimal number of change point for time series
cp.1 <- cpt.meanvar(act.1$std_conductivity, method = "PELT", penalty = "CROPS", pen.value = c(5, 500))
pen.value.full(cp.1) #investigate penalty trend
plot(cp.1, diagnostic = T) #investigate penalty trend visually
plot(cp.1, ncpts = 6) #plot number of optimal segments to double check

#run change point with optimal number of CP
cp.1 <- cpt.meanvar(act.1$std_conductivity, method = "PELT", Q = 6)
plot(cp.1) #visualize
cpts(cp.1) #investigate position of CPs on x-axis
act.1$date[111] #examine suggested CP of interest, here as point 111 on x-axis

#add the corresponding date of CP to df
anda.f$est_start[1] <- format(act.1$timestamp[111], format = "%Y-%m-%d")
```

Script B4. Change point on improved timeframe. Shown for year 2016.

```
#create binary levels one for each state of conductivity data: wet, dry, intermediate
yr.16 <- yr.16 %>%
  mutate(cond_bin = factor(NA, levels = c(2, 1, 0))) %>%
  mutate(cond_bin = case_when(std_conductivity > 0.90 ~ factor(2, levels = c(2, 1, 0)), #2 = wet
                              std_conductivity < 0.01 ~ factor(0, levels = c(2, 1, 0)), #0 = dry
                              std_conductivity < 0.90 & std_conductivity > 0.01
                              ~ factor(1, levels = c(2, 1, 0)), #1 = intermediate
                              TRUE ~ cond_bin))


#creating group for each cond_bin interval
yr.16 <- yr.16 %>%
  group_by(individ_id, year(timestamp)) %>%  #separate on individual level and by year
  mutate(group = rleid(cond_bin)) #create column with id per unique interval

#remove extra column
yr.16$`year(timestamp)` <- NULL


#filtering out wet data, only interested in these
yr.16 <- yr.16 %>%
  filter(cond_bin == 2)

#finding length of wet data intervals
tmp.16 <- yr.16 %>%
  #separate groups for each individual, each year
  group_by(year(timestamp), individ_id, group) %>%
  # compute time differences (i.e. length of each period)
  mutate(event_duration_min = 10 + as.numeric(difftime(timestamp[n()],
                                                       timestamp[1], units = "min"))) %>%
  slice(1) %>% # simplify dataset and select only one row per group
  ungroup()

#remove extra column
tmp.16$`year(timestamp)` <- NULL

#find number of minutes spent on water per day
tmp.16 <- aggregate(data = tmp.16, event_duration_min ~ individ_id + date(timestamp),
                    FUN = sum)
names(tmp.16)[2] <- "timestamp" #change name of column to timestamp

#
#
#
#Change point

#empty df to store all estimates from Change point analysis
anda.f <- data.frame(year = rep("NA", 48)) #anda.f = df females anda
#add rest of the columns
anda.f$ID <- "NA" #individuals ID
anda.f$est_start <- "NA" #estimated breeding start
anda.f$colony <- "Anda" #colony of origin
```

```r
#filtering out individual of interest
act.1 <- filter(avg_act, individ_id == "NOS-6198715")

#find optimal number of change point for time series
cp.1 <- cpt.meanvar(act.1$std_conductivity, method = "PELT", penalty = "CROPS", pen.value = c(5, 500))
pen.value.full(cp.1) #investigate penalty trend
plot(cp.1, diagnostic = T) #investigate penalty trend visually
plot(cp.1, ncpts = 6) #plot number of optimal segments to double check

#run change point with optimal number of CP
cp.1 <- cpt.meanvar(act.1$std_conductivity, method = "PELT", Q = 6)
plot(cp.1) #visualize
cpts(cp.1) #investigate position of CPs on x-axis
act.1$date[111] #examine suggested CP of interest, here as point 111 on x-axis

#add the corresponding date of CP to df
anda.f$est_start[1] <- format(act.1$timestamp[111], format = "%Y-%m-%d")
```

Script B5. Preparing data for statistical analysis

```
#Datasets of estimated breeding start

m <- read_excel(path = "~/change_point_males_int.xlsx", sheet = "Sheet1")
m$sex <- "male"

f <- read_excel(path = "~/change_point_females_int.xlsx", sheet = "Sheet1")
f$sex <- "female"

uk <- read_excel(path = "~/cp_uk_sex_int.xlsx", sheet = "Sheet1")
uk$sex <- "unknown"

e <-  read_excel(path = "~/extra.xlsx", sheet = "Sheet1")
e$sex <- "unknown"


#combine all dfs
all.df <- rbind(m, f, uk, e)

#
#
#

#Population sizes
#Sklinna
s <- read_excel(path = "~/pop_size_sklinna.xlsx", sheet = "Sheet1")
#Anda
a <- read_excel(path = "~/Pop str. krykkje Anda 2005-2022.xlsx", sheet = "Sheet1")
#Runde
r <- read_excel(path = "~/Pop str. krykkje Ålesund 2011-2022.xlsx", sheet = "Sheet1")


pop <- rbind(a, r, s) #combine all population data
all.df <- left_join(all.df, pop, by = c("colony", "year")) #add population data to df with estimates

#
#
#SST values
sst <- read.csv("SST_NOAA_JanJune.csv", sep = ";", header = T) #import files with SST data
sst <- sst %>% filter(sst$Year %in% c(2011:2021)) #extract years of interest


#Winter SST
sst.winter <- sst %>% filter(month %in% c(1:4)) #filter out months jan-march

#pivot longer
sst.winter <- sst.winter %>%
  pivot_longer(cols = c("Anda", "Sklinna", "Runde"), names_to = "colony", values_to = "SST")

#calculate mean SST in the months jan-march
sst.winter <- aggregate(data=sst.winter, SST ~ Year + colony, FUN=mean)
sst.winter <- sst.winter[-c(1,12,13, 14, 15,16, 21, 23,24, 25, 33),] #remove rows
names(sst.winter)[3] <- "SST_winter" #rename column
names(sst.winter)[1] <- "year" #rename column
```

```
#add SST winter data to df with estimates
all.df <- left_join(all.df, sst.winter, by = c("colony", "year"))



#Spring SST
sst.spring <- sst %>% filter(month %in% c(4:6)) #filter out months april-june

#pivot longer
sst.spring <- sst.spring %>%
  pivot_longer(cols = c("Anda", "Sklinna", "Runde"), names_to = "colony", values_to = "SST")


#calculate mean SST in the months april-june
sst.spring <- aggregate(data=sst.spring, SST ~ Year + colony, FUN=mean)
sst.spring <- sst.spring[-c(1,12,13, 14, 15,16, 21, 23,24, 25, 33),] #remove rows with no data
names(sst.spring)[3] <- "SST_spring" #remane column
names(sst.spring)[1] <- "year" #rename column

#add SST spring data to df with estimates
all.df <- left_join(all.df, sst.spring, by = c("colony", "year"))



#Lagged SST

SST_lagged <- sst %>% filter(month %in% c(1:4)) #filter out months jan-march
#pivot longer
SST_lagged <- SST_lagged %>%
  pivot_longer(cols = c("Anda", "Sklinna", "Runde"), names_to = "colony", values_to = "SST")


#calculate mean SST in the months jan-march
SST_lagged <- aggregate(data=SST_lagged, SST ~ Year + colony, FUN=mean)

SST_lagged$SST_lagged <- lag(SST_lagged$SST, n=1) #shift SST values one row down
names(SST_lagged)[1] <- "year" #rename column
SST_lagged$SST <- NULL #remove column

#add SST lagged data to df with estimates
all.df <- left_join(all.df, SST_lagged, by = c("colony", "year"))

#
```

```
#NAO
 #import file
nao <- read.delim("norm.nao.monthly.b5001.current.ascii.table.txt", sep = "", row.names = NULL)
names(nao)[1] <- "year" #rename column

#filter years of interest
target <- c(2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020, 2021)
nao <- nao %>%
  filter(year %in% target)

#keep only months of interest
nao <- nao[, c(1, 2, 3, 4,  13)]
nao <- nao %>%
  mutate(Dec = lag(Dec)) #shift values of december one row down

nao <- nao %>%
  pivot_longer(cols = c("Jan", "Feb", "Dec", "Mar"), names_to = "month", values_to = "NAO")

#find winter average
nao <- aggregate(data=nao, NAO ~ year, FUN=mean)

#remove 2011
nao <- nao %>%
  filter(!year == 2011)

#add NAO to df with estimates
all.df$year <- as.character(all.df$year)
all.df <- left_join(all.df, nao, by="year")


#
#
#

#drift

colonies <- rbind(m, f, uk, e) #combine all dfs with estimates
#calculate mean breeding start per colony per year
colonies <- aggregate(data = colonies, est_start ~ year + colony, FUN = mean)
colonies$est_start <- yday(colonies$est_start) #convert dates to day of year

#pivot wider
colonies <- colonies %>%
  pivot_wider(names_from = colony, values_from = est_start)


#create empty df to store information
df <- data.frame(year = rep(2012:2021, 2))
df$colony1 <- "NA" #create column for colony one in pair
df$colony2 <- "NA" #create column for colony 2 in pair
df$colony1[1:10] <- "Anda" #first colony 1 = Anda
df$colony2[1:10] <- "Sklinna" #first colony 2 = Sklinna
df$colony1[11:20] <- "Sklinna" #second colony 1 = Sklinna
```

```
df$colony2[11:20] <- "Runde" #second colony 2 = Runde
df$diff <- NA #difference in mean breeding start between colonies 1 and 2
df$drift10 <- NA #drift at depth 10m
df$drift20 <- NA #drift at depth 20m
df$drift30 <- NA #drift at depth 30m


#calculate difference between colony 1 and 2
#difference between mean breeding start Anda - Sklinna
df$diff[1:10] <- colonies$Anda - colonies$Sklinna

#difference between mean breeding start Sklinna - Runde
df$diff[11:20] <- colonies$Sklinna - colonies$Runde
df$diff <- as.numeric(df$diff) #convert to numeric
```

Script B6. VIF test

```
vif_func<-function(in_frame,thresh=10,trace=T,...){

  library(fmsb)

  if(any(!'data.frame' %in% class(in_frame))) in_frame<-data.frame(in_frame)

  #get initial vif value for all comparisons of variables
  vif_init<-NULL
  var_names <- names(in_frame)
  for(val in var_names){
    regressors <- var_names[-which(var_names == val)]
    form <- paste(regressors, collapse = '+')
    form_in <- formula(paste(val, '~', form))
    vif_init<-rbind(vif_init, c(val, VIF(lm(form_in, data = in_frame, ...))))
  }
  vif_max<-max(as.numeric(vif_init[,2]), na.rm = TRUE)

  if(vif_max < thresh){
    if(trace==T){ #print output of each iteration
      prmatrix(vif_init,collab=c('var','vif'),rowlab=rep('',nrow(vif_init)),quote=F)
      cat('\n')
      cat(paste('All variables have VIF < ', thresh,', max VIF ',round(vif_max,2), sep=''),'\n\n')
    }
    return(var_names)
  }
  else{
```

```
    in_dat<-in_frame

    #backwards selection of explanatory variables, stops when all VIF values are below 'thresh'
    while(vif_max >= thresh){

      vif_vals<-NULL
      var_names <- names(in_dat)

      for(val in var_names){
        regressors <- var_names[-which(var_names == val)]
        form <- paste(regressors, collapse = '+')
        form_in <- formula(paste(val, '~', form))
        vif_add<-VIF(lm(form_in, data = in_dat, ...))
        vif_vals<-rbind(vif_vals,c(val,vif_add))
      }
      max_row<-which(vif_vals[,2] == max(as.numeric(vif_vals[,2]), na.rm = TRUE))[1]

      vif_max<-as.numeric(vif_vals[max_row,2])

      if(vif_max<thresh) break

      if(trace==T){ #print output of each iteration
        prmatrix(vif_vals,collab=c('var','vif'),rowlab=rep('',nrow(vif_vals)),quote=F)
        cat('\n')
        cat('removed: ',vif_vals[max_row,1],vif_max,'\n\n')
        flush.console()
      }

      in_dat<-in_dat[,!names(in_dat) %in% vif_vals[max_row,1]]

    }

    return(names(in_dat))

  }

}
```

Script B7: Model fitting GAMM and LME. Shown for spring SST model structure

```
#GAMM fitting
gam.spring <- gamm4(est_start ~ s(SST_spring, k=3, bs="ts") + s(NAO, k=3, bs="ts")
                    + s(colony1, k=3, bs="ts") + s(pairs, k=3, bs="ts"),
                    random = ~ (1|year) + (1|ID), data=all.df)

#LMER fitting
all.df$SST_spring_scaled <- scale(all.df$SST_spring) #scaling spring SST
all.df$NAO_scaled <- scale(all.df$NAO) #scaling NAO
all.df$pop.size_scaled <- scale(all.df$pop.size) #scaling population size
lmer.spring <- lmer(est_start ~ SST_spring_scaled + colony + pop.size_scaled + NAO_scaled +
                      (1|year) + (1|ID),  data = all.df)
```

6 References

Ådlandsvik, B. 2022. 'LADiM Documentation'. Havforskningsinstituttet. https://www.hi.no/hi/nettrapporter/rapport-fra-havforskningen/2013/ladimlicereport_med_forside.

Albertsen, J., A. D. Sandvik, L. Asplin, V. S. Lien, and J. Skardhamar. 2022. 'LADiM Documentation'. 35. Havforskningsinstituttet. https://hdl.handle.net/11250/3045336.

Anderson, D. J., and P. J. Hodum. 1993. 'Predator Behavior Favors Clumped Nesting in an Oceanic Seabird'. *Ecology* 74 (8): 2462–64. https://doi.org/10.2307/1939597.

Angelier, F., B. Moe, C. Clement-Chastel, C. Bech, and O. Chastel. 2007. 'Corticosterone Levels in Relation to Change of Mate in Black-Legged Kittiwakes'. *The Condor* 109 (3): 668–74. https://doi.org/10.1093/condor/109.3.668.

Anker-Nilssen, T., A. L. Fayet, and T. Aarvak. 2023. 'Top-down Control of a Marine Mesopredator: Increase in Native White-tailed Eagles Accelerates the Extinction of an Endangered Seabird Population'. *Journal of Applied Ecology*, January, 1365-2664.14343. https://doi.org/10.1111/1365-2664.14343.

Barrett, Robert T., and Robert W. Furness. 1990. 'The Prey and Diving Depths of Seabirds on Hornøy, North Norway after a Decrease in the Barents Sea Capelin Stocks'. *Ornis Scandinavica (Scandinavian Journal of Ornithology)* 21 (3): 179–86. https://doi.org/10.2307/3676777.

Barrett, R.T., S. Lorentsen, and T Anker-Nilssen. 2006. 'The Status of Breeding Seabirds in Mainland Norway'. *Atlantic Seabirds* 8 (3): 97–126.

Bates, D., M. Mächler, B Bolker, and S. Walker. 2015. 'Fitting Linear Mixed-Effects Models Using Lme4.' *Journal of Statistical Software* 67 (1): 1–48. https://doi.org/10.18637/jss.v067.i01.

Beaugrand, G. 2003. 'Long-Term Changes in Copepod Abundance and Diversity in the North-East Atlantic in Relation to Fluctuations in the Hydroclimatic Environment'. *Fisheries Oceanography* 12 (4–5): 270–83. https://doi.org/10.1046/j.1365-2419.2003.00248.x.

Bech, C., I. Langseth, B. Moe, M. Fyhn, and G. W. Gabrielsen. 2002. 'The Energy Economy of the Arctic-Breeding Kittiwake (Rissa Tridactyla): A Review'. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 133 (3): 765–70. https://doi.org/10.1016/S1095-6433(02)00153-8.

Bogdanova, M., F. Daunt, M. Newell, R. Phillips, M. Harris, and S. Wanless. 2011. 'Seasonal Interactions in the Black-Legged Kittiwake, Rissa Tridactyla: Links between Breeding Performance and Winter Distribution'. *Proceedings. Biological Sciences / The Royal Society* 278 (July): 2412–18. https://doi.org/10.1098/rspb.2010.2601.

Burr, Z.M., Ø. Varpe, T. Anker-Nilssen, K. E. Erikstad, S. Descamps, Robert T. Barrett, Claus Bech, et al. 2016. 'Later at Higher Latitudes: Large-scale Variability in Seabird Breeding Timing and Synchronicity'. *Ecosphere* 7 (5). https://doi.org/10.1002/ecs2.1283.

Burthe, S., F. Daunt, A. Butler, D. A. Elston, M. Frederiksen, David Johns, Mark Newell, Stephen J. Thackeray, and Sarah Wanless. 2012. 'Phenological Trends and Trophic Mismatch across Multiple Levels of a North Sea Pelagic Food Web'. *Marine Ecology Progress Series* 454 (May): 119–33. https://doi.org/10.3354/meps09520.

Carroll, M. J., A. Butler, E. Owen, S. R. Ewing, T. Cole, J. A. Green, L. M. Soanes, et al. 2015. 'Effects of Sea Temperature and Stratification Changes on Seabird Breeding Success'. *Climate Research* 66 (1): 75–89. https://doi.org/10.3354/cr01332.

Chardine, J. W. 1983. 'Aspects of the Breeding Behaviour of the Kittiwake (Rissa Tridactyla) before Egg-Laying'. Doctoral thesis, Durham: Durham. http://etheses.dur.ac.uk/7857/.

Cherel, Y., P. Quillfeldt, K. Delord, and H. Weimerskirch. 2016. 'Combination of At-Sea Activity, Geolocation and Feather Stable Isotopes Documents Where and When Seabirds Molt'. *Frontiers in Ecology and Evolution* 4. https://www.frontiersin.org/articles/10.3389/fevo.2016.00003.

Chivers, L., M. Lundy, K. Colhoun, S. Newton, J. Houghton, and N Reid. 2012. 'Foraging Trip Time-Activity Budgets and Reproductive Success in the Black-Legged Kittiwake'. *Marine Ecology Progress Series* 456 (June): 269–77. https://doi.org/10.3354/meps09691.

Christensen-Dalsgaard, S., R. May, R. Barrett, M. Langset, B. Sandercock, and S. Lorentsen. 2018. 'Prevailing Weather Conditions and Diet Composition Affect Chick Growth and Survival in the Black-Legged Kittiwake'. *Marine Ecology Progress Series* 604 (October): 237–49. https://doi.org/10.3354/meps12744.

Christensen-Dalsgaard, S., R. May, and S. Lorentsen. 2018. 'Taking a Trip to the Shelf: Behavioral Decisions Are Mediated by the Proximity to Foraging Habitats in the Black-Legged Kittiwake'. *Ecology and Evolution* 8 (2): 866–78. https://doi.org/10.1002/ece3.3700.

Collins, P. M., J. A. Green, K.H. Elliott, P. J. A. Shaw, L. Chivers, Sc. A. Hatch, and L. G. Halsey. 2020. 'Coping with the Commute: Behavioural Responses to Wind Conditions in a Foraging Seabird'. *Journal of Avian Biology* 51 (4). https://doi.org/10.1111/jav.02057.

Coulson, J. C. 2011. *The Kittiwake*. Poyser Monographs. T. & AD Poyser.

Coulson, J. C., and J. M. Porter. 2008. 'Reproductive Success of the Kittiwake Rissa Tridactyla: The Roles of Clutch Size, Chick Growth Rates and Parental Quality'. *Ibis* 127 (4): 450–66. https://doi.org/10.1111/j.1474-919X.1985.tb04841.x.

Dale, T., F. Rey, and B. R. Heimdal. 1999. 'Seasonal Development of Phytoplankton at a High Latitude Oceanic Site'. *Sarsia* 84 (5–6): 419–35. https://doi.org/10.1080/00364827.1999.10807347.

Descamps, S., F. Ramírez, S. Benjaminsen, T. Anker-Nilssen, Robert T. Barrett, Z. Burr, S. Christensen-Dalsgaard, et al. 2019. 'Diverging Phenological Responses of Arctic Seabirds to an Earlier Spring'. *Global Change Biology* 25 (12): 4081–91. https://doi.org/10.1111/gcb.14780.

Deurs, M., R. Hal, M. T. Tomczak, S. H. Jónasdóttir, and P. Dolmer. 2009. 'Recruitment of Lesser Sandeel Ammodytes Marinus in Relation to Density Dependence and Zooplankton Composition'. *Marine Ecology Progress Series* 381 (April): 249–58. https://doi.org/10.3354/meps07960.

Dias, M. P., R. Martin, E. J. Pearmain, I. J. Burfield, Cleo Small, R. A. Phillips, O. Yates, B. Lascelles, P. G. Borboroglu, and J. P. Croxall. 2019. 'Threats to Seabirds: A Global Assessment'. *Biological Conservation* 237 (September): 525–37. https://doi.org/10.1016/j.biocon.2019.06.033.

Dinno, A. 2017. 'Dunn's Test of Multiple Comparisons Using Rank Sums'. https://cran.r-project.org/package=dunn.test.

Dippner, J. W. 1997. 'Recruitment Success of Different Fish Stocks in the North Sea in Relation to Climate Variability'. *Deutsche Hydrographische Zeitschrift* 49 (September): 277–93. https://doi.org/10.1007/BF02764039.

Dupont, N., E. Bagøien, and W. Melle. 2017. 'Inter-Annual Variability in Spring Abundance of Adult Calanus Finmarchicus from the Overwintering Population in the Southeastern Norwegian Sea'. *Progress in Oceanography* 152 (March): 75–85. https://doi.org/10.1016/j.pocean.2017.02.004.

Durant, J. M., D. Ø Hjermann, Geir Ottersen, and N. C. Stenseth. 2007. 'Climate and the Match or Mismatch between Predator Requirements and Resource Availability'. *Climate Research* 33 (3): 271–83. https://doi.org/10.3354/cr033271.

Durant, J. M., Y. V. Krasnov, N. G. Nikolaeva, and N. C. Stenseth. 2012. 'Within and between Species Competition in a Seabird Community: Statistical Exploration and Modeling of Time-Series Data'. *Oecologia* 169 (3): 685–94. https://doi.org/10.1007/s00442-011-2226-3.

Eerkes-Medrano, D., R. J. Fryer, K. B. Cook, and P. J. Wright. 2017. 'Are Simple Environmental Indicators of Food Web Dynamics Reliable: Exploring the Kittiwake–Temperature Relationship'. *Ecological Indicators* 75 (April): 36–47. https://doi.org/10.1016/j.ecolind.2016.12.019.

Ens, B.J., S. Choudhury, and J.M. Black. 1996. 'Mate Fidelity and Divorce in Monogamous Birds'. In *Partnership in Birds: The Study of Monogamy*, 345–94. Oxford University Press.

Erikstad, K. E., P. Fauchald, T. Tveraa, and H. Steen. 1998. 'On the Cost of Reproduction in Long-Lived Birds: The Influence of Environmental Variability'. *Ecology* 79 (5): 1781–88. https://doi.org/10.1890/0012-9658(1998)079[1781:OTCORI]2.0.CO;2.

Erikstad, K.E., S. Benjaminsen, T. K. Reiertsen, M. Ballestros, and H. Strøm. 2018. 'Modellering av svømmetrekket til lomvi (Uria aalge) fra Bjørnøya til norskekysten. Utvikling av ny metodikk for bruk av lysloggere (GLS),dykkeloggere (TDR) og sjøtemperaturer (SST) til kartlegging av svømmetrekket hos alkefugl'. NINA Rapport 1546. Norsk Institutt for Naturforskning (NINA). http://hdl.handle.net/11250/2575364.

Fauchald, P., T Anker-Nilssen, R. T. Barrett, J.O. Bustnes, B. Bårdsen, S. Christensen-Dalsgaard, S. Descamps, et al. 2015. 'The Status and Trends of Seabirds Breeding in Norway and Svalbard'. 1151. Tromsø: Norwegian Polar Institute. https://brage.nina.no/nina-xmlui/handle/11250/2397703.

Frederiksen, M., T. Anker-Nilssen, G. Beaugrand, and S. Wanless. 2013. 'Climate, Copepods and Seabirds in the Boreal Northeast Atlantic – Current State and Future Outlook'. *Global Change Biology* 19 (2): 364–72. https://doi.org/10.1111/gcb.12072.

Frederiksen, M., M. Edwards, R. A. Mavor, and S. Wanless. 2007. 'Regional and Annual Variation in Black-Legged Kittiwake Breeding Productivity Is Related to Sea Surface Temperature'. 2007. https://click.endnote.com/viewer?doi=10.3354%2Fmeps07126&token=WzE5Nzg3NTQsIjEwLjMzNTQvbWVwczA3MTI2Il0.4_sPaxLLBxoUFXCEMrBGh_juNvY.

Frederiksen, M., M. P. Harris, F. Daunt, P. Rothery, and S. Wanless. 2004. 'Scale-Dependent Climate Signals Drive Breeding Phenology of Three Seabird Species'. *Global Change Biology* 10 (7): 1214–21. https://doi.org/10.1111/j.1529-8817.2003.00794.x.

Frederiksen, M., Sarah Wanless, Michael P. Harris, Peter Rothery, and Linda J. Wilson. 2004. 'The Role of Industrial Fisheries and Oceanographic Change in the Decline of North Sea Black-Legged Kittiwakes'. *Journal of Applied Ecology* 41 (6): 1129–39. https://doi.org/10.1111/j.0021-8901.2004.00966.x.

Galbraith, H. 1983. 'The Diet and Feeding Ecology of Breeding Kittiwakes *Rissa Tridactyla*'. *Bird Study* 30 (2): 109–20. https://doi.org/10.1080/00063658309476785.

Gill, V. A., S. A. Hatch, and R. B. Lanctot. 2002. 'Sensitivity of Breeding Parameters to Food Supply in Black-Legged Kittiwakes Rissa Tridactyla: Sensitivity of Breeding Kittiwakes to Food'. *Ibis* 144 (2): 268–83. https://doi.org/10.1046/j.1474-919X.2002.00043.x.

Goutte, A., F. Angelier, C. Bech, C. Clément-Chastel, G. Dell'Omo, G. W. Gabrielsen, Á. Z. Lendvai, et al. 2014. 'Annual Variation in the Timing of Breeding, Pre-breeding Foraging Areas and Corticosterone Levels in an Arctic Population of Black-Legged Kittiwakes'. *Marine Ecology Progress Series* 496 (January): 233–47. https://doi.org/10.3354/meps10650.

Goutte, A., F. Angelier, C. C. Chastel, C. Trouvé, B. Moe, C. Bech, G. W. Gabrielsen, and O. Chastel. 2010. 'Stress and the Timing of Breeding: Glucocorticoid-Luteinizing Hormones Relationships in an Arctic Seabird'. *General and Comparative Endocrinology* 169 (1): 108–16. https://doi.org/10.1016/j.ygcen.2010.07.016.

Grissot, A., C. Borrel, M. Devogel, L. Altmeyer, M. K. Johansen, H. Strøm, and K. Wojczulanis-Jakubas. 2023. 'Use of Geolocators for Investigating Breeding Ecology of a Rock Crevice-Nesting Seabird: Method Validation and Impact Assessment'. *Ecology and Evolution* 13 (3). https://doi.org/10.1002/ece3.9846.

Hamer, K. C., P. Monaghan, J. D. Uttley, P. Walton, and M. D. Burns. 2008. 'The Influence of Food Supply on the Breeding Ecology of Kittiwakes Rissa Tridactyla in Shetland'. *Ibis* 135 (3): 255–63. https://doi.org/10.1111/j.1474-919X.1993.tb02842.x.

Harris, M. P., and S. Wanless. 1997. 'Breeding Success, Diet, and Brood Neglect in the Kittiwake (Rissa Tridactyla) over an 11-Year Period'. *ICES Journal of Marine Science* 54 (4): 615–23. https://doi.org/10.1006/jmsc.1997.0241.

Hatchwell, B. J. 1988. 'Intraspecific Variation in Extra-Pair Copulation and Mate Defence in Common Guillemots Uria Aalge'. *Behaviour* 107 (3–4): 157–85. https://doi.org/10.1163/156853988X00331.

Haynes, K., I. A. Eckley, and P. Fearnhead. 2014. 'Efficient Penalty Search for Multiple Changepoint Problems'. arXiv. http://arxiv.org/abs/1412.3617.

Hernández-Matías, A., L. Jover, and X. Ruiz. 2003. 'Predation on Common Tern Eggs in Relation to Sub-Colony Size, Nest Aggregation and Breeding Synchrony'. *Waterbirds* 26 (3): 280–89. https://doi.org/10.1675/1524-4695(2003)026[0280:POCTEI]2.0.CO;2.

Hestem, M. 2019. 'Should I Stay or Should I Go? : Geolocators Reveal Different Winter Home Ranges and -Activity Patterns in Sympatrically Breeding Razorbills (Alca Torda)'. Norwegian University of Life Sciences (NMBU). https://hdl.handle.net/11250/2642390.

Hjermann, D. Ø, N. C. Stenseth, and G. Ottersen. 2004. 'Indirect Climatic Forcing of the Barents Sea Capelin: A Cohort Effect'. *Marine Ecology Progress Series* 273 (June): 229–38. https://doi.org/10.3354/meps273229.

IUCN. 2017. 'IUCN Red List Report 2017-2020'. IUCN Red List 2017-2020. https://nc.iucnredlist.org/redlist/resources/files/1630480997-IUCN_RED_LIST_QUADRENNIAL_REPORT_2017-2020.pdf.

Kaartvedt, S. 2000. 'Life History of Calanus Finmarchicus in the Norwegian Sea in Relation to Planktivorous Fish'. *ICES Journal of Marine Science* 57 (6): 1819–24. https://doi.org/10.1006/jmsc.2000.0964.

Kålås, J., S. Henriksen, S. Skjelseth, and Å. Viken. 2010. *Environmental Conditions and Impacts for Red List Species*.

Killick, R., P. Fearnhead, and I. A. Eckley. 2012. 'Optimal Detection of Changepoints with a Linear Computational Cost'. *Journal of the American Statistical Association* 107 (500): 1590–98. https://doi.org/10.1080/01621459.2012.737745.

Killick, Rebecca, and Idris A. Eckley. 2014. 'Changepoint: An R Package for Changepoint Analysis'. *Journal of Statistical Software* 58 (3). https://doi.org/10.18637/jss.v058.i03.

Kokko, H., M. P. Harris, and S. Wanless. 2004. 'Competition for Breeding Sites and Site-Dependent Population Regulation in a Highly Colonial Seabird, the Common Guillemot Uria Aalge'. *Journal of Animal Ecology* 73 (2): 367–76. https://doi.org/10.1111/j.0021-8790.2004.00813.x.

Kostianoy, Andrey G., Jacques Nihoul, and Vyacheslav Rodionov. 2004. *Physical Oceanography of Frontal Zones in the Subarctic Seas*.

Lauria, V., M.J. Attrill, J.K. Pinnegar, A. Brown, M. Edwards, and S. C. Votier. 2012. 'Influence of Climate Change and Trophic Coupling across Four Trophic Levels in the Celtic Sea'. 2012. https://click.endnote.com/viewer?doi=10.1371%2Fjournal.pone.0047408&token=WzE5Nzg3NTQsIjEwLjEzNzEvam91cm5hbC5wb25lLjAwNDc0MDgiXQ.3RzEMttLE7jGabgfnFqqmTtsUTw.

Lewis, S., D. A. Elston, F. Daunt, B. Cheney, and P. M. Thompson. 2009. 'Effects of Extrinsic and Intrinsic Factors on Breeding Success in a Long Lived Seabird'. *Oikos* 118 (4): 521–28. https://doi.org/10.1111/j.1600-0706.2008.17308.x.

Lewis, S., S. Wanless, P. Wright, M. Harris, J. Bull, and D. Elston. 2001. 'Diet and Breeding Performance of Black-Legged Kittiwakes Rissa Tridactyla at a North Sea Colony'. *Marine Ecology Progress Series* 221: 277–84. https://doi.org/10.3354/meps221277.

Lisovski, S., S. Bauer, M. Briedis, S. C. Davidson, K. L. Dhanjal-Adams, M. T. Hallworth, J. Karagicheva, et al. 2020. 'Light-Level Geolocator Analyses: A User's Guide'. *Journal of Animal Ecology* 89 (1): 221–36. https://doi.org/10.1111/1365-2656.13036.

Mercier, G., N. G. Yoccoz, and S. Descamps. 2021. 'Influence of Reproductive Output on Divorce Rates in Polar Seabirds'. 2021. https://click.endnote.com/viewer?doi=10.1002%2Fece3.7775&token=WzE5Nzg3NTQsIjEwLjEwMDIvZWNlMy43Nzc1Il0.Zkd1OxydWkAGkEIHfWbU_akkJC4.

Merkel, B., S. Descamps, N. G. Yoccoz, J. Danielsen, F. Daunt, K. E. Erikstad, A. V. Ezhov, et al. 2019. 'Earlier Colony Arrival but No Trend in Hatching Timing in Two Congeneric Seabirds (*Uria* Spp.) across the North Atlantic'. *Biology Letters* 15 (10): 20190634. https://doi.org/10.1098/rsbl.2019.0634.

Moe, B., L. Stempniewicz, D. Jakubas, F. Angelier, O. Chastel, F. Dinessen, G. W. Gabrielsen, et al. 2009. 'Climate Change and Phenological Responses of Two Seabird Species Breeding in the High-Arctic'. *Marine Ecology Progress Series* 393 (October): 235–46. https://doi.org/10.3354/meps08222.

Møller, A. P., E. Flensted-Jensen, and W. Mardal. 2006. 'Rapidly Advancing Laying Date in a Seabird and the Changing Advantage of Early Reproduction'. *Journal of Animal Ecology* 75 (3): 657–65.

Møller, E. F., M. Maar, S. H. Jónasdóttir, T. G. Nielsen, and K. Tönnesson. 2012. 'The Effect of Changes in Temperature and Food on the Development of Calanus Finmarchicus and Calanus Helgolandicus Populations'. *Limnology and Oceanography* 57 (1): 211–20. https://doi.org/10.4319/lo.2012.57.1.0211.

Monaghan, P. 1996. 'Relevance of the Behaviour of Seabirds to the Conservation of Marine Environments'. *Oikos* 77 (2): 227–37. https://doi.org/10.2307/3546061.

———. 2007. 'Early Growth Conditions, Phenotypic Development and Environmental Change'. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363 (1497): 1635–45. https://doi.org/10.1098/rstb.2007.0011.

Montero, José T., Mauricio Lima, Sergio A. Estay, and Enrico L. Rezende. 2021. 'Spatial and Temporal Shift in the Factors Affecting the Population Dynamics of Calanus Copepods in the North Sea'. *Global Change Biology* 27 (3): 576–86. https://doi.org/10.1111/gcb.15394.

Nicoll, M. A. C., N. C. Cole, C. Horswill, C. G. Jones, N. Ratcliffe, K. Ruhomaun, V. Tatayah, and K. Norris. 2022. 'No Detectable Effect of Geolocator Deployment on the Short- or Long-Term Apparent Survival of a Tropical Seabird'. *Ibis* 164 (4): 1201–12. https://doi.org/10.1111/ibi.13094.

Olin, A., N. Banas, P. Wright, M. Heath, and R. Nager. 2020. 'Spatial Synchrony of Breeding Success in the Blacklegged Kittiwake Rissa Tridactyla Reflects the Spatial Dynamics of Its Sandeel Prey'. *Marine Ecology Progress Series* 638 (March): 177–90. https://doi.org/10.3354/meps13252.

Olsen, E., S. Aanes, S. Mehl, J. Holst, A. Aglen, and H. Gjøsæter. 2010. 'Cod, Haddock, Saithe, Herring, and Capelin in the Barents Sea and Adjacent Waters: A Review of the Biological Value of the Area'. *ICES J. Mar. Sci.* 67 (January): 87–101. https://doi.org/10.1093/icesjms/fsp229.

Ottersen, G., B. Planque, A. Belgrano, E. Post, P. C. Reid, and N. C. Stenseth. 2001. 'Ecological Effects of the North Atlantic Oscillation'. *Oecologia* 128 (1): 1–14. https://doi.org/10.1007/s004420100655.

Paredes, R., A. M. A. Harding, D. B. Irons, Daniel D. Roby, R. M. Suryan, R. A. Orben, H. Renner, R. Young, and A. Kitaysky. 2012. 'Proximity to Multiple Foraging Habitats Enhances Seabirds' Resilience to Local Food Shortages'. *Marine Ecology Progress Series* 471 (December): 253–69. https://doi.org/10.3354/meps10034.

'QGIS Geographic Information System.' 2023. QGIS Association. http://www.qgis.org/.

R Core Team. 2022. 'R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing'. Vienna, Austria. https://www.R-project.org/.

Régnier, T., F. M. Gibb, and P. J. Wright. 2017. 'Importance of Trophic Mismatch in a Winter-Hatching Species: Evidence from Lesser Sandeel'. *Marine Ecology Progress Series* 567 (March): 185–97. https://doi.org/10.3354/meps12061.

Reygondeau, G., and G. Beaugrand. 2010. 'Future Climate-Driven in Distribution of Calanus Finmarchicus'. *Global Change Biology* 17 (October): 756–66. https://doi.org/10.1111/j.1365-2486.2010.02310.x.

Roberts, B. D., and S. A. Hatch. 1993. 'Behavioral Ecology of Black-Legged Kittiwakes during Chick Rearing in a Failing Colony'. *The Condor* 95 (2): 330. https://doi.org/10.2307/1369356.

Ropert-Coudert, Y., A. Kato, N. Poulin, and D. Grémillet. 2009. 'Leg-Attached Data Loggers Do Not Modify the Diving Performances of a Foot-Propelled Seabird'. *Journal of Zoology* 279 (3): 294–97. https://doi.org/10.1111/j.1469-7998.2009.00619.x.

Rotics, S., M. Kaatz, S. Turjeman, D. Zurell, M. Wikelski, N. Sapir, U. Eggers, W. Fiedler, F. Jeltsch, and R. Nathan. 2018. 'Early Arrival at Breeding Grounds: Causes, Costs and a Trade-off with Overwintering Latitude'. 2018. https://click.endnote.com/viewer?doi=10.1111/1365-2656.12898&route=7.

Runde, O. J., and R. T. Barrett. 1981. 'Variations in Egg Size and Incubation Period of the Kittiwake Rissa Tridactyla in Norway'. *Ornis Scandinavica* 12 (1): 80. https://doi.org/10.2307/3675908.

Sandvik, H., R. T. Barrett, K. E. Erikstad, M. S. Myksvoll, F. Vikebø, Nigel G. Yoccoz, T. Anker-Nilssen, et al. 2016. 'Modelled Drift Patterns of Fish Larvae Link Coastal Morphology to Seabird Colony Distribution'. *Nature Communications* 7 (1): 11599. https://doi.org/10.1038/ncomms11599.

Sandvik, H., T. Coulson, and B. Sæther. 2008. 'A Latitudinal Gradient in Climate Effects on Seabird Demography: Results from Interspecific Analyses'. *Global Change Biology* 14 (4): 703–13. https://doi.org/10.1111/j.1365-2486.2007.01533.x.

Shultz, M., J. Piatt, A. Harding, A. Kettle, and T. Van Pelt. 2009. 'Timing of Breeding and Reproductive Performance in Murres and Kittiwakes Reflect Mismatched Seasonal Prey Dynamics'. *Marine Ecology Progress Series* 393 (October): 247–58. https://doi.org/10.3354/meps08136.

Skjoldal, H.R, P. Dalpadado, and A Dommasnes. 2004. *The Norwegian Sea Ecosystem*. Trondheim, Norway: Tapir Academic Press.

Stephens, D. W., and J. R. Krebs. 1986. *Foraging Theory*. Princeton, NJ: Princeton University Press.

Stige, L., G. Ottersen, K. Brander, K. Chan, and N. C. Stenseth. 2006. 'Cod and Climate: Effect of the North Atlantic Oscillation on Recruitment in the North Atlantic'. *Marine Ecology Progress Series* 325 (November): 227–41. https://doi.org/10.3354/meps325227.

Utne, K. R., S. S. Hjøllo, G. Huse, and M. Skogen. 2012. 'Estimating the Consumption of Calanus Finmarchicus by Planktivorous Fish in the Norwegian Sea Using a Fully Coupled 3D Model System'. *Marine Biology Research* 8 (5–6): 527–47. https://doi.org/10.1080/17451000.2011.642804.

Votier, S. C, B. J. Hatchwell, M. Mears, and T. R. Birkhead. 2009. 'Changes in the Timing of Egg-Laying of a Colonial Seabird in Relation to Population Size and Environmental Conditions | EndNote Click'. 2009. https://click.endnote.com/viewer?doi=10.3354%2Fmeps08258&token=WzE5Nzg3NTQsIjEwLjMzNTQvbWVwczA4MjU4Il0.__xCmzTasDYB9AWovTEKyHIzHmI.

Wanless, S., M. Frederiksen, J. Walton, and M. P. Harris. 2009. 'Long-Term Changes in Breeding Phenology at Two Seabird Colonies in the Western North Sea'. *Ibis* 151 (2): 274–85. https://doi.org/10.1111/j.1474-919X.2008.00906.x.

Weydmann, A., W. Walczowski, J. Carstensen, and S. Kwaśniewski. 2018. 'Warming of Subarctic Waters Accelerates Development of a Key Marine Zooplankton Calanus Finmarchicus'. *Global Change Biology* 24 (1): 172–83. https://doi.org/10.1111/gcb.13864.

Wood, S., and F. Scheipl. 2020. 'Gamm4: Generalized Additive Mixed Models Using "mgcv" and "Lme4"'. https://CRAN.R-project.org/package=gamm4.

Wooller, R. D., and J. C. Coulson. 1977. 'Factors Affecting the Age of First Breeding of the Kittiwake Rissa Tridactyla'. *Ibis* 119 (3): 339–49. https://doi.org/10.1111/j.1474-919X.1977.tb08252.x.