Environmental factors affecting the phenology of the Atlantic puffin (*Fratercula arctica*) in the Westman Islands, Iceland

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Master's thesis

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ABSTRACT

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The timing of annual life-history events such as reproduction is a critical component of how animals respond to climate change. I studied the timing of reproduction and reproductive success of the largest population of Atlantic puffins (*Fratercula arctica*) in the world, located in the Westman Islands, Iceland. Puffins are considered to be excellent bioindicators for the overall status of their ecosystem due to the bird's long lifespan and specialist coastal foraging.

So far, attempts to understand the potential impacts of climate variation on seabirds have studied relationships between oceanographic features and the birds' distribution and demographic parameters. I add to these studies by exploring the effects on chick numbers and timing of breeding through changes in SST, salinity and large-scale oceanic (SPG) and climate (wNAO) proxies. To get a sense of the population's demography, I used a long-term time series of observational data on annual productivity and the average fledging dates of chicks. I discovered, that since 2006, the puffins have been breeding approximately three weeks later, and after 2015, there has been almost a 100-fold increase in productivity, with an annual increase of roughly 871 individual birds. Of the climate proxies, wNAO and SPG showed a significant correlation with productivity and fledging dates, respectively.

This thesis suggests that the puffin population of the Westman Islands is currently on the rise, and that the ocean climate proxies wNAO and SPG play a role in their population fluctuations.

Keywords:
Breeding phenology, fledgling productivity, Fratercula arctica, climate change, trophic mismatch, Iceland

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1. INTRODUCTION

1.1. Climate change

Climate is a term used to describe the average weather over a long (e.g. 30-year) period (IPCC, 2021; Jenouvrier, 2013). Climate change is not a spatially uniform process and different populations of the same species may have various responses to change, depending on the nature and strength of the change in their particular environment (Descamps *et al.*, 2019; Durant *et al.*, 2004; Stenseth & Mysterud, 2002). Current climate change is a process of highly fluctuating rates of temperature change across all environments (IPCC, 2021). IPCC reported in 2021 of melting glaciers, rising sea temperatures and the decrease of ice sea cover (IPCC, 2021).

Within terrestrial ecosystems, the start of spring is advancing more dramatically in the northern parts of the Earth compared to southern latitudes (Stenseth & Mysterud, 2002). These climatic changes are predicted to have devastating effects on wildlife by altering the food web structure, phenology and ultimately the demography of populations in the Arctic as well as on a global scale (IPCC, 2021). Strong, negative responses of species that are sensitive to these changes in climatic conditions can have direct impacts on all trophic levels of the entire ecosystem (Hansen *et al.*, 2021).

Phenology is the study of the timing of seasonal plant and animal activity in tune with environmental factors (Edwards & Richardson, 2004). The timing of annual life-history events such as reproduction is a critical component of how animals respond to climate change (Descamps *et al.*, 2019). The phenology of a species aims to synchronize the timing of key life-history events such as reproduction and migration with environmental conditions in order to maximize its fitness (Stenseth & Mysterud, 2002). Phenological changes as responses to climate change are widely reported in all environment types from terrestrial to marine (Charmantier & Gienapp, 2014). Most of these reported changes in timing of life-history events seem to focus on springtime. For instance, abundance peaks of prey fish species affect the breeding success of the predator birds. There is mounting evidence across many piscivorous seabird taxa, that as the timing of these peaks shifts due to warming waters, the mean migration dates and mean breeding dates of the bird populations shift accordingly (Hipfner, 2008).

Oceans have high capacity to store heat, thus having a low temperature variability on the shortterm. Due to this characteristic, many marine ectotherms have adapted to a very specific temperature environment (known as stenothermia), most pronounced during times of reproduction (Frederiksen *et al.*, 2013).

In oceans, the temperatures have increased gradually in the last 50 years, with periods of rapid and intense warming fluctuating with slower and moderate warming periods (Beaugrand *et al.*, 2015). These rapid periods have caused abrupt, large, and persistent changes in the state of the environment known as regime shifts (Beaugrand *et al.*, 2015). Studying the changes in climate (30 year averages) and the effects of those changes to the ecology and demography of long-lived seabirds requires long time series'. This is because often the relationships between environmental parameters and species are complex, meaning there are likely many kinds of fluctuations that cannot be predicted simply by surveying a population over one or two generations. Unfortunately, there are only a few long-term ecological time series data available on wildlife populations. Therefore, determining the effects of climate on species that have long lifespans (such as many seabirds) is difficult (Descamps *et al.*, 2017; Hansen *et al.*, 2021). How organisms respond to regime shifts compared to periods of slower change can be highly variable. Therefore, in addition to obtaining long-term datasets, understanding the non-linearity and variations in warming rates is important when making assessments on biotic responses to climate change (Descamps *et al.*, 2017).

To understand how oceanic changes caused by changes in the climate affect marine food webs, it is important to find reliable indicators of resource availability. Sea surface temperatures (SST) and concentration of chlorophyll a have been shown to describe the spatial and temporal of changes of ocean primary productivity well (Behrenfeld *et al.*, 2006). Although these indicators mainly describe effects on lower trophic levels, this information could be used to indirectly predict higher trophic level responses to the changing climate conditions (Carroll *et al.*, 2016).

1.2. Trophic mismatch

The annual seasonal cycle accounts for much of the total temporal variability of mid- and high-latitude marine ecosystems. Although the general pattern of the seasons repeats each year, climate change has produced detectable changes in intensity of weather patterns and the timing of spring onset (Bertram *et al.,* 2001; Serreze & Barry, 2011). For many seabirds, particularly species living in high latitudes, the optimal time for important life-history events such a migration and reproduction is often strictly limited due to seasonal changes in the weather conditions and food availability. Because of this, the failure to adapt phenology according to the changing environment can have major fitness consequences. In general, how a bird species should optimally adjust its breeding date in response to climate change depends to a large extent on the response of other parts of the food chain during the time of selection (Visser *et al.,* 2004). This phenomenon often appears as a "bottom-up" process (Fig. 1), where the fluctuations in lower trophic levels (in this case plankton abundance and the resulting availability of fish stock for food) control the survival and reproductive success of species higher in the food chain (for instance seabirds) (Kitaysky & Golubova, 2000).

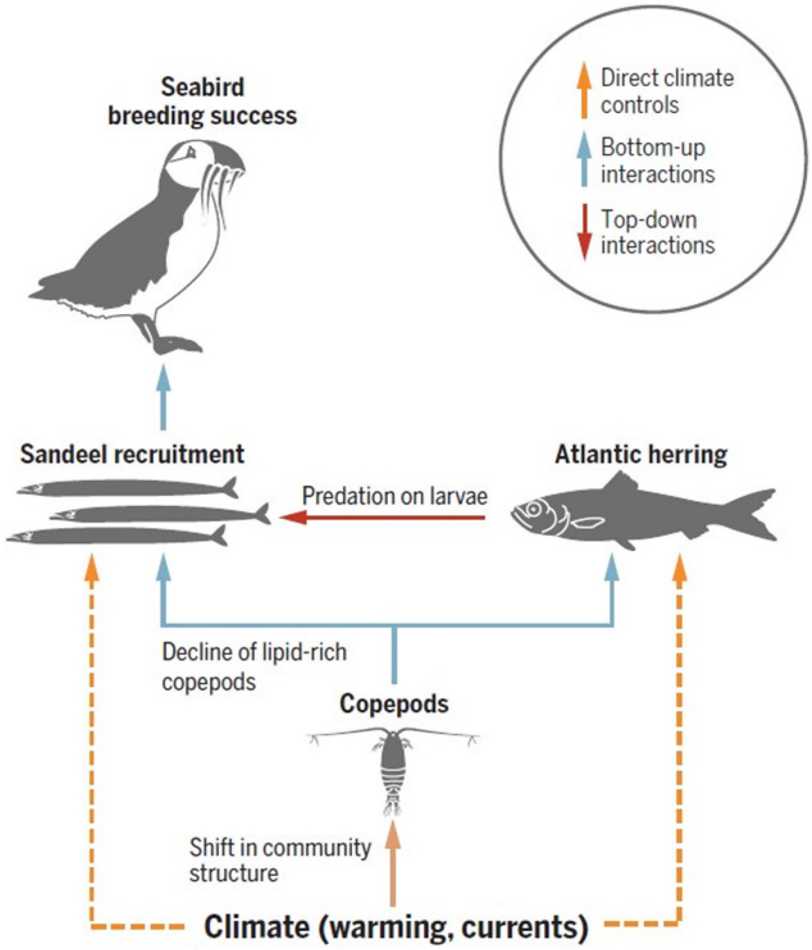

Figure 1. Bottom-up and top-down interactions of climate change in the North Sea. The replacement of the lipid rich *Calanus finmarchicus* by lipid poor *C. helgolandicus* results in declines in sandeel recruitment growth, causing poor seabird breeding success. Modified from Sydeman *et al.*, 2015.

The Arctic ecosystem is shown to be the most affected by global warming (Serreze & Barry, 2011). The rapid pace of warming has caused significant alterations in the Arctic marine system, one of the most evident being the disruption of trophic interactions. Keeping in mind the short time window at high latitudes when animals and plants can reproduce and grow, Arctic species are highly dependent on their phenology to synchronize with the peak resource availability (Descamps *et al*., 2019). Failure to synchronize leads to a phenomenon known as a trophic mismatch (Durant et al., 2004; Sydeman et al., 2015).

The basis of the trophic mismatch hypothesis is that predators breed more successfully in years where their breeding cycle best overlaps (i.e. matches) with the seasonal peak of abundance of their prey (Hipfner, 2008). In marine ecosystems, climate change has caused an

increase in the frequency and severity of mismatches in recent years (Edwards & Richardson, 2004).
Changes in prey availability have been shown to influence several demographic parameters (Frederiksen *et al.*, 2004). For instance, successful reproduction of several seabird species in the northwest Atlantic has been linked to the availability and timing of the coastal movements of the capelin (*Mallotus villosus*), a small forage fish (Durant *et al.*, 2003). One of the earliest studies was carried out in 1990, where Aebischer *et al.* successfully linked variations in climate conditions to a relationship between prey availability and breeding success of seabirds in the North Atlantic (Aebischer *et al.*, 1990).

Another example of a documented trophic mismatch comes from a colony of Atlantic puffins on the islands of Røst in Norway. The Norwegian spring-spawning herring (*Clupea harengus*) stock has experienced great fluctuation in recent decades, presumably as a response to temperature change and overfishing in the ocean (Gullestad *et al.*, 2014). Because of this, on years when herring stocks have been low, the puffin colony has suffered major, and on some years even total, breeding failures. When the availability of herring does not match the puffins' requirements at the most crucial time of their breeding season, chick survival plummets. However, even on years of high herring productivity, the puffins' breeding fails if the timing of the stock's peak abundance is too late in the season or if they drift too away from the colony. Mismatch can thus be considered both in terms of abundance as well as timing (Durant *et al.*, 2006).

1.3. Seabirds as biomonitors for climate change

Birds are among the best-studied groups of living organisms (Jenouvrier, 2013). Seabirds, one of the most threatened groups of birds (Birdlife International, 2018), can be found in all the world's oceans, their habitats spanning everywhere from shores and coasts to the open sea. Seabirds breed on land, typically in colonies, and spend most of their life above water, making them an easy study subject compared to most other marine animals (Dias *et al.*, 2019; Frederiksen *et al.*, 2013). For instance, their numbers are tracked with relatively less effort during the breeding season and large quantities of data can be collected from one colony in a short period of time (Furness & Camphuysen, 1997). As a result of this, detailed documentation of seabird ecology and life-histories of many populations exist, making them good biomonitors (or bioindicators) of the condition of marine ecosystems (Dias *et al.*, 2019; Furness & Camphuysen, 1997; Irons *et al.*, 2008).

However, to function as an effective biomonitor, the species must be sensitive to changes in the variable that it is used as a proxy for. The response of the biomonitor should be predictable, and not caused by any other factor, or a mix of factors. The speed of the response is also important because lagged responses are less reliable and often result in information that is too little, too late. For example, many seabirds take between four to five years to reach maturity. So, changes in the numbers of breeding birds would be considered a poor bioindicator, since the effects of changes can often be seen with a lag of many years. A better measurement in this case would be a more immediate response, such as breeding success (Furness & Camphuysen, 1997).

The effects of climate variability on seabirds are most notably seen directly through life-history effects, such as changes in the reproductive output, and indirectly through a change in prey availability (Jenouvrier, 2013). So far, direct effects have been documented in the timing of breeding, breeding proportion, breeding success and adult survival (Sandvik *et al.*, 2012). Seabirds are found high in the trophic levels and are considered prolific ocean upper predators. Their prey includes a wide variety of organisms on different trophic levels, each with populations that can fluctuate highly in response to climate change, so changes in food availability is a very effective tool when studying the effects of climate change on seabirds (Durant *et al.*, 2004). For example, in the Gulf of Alaska, a regime shift in 1977 caused a trophic cascade in the local marine ecosystem, which caused declines in the local seabird populations due to changes in the prey abundance (Bertram *et al.,* 2001).

Seabirds typically have low birth rate, with many species laying a single egg in a breeding season, compensated for by a long lifespan. Because of this low fertility, most seabirds have very little flexibility in their breeding response to the fluctuating climate variables compared to terrestrial birds. With global warming comes the increased risk of mismatch between peak food availability and the timing of hatching (the period when most energy is required), that can have a major impact on the fledging success of seabirds (Guillemain *et al.*, 2013). However, since many species take years to reach maturity, the effects of climate signals may take years to show in a colony (Durant *et al.*, 2006; Sandvik *et al.*, 2012).

Birds are in general well cued to year-to-year variation in weather parameters and can relatively easily adapt their reproduction timing to match the temperature (Carey, 2009). However, it is much more difficult for birds to assess the timing of peak abundance of food since egg-laying typically occurs well before (Visser *et al.*, 2004). So, to synchronize their reproductive efforts to match nestling growth period with peak food abundance, other environmental cues are required. Different cues can be combined to produce a physiological response which translates the information received from the environmental cues into a laying date (Visser *et al.*, 1998). Problems arise when climate change affects some, but not all, of the important cues birds use. For instance, one important cue for the timing of reproduction is photoperiod (day length). The change in photoperiod is always the same, since it is dictated by the rotation of the Earth around itself and the Sun, so it alone cannot be used to find out the optimal breeding time. The strength of photoperiod as an environmental cue depends on the strength and nature of the effects of climate change on additional cues (e.g., sea-surface temperature or plankton abundance) used by birds to time reproduction (Lambrechts & Perret, 2000). Climate change makes these additional cues unpredictable, which can lead to mistiming, i.e., the timing of chick feeding does not match the timing of the peak abundance of the food source anymore. Thus, it is important to focus on these supplementary cues when studying the adaptation of species to climate change (Visser *et al.,* 2004)

1.4. Puffin as a study species

The Atlantic puffin (*Fratercula arctica*, hereafter puffin) is a long-lived seabird of the *Alcidae* family endemic to the North Atlantic Ocean (Fig. 2). They are predators high in the food web, and as is the case with most seabirds, tend to respond to climate change through a bottom-up process. Puffins' breeding range stretches from the Arctic coasts and Northern Europe to Canada, with most southern colonies found in France and USA (Kersten *et al.*, 2021). There are three subspecies of puffins, and the one I studied, *Fratercula arctica arctica*, is most commonly found in Iceland, where estimated 2.5 - 3 million pairs account for approximately 40% of the world's population. In 2015, the global species' Red-list status was changed from "Least Concern" to "Vulnerable" (IUCN, 2019).

Figure 2. An adult ringed puffin in its breeding plumage. Photo © Rodrigo Martinez Catalan.

Puffins feed on small forage fish no more than 10cm long (Kress *et al.*, 2017). Worldwide, over 50 different fish species as well as a number of invertebrates have been documented as puffins' prey (Harris & Wanless, 2011). Normally in a colony one or two species of prey are favoured. Depending on the size of the prey, puffins have been documented carrying as much as 80 individual preys in their beak at any one time (Barrett, 2015).

Puffins spend most of their lives in the open ocean, and only come to land to breed during the spring and summer months. They nest in large colonies on cliffs, where each bonded pair has a nest burrow of their own. They lay only a single egg per breeding season. Incubation is a duty shared by both parents and lasts for 42 days (Harris & Wanless, 2011). Both parents feed the chick with small fish and zooplankton (predominantly sandeel and Northern krill [*Meganyctiphanes norvegicus*] in the Westman Islands), until it fledges at five to six weeks old. Chicks fledge at night, and fly straight out to sea (Ashcroft, 1979). In earlier studies, puffin chick's development has been linked to mean sea-surface temperature (hereafter SST). Below a certain threshold value in temperature, fledging does not occur. This relationship has been explained by an indirect effect of SST on puffins' food supply as well as direct effect of SST on the chick's metabolism (Durant *et al.*, 2006).

Puffins are upper predators in the North Atlantic, and as is the case with most seabirds, tend to respond to climate change through a bottom-up process (Hansen *et al.*, 2021). This means that when a change in a puffin colony is linked to a change in climatic conditions, it can be expected that significant changes are occurring in other trophic levels of their ecosystem as well (Hansen *et al.*, 2021). Puffins have a strong breeding site fidelity, an extended chick-rearing period and they breed in big colonies (Kress *et al.*, 2017). These traits make them relatively easy to monitor compared to for example the timing of plankton blooms or fish abundance.

1.5. Environmental variables in marine ecology

1.5.1. Temperature and salinity

Ocean surface temperature (SST) is one of the most used environmental variables in studies of marine ecology. Because of its reported effects on the behaviour, physiology, distribution and migration of free-living organisms, temperature is crucial to the function and structure of ecosystems. Seasonal temperatures vary significantly even in oceans, with surface waters warmer during summertime than in winter. Changes in biological activity are great as winter progresses to summer, so the timing and magnitude of warming can be a major contributing factor to the condition of the ecosystems (Bertram *et al.*, 2001).

Uncharacteristically warm sea surface temperatures have in some cases been linked to long-term climatic changes caused by global warming (Gjerdrum *et al.*, 2003). Changing SSTs have in some occasions helped to explain large and swift changes in fish and seabird populations worldwide (Descamps *et al.*, 2017; Durant *et al.*, 2004; Irons *et al.*, 2008). As temperatures are on the rise in many places, it is of critical importance to predict the effect of these changes on the demography and dynamics of organisms to identify vulnerable populations and anticipate extinction (Gjerdrum *et al.*, 2003)

Together, salinity and sea surface temperatures in the waters off South-Iceland reflect the amount of warm and saline Atlantic Surface Water (ASW) that flows northwards from the south via the Irminger current (Fig. 3). The northern Atlantic waters around Iceland are generally colder and less saline, so these ASW pulses have a negative effect on the nutrient availability of the north, thus decreasing the area's productivity (Hanna *et al.*, 2006).

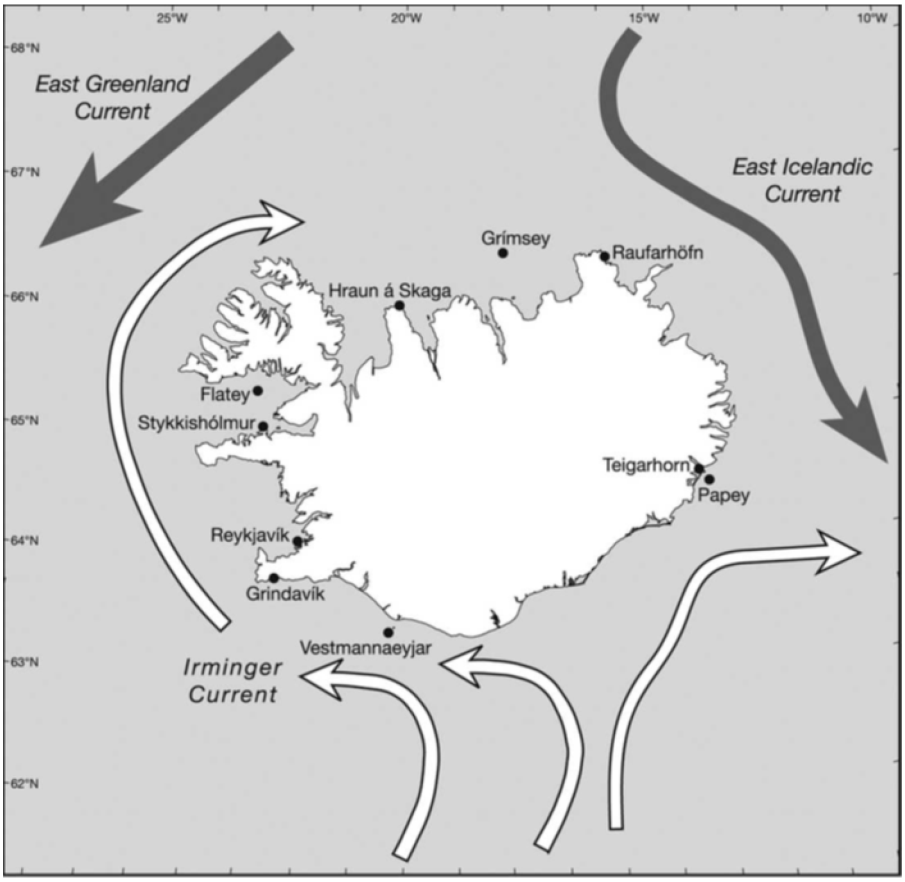

Figure 3. Map of Iceland with all the major currents depicted. Figure from Hanna *et al.,* 2006

1.5.2. wNAO

The North Atlantic Oscillation (NAO hereafter) has become an increasingly popular proxy for climate variations in the Northern Hemisphere (Oro, 2014; Stenseth *et al.*, 2003), which is defined as the difference in atmospheric sea level pressure between Stykkisholmur/ Reykjavik, Iceland and Lisbon, Portugal (Descamps *et al.*, 2013; Hovinen *et al.*, 2014). It has been linked to various climatic variables, including precipitation and temperature, and is considered to be the main mode of climatic variability in mid- and high latitudes (Hovinen *et al.,* 2014; Hurrell *et al.,* 2003*)*.

The NAO indirectly reflects the strength of the westerlies and the movement of air and wind-driven surface water and is thus linked to SST. When the NAO index is negative, the conditions in Iceland are mainly dry and the sea temperatures are low (reduced inflow of Atlantic water into the Arctic), whereas a positive index is related to humidity and warmer air temperatures (intensified inflow of Atlantic water into the Arctic) (Durant *et al.*, 2004; Hovinen *et al.*, 2014; Hurrell *et al.*, 2003).

The NAO has been shown to be linked to the phenology and population dynamics of several species of seabirds (Guillemain *et al.*, 2013; Hubálek, 2004; Hurrell *et al.*, 2003), for example by affecting the abundance of zooplankton and key fish prey (Durant *et al.*, 2006), but the effects are complex as they differ with latitude and even between different populations (Durant *et al.*, 2004)

The NAO has been shown to be strongest during the winter months (December to March), with far-reaching effects on phyto- and zooplankton communities in the subsequent spring and summer seasons (Hurrell *et al.*, 2003). By affecting the plankton assemblages, the winter NAO (wNAO) has been related to the life-history of numerous seabird species, most notably on reproductive success (Descamps *et al.,* 2013; Durant *et al.,* 2006).

From the perspective of this study, the NAO gives us a proxy on the weather conditions at a given time in the sea. The more windy or stormy the weather is, the more sea surface mixes, destroying the surface water layering and deepening the surface mixed layer, thus perturbating surface warming and hindering the onset of the phytoplankton bloom (e.g., Hurrell *et al.*, 2003).

1.5.3. SPG

The North Atlantic subpolar gyre (hereafter SPG) is a large counterclockwise rotating body of cold and low-saline subarctic water in the North Atlantic which dominates the physical oceanography of the central northern region (Hátún *et al.,* 2016). The SPG index (or the SGI) is calculated from sea surface heights, which reflect both the composition of water masses and the associated currents (Descamps *et al.*, 2013; Hátún *et al.*, 2016). The SPG is linked to the NAO, but it has been argued that SPG relates more closely to oceanographic conditions and therefore is a better proxy to explain variation in food availability and distribution of seabirds (Descamps *et al.*, 2013). The SGI has been used as a global proxy to assess oceanographic conditions and changes in marine ecosystems in the North Atlantic (Fluhr *et al.*, 2017; Sandvik *et al.*, 2012).

Marine ecosystems can undergo rapid and dramatic changes in their biological and physical properties over long periods of time. In 1996, an abrupt ecosystem shift occurred in the North-East Atlantic Ocean, when a great quantity of warm and saline waters from the south flowed up to the north (Beaugrand & Reid, 2012; Fluhr *et al.*, 2017; Hátún *et al.,* 2017). The temperature rose by more than 1°C in South Iceland between 1996- and 2003 (Hansen *et al.*, 2021). This rise is associated with the 70-year cycle of the Atlantic Multidecadal Oscillation (AMO) and simultaneous contraction of the SPG. A decrease in the SPG led to warming and salinification of the waters around the south of Iceland (Hátún *et al.*, 2005). This regime shift has been associated with pronounced changes in the physical environment (e.g., SST, salinity) and free-living organisms. For example, a species of copepod (*Calanus finmarchicus*) decreased briefly in abundance in the southern parts of Iceland after the shift in the gyre (Descamps *et al.*, 2013).

Due to its effect on temperature, salinity and nutrients of water masses in the north Atlantic Ocean, changes in the SPG impact the phytoplankton and zooplankton communities through trophic cascades or amplifications (Fluhr *et al.*, 2017). During warm cycles of AMO (like the one currently ongoing), the eastern part of the SPG responsible for directing cold and nutrient-rich waters towards Iceland retracts westwards and is replaced by inflow of ASW (Atlantis Surface Water, see ch. 4.1.) The SPG index shows the strength or intensity of the cold and nutrient rich current toward Iceland.

1.6. In this study

Attempts to understand the potential impacts of climate variation on seabirds have studied relationships between oceanographic features and the birds' distribution and demographic parameters. In the following, I use similar methods to explore the potential effects on puffins by changes in SSTs, salinity and large-scale ocean climate proxies.

In order to examine the effects of aforementioned oceanographic parameters on these Atlantic predators, I used annual productivity and the average fledging dates of chicks in a colony of puffins in southern Iceland.

Since most previous studies have concluded that large, rapid environmental changes have a negative impact irrespective of the direction of change, I hypothesized, that the rapid changes observed in the climate are negatively affecting the puffin population in the Westman Islands.

2. MATERIALS AND METHODS

2.1. Study area: Westman Islands, Iceland

Westman Islands (N63°25’37.28”, W20°16’9.54”) or Vestmannaeyjar, is a geologically young archipelago consisting of 16 islands in total, located off the southern coast of Iceland (Fig. 4). The biggest and the only inhabited island in the system is called Heimaey (13,4km²), with a population of approximately 4300. More than 30 species of birds regularly breed in the Westman Islands, including guillemots, gannets, kittiwakes, skuas and puffins. The birds nest in their millions among the cliffs and grassy ledges of the volcanic islands, including the world’s largest colony of puffins (approximately one million breeding pairs) (Hansen *et al.*, 2021).

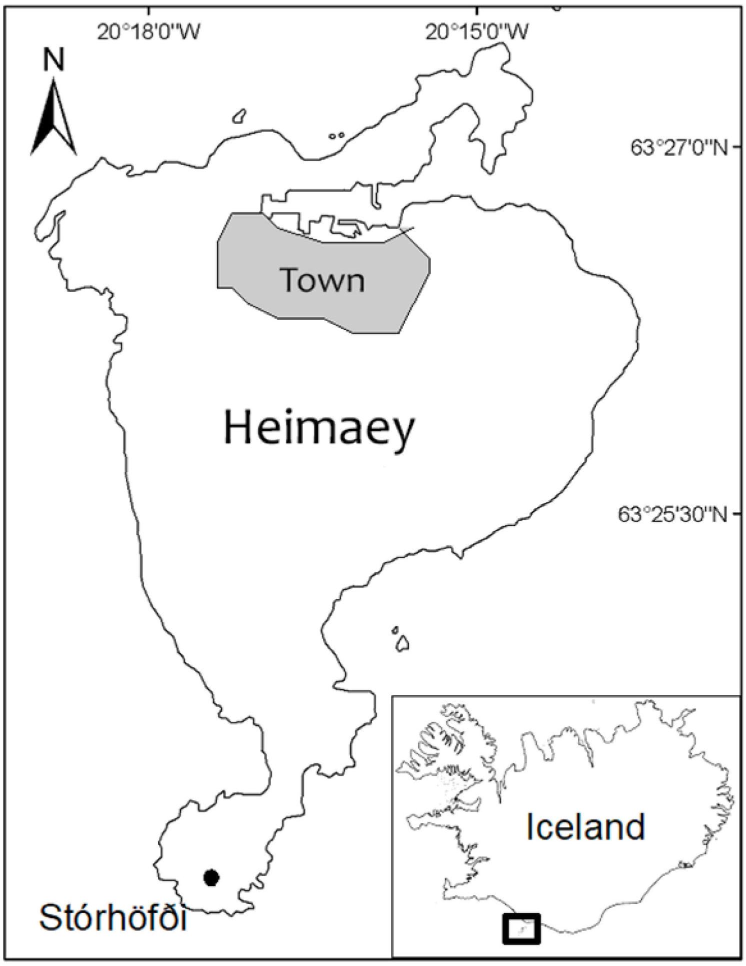

Figure 4. Map of the main island of the Westman Islands archipelago, Heimaey. The puffin colony that was studied for this thesis is found in the cliffs of Stórhöfði in the south of the island, marked on the map. Smaller map shows the location of the Westman Islands in Iceland. Map modified from Manson & Jónsson 2006, unpublished.

The data was extracted from the national ringing database of the Icelandic Institute of Natural History and is used with their permission. For this study, two ringing locations were extracted: Stórhöfði, the southernmost point of Heimaey, and the town of Vestmannaeyjabær. From this dataset I took the fledging dates to be used as a phenology marker, as well as the total number of fledged birds each year.

Vast majority of the birds were ringed by two ringers, Óskar J. Sigurđsson (1953-2014) and Sigurgeir Sigurđsson (1971-1992). Óskar J. Sigurđsson was the local lighthouse keeper at Stórhöfði and mostly ringed the puffins there, but after 1990 he also contributed to the ringing of the town's pufflings that his son rescued. Sigurgeir Sigurđsson was responsible for ringing the town's pufflings. From 2015 onward, the ringing of fledglings brought to the

Puffling Rescue Center in Heimaey has been done by the staff of South Iceland Nature Research Centre (Fig. 5).

Figure 5. On the left, a puffling approximately a week away from shedding its last down feathers. On the right, a fully-fledged bird ready to leave the nest.

2.3. Fledglings in town

The nestlings usually leave their burrows at night, presumably to avoid predators (Myrberget & Harris, 1988). Many of them are attracted to the lights of the nearby town, and instead of the ocean, they fly straight into town and get lost on the streets. The fledging season ranges from four to up to eight weeks, and in a productive year it literally rains pufflings in the town of Heimaey. For most of the last century, there has been a tradition of puffling rescue by the residents of the island. Families equipped with cardboard boxes and flashlights walk the streets at night, looking for the birds. They pick up the pufflings and put them in the safety of the cardboard boxes for the night. In the morning, the puffings are brought in for registration by puffin rescue center run by the Þekkingarsetur Vestmannaeyja for data collection (weight, wing length, number of pufflings). Afterwards they are released to the sea (see Fig. 6).

Figure 6. Successful releases of pufflings rescued from the town (Photos © Margrét L. Magnúsdottir).

2.4. Puffling Patrol data

In 2003, Páll M. Jónsson, a local marine biologist, started a citizen science project based on the puffling rescue called “Pysjueftirlitið,” or the “Puffling Patrol” (Fig. 7). The aims of this ongoing project is to gather data from the birds that can be utilized in future studies of the colony. The resident scientists measure body mass, and wing length from the rescued pufflings brought in by the public. The measurements were supervised by Páll M. Jónsson (2003 – 2007) and Margrét L. Magnúsdóttir 2007 - present). We merged the data from Puffin Patrol with the ringing data we received from the Institute of National History for more accurate results.

Figure 7. On the left, a puffling caught in town in the process of being weighed and measured before releasing it to the ocean. On the right, the logo of the Puffin Patrol (pictures © Rodrigo Martinez Catalan and Margét L. Magnúsdóttir).

2.5. Environmental variables

For the purpose of analysing the changes in puffin phenology against the changes in the local environment over time, data were requested from research institutes as well as downloaded online. The following section contains more detailed information about the environmental factors chosen. In total, four climate indices were used as covariates (Fig. 8).

Figure 8. Time-series trends of the environmental covariates used in this thesis.

From our study area, we have an annual average of SST and salinity. The SST data spans from 1938 to 2018, and salinity (marked as Practical Salinity Units, or PSU, from now on) starts in 1947 (Fig. 7). The SST and salinity data were acquired from the Icelandic Meteorological Office and the Icelandic Marine Research Institute.

We considered the winter NAO (wNAO) index, calculated as a mean value from December to March. We are using data with index values measured monthly starting from 1938. NAO index was retrieved from the National Center for Atmospheric Research. https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based

The SPG index was kindly provided by Dr. Léon Chafik from Stockholm University. It is an annual index starting from 1938. This index is used in this study to reflect the annual oceanographic conditions in the waters around the Westman Islands.

2.6. Data analysis

The data analysis was conducted using the RStudio software ver. 1.4.1103 (R Studio Team, 2020). First, I used a breakpoint analysis to compare different models and to find out which type of analysis method best suited this particular dataset. The breakpoint analysis allows me to fit two different regression slopes before and after an arbitrary point in the predictor variables, within a linear model framework. The analysis works by testing all of the possible breakpoints and selects the most appropriate breakpoint by maximising the model likelihood. In essence, breakpoint analysis returns the point in the data where significant changes are most likely to have occurred. Since there are considerable gaps in the early years of the dataset, this analysis was run twice; first with all the years included, and second starting from after the last gap year.

Based on the results of the breakpoint analysis, I decided to use generalized linear models (GLMs) for all research questions. The GLM works by generalizing linear regressions to allow linear models to be related to response variables with different distributions. This allows different types of measurements and values to be analysed against each other. I assumed normal (Gaussian) distribution in my models and collected the AICs (Akaike's Information Criterion) from each one. AIC is an estimate of prediction error and assesses the informative quality of a statistical models. The lower the AIC, the better fit the used model is for the dataset.

The more complex the models are (more degrees of freedom), the larger datasets they require, and in the case of my study, the time series of my dataset was relatively short, coupled with significant amounts of autocorrelation. I first considered the short-term (year to year) fluctuations by analysing the detrended time series. Detrending means removing a trend (a change in the mean over time) from a time series. When you detrend data, you remove an aspect from the data that you think is causing some kind of error or skew. For example, you might detrend data that shows an overall increase, in order to see smaller, more subtle changes. Second, I considered raw data and focused on the long-term fluctuations (i.e., trend). I used the criterion of $P < 0.05$ to reject a null hypothesis.

3. RESULTS

3.1. How has puffin productivity changed between 1938 – 2020?

In 2015, a significant change in the population productivity occurred (see fig. 9). Before this change, the annual increase of puffins in the colony was on average 11 individuals (p=0.002, with confidence limits 4.37 – 18.4). After 2015, there has been almost a 100-fold increase in productivity, with an annual increase of roughly 871 individual birds (p<0.001, with confidence limits 618.06 – 1124.09) (table 1). Figure 11 shows, how the prediction of the AIC analysis for the best model fits the data.

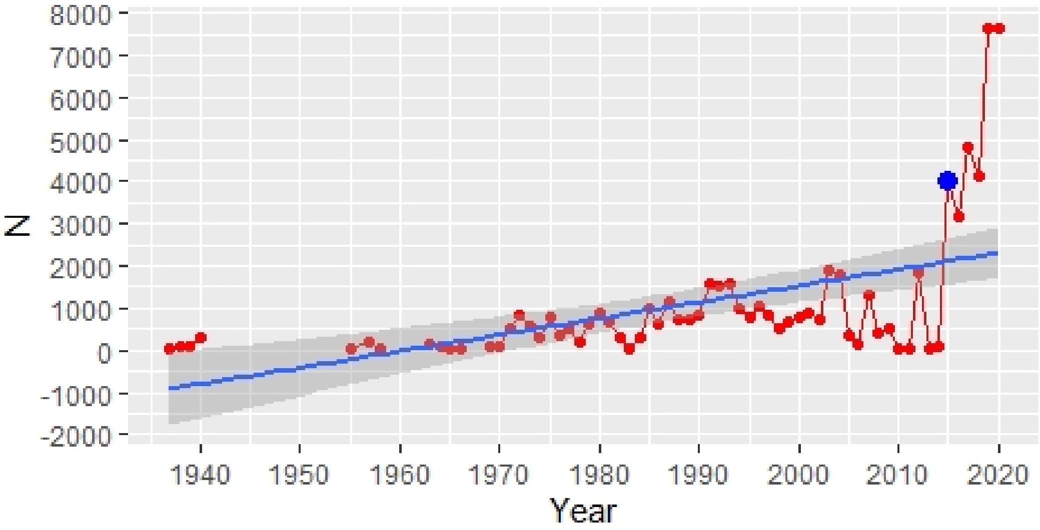

Figure 9. A time-series displaying number of pufflings caught each year in the Westman Islands from 1938 to 2020, with the breakpoint year (2015) marked in blue, and a regression line with standard errors shown in grey.

Table 1. The summary of GLM analysis on puffin productivity in the Westman Islands from 1938 to 2020. Year gives the average annual increase in fledgling numbers before the year 2015 with confidence limits and p-value, whereas Year*threshold shows the annual average increase in productivity after the change in 2015.

Predictors	*Estimates*	*CI*	*p*
(Intercept)	-21996.03	-35913.57 – -8078.49	**0.003**
Year	11.38	4.37 – 18.40	**0.002**
threshold	-1753124.26	-2263583.79 – -1242664.72	**<0.001**
Year*threshold	871.08	618.06 – 1124.09	**<0.001**
Observations	63		
R^2	**0.886**		

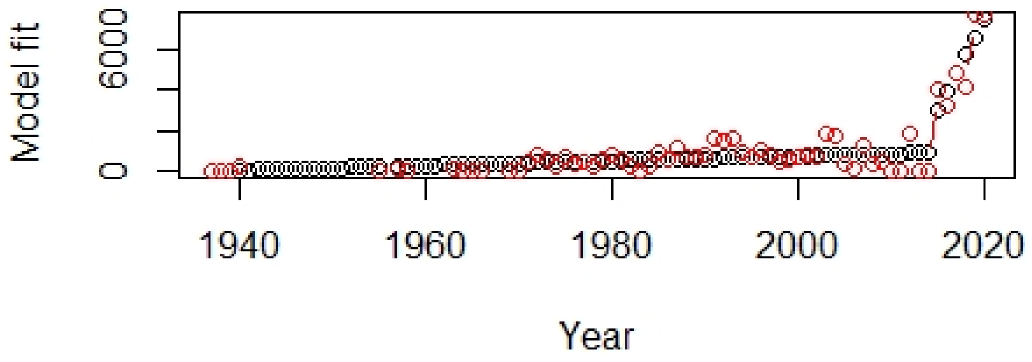

Figure 10. A graph showing the fit of the best model predicted by AIC (black) against the number of pufflings (red).

3.2. How has the fledging phenology changed between 1938 – 2020?

A significant change in the mean annual fledging date of the puffins was in 2006, from which on the average fledging date moved to 17,5 days later than before ($p<0.001$, with confidence limits 12.06 – 22.98) (fig. 12). No relationship between years and fledging dates was found, so that interaction was excluded from the analysis, assuming there were no time trends before or after the point of change in 2006 (Table 2).

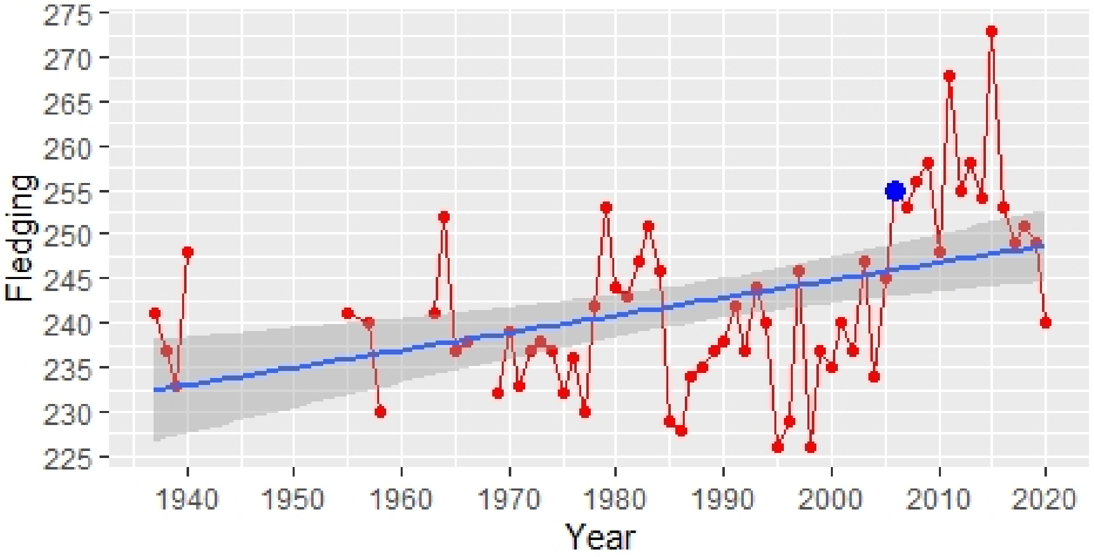

Figure 11. A time-series displaying the mean fledging dates of the pufflings in the Westman Islands from 1938 to 2020, with the breakpoint year (2006) marked in blue, and a regression line with standard errors shown in grey.

Table 2. The summary of the GLM analysis on puffin breeding phenology in the Westman Islands from 1938 to 2020. Threshold shows how much on average the fledging dates changed after the breakpoint of 2006, with confidence limits and p-value.

Predictors	*Estimates*	*CI*	*p*
(Intercept)	312.9	97.79 – 528.01	**0.006**
Year	-0.04	-0.15 – 0.07	0.5
threshold	17.52	12.06 – 22.98	**<0.001**
Observations	63		
R²	**0.51**		

3.3. What is the relationship between productivity and fledging dates?

No relationship between mean fledging dates and number of pufflings in the Westman Islands was found (table 3). Although the p-value marks significance (p=0.037), the slope is indistinguishable from 0 (confidence limits 0-0.01), meaning these two covariates have no relevant correlation with each other.

Table 3. The summary of GLM analysis displaying the relationship between puffin productivity and mean fledging dates with confidence limits and p-values.

	Fledging		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	240.03	236.85 - 243.22	**<0.001**
N	0	0 - 0.01	**0.037**
Observations	60		
R²	**0.072**		

3.4. Which environmental factors are affecting puffin phenology and productivity?

Considering the number of pufflings (N), significant correlation was only found with wNAO (p=0.026, fig. 12). There was no correlation with SPG (p=0.088), PSU (p=0.238) or SST (p=0.560).

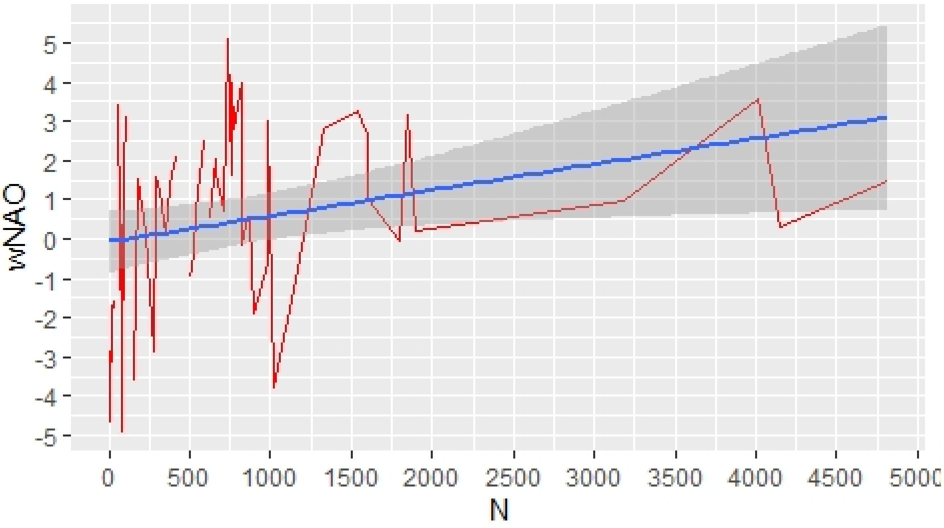

Figure 12. Line plot showing the result of the GLM analysis of number of pufflings and wNAO index. Correlation (p=0.026) is shown with a blue line.

With mean fledging dates, the only significant correlation found was with SPG (p=0.004, fig. 13). No correlation was found on any of the other environmental covariates (p-values between 0.370 – 0.632). All results are shown in table 4.

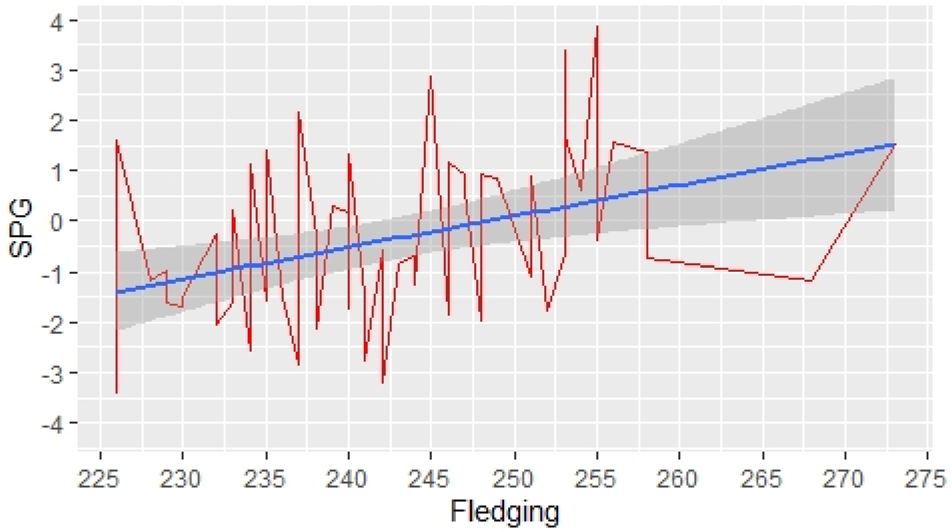

Figure 13. Line plot displaying the result of the GLM analysis of average fledging dates and SPG index. The blue line shows the correlation (p=0.004).

Table 4. The summary of GLM analyses on the relationships between the puffin population parameters and the environmental variables, with p-values, confidence limits, degrees of freedom and R-squared values. The boldened rows show significant results.

Response variable	*Predictors*	*Estimates*	*CI*	*p*	*Observations*	*df*	*R²*
Number of pufflings	**wNAO**	**133.66**	**19.12 - 248.19**	**0.026**	**56**	**1**	**0.088**
	SPG	134.15	-17.35 - 285.65	0.088	60	1	0.049
	PSU	-837.24	-2211.51 - 537.04	0.238	53	1	0.027
	SST	-210.22	-913.58 - 493.15	0.56	60	1	0.024
Average fledging date	wNAO	0.28	-0.86 - 1.42	0.632	56	1	0.004
	SPG	**2.21**	**0.78 - 3.64**	**0.004**	**60**	**1**	**0.137**
	PSU	-5.45	-18.9 - 7.99	0.43	53	1	0.012
	SST	3.19	-3.73 - 10.12	0.37	60	1	0.155

4. DISCUSSION

4.1. Changes in the puffin productivity

The data I used to evaluate puffin productivity was large and it provided me with a long timeline of the Westman Islands colony. Because of the length of the time series, it consisted of different individuals who ringed and counted the fledged chicks. There have likely been differences in for instance work effort, style, time and place between individuals that could have an effect on data accuracy. In addition, since 2003, I had additional data from the Puffling Patrol, which only takes into account the fledglings that fly into town. The proportion of fledglings that fly into town each year varies highly, and the exact reason behind this phenomenon is uncertain. The number of chicks that fly straight from the colonies to the sea is unknown. Recently, a study by Hansen *et al.* showed a population decline in the Westman Islands colonies using hunting data from 1880 to 2008 (Hansen *et al.*, 2021). However, the data I used ranged all the way to 2020, and what I have discovered is, that after a short crash in productivity around 2010, the puffin population of Westman Islands has seen an almost exponential growth spurt since 2015. In the future, perhaps a more standardized method of assessing productivity is needed (for example, regular burrow monitoring during the breeding season). This, however, would requires long-term efforts and planning, and the development of standardized methods.

4.2. Changes in the phenology

Since 2006, the puffins have been fledging approximately three weeks later. The reasons behind this shift are still unknown. This finding is the opposite of what I expected to see, since previous studies have shown, that warming climate advances spring phenologies, rather than delays them.

In a recent paper by Descamps *et al.* (2019), they reported that diving birds, particularly those of the *Alcidae* family, have shown a lack of significant phenological change over the last decades. They speculate, that within this family, global warming and spring advancement would not have a strong influence. They suggest that pursuit-diving seabirds such as puffins have access to wider environmental space and show larger foraging plasticity, therefore being able to breed successfully independent of spring onset. Naturally, confirming these speculations require additional colony level studies, but it could shed some light on what I have seen in the Westman Islands colonies. After 2006 the chicks in the colony have fledged on average three weeks later than before, which was the opposite direction of what I initially expected to see. This could indicate foraging plasticity (change of main food source from sandeel to krill), but more studies are needed to confirm this.

4.3. The mismatch

Typically, when spring is early and warm, plankton blooms earlier and causes breeding seabirds to miss the peak availability of their food resources. This mismatch, as mentioned earlier, reduces the reproductive performance of birds. If ocean temperatures continue to rise and cause further advancement of springtime, we should expect to see an even greater reduction of breeding success in future cohorts, unless they successfully adapt their phenology to these shifts (Bertram *et al.*, 2001).

Because seabirds are at a high trophic level, and often take prey from different levels, their relationship with climate becomes complex (Durant *et al.*, 2006). A temperature that is favourable for seabirds and their prey might not be favourable for the prey species' food resource. For example, in the 1990s it was discovered, that changes the population dynamics of Black-legged kittiwakes and SST coincided with marine regime shifts in the Northern Hemisphere. These regime shifts were the result of changes in plankton assemblages, which also coincided with reported declines in fish stocks (Descamps *et al.*, 2017). In essence, the environment turned unfavourable for the kittiwakes because of the reduction in the availability of its own prey (Durant *et al.*, 2006).

Because of this reported link between seabird population dynamics and plankton, I wanted to study the relationship between plankton abundance and the demographic parameters of the puffin colony. However, the data that was available to me (Continuous Plankton Recorder data, CPR) has numerous gaps, especially during the critical periods I was interested in (the points of change in the demographical data), so I had to exclude this analysis from this study.

At present, climate change can often be witnessed as an advancement of spring phenology in the animal kingdom (Visser *et al.*, 2004). Since species in different trophic levels have different response mechanisms to changing weather patterns and rising temperature, and thus time their phenologies in different ways, trophic mismatches have been increasingly reported. It is believed that mismatches caused by climate changes will become a general phenomenon in ecosystem around the world (Visser *et al.*, 2004).

4.4. Environmental variables

Rapid changes in ocean temperatures have often been thought to be at the origin of regime shifts in marine ecosystems, even though the exact reasons as to why that is are still largely unknown (Beaugrand *et al.*, 2015; Descamps *et al.*, 2017). In Røst, Norway, Durant *et al.* documented an indirect effect of SST on puffins through changes in their prey resources. Fledging success was related to both SST and food availability. Mismatch occurred when SST dropped. They concluded that the birds' feeding biology is a major factor in how changes in sea temperature affect their reproduction. Planktivorous birds' reproductive success was negatively correlated with SST, whereas piscivorous birds had a positive correlation (Durant *et al.*, 2006). In my study population, I found no correlation between the productivity and SST. However, using a different time-series data of the same puffin colony, Hansen *et al.* (2021) found that SST explains 88% of variation in puffin production (Hansen *et al.*, 2021). This significant difference in results may be due to the differences in the quality of the time-series data used, or other methodology. To understand these differences, further analyses would be required.

It has previously been reported, that when wNAO index is high, puffins tend breed earlier. However, a study in 2004 by Durant *et al.* showed two different regimes, one with a negative relationship between wNAO and timing of breeding, and another regime where timing was independent of wNAO (Durant *et al.*, 2004). What I discovered was a relationship with the actual number of chicks and the wNAO index ($R_2 = 0.088$, $p = 0.026$). When the wNAO index was lower, puffling numbers crashed. Timing did not correlate with the index.

I also discovered a correlation between the SPG index and fledging dates ($R_2 = 0.137$, $p = 0.004$). When the SPG index was high (weak Subpolar Gyre circulation), the puffins tended to fledge later. The reasons behind this are still unknown. However, considering that SPG index shows the strength or intensity of the cold and nutrient rich current, one hypothesis would be that this colder current is less favourable for plankton blooms as opposed to the warm and more saline current indicated by a higher SPG index. Plankton might take longer to bloom in the colder current, and thus through trophic interactions, the peak sandeel and krill abundance is later, which then causes the puffins to fledge later. Another possible scenario could be that it takes longer than average for the pufflings to grow big enough to fledge because of the delay in food resources. These scenarios are both purely hypothetical and will need further studies to confirm.

The NAO index is generally accepted as a reliable proxy for the North Atlantic climate, for it catches most of the variation in many oceanographic as well as atmospheric parameters (Stenseth *et al.*, 2003). For assessing the conditions in the North Atlantic marine ecosystem, SPG is being more frequently used. It is recommended that when analysing marine climate, NAO and SPG should both be used in synergy, even though they do correlate with each other. By affecting the temperature and the salinity of water, changes in the SPG reflects the oceanic conditions experienced by marine organisms more directly than the NAO index, which is bases on atmospheric pressure (Fluhr *et al.*, 2017; Hátún *et al.*, 2017).

There is a considerable variation of responsiveness to changing climatic conditions between seabird species and even between different populations of the same species (Barrett *et al.*, 2012; Kitaysky & Golubova, 2000). However, it has been argued that out of all life-history traits, offspring production is the one that universally responds to climatic variations, regardless of species (Sandvik *et al.*, 2012; Visser *et al.*, 2004). Our study supports this theory by reporting that, although not much correlation was discovered, the puffling numbers generally explained the variations in time slightly better than the fledging dates. Although, as can be observed from the summary tables of the analyses, singular variables, regardless of having a significant correlation, did only explain small fractions of the overall variation. In hindsight, to explain more of the variations in the colony with these variables, the variables should have been tested together as a multiple regression analysis, for they most likely have a combined effect.

4.5. Puffins and the Westman's

Hansen et al. hypothesized in 2021, that the lesser sandeel stocks might be the key factor explaining the population dynamics of puffins in the Westman Islands. Previous studies on sandeel recruitment have shown, that warmer winter temperatures cause higher mortality and lower fecundity on the sandeel stocks (Arnott & Ruxton, 2002; Frederiksen *et al.*, 2011). In addition to this, their abundance also decreases if the temperatures are too low. In essence, strong increases or decreases of SST in the waters around Iceland could cause food shortages for the puffins and this way affect the productivity of the population. For this thesis, it would have been interesting to analyse our data against a time series of sandeel stocks in south Iceland. Unfortunately, the data was not available to us.

Puffins, like many seabirds, have an integral place in human culture and economy. In Iceland, for example, puffins are considered to be the most important of birds, for tourism as well as in the hearts of the locals, as can be seen from the ongoing puffling rescue efforts of the people of the Westman Islands. Sadly, however, since the mid-20th century, seabird numbers have plummeted globally by a colossal 70%. This is an alarming decline that poses a serious threat to marine ecosystems and human societies alike, underlining the importance of seabird conservation (Kersten *et al.*, 2021).

4.6. Conservation and climate change

At present, there is a pressing demand for more population predictions to future climate conditions in order to implement new, necessary conservation strategies (Jenouvrier, 2013). Thanks to their positions as top predators, seabirds' response to climate change is a good bioindicator of the overall state of the food web. Thorough ecological studies on food webs and their relationships with the environment is needed, and in this context, studies of seabird populations could be of great value.

One of the most important issues facing ecologists today is understanding and predicting species' population-level responses to climate change (Beaugrand & Reid, 2012). Will populations increase or decline? Will their ranges shift, expand or contract? Are they in danger of facing extinction? To answer these questions, one is required to have an understanding of the thermal tolerance, trophic relationships and dispersal capacity of the organism in question. What makes achieving this understanding particularly difficult for seabirds, is that for species high in the food chain, trophic effects are often more significant than direct effects of surrounding climate (Frederiksen *et al.*, 2013).

Climate change is a global phenomenon. However, most analysis of its ecological effects on organisms have so far been in a local, single population scale. In addition, even though temperatures are on the rise in general, cyclical climatic and oceanic oscillations also play an important role in the changes observed in marine ecosystems (Hurrell *et al.*, 2003). Furthermore, an alteration of ecological systems by the loss of top trophic levels due to overfishing, pollution, and the introduction of alien species can have an impact on the accuracy of the study results (Irons *et al.*, 2008).

One of the most important limiting factors in the studies of climate effects on animals is the shortness of available data. Most time series are too short study climatic effects since climate is a long concept. It is difficult to see patterns and relationships unless we have data of sufficient lengths. Additionally, due to the monotonic trend of the time-series data, there is an increased amount of temporal autocorrelation, which, if not addressed, should at least be acknowledged.

4.7. Conclusions

To understand the complex effects of climate change on the marine environment, we must first find out what biological mechanisms are involved (Durant *et al.*, 2006). For instance, variations in life history and foraging ecology could serve as a basis for grouping species' responses to climate change, which could able us to predict (Stenseth & Mysterud, 2002). Results from my study of this one big colony of puffins offers insight to the local mechanisms on how this particular population responds to changes in the climate of their ecosystem. However, since global change rates and seabird species' responses vary spatially and temporally (Descamps *et al.*, 2017), these findings cannot be used as a generalization for the whole group.

Last but not least, expanding the climatic effects across the entire life cycle of the organism is crucial, because they can differ in a multitude of ways depending on the season, phases or stage of the life cycle. Although studies quantifying the effect of individual environmental factors on individual life-history events of individual population, like in this thesis, are very important in order to add to our understanding of the effects on a particular population, they do not provide a complete understanding of the species' response to climate change (Jenouvrier, 2013). To avoid erroneous predictions, it is vital to look at the bigger picture, in this case the responses of different populations throughout their entire life cycles.

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7. APPENDICES

7.1. R-scripts

```
#Questions 1 & 2, just change the variables in the code
setwd("C:/Users/petri/Dropbox/My PC (DESKTOP-LU5TS78)/Desktop/GRADU/R")
Question2<-read.csv("question2.csv", header=T, sep=",", stringsAsFactors = T,
fileEncoding="UTF-8-BOM")
#fileEncoding="UTF-8-BOM" removes the ï.. from the header
#installing necessary files
# Check if the packages are installed, if needed install them and load them:
if(!require(devtools)) install.packages("devtools") ; require(devtools)
if(!require(poptrend)) install_github("jknape/poptrend") ; require(poptrend)
if(!require(MuMIn)) install.packages("MuMIn") ; require(MuMIn)
if(!require(sjPlot)) install.packages("sjPlot") ; require(sjPlot)
if(!require(sjlabelled)) install.packages("sjlabelled") ; require(sjlabelled)
if(!require(sjmisc)) install.packages("sjmisc") ; require(sjmisc)
Question2
class(Question2$Year)
class(Question2$Fledg..Date)
class(Question2$N)
#Change class from integer to numeric
Question2$Year<-as.numeric(Question2$Year)
class(Question2$Year)
Question2$Fledg..Date<-as.numeric(Question2$Fledg..Date)
Question2$N<-as.numeric(Question2$N)
#Change the name of Fledging date
names(Question2)[names(Question2) == "Fledg..Date"]<- "Fledging"
# THRESHOLD MODELS:
#We will test different linear models,
#with a different trend before and after a threshold,
#and test which one seems to work best:
# AICc of the homogeneous model, where only one linear trend applies to all the data:
Question2$threshold <- 0
```

```
# This is the simple linear model fit, with normal ("gaussian") residuals:
f <- glm(N ~ Year*threshold, family=gaussian(link="identity"), data=Question2)
# We calculate the corrected Akaike Information Criterion (AICc) for this model:
MuMIn::AICc(f)
# we prepare and empty list to store the AICc values:
devprof<-vector()
# we test all years "y", from the earliest to the latest in the dataset.
for(y in min(Question2$Year):max(Question2$Year)){
  # we make two categories of years: "0" if they are before the threshold, "1" otherwise.
  Question2$threshold <- ifelse(Question2$Year < y, 0, 1)
  # we fit our model, with a different slope for each category ("before threshold" and "after threshold")
  f <- glm(N~Year*threshold, family=gaussian(link="identity"), data=Question2)
  # we collect the AICc for this model:
  k<-MuMIn::AICc(f)
  # we add it to our list of AICc:
  devprof<-rbind(devprof,k)
}
# We make a plot of AICc vs. year of the threshold. The lowers value is the "most economical" model (good fit, as simple as possible).
years <- min(Question2$Year):max(Question2$Year)
plot(devprof~years, xlab="Year", ylab="AICc", type='b')
#We will extract the year corresponding to the best possible threshold:
tippingpoint <- years[min(which(devprof==min(devprof)))]
print(paste("Threshold year:", as.character(tippingpoint)))
print(paste("AICc: ", as.character(round(min(devprof)))))
#We can now re-run that best model and look at it:
Question2$threshold <- ifelse(Question2$Year < tippingpoint, 0, 1) # we add that to our dataset
model <- glm(N~Year*threshold, family=gaussian(link="identity"), data=Question2)
MuMIn::AICc(model)
summary(model)
tab_model(model)
#We proceed to plot the predictions of the model, together with the real data:
```

```
# Plot the predictions:
predicted <- predict(model, newdata = Question2, se.fit=T)
plot(Question2$Year, predicted$fit, type='b')
xlab="Year", ylab="Model fit")
points(Question2$Year, Question2$N, col='red', type='b')
#Make a nice plot to present
Question2 %>%
  ggplot(aes(x=Year, y=N, group=2)) +
  geom_line(color="Red")+
  geom_point(color="Red") +
  geom_point(x=2015, y=4007, color="Blue", size=3) +
  scale_x_continuous(breaks = scales::pretty_breaks(n = 10)) +
  scale_y_continuous(breaks = scales::pretty_breaks(n = 10)) +
  geom_smooth(method=lm)

#Question 3
f <- glm(Fledging ~ N, family=gaussian(link="identity"), data=Fulldata)
summary(f)
tab_model(f)

#Question 4, just change the variables in the code
setwd("C:/Users/petri/Dropbox/My PC (DESKTOPLU5TS78)/Desktop/GRADU/Env")
env <- read.csv("Env.csv")
install.packages("ggplot2")
install.packages("reshape2")
library(ggplot2)
library(reshape2)
#plot all the env. variables to one picture
ggplot(env) +
  geom_line(aes(x=Year, y=SST), col="blue") +
  geom_line(aes(x=Year, y=SPG), col="green") +
  geom_line(aes(x=Year, y=PSU), col="red") +
  geom_line(aes(x=Year, y=wNAO), col="yellow")
```

```
menv <- melt(env, id="Year")
ggplot(menv, aes(x=Year, y=value)) +
  geom_line(aes(col=variable)) +
  facet_wrap(.~variable, scales="free_y", ncol = 1) +
  geom_vline(xintercept = c(1996, 2003))
Fulldata <- merge(Question2, env)
#GLM analysis
M <- glm(Fledging~SST, data=Fulldata, family="gaussian")
with(summary(M), 1 - deviance/null.deviance)
summary(M)
tab_model(M)
#plot the predictions
plot(Fulldata$Fledging~Fulldata$wNAO)
ggplot(Fulldata) +
  geom_line(aes(x=Year, y=scale(Fledging)), col="blue") +
  geom_line(aes(x=Year, y=scale(wNAO)), col="red") +
  ylab("wNAO")
#visualize significant results
Fulldata %>%
  ggplot(aes(x=N, y=wNAO, group=2)) +
  geom_line(color="Red") +
  scale_x_continuous(breaks = scales::pretty_breaks(n = 10)) +
  scale_y_continuous(breaks = scales::pretty_breaks(n = 10)) +
  geom_smooth(method=lm)
```

7.2. Table of annual mean values of data used

Year	Number of pufflings	Fledging date (julian)	PSU	wNAO	SPG	SST
1938	87	237		1.79	-2.83	9.517
1939	80	233		0.37	-1.62	9.250
1940	280	248		-2.86	-1.95	10.317
1941				-2.31	-0.27	9.483
1942				-0.55	0.41	10.467
1943				1.48	0.31	9.550
1944				0.61	-0.89	9.567
1945				1.64	1.04	9.933
1946				0.27	1.68	9.917
1947			35.21	-2.71	0.3	9.967
1948			34.96	1.34	-2.45	9.667
1949			34.95	1.87	-3.42	9.567
1950			34.98	1.4	-3.7	9.083
1951			34.87		-4.18	9.567
1952				0.83	-3.05	9.324
1953			35.01	0.18	-1.83	8.350
1954				0.13	0.51	9.483
1955	15	241		-2.52	-1.46	9.583
1956			35.06	-1.73	-0.09	9.417
1957	180	240	34.34	1.52	0.18	9.383
1958	60	230	35.18		-1.7	9.767
1959				-0.37	-0.36	9.648
1960			35.03	-1.54	-2.45	9.317
1961			35.25	1.8	-2.19	10.067
1962			35.13	-2.38	-3.34	9.517
1963	155	241	35.09	-3.6	-2.75	9.433
1964	74	252	34.82	-2.86	-1.78	9.217
1965	11	237	34.99	-2.88	-1.41	9.101
1966	13	238	35.22	-1.69	-0.28	9.218
1967				1.28	-0.83	9.314
1968			35.09		-1.7	9.088
1969	82	232		-4.89	-0.25	9.236
1970	81	239		-1.89	0.3	8.872
1971	501	233	34.98	-0.96	0.21	8.910
1972	850	237	34.01	0.34	0.37	9.392
1973	583	238	34.77	2.52	-1.78	9.173
1974	319	237	35.02	1.23	-1.81	8.891
1975	761	232	34.81	1.63	-2.03	9.354
1976	377	236	34.9	1.37	-1.5	8.653
1977	500	230	34.99		-1.5	9.137
1978	222	242	34.98	0.17	-0.57	9.074
1979	624	253	35		-0.65	9.179
1980	876	244	34.51	0.56	-0.69	8.361

1981	661	243	35.01	2.05	-0.84	9.385
1982	287	247	34.79	0.8	0.95	8.970
1983	61	251	34.94	3.42	-1.11	8.911
1984	287	246	34.86	1.6	-1.84	8.469
1985	982	229	34.97	-0.63	-0.98	9.047
1986	627	228	34.83	0.5	-1.16	9.092
1987	1164	234	34.96	-0.75	-2.56	9.134
1988	709	235	34.92	0.72	-1.56	9.199
1989	738	237	34.86	5.08	-1.17	9.059
1990	816	238	34.94	3.96	-2.12	8.747
1991	1602	242	34.79	1.03	-3.19	9.135
1992	1535	237	34.96	3.28	-2.51	9.441
1993	1595	244	34.77	2.67	-1.27	8.714
1994	985	240	34.84	3.03	-1.73	8.987
1995	761	226	35.07	3.96	-3.44	9.146
1996	1025	229	35.02	-3.78	-1.59	8.989
1997	820	246	34.97	-0.17	1.15	9.589
1998	531	226		0.72	1.61	9.225
1999	663	237	34.68	1.7	1.93	9.488
2000	770	235	35.06	2.8	1.4	8.944
2001	891	240	34.86	-1.9	1.33	9.077
2002	712	237	34.97	0.76	2.15	9.345
2003	1899	247	34.88	0.2	0.6	9.116
2004	1793	234	35.05	-0.07	1.14	10.005
2005	350	245	34.88	0.12	2.88	9.509
2006	135	255	35.14		3.87	9.209
2007	1333	253	34.98	2.79	3.38	9.199
2008	412	256	35.11	2.1	1.56	9.129
2009	525	258	35.09	-0.41	1.35	9.811
2010	11	248	34.63	-4.64	0.92	10.017
2011	34	268	34.67	-1.57	-1.18	9.744
2012	1848	255	34.91	3.17	-0.36	9.268
2013	23	258	34.84	-1.97	-0.75	9.297
2014	100	254	34.78	3.1	0.63	8.641
2015	4007	273	34.84	3.56	1.54	9.566
2016	3179	253	34.89	0.98	1.69	8.532
2017	4813	249	34.54	1.47	0.84	9.312
2018	4150	251	34.84	0.3	0.91	9.006