



# **Climate variability, plankton and seabirds: a discussion on trophic interactions in the North Atlantic**

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**Faculty of Life and Environmental Sciences  
University of Iceland  
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# Climate variability, plankton and seabirds: a discussion on trophic interactions in the North Atlantic

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10 ECTS report submitted in fulfillment of  
*LÍF038M, a "research project in biology for foreign students"*

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Reykjavik, May 2013

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# Abstract

Iceland is an important habitat for seabirds in the northern Atlantic, and because the effects of global climate change are manifesting to a greater extent at higher latitudes, it is necessary to understand how climate is affecting seabirds around Iceland. The effects of climate change can be exhibited through direct or indirect ecosystem effects, and the relative importance of each type of control is an essential aspect of understanding ecosystem functioning for management purposes. This paper synthesizes literature that deals with the effects of oceanographic and ecosystem features, such as sea surface temperature (SST) and lower trophic level characteristics that have the potential to influence high trophic level seabirds. The concept of bottom-up control has been suggested to explain ecosystem dynamics in several cases in the northern Atlantic. Therefore, effects of climate on lower trophic levels and trophic coupling to higher trophic levels should be well documented in systems where bottom-up control is plausible. Additionally, this paper addresses to what extent SST can explain Icelandic great cormorant (*Phalacrocorax carbo carbo*) and common eider (*Somateria mollissima*) population fluctuations in Breiðafjörður, Iceland. Neither analysis found significant models to explain population variation in either species, however, in both cases there were results that suggested SST may be positively related to success. This paper suggests that other potential mechanisms, such as extreme weather events and indirect effects through trophic interactions, should also be addressed in the context of the cormorant and eider populations of Iceland.



*Dedication*

*For the birds.*





# **Preface**

This project is the final 10 ECTS report for the course “Research project in biology for foreign students” (LÍF038M). These credits are to be applied towards the completion of a Master’s of Science degree through the Joint Nordic Master’s Programme in Marine Ecosystems and Climate, which is hosted in part by the University of Iceland.



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# 1 Background

The waters around Iceland provide some of the most important habitat for seabirds in the northeast Atlantic. Furthermore, it has been suggested that the marine ecosystems around Iceland are highly susceptible to climate change (Astthorson *et al.*, 2007). There has been a gradual increase in salinity and temperature since 1996 (Anonymous, 2005) and the increase in temperature has been attributed to the observed changes due to the North Atlantic Oscillation (NAO) (Anonymous, 2004), rather than to anthropogenic climate change. However, studies based on previous climate variability can be used to understand future responses to climate change. The NAO has been shown to be correlated to North Sea zooplankton, European sardine (*Sardina pilchardus*) and herring (*Clupea harengus*), salmon (*Salmo salar*), benthic foraminifera and the Southern Norway dipper (*Clinclus cinclus*) (Ottersen *et al.*, 2001). As a higher trophic level group seabirds are an integral part of ecosystem dynamics through their role as predators and also have the potential to be affected by oceanographic conditions and climate variation.

In a simplified view, there are two primary water masses around Iceland that originate in different places and are responsible for variations in water mass characteristics around Iceland (Fig. 1-1). The NAO affects the abundance and distribution of these water masses around Iceland. The Atlantic water mass from the south carries warm, saline water primarily along the west coast of Iceland, whereas the less saline and colder polar water, originating in the Arctic Ocean, is carried from the north. Therefore, the waters around Iceland are largely made up of a product of mixed Atlantic and Arctic waters (Astthorson *et al.*, 2007). Strong inflow of Atlantic water increases sea surface temperatures (SST) around Iceland and may also increase the advection of zooplankton into Icelandic waters. SST has been shown to be a proxy for phyto- and zooplankton growth (Richardson and Schoeman, 2004; Astthorson *et al.*, 2007). It has been shown that SST warming increases phytoplankton abundance in cooler places, but decreases production in warmer places (Richardson and Schoeman, 2004). It has also been shown that an increased temperature has positive effects on growth and increases development in Icelandic zooplankton (Astthorson *et al.*, 2007). Therefore, the oceanographic effects correlated with the North Atlantic Oscillation are important for the plankton abundance and distributions in Icelandic waters, which may be important in understanding the indirect effects on seabird success.



Figure 1-1. Surface currents around Iceland (from Astthorson *et al.*, 2007).

Certain aspects of seabird behavior and physiology make them susceptible to changes in climate and water mass characteristics; however, the effects may manifest as positive or negative responses within populations or species. Seabirds, a high trophic level group, have the potential to be affected indirectly through trophic relationships and directly by climate variation (Stoleson and Bessinger, 1999; Williams, 1996; Durant *et al.*, 2004). Examples of direct influences include temperature causing physiological constraints on a species or directly causing mortality to individuals of a species, while indirect influences consist of multiple steps of effect, such as those through multiple trophic levels. Previous work has stated that indirect effects are more likely to affect seabirds than direct effects (Durant *et al.*, 2004). Understanding how individual species are affected by the different factors that influence ecosystem dynamics is an essential part of conservation efforts, especially in terms of the relative importance of top-down and bottom-up indirect effects on high trophic level species.

## Objectives

This project aims to synthesize literature and review cases of the mechanisms that have the potential to influence seabird success, with a focus on North Atlantic ecosystems. The included literature survey will focus on relevant studies and theories about climate and trophic interactions propagating from the lower trophic levels to seabird success, and will also discuss potential direct effects of climate on seabird success. Therefore, this study contributes to the understanding of ecosystem dynamics that are necessary to make management decisions. Further, in light of a temperature increase in Breiðafjörður, Iceland over the past 30 years and a known increase in cormorant (*Phalacrocorax carbo carbo*) populations, this paper will present a brief analysis of cormorant population increase and sea surface temperature in Breiðafjörður. Eider (*Somateria mollissima*) populations have also recently exhibited anomalous population characteristics. In response to these observations, this study will also analyze eider populations and SST to examine if irregularities occurring in eider populations can be explained to any extent by SST







## **2 Indirect effects of climate variation and plankton on seabird success**

Several studies provide support for the concept of bottom-up control regulating higher trophic levels (Frederiksen *et al.*, 2006; Grémillet and Boulinier, 2009; Aebischer *et al.*, 1990, Jenouvrier *et al.* 2003; Frederiksen *et al.* 2004; Sandvik *et al.*, 2005), where bottom-up control can be viewed as a positive relationship between predator and prey populations. This section will explore the previous studies on bottom-up effects and trophic couplings to better understand potential influences on seabird success. This includes addressing the physical factors, such as sea surface temperature, that may affect both phyto- and zooplankton populations around Iceland, and subsequently seabird success. It is also necessary to note that other forms of trophic coupling such as top down-control and wasp-waist control are also able to act on ecosystem dynamics simultaneously (Cury *et al.*, 2000; Fauchald *et al.*, 2011), however these patterns of ecosystem control will not be discussed in this project. Indirect effects are important to consider because the consequences of such effects fall outside of normal seabird conservation efforts. For example, prominent seabird conservation actions include creating marine protected areas, removing invasive species and reducing by-catch. However, indirect effects of climate change on food resources are not manageable with such methods (Croxall *et al.*, 2012).

### **2.1 Weather and SST as proxies for seabird success**

One of the earliest studies to link relationships between weather and prey availability to reproductive success in North Atlantic seabirds was Aebischer *et al.*'s (1990) study on four trophic levels and weather in the North Sea between 1955 and 1987. This study revealed that westerly weather, phytoplankton, zooplankton, herring and black-legged kittiwakes (*Rissa tridactyla*) all show the same pattern over time, declining at same rate until ~1980 and then showing a marked recovery. Although this study appeared to show strong correlations across trophic levels, this study also discussed the concern of ascribing a causal relationship to these parallel trends because, for example, weather could be affecting each of the trophic levels directly rather than bottom-up processes controlling the entire system. This is an important concern to keep in mind when studying trophic interactions, and causal relationships should only be suggested if there is ecological reasoning to support the observed correlations. However, regardless of the specific mechanisms affecting each trophic level, it can be taken from this study that weather affected all trophic levels, either directly or indirectly. In regards to kittiwakes specifically, the weather explained only 47% of variation in timing of breeding, and because food availability is also a known determinant of bird breeding success, it can be expected that both weather and prey influenced kittiwake laying date, clutch size and chick success.

Combined with the concern about global climate change, Aebischer *et al.*'s study led to many new studies with a directed focus on understanding the indirect effects of climate

change on seabirds. There is currently a wide range of available literature, with many studies discussing the effects of climate on seabirds, through climate's effects on lower and mid-trophic level species. The results presented in the literature vary and demonstrate that there may not be consistent trends due to the uniqueness of each species life history traits, feeding behavior, physiological constraints and species distributions. For example, Lauria *et al.* (2012) reviewed the influence of climate change and trophic coupling across four trophic levels in the Celtic Sea and found trends that do not agree with the concepts of bottom-up control. Although this study found differing trends from Aebischer *et al.* (1990) the authors agreed with prior studies (Frederiksen *et al.*, 2007; McGinty *et al.*, 2011), which reported that the strength of bottom-up control can vary regionally. Therefore, long-term studies examining multiple trophic levels over the same spatial scale are valuable for uncovering regional ecosystem responses to climatic variation (Aebischer *et al.*, 1990; Frederiksen *et al.*, 2006; Lauria *et al.*, 2012), and less comprehensive studies also show important linkages between climate and trophic levels (Weimerskirch *et al.*, 2001; Österblom *et al.*, 2006; Arnott and Ruxton, 2002; Astthorson and Gislason, 1998).

In the northeast Atlantic, Durant *et al.* (2003) found that SST indirectly affected Atlantic puffin (*Fratercula arctica*) fledging success through its effects on plankton, such that a higher SST in the Norwegian coastal current benefited the puffin breeding in Røst, Norway. Further, both the quality and quantity of herring were related to puffin fledging success (Durant *et al.* 2003). In regards to SST and the direction of influence on seabird success, this result contradicts the direction of SST influence that is presented different regional studies. This study proposed a hypothetical chain of events that would indirectly influence puffin success, in which the water movement of the Norwegian current influences SST, which directly affects plankton abundance, and ultimately influences the success of young herring. Based on this causal sequence, in colder years, puffins experienced reduced food availability during chick rearing in June-August, resulting in a decreased fledging success. However, the relationships are likely more complicated, and the authors suggest that the northward drift of larval or juvenile herring may also have had a strong effect on puffin success. Therefore, in a subsequent study, by including the timing of the arrival of the herring that drift north, the model was improved; 11% of puffin breeding success was explained by the timing of the arrival of herring (Durant *et al.* 2005).

Frederiksen *et al.* (2006) linked plankton dynamics to seabird success and suggested that because plankton populations are affected by climate, seabirds are indirectly affected by climate. Specifically, this study showed that over a three year period, there was a positive association between phyto- and zooplankton abundance and sand eel (*Ammodytes marinus*) growth, and a further increase in seabird breeding productivity from previous years (2006). This study tested whether bottom up or top-down effects control lesser sandeel populations, and whether seabirds are linked to overall sandeel abundance or individual fish size. The biomass of larval sandeel was linked to plankton, indicating the influences of bottom-up control, and both the biomass and individual sandeel size were linked to bird success. Ultimately, this study indicated that changes in plankton communities caused by climate variation could affect top predators through the dynamics of a mid-trophic level fish. However, the study found patterns that cannot be explained by bottom-up control, for example failing recruitment to sandeel stocks and low seabird breeding in 2004 were not explained by low sandeel biomass in 2003, and therefore the study does not argue that top-down effects play no role. This study also supported the idea that a species that feeds on many prey items would be more affected by general biomass of a prey species, whereas a

species specialized in one prey type would be more affected by the quality of that prey type.

In less comprehensive studies that do not address all trophic levels in a system, sea surface temperature (SST) has been shown to be a proxy for seabird success in many species from several marine systems around the globe. In the California current system, a long-term increase in temperature has been linked with a 40% decline in pelagic seabird abundance (Veit *et al.*, 1996). In a different global system, Weimerskirch *et al.*, (2001) present results on the yellow-nosed albatross (*Diomedea chlororhynchos*) in the Indian Ocean that indicate cold years produce adults with better body condition and larger meals brought to chicks, while during warmer years there were lower provisioning rates, lower adult mass, and lighter chicks at fledging. Both of these studies, in California and the Indian Ocean, demonstrate that an increase in SST is not directly affecting seabird success, but is affecting lower trophic levels that subsequently affect seabirds.

Indirect effects of climate on important seabird prey species have been shown in additional cases in north Atlantic systems, and may therefore be impacting seabird populations. In the North Sea, warm temperatures were correlated with poorer than average recruitment of sandeels, an important prey species for many seabirds (Arnott and Ruxton, 2002). The study suggested that sandeels are already at the southern range for their species in the North Sea, so an increase in temperature pushes them outside of their natural temperature tolerance. In addition, the results of this study showed a positive association between recruitment and *Calanus* spp. copepod (Stage V and VI) abundance around the time of sandeel larval hatching, suggesting that the availability of *Calanus* as a prey species is very important for young sandeel survival. Stage V and VI *Calanus* are probably too big to be consumed by sandeel larvae, however their abundances provide an estimate to the abundances of *Calanus* nauplii. The findings in this study demonstrated a complex system of climate affecting sandeel abundances indirectly and directly.

It is also important to elucidate that complex interactions can exist, such that they are only uncovered through detailed analysis of specific inter-species interactions. For example, Österblom *et al.*, (2006) described the common guillemot's (*Uria aalge*) response to changes in the zooplankton-feeding sprat (*Sprattus sprattus*). The main predator of sprat is cod (*Gadus morhua*), and as cod populations fluctuated, sprat populations responded to the released predation pressure. With an increase in sprat stock abundance, a decrease in energy content (weight) per sprat was found and as a result, there was a subsequent decrease in chick body mass at fledging. As sprat stock later diminished and the energy content per individual sprat increased, chick fledging body mass recovered. This example demonstrates that a simple increase in prey abundance may not be a justifiable explanation for increase in seabird success, and again indicates the complexity of interactions across several marine trophic levels.

## **2.2 Plankton dynamics affect higher trophic levels**

In a simplified situation, temperature and climate oscillations affect phytoplankton growth and distribution (Menge, *et al.*, 2009; Beaugrand *et al.*, 2000) and changes in plankton dynamics propagate up the food web and affect higher trophic levels (Richardson and

Schoeman 2004; Österblom *et al.*, 2006). In addition to the studies presented above that link multiple trophic levels to seabird success (Aebischer *et al.*, 1990; Frederiksen *et al.*, 2006), the following studies have linked plankton to success in other higher trophic levels. Beaugrand *et al.* (2003) suggest that rising temperatures in the North Sea since the mid-1980s has caused a decrease in the survival of young cod through bottom-up control by changing the plankton dynamics. Additionally, Ware and Thomson (2005) found that fish production in the continental margin of northwest North America is controlled by phytoplankton, through zooplankton to resident fish populations.

Beyond the effects of the abundance of phytoplankton on seabird success, it has been demonstrated in several species that the timing of a peak in phytoplankton can have important implications for seabird success. Scott *et al.* (2006) found that black-legged kittiwake and common guillemot breeding success was linked to the timing of the phytoplankton bloom; the effects of which propagated up the food web to influence seabird prey and seabird success. In high latitude Atlantic marine environments, the onset of the temporally pulsed spring-bloom is a critical seasonal event that has vast ecological consequences. Therefore, addressing seabird prey in the context of the unique phytoplankton bloom system that characterizes the northern Atlantic is important. A strong spring peak in phytoplankton characterizes the high-latitude spring bloom system, the mechanisms of which were described by Svedrup's critical-depth model (1953). The model described that a spring yearly peak in phytoplankton biomass occurs when the light and nutrients conditions are sufficient for photosynthesis and the water column has stabilized into stratified layers; the mixed layer must be shallower than the depth at which net primary production equals net respiration. The result is a peak in phytoplankton biomass, which declines once the nutrients have been depleted. Natural yearly variation in the timing of plankton production exists, and the peak in the north Atlantic ecosystem can vary year to year by as much as six weeks (Cushing, 1990).

Based on the understanding of the spring-bloom system the temporal match-mismatch hypothesis was developed, which describes that the timing of the peak of a consumer's food must be temporally matched by its life-history stages, such as the production of offspring (Cushing, 1990). The match-mismatch hypothesis is plausible in the northern high latitude spring-bloom system due to the transitory timing of phytoplankton blooms. Durant *et al.* (2005) expanded the match-mismatch hypothesis to include the abundance of food, not only the timing of the peaks, as an important factor. The match-mismatch hypothesis has been demonstrated by several seabird studies (Burthe *et al.*, 2012; Durant *et al.*, 2007; Watanuki *et al.*, 2009), and has also been applied to spatial, rather than temporal scales (Gremillet *et al.*, 2008). In the Benguela upwelling zone, Gremillet *et al.* (2008) showed that there was a strong spatial mismatch between copepods and pelagic fish, and also between seabirds and the pelagic fish that they feed on. Both the temporal onset of the phytoplankton blooms in Iceland, and the abundance of those blooms could be indirectly contributing to the success of seabirds in the area.

Sigurðardóttir (2012) reiterates a point made in Thordardottir's (1994) paper, that the coastal waters around Iceland may be important for copepods, a primary zooplankton type in Iceland, due to the high annual mean phytoplankton production. Neritic species of zooplankton, or those that inhabit coastal waters, are more common in Iceland; the abundance of zooplankton in coastal waters was found to be approximately four times higher than offshore Atlantic water (Gislason and Astthorson, 1995). In a study on zooplankton in Breiðafjörður, a significant positive correlation between the abundance of

total zooplankton and chlorophyll *a*, and between zooplankton and temperature one and two weeks prior to sampling were shown, demonstrating a link between trophic levels (Sigurðardóttir, 2012). This study also showed that in Breiðafjörður there were differences in zooplankton abundances and compositions between years and the timing of peaks in zooplankton abundances differed between years, which may have implications for higher trophic levels, such as seabirds, due to the sensitive timing of life history stages.

Climate has been shown to affect zooplankton abundances and fish success in waters north of Iceland (Astthorson and Gislason, 1998). In this study, Astthorson and Gislason (1998) show that zooplankton abundance was higher than average during warmer years and the mean weights of capelin were higher during warmer years. There was not a strong correlation between zooplankton and capelin weights-at-age or capelin biomass, although the data suggested that to some degree the trends in capelin followed those of zooplankton. The relationship between environmental conditions and capelin biomass here was not entirely clear, but this study does suggest a degree of linkage between this pelagic fish stock and oceanographic conditions. The positive correlation between temperature and capelin success in the waters north of Iceland did not agree with the trend found by Arnott and Ruxton (2002), in which warm temperatures were correlated with poorer than average sandeel recruitment in the North Sea. The differences in response by mid-trophic level fishes to temperatures in these two systems could be explained by a combination of food abundance and physical constraints acting on sandeels. As mentioned in Arnott and Ruxton's study, capelin in the North Sea are at the most southern limit of their distribution and success is thus constrained by oceanographic conditions. Whereas capelin in the waters north of Iceland are not experiencing range limitations and may therefore be influenced more by indirect ecosystem effects, rather than oceanographic conditions.

## 2.3 Conclusions

The link between seabirds and lower trophic levels is difficult to generalize because different species feed at different trophic levels, and each level has the potential to be influenced directly by climate or indirectly through various forms of ecosystem control. Because seabirds exist within high trophic levels, they can be affected by climate in several interconnected ways. Durant *et al.* (2004) present this idea in a clear way: a warming temperature may affect a seabird species and its prey source in the same way; however the prey of the seabird's prey may be affected by a warming temperature in a different way. Based upon reviewing relevant literature, it appears that interactions are complicated and regional and specific studies are needed to understand local mechanisms.





### 3 Direct effects of climate variation on seabird success

Seabirds also face direct effects of climate change, such as impacts on energetics, reproduction and direct mortality from weather conditions (Stenseth *et al.*, 2004). Effects on metabolic processes during important life stages, such as reproduction or molt, may have substantial effects (Durant *et al.*, 2004). As endotherms, seabirds must maintain their core body temperatures by using either stored energy or ingested energy. There is a range of temperatures in which the metabolism is not affected by ambient temperature, which is known as the thermoneutral zone (TNZ) (Schmidt-Nielssen, 1997), and when the ambient temperature extends outside of the TNZ the bird must incur extra energy costs (Durant *et al.*, 2004). During the breeding season the costs of the thermal stress on eggs and chicks are also placed on the parents (Durant *et al.*, 2004).

Further direct stresses on reproduction include the maintenance of egg temperature, because if it drops below a certain temperature, the development of the embryo may stop (Stoleson and Bessinger, 1999). Therefore, in colder temperatures an increased amount of heat transfer from parent offspring may increase the costs of incubation. Also, in a colder ambient temperature, the cost of re-warming the egg after foraging trips is higher (Williams, 1996). Although it is possible that embryo development may stop in colder temperatures, adult individual mortality due to temperature is not a commonly known cause of death in seabirds (Durant *et al.*, 2004). Based on these physiological constraints in colder climates, it can be expected that an increase in temperature may have beneficial consequences; although, if temperatures increase too much and if the ambient temperature extends above the TNZ of seabird species in the northern Atlantic, there may be associated energy costs that decrease fitness.

Another less obvious direct effect of climate change that may be beneficial for seabirds is the opening of nesting sites due to the melting of snow and ice. For example, in Kongsfjorden, Svalbard the opening of sea ice earlier in the season, as opposed to later, allowed for higher number of nesting sites and larger clutch sizes in the common eider (*Somateria mollissima*) (Mehlum, 2012). In the northern Atlantic, where increase in temperature due to climate change has been known to be greater than in other regions (Pachauri and Reisinger, 2007), direct effects of climate change may play a role in determining seabird success. However, due the assorted potential mechanisms and the power of their effects, the strength of indirect effects may have more powerful consequences on seabird fitness in the North Atlantic. This agrees with other published work that says indirect effects likely have greater impacts on seabirds than direct effects (Durant *et al.*, 2004).



## 4 Great cormorant (*Phalacrocorax carbo*) populations in Iceland

### 4.1 Introduction

There has been concern about a national decline in seabird populations in Iceland (Garðarsson, 2006a; Bornaechea and Garðarsson, 2006; Garðarsson, 2006b; Hallgrímsson, 2011) and this decline has been attributed to a decline in sandeel stocks (*Ammodytes* spp.). However, parallel to this decline, the number of great cormorants, (hereafter ‘cormorants’) has greatly increased over the past several decades throughout Europe, including in Iceland (Bregnballe *et al.*, 2011). In Western Europe the increase has been extreme, having increased from several thousand to 150,000 breeding pairs over the past centuries (Bregnballe *et al.* 2003). Previous studies have concluded that these increases in populations are in part due to the improved protection status in the European Union and a decrease in environmental contaminants (Bondewijn and Dirksen, 1995, Van Eerden and Gregersen, 1995), and as a result of the population increase, the breeding population is expanding northward (Lehikoinen, 2006). Lehikoinen (2006) also discusses the idea that in places such as the Baltic Sea, more suitable habitats for cormorants are arising as a result of eutrophication increasing the abundance of small fish prey species.

These rapid expansions of cormorant populations in specific locations have been observed and documented by several local studies. For example in the Finnish archipelago, the cormorants first started breeding in 1996 and within nine years the population increased from 10 pairs to 2,930 pairs in 2004 (Lehikoinen, 2006). In Greenland, cormorant populations have been increasing and White *et al.* (2011) have shown that the rates of change are correlated with increasing SST, but also likely because of the improved protection. This study discusses that the increase in temperature could be affecting cormorants directly or indirectly due to the effects of prey distribution. Because cormorants have a partially wettable plumage (Grémillet *et al.*, 2005) it is plausible that they are poorly insulated and would be limited by latitude, but with an increase in SST they would be more able to survive in typically cold northern waters. A recent expansion of cormorant population size and spatial distribution of the sub species *Phalacrocorax carbo carbo* has also been taking place in Iceland (Garðarson, 2008)(Fig 4-1), although the cause of this expansion has not yet been confirmed.

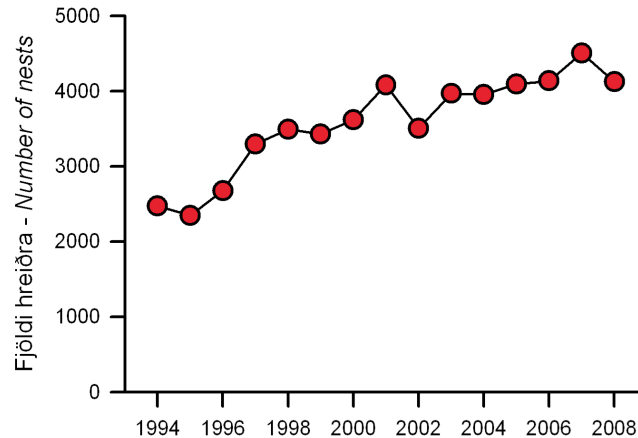


Figure 4-1. Documented increase in number of cormorant nests from 1994–2008 in Iceland (from Garðarsson, 2008).

In Iceland, breeding colonies diminished to only Breiðafjörður and Faxaflói bays, but used to also breed in northern Iceland and other areas (Hilmarsson, 2011). However, after a marked crash in population size in 1992, the total number of great cormorants breeding in Iceland has been increasing in Breiðafjörður and Faxaflói bays. In 2008 the total number of breeding pairs was 4,127 (Garðarsson, 2008), and the number continued to increase until 2010 and has since plateaued. The expansion of breeding sites in Iceland and the increase in population size show detailed patterns; for example, the increase in colony size is only in certain areas while some colonies are declining in size (Garðarsson, 2008). Concurrently in Breiðafjörður, recent average SST has been rising. A previous study published in 2004 reports that SST had steadily increased since 1995 based on values calculated from the relationship between SST from Flatey in Breiðafjörður (May–August) and surface temperatures in Stykkisholmur (Jonasson, 2004). As mentioned previously, this increase in temperature has the potential to impact seabirds directly or indirectly through lower trophic levels, and climate change has been documented to cause negative impacts on some Arctic species, while creating a boon to others (as described in White *et al.*, 2011). Oceanographic conditions during the time of seabird breeding, which are largely susceptible to climate change, have the potential to influence the availability of prey and subsequently, seabird breeding success (Scott *et al.*, 2006).

Based on White *et al.*'s (2011) study on cormorants in Greenland, it would be expected that the increase in cormorant populations in Iceland is similarly directly influenced by an increase in SST. However, it is possible that consequences of the increase in temperature could manifest as direct effects on physiology or indirect effects through lower trophic levels in Iceland. This section of the paper will begin to explore trends in cormorant populations and SST in Breiðafjörður in order to discuss the potential direct and indirect effects that may be responsible for the increase in cormorant populations. However, a thorough analysis of mechanisms influencing cormorant populations will not be presented in this paper, it is rather an exploration and discussion of possible influencers.

## 4.2 Methods

### 4.2.1 Study species

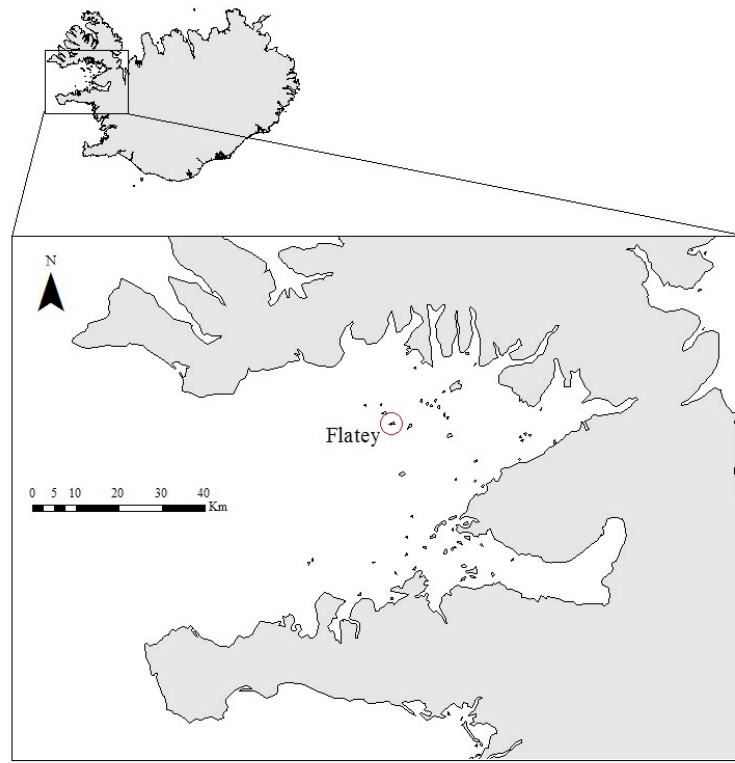
The great cormorant is a visually foraging pursuit-diving fish eater that can dive for many bottom-dwelling fish and crustaceans. All around Iceland bull-rout (*Myoxocephalus scorpius*) is the main food source for cormorants in all seasons, but other common prey species include lumpsucker (*Cyclopterus lumpus*), flatfishes (Pleuronectiformes) including saithe (*Pollachius virens*), butterfish (*Pholis gunnellus*), and cod (Lilliendahl and Solmundsson, 2006). Sandeels and char (*Salvelinus alpinus*) were rare, but were also present in cormorant diets (Lilliendahl and Solmundsson, 2006). Cormorants can be classified as a generalist feeder because they rely on a range of prey types (Cosolo *et al.*, 2010). Cormorants also feed primarily in waters shallower than 20 m (Garðarsson, 2008). Lehikoinen *et al.* (2011) demonstrated their foraging flexibility with the cormorants in Finland who shifted their diet over an eight-year period (2002–2010). This diet switching could be due to the relative availability of food; because cormorants are generalists, variations in the relative abundances of available prey species may not have a large effect of their success, whereas species with narrow ranges of acceptable prey may be more affected (Lehikoinen *et al.*, 2011). A study from the Minho River in northwest Iberia demonstrated that great cormorants do not have to move with a preferred prey resource; rather they have the ability to adapt to changing resource conditions (Dias *et al.*, 2012). Dias *et al.* (2012) found that most of the variation in great cormorant diet in this region was attributed to variation in river discharge.

It has also been stated that cormorants have the highest foraging yield of any marine species (Grémillet *et al.*, 2004), and may therefore be of interest to fisheries and marine managers because of their potential to affect fish stocks (see Lilliendahl and Solmundsson, 2006 and references therein). There are currently conflicting views about the potential danger of cormorant populations to fish stocks; it has been demonstrated that cormorants do not affect fish stocks (Lehikoinen *et al.*, 2011), while in other cases it has been put forth that cormorant populations should be managed because of their harm to fish stocks (Steffens, 2010). In contrast to the possible negative effects to human interests, cormorants have been shown to be useful indicators of ichthyofauna (Dias *et al.*, 2012).

### 4.2.2 Study site

Breiðafjörður is located in the West of Iceland and is a wide and deep fjord (approximately 50 x 150km)(Fig. 4-2) with a bottom depth that reaches 200m, although large areas are also only 20m in depth (Sigurðardóttir, 2012). To the north of the bay is the West Fjords Peninsula and to the south of the bay is the Snæfellsnes Peninsula. The bay hosts extensive intertidal areas with over 3,000 skerries and islands, one role of which is to host seabirds during the breeding season. Breiðafjörður is an important habitat for a range of species and has extensive algal ‘forests’ that help support the ecosystem (Petersen *et al.*, 1997). The health of Breiðafjörður is also important for the Icelandic economy because it is a fishing ground for the lumpsucker, Iceland scallop (*Chlamys islandica*), Atlantic cod, pink shrimp (*Pandulus borealis*) and others (Petersen *et al.*, 1997; Jonasson *et al.*, 2006). The area is a “conservation area”, in which the goals are to conserve ecological and cultural features while allowing sustainable use of the area as a fishing ground, tourism location, and source

for algae harvesting (Petersen *et al.*, 1997). More recently, Breiðafjörður was suggested to be designated a Ramsar Convention site and a UNESCO World Heritage site (Stefánsson *et al.*, 2008).



*Figure 4-2. Map of Breiðafjörður, Iceland with the location of SST measurements on Flatey marked.*

### **4.2.3 Data sources**

Cormorant nests were counted every year from 1994–2012 on one surveying day between the dates of May 9-31, when most nests contain eggs or small young (Garðarsson, 2008). Spatial boundaries for groups of colonies were created to make 12 areas and the total number of nests in each area was counted during aerial surveys conducted by Arnþór Garðarsson (2008). For the sake of this study only total nest numbers in the entire bay were used because SST data is only from one central site in the bay, and it would therefore not be applicable to divide the cormorant data into smaller spatial groups.

Data for SST was collected by a monitoring station near Flatey, an island in the center of the bay, in Breiðafjörður, Iceland ( $65^{\circ}22'N$   $22^{\circ}55'W$ )(Fig 4-2). Temperature values were recorded every other day between the years 1991-2011. The raw data was provided by Erla Björk Örnólfsdóttir, formerly at Vör Marine Research Center at Breiðafjörður, however, the data was originally collected by the Marine Research Institute in Iceland (Hafrannsóknastofnun). Data from 2012 have been removed from all analyses because the raw values remained between 0-2 C° from January-May when all other years showed a marked increase in temperature.

#### **4.2.4 Statistical analysis**

Monthly and seasonal averages of SST were used for statistical analysis. Linear regressions were used to address if monthly or seasonal temperatures explained any of the variation in cormorant nest numbers over the examined years. If there appeared to be outliers, they were removed and the analysis was completed again. Monthly average SST values were calculated by taking the average of all sampling days within that month. Temperatures were recorded every other day, as a result months with 30 days had 15 recorded temperatures and months with 31 days had 16 recorded temperatures. An extra sampling day occurred in February in order to maintain 15 sampling days. Only winter and spring seasonal temperatures were used for seasonal analysis, and were calculated from the original values that were recorded every second day. Winter months were classified as December-March and spring months were classified as April-May. Months with more than one sampling day missing and seasons with more than one day per month missing were removed from analysis because averages became skewed and unrepresentative of the true monthly SST values.

In order to determine which months of the year exhibit the most extreme temperatures and may therefore be causing limitations or boons for seabird success, analyses were performed to better understand the patterns of SST throughout the year. A linear ANOVA model was first used to confirm a significant difference between average monthly temperatures. A post-hoc Tukey's HSD test was then used to determine which months were significantly different from each other. Further, due to the large number of comparisons made by the Tukey's HSD test, a Bonferroni adjustment on the confidence interval was used in order to ensure accurate rejections of null hypotheses.

### **4.3 Results**

Of the linear regressions used to address if monthly or seasonal temperatures explained any of the variation in cormorant nest numbers, the only significant model that showed a substantial relationship was between February SST and the total cormorant nest number. This model explained 37.5% of the variation in cormorant nest numbers over the study period ( $p=0.0091$ )(Fig. 4-3). The model for the month of March was also significant, but showed no linear relationship ( $p=0.0489$ , adjusted  $R^2=0.183$ ). Similarly, the model for the spring temperature was significant and showed no linear relationship when all data points were included ( $p=0.0484$ ,  $R^2=0.184$ )(Fig. 4-4). However, in the model for spring temperature there were possible outliers, one extremely low cormorant nest number and one notably high value. When these values were removed from the analysis the model was highly insignificant ( $p=0.374$ ).

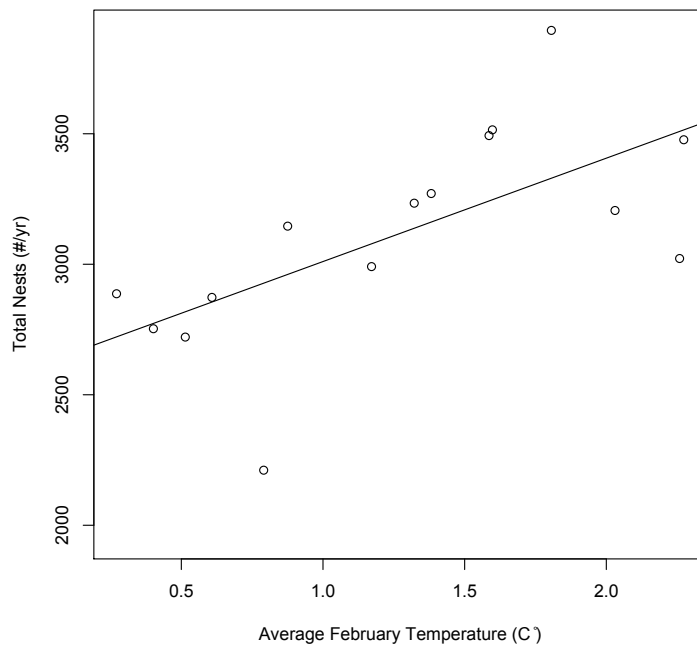


Figure 4-3. Relationship between average SST in February and the total number of cormorant nests in Breiðafjörður. Each point represents a year between 1996-2011, excluding 1998 ( $p=0.0091$ , adjusted  $R^2=0.375$ ).

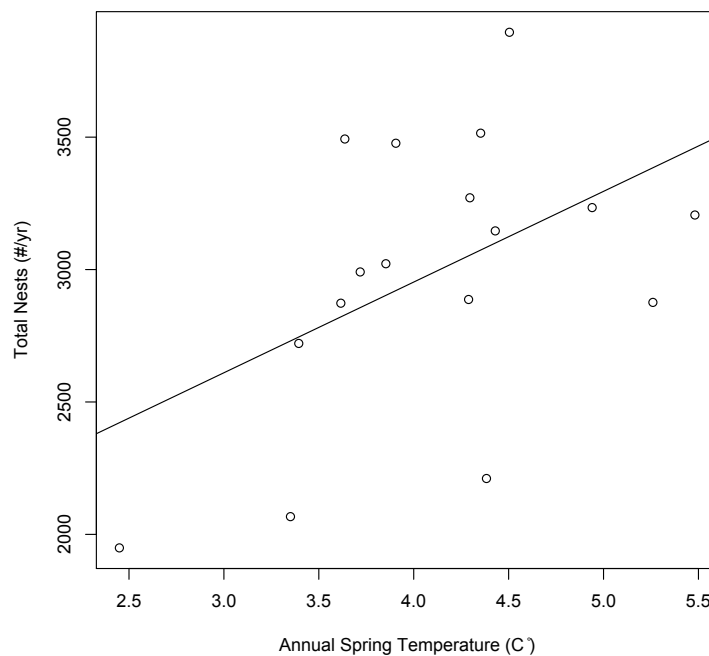
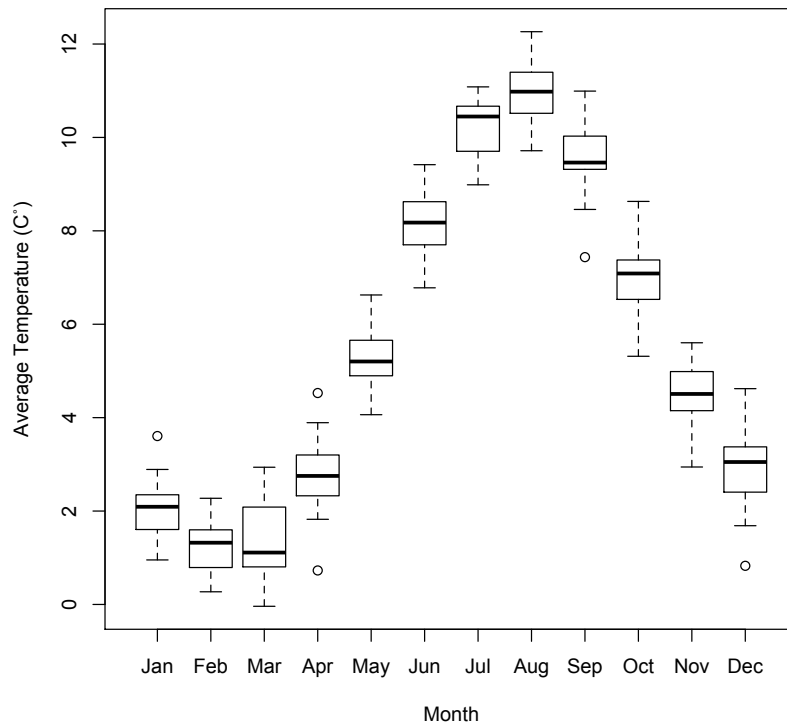


Figure 4-4. Relationship between average spring SST and the total number of cormorant nests in Breiðafjörður. Each point represents a year between 1994-2011, excluding 1997 ( $p=0.0484$ , adjusted  $R^2=0.184$ ).



There is a wide range of monthly average temperatures throughout the year in Breiðafjörður (Fig. 4-5). The coldest months of the year are February and March and the warmest are July and August. February and March were not significantly different from each other ( $p=0.99$ ) but were significantly colder than all months of the year ( $p < 0.001$  for all comparisons), excluding January (February:  $p=0.074$ , March:  $p=0.347$ ).



*Figure 4-5. Average monthly SST values for the years 1994-2011 from Flatey, Breiðafjörður.*

## 4.4 Discussion

The correlation between increase in SST and increase in cormorant numbers in February could be a manifestation of effects of climate, however in this case a causal relationship cannot be ascribed. Therefore, it is not possible with this limited analysis to conclude that SST is contributing to the increase in cormorant populations in Iceland. February, however, is one of the two coldest months of the year in Breiðafjörður, and may therefore be responsible for limiting the population increase. Cormorants begin their pre-breeding activity in February, when they attain their breeding plumage (Jón Einar Jónsson, personal communication, May 20, 2013), and the temperatures in February could therefore be influencing breeding behavior and success. Perhaps, due to higher thermoregulatory costs during colder periods, the energy allocated to breeding efforts is reduced.

As previously mentioned, this analysis was only intended to briefly explore mechanisms

for the increase in cormorant populations around Iceland. It is already documented that both temperature and cormorant populations are increasing in Breiðafjörður, therefore the method of statistical analysis applied in this study may have produced misleading results. A correlation between the variables suggests causation in a case like this, however it is important to recognize that many factors could be increasing cormorant populations independently and separately from an increase in local SST. A more advanced method for statistical analysis that tests for true causality should be applied to understand if SST is influencing the cormorant populations.

In the context of direct and indirect effects, cormorant population increase in Iceland may be a result of both factors. A direct effect from the increasing SST in Breiðafjörður may allow for greater success in cormorants because they are not as limited by their wettable plumage, as was shown to be the case in Greenland (White *et al.*, 2011). Because of their wettable plumage they are susceptible to heat loss when diving in cold waters. Therefore, increasing populations of cormorants in Iceland may be related to the reduced thermoregulatory costs in warmer years, when ambient water temperatures are closer to their TNZ. Additionally, around Iceland there must be sufficient prey resources to match the energetic requirements of foraging in colder waters. Enstipp *et al.* (2007) report that in high prey density, great cormorants can reach their required foraging more easily. In Iceland, there may be both reduced energetic costs from warming waters, and sufficient prey to support the energetic needs of cormorants, thus increasing their populations. It is also interesting to note that around Iceland, the abundance of the cormorant's main prey species, bull-rout, appeared to have been decreasing between 1994-2005 (Kasper, 2010), which suggested that it is not prey dynamics of bull-rout that are controlling the cormorant population. The apparent decrease in bull-rout could be only a result of bull-rout moving from the area of survey effort rather than a true decrease in their abundance occurring. The prey dynamics of alternative prey species, beyond bull-rout, could also be affecting cormorant populations. Long-term studies across several trophic levels must be done in order to address this, as seen in other studies addressing many trophic levels (Aebischer *et al.*, 1990; Frederiksen *et al.*, 2006). With a more complete data set including climate conditions, phyto- and zooplankton, and mid-trophic level seabird prey species, potential indirect effects through bottom-up control could be explored to understand the relative influence of indirect versus direct effects on cormorant success.

Additional mechanisms for the cormorant increase in Iceland may also be occurring. For example, cormorants may be more vulnerable to extreme weather events, rather than changes in mean climate characteristics (Frederiksen *et al.*, 2008). In seabirds, mortality from climate is rare but when climate is the cause of direct mortality, it is usually through starvation due to the absence of prey or the inaccessibility of prey due to bad weather (Durant *et al.*, 2004). In the Isle of May, Scotland, large-scale mortality events in the European Shag (*Phalacrocorax aristotelis*) have been linked to strong winter gales (Frederiksen *et al.*, 2008). In Danish cormorants (*Phalacrocorax carbo sinensis*) it has been shown that severe winters increase mortality more strongly when populations are high, likely because harsh conditions reduce high quality habitat (Frederiksen and Bregnballe, 2000). Perhaps, the rate of extreme weather events is more responsible for controlling cormorant populations in Iceland than mean climate characteristics. Therefore, further investigations should be done to understand if there is a reduced occurrence of severe weather events in Iceland over the recent years, which may be releasing the cormorant population from climate induced mortality.

In general, further population monitoring should be done to understand other possible mechanisms causing the increase in cormorants and to monitor the ecosystem effects from an increasing population. A full analysis of all trophic levels in Breiðafjörður would be useful in understanding the cormorant increase, but would also inform about other interactions in the bay and the potential effects on many high trophic level species. Information on the mechanisms controlling high trophic levels species is essential for the conservation and preservation of high trophic levels species, which are important to ecosystem functioning.



# 5 Common eider (*Somateria mollissima*) and sea surface temperature in Breiðafjörður, Iceland

## 5.1 Introduction

Like all seabirds, common eider (*Somateria mollissima*, hereafter ‘eider’) populations have the potential to be influenced positively or negatively by several factors in the marine environment. Weather and SST, for example, have the potential to be directly and indirectly influencing eider success through physiological constraints. For example, colder winters may require female eiders to use fat reserves intended for the breeding season (Systad *et al.*, 2000), and it has been shown that eider female body condition prior to breeding is positively related to clutch size (Erikstad *et al.*, 1993) and egg size (Hanssen *et al.*, 2002), and negatively related to cases of brood abandonment (Bustnes and Erikstad, 1991). In colder years, females may also skip breeding in order to maximize reproductive output over their entire lifespan (Coulson, 1984). In a study on Icelandic eiders, only a minor effect of weather on eider nest numbers was found, but rare years of severe weather were correlated with lower breeding numbers (Jónsson *et al.*, in press). Descamps *et al.* (2010) shows that winter NAO values are linked to pre-laying body mass in two arctic populations, however, the mechanisms linking the climate oscillation to eider mass differed between population. In the Canadian Arctic the pre-laying body mass was related to the NAO conditions in the same year, which implied a direct effect of climate, while in Grindøya, Norway a lagged response to winter NAO index suggested indirect influence through the food chain (Descamps *et al.*, 2010).

In regards to indirect effects, bottom-up effects propagating from lower trophic levels and prey dynamics may be controlling yearly success in the eider populations around Iceland. Timing of nesting needs to be matched with peak food abundances in avian species (Both *et al.*, 2006), in agreement with the match-mismatch hypothesis (Cushing, 1990). Breeding later in the season has been associated with a decline in clutch size (Arnold *et al.*, 2004), and if nesting occurs later to match peak food abundances, prey phenology has the potential to influence populations. Eiders may also experience bottom-up effects through the dynamics of a primary prey species, the blue mussel (*Mytilus edulis*), which responds well to colder winter temperatures (Beukema, 1993). Therefore, successful years of seabirds breeding can be sensitive and influenced from many directions, and as discussed in previous sections, there are a plethora of direct and indirect effects that can be influencing populations.

Eider numbers in Iceland are estimated to be 250,000 pairs, making them the most abundant waterfowl in Iceland (Asbirk *et al.*, 1997), and Breiðafjörður (Fig. 4-2) hosts approximately 25% of the eiders in Iceland during wintering, molting and breeding activities (Grimmett and Jones, 1989). Recently there has been interest in specific years of

breeding success in eiders; specifically, 2011 was a year of comparatively low numbers of young eiders in Breiðafjörður. In response to these observations, this study will address the number of female and young eiders in relation to SST to examine if anomalies occurring in eider populations can be explained to any extent by SST.

## **5.2 Methods**

### **5.2.1 Study species**

The common eider is a large, resident sea duck in Iceland that breeds on the coast and forms large flocks during the non-breeding seasons (Jónsson *et al.*, 2009). This short distance migrant species has the capability of feeding on a range of prey types, and is therefore able to survive under a range of conditions (Leopold *et al.*, 2001). In general, the eider feeds primarily on the blue mussel and other bivalve molluscs (*Bivalvia*) (Leopold *et al.*, 2001; Kristjánsson *et al.* 2013), however, in Breiðafjörður during the spring, it has been shown that the most common prey species is a chiton, and not the blue mussel. Overall, the eider has been documented to show flexibility and feed on prey such as sea urchins, fish eggs and chitons (Kristjánsson *et al.* 2013). During the laying and incubation periods female eiders rely on endogenous fat reserves because they do not feed at all (Parker and Holm, 1990). In Iceland, the common eider is an economically important species due to the collection of down for use in commercial items, and is therefore largely monitored and managed. They have been protected from hunting since 1850 and from public egg collection since 1787 (as cited in Jónsson *et al.*, 2013).

### **5.2.2 Data sources**

Eider brood counts were made twice each year in June and July for the years 2007-2012 in and around Breiðafjörður. The data were collected by the means of vehicular surveys, an observational method that has been previously documented to count avian species (Diem and Lu, 1960; Oates and Crawford, 1983). During these counts, the number of females and the number of young were counted separately. The data were provided by Jón Einar Jónsson from the Snæfellsnes Research Center.

### **5.2.3 Statistical analysis**

Similarly to the cormorant analysis, linear regressions were used to address if spring or winter temperatures explained any of the variation in eider populations between 2007-2011. All methods for determining seasonal SST averages are as described in Section 4, and data from 2012 have been removed from all analyses because the raw values remained between 0-2 C° from January-May when all other years showed a marked increase in temperature. Due to the limited amount of data, only seasonal temperatures, not monthly, were used in this analysis. Additionally, in order to understand if there was any variation in spring and winter temperatures over the short span of study years, a general linear ANOVA model was used to compare temperatures between years.

## 5.3 Results

In regards to the eider populations and SST, no significant relationships between female or young counts for either June or July were found. Although, the young numbers are noticeably low in 2011, there was no significant relationship to temperature found (Tab. 5-1). The average spring temperature in 2011 is lower than the previous four years, despite no significant differences found in the statistical models. Additionally, when comparing average spring temperatures between the years 2007-2011, and average winter temperatures over the same years, no significant differences between the years for either season were found.

Year	Winter Average SST $\pm$ SD	Spring Average SST $\pm$ SD	June Young Count	July Young Count
2007	2.3 $\pm$ 0.9	4.3 $\pm$ 1.3	636	812
2008	1.3 $\pm$ 0.8	4.3 $\pm$ 1.5	2070	486
2009	2.3 $\pm$ 1.0	4.4 $\pm$ 1.6	1406	347
2010	2.4 $\pm$ 0.8	4.5 $\pm$ 1.7	1240	346
2011	1.9 $\pm$ 1.1	3.9 $\pm$ 1.5	205	58

Table 5-1. Average seasonal temperatures and young eiders counts made twice each year between 2007-2011 Breiðafjörður, Iceland.

## 5.4 Discussion

No models were found to explain the variation in eider populations over the examined years. These results imply that other factors, aside from SST, are likely explaining anomalies in the eider populations. However, the average spring temperature in 2011, when the number of eider young was low, is noticeably lower than the previous years. Due to the low number of available sample years in this analysis ( $n=5$ ) a complete analysis may not currently be possible. With a longer temporal scale it would be possible to better understand if SST is a mechanism affecting eider breeding success. However, the lower spring temperature in 2011 suggests that further analysis should be done when a longer data set is available, especially because other studies suggest that weather is correlated with success of species in the Anatidae family (Drever and Clark, 2007; Jónsson and Gardarsson, 2001; Systad *et al.*, 2000; Coulson, 1984). For example, eider clutch size is higher when nesting occurs earlier, and earlier nesting is more likely after milder winters (Jónsson *et al.*, 2009).

The results suggest that perhaps lower SST during the spring months of that year were affecting eider breeding success, either through direct or indirect effects. In agreement with this concept, it has been shown that the nest success of five duck species in Saskatchewan, Canada, was positively correlated with spring temperature (Drever and Clark, 2007). Additionally, it has been shown that the proportion of paired mallards (*Anas*

*platyrhynchos*) was positively correlated with mean monthly temperature (Jónsson and Gardarsson, 2001). The explanation of SST conditions prior to breeding directly affecting nesting success would agree with previous studies that say females may have to use fat reserves during colder winters (Systad *et al.*, 2000) which affects clutch size, egg size, and levels of parental care (Erikstad *et al.*, 1993; Hanssen *et al.*, 2002; Bustnes and Erikstad, 1991), and they may also skip breeding in order to maximize reproductive output over their entire lifespan (Coulson, 1984).

In the context of indirect versus direct effects on eider populations in Iceland, both mechanisms of ecosystem control are likely working simultaneously. However, Jónsson *et al.* (2009) suggest that because Iceland is not the coldest part of the eider range, the effects of weather are more significantly indirect than direct. As put forth in the previous section, further analysis of potential indirect effects through trophic relationships should be explored in order to understand if lower trophic levels, such as plankton, are affecting avian success. It has also been suggested that severe winters may be affecting the predators of eiders, as well as eiders themselves (Drever and Clark, 2007), indicating the occurrence of indirect effects.

As suggested for cormorant populations, perhaps the effects of extreme local weather events should be focused on rather than mean climate characteristics, such as SST, in order to better understand the drivers of anomalous years in eider populations. Jónsson *et al.*, (in press) found that weather effects were limited to causing declines in breeding numbers during individual years of anomalous weather, such as years with sea ice or severe weather conditions. To understand the cause of a low young eider number in 2011, an analysis of extreme weather events should be done because perhaps the occurrence of severe weather conditions caused a decline in young production. In general, due to the changing of the global climate and the economic importance of eiders to Iceland, further monitoring and analysis of temperature, extreme weather events and eider populations should continue.



## 6 Conclusions

In the case of Icelandic seabird populations there are likely differing mechanisms affecting species success. Therefore, regional and specific studies are necessary, and logical explanations that are justified and explained by collected data need to be used to explain the mechanisms determining success in high trophic level species. For example the cormorants in Iceland are unique in their increase, and therefore require a focused study to address mechanisms for the increase. Additionally, anomalies in eider populations in Breiðafjörður should be further explored because the relationship between SST and eider young was not well explained by the results.

As discussed in this paper, the interactions among trophic levels are complex yet have the potential to vastly influence ecosystem functioning. It is therefore necessary to maintain ecological perspectives when addressing conservation measures. An ecosystem approach still requires detailed case studies to understand the responses in different species and varying geographical areas because species respond differently to climate change; different populations of mid-trophic level fish had contrasting responses to SST increase (Astthorson and Gislason, 1998; Arnott and Ruxton, 2002), as did different seabird populations globally (Veit *et al.*, 1996; Weimerskirch *et al.*, 2001; Durant *et al.*, 2003). The relative influence of direct and indirect effects is necessary to understand what factors are influencing populations, and even more specifically the effects of bottom-up and top-down ecosystem control. Ecosystem functioning is important in light of the elevated effects of global climate change in the North Atlantic compared to other regions (Pachauri and Reisinger, 2007), and the potential for climate to influence top predators directly or indirectly through the food chain is necessary to understand.



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