THE EFFECT OF CLIMATE VARIATION AND FOOD AVAILABILITY ON BREEDING SUCCESS IN ATLANTIC PUFFINS AT HJELMSØYA, NORTHERN NORWAY

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ABSTRACT

The colony of Atlantic puffins (*Fratercula arctica*) at Hjelmsøya, in Northern Norway has experienced extensive annual fluctuations in breeding success. To investigate how climate variability affects the population dynamics of this iconic seabird, I have analysed data on breeding success for this colony for the past 10 years. Through analysis of the time-series data I wished to investigate which climate and oceanographic conditions that best explained the variance in breeding success. My hypotheses were that 1) the short-time variation apparent in breeding success is best explained by climatic conditions in the months leading up to the breeding season, and that 2) this effect will be most apparent indirectly, through the availability of prey. Where earlier studies mainly consider the NAO index as a parameter for climate variability, I have included several other teleconnections to account for other modes of climate variability in the Northern Atlantic. The abundance of cod larvae in the Barents Sea was the single variable that explained most of the variance in breeding success, having a significant positive effect on breeding. I found that the effect of climate on breeding success for the puffin colony at Hjelsmøya was most apparent indirectly, through the availability of cod larvae in the Barents Sea, which had a significant positive effect on breeding success. While commonly used climate teleconnection patterns, such as NAO, could only weakly explain the variance in breeding success, the effect of NAO on abundance of cod larvae was considerably stronger. This supports the hypothesis that the effect of climate is most apparent indirectly, through the availability of prey. In addition, the multiple regression model explaining most of the variance was the model including NAO, cod larvae abundance and cod larval drift as covariates. Thus, the causal pathway by which climate seems to influence breeding success is by its effects on oceanic currents affecting larval drift and thereby the amount of fish larvae available to the puffins breeding at Hjelmsøya.

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1 INTRODUCTION

At the top of the marine food chain are the seabirds, the most numerous and visible of marine top predators, offering an insight into the change and status of an environment where most other components are hidden under water. The population dynamics of marine predators are affected by a combination of factors including climate fluctuations and human influences (Frederiksen *et al.* 2004; Sandvik *et al.* 2012). Knowledge of how different factors influence the population dynamic of seabirds is of fundamental importance when interpreting and predicting the effects that climate and anthropogenic factors have on a population's trajectory (Lande *et al.* 2003; Sandvik *et al.* 2014).

Several studies have focused on how climate variability affects population dynamics, or more specifically, along which pathways climate influences different seabirds' life-history traits, such as offspring production and recruitment (Durant *et al.* 2003; Sandvik *et al.* 2012; Watanuki & Ito 2012; Yannic *et al.* 2014). The pathway along which climate variability influence population dynamics have generally been most clearly demonstrated through its effect on reproductive success (Durant *et al.* 2003). This is because birds typically adjust their breeding decisions to match food availability, making them sensitive to variation in oceanographic conditions (Lack 1968; Barrett 2002; Durant *et al.* 2003). Climate may affect breeding success directly, by increasing individual mortality and thereby reducing breeding success (Sandvik *et al.* 2005; Yannic *et al.* 2014), or indirectly through the availability and quality of prey in the foraging areas (Durant *et al.* 2003; Scott *et al.* 2006; Sandvik *et al.* 2012; Watanuki & Ito 2012). To be able to get a broader understanding of the development of marine ecosystems, it is important to understand how seabird populations are affected by climatic and oceanographic conditions, and how it affects key organisms at lower trophic levels (Frederiksen *et al.* 2013).

The marine ecosystems are affected by climate through various climatic features influencing the oceanographic conditions (Mesquita *et al.* 2015). Teleconnection indices of large-scale atmospheric circulation patterns are commonly used when studying the effect of climate on population dynamics (Durant *et al.* 2004; Mesquita *et al.* 2015). Many studies have looked at the correlation between population dynamics in seabirds and teleconnection indices (Durant *et al.* 2004; Devney *et al.* 2009; Mesquita *et al.* 2015). In the Northeast Atlantic, the most common proxy used is the North Atlantic Oscillation (NAO), which is an anomalous dipole in atmospheric pressure between the low-pressure system in the North Atlantic (Iceland) and the subtropical high-pressure system in the south (Azores) (Barnston & Livezey 1987; Mesquita *et al.* 2015).

Several studies have investigated the relationship between breeding success and NAO as a proxy for climate fluctuations (Durant *et al.* 2003; Durant *et al.* 2004; Sandvik *et al.* 2012; Mesquita *et al.* 2015). However, Mesquita *et al.* (2015) argue that the NAO index is only one of a number of modes of climate variability in the Northern Atlantic, and that other modes of climate variability must be considered. In addition, the effect of teleconnection patterns such as the NAO index is often mediated by oceanographic conditions such as sea temperatures and oceanic currents, which affect the distribution and growth rate of ecologically important organisms such as zooplankton and fish larvae (Durant *et al.* 2003; Vikebø *et al.* 2010; Vikebø *et al.* 2011; Myksvoll *et al.* 2013; Sandvik *et al.* 2014; Myksvoll *et al.* 2015).

The reproduction of piscivorous seabirds along the coast of Norway is highly dependent on the availability of fish larvae and juvenile fish, such as first year Norwegian spring-spawning herring (*Clupea harengus L.*) and Northeast Atlantic cod (*Gadus morhua)* (Durant *et al.* 2003; Fauchald *et al.* 2015b). These, in turn, are dependent on the availability of zooplankton, which is known to fluctuate with climate conditions, as they drift from their spawning grounds along the Norwegian coast from the Norwegian Sea (herring) to their nursing grounds in the Barents Sea (herring and cod) (Durant *et al.* 2003; Vikebø *et al.* 2010). A rapid northward displacement to the main nursing areas have been documented to be important for larval survival (Vikebø *et al.* 2010). The currents carrying eggs and larvae are affected by climatic conditions, such as wind direction and strength. Stronger winds lead to stronger currents (Vikebø *et al.* 2010), which have been associated with a strong positive NAO (Blindheim *et al.* 2000). Increased northerly winds in the Norwegian Sea have also been demonstrated to force the larval drift out to the continental shelf, increasing the displacement of larvae to the Barents Sea (Sætre *et al.* 2002).

The Norwegian seabird population contributes to more than 25 % of the population breeding in Europe (Fauchald *et al.* 2015a), which means that Norway has a considerable international management responsibility (Anker-Nilssen *et al.* 2015). In Norway, all monitoring of seabird populations is carried out by the national seabird mapping and monitoring programme SEAPOP (short for seabird populations). The main focus of SEAPOP is to establish and maintain long-term data series that describe the population dynamics of a geographically and ecologically representative sample of those of our seabird populations that are believed to be most vulnerable to external influences (Anker-Nilssen *et al.* 2015). Seabird population along the coast of Norway are experiencing a decline (Fauchald *et al.* 2015a). The trends are, however, not uniform; in the Norwegian Sea, the breeding populations of common guillemots and puffins show a clear negative trend the last 25 year, while increasing in the Barents Sea area (Fauchald *et al.* 2015b).

The Atlantic puffin is one of the most numerous seabirds breeding in Norway, aggregating in large breeding colonies from Sogn og Fjordane county in the South to Svalbard in the North (Harris & Wanless 2011). One of the key locations where the Atlantic puffin is monitored is Hjelmsøya, located 71^0 North in the Barents Sea. The breeding population of this colony is experiencing annual fluctuations. The latest annual report from SEAPOP (Anker-Nilssen *et al.* 2014), however, documents a general increase in the population size. This is in contrast with key locations in the Norwegian Sea, where the breeding populations have a clear negative trend from 2004-2014 (Anker-Nilssen *et al.* 2014; Anker-Nilssen *et al.* 2015) .

Causal studies offer a unique insight into the status of the marine environment (Piatt *et al.* 2007), as well as being important when working out suitable management plans (Fauchald *et al.* 2015b). Several studies have focused on what effect climate have on breeding strategies and breeding success of Atlantic puffins (Durant *et al.* 2003; Durant *et al.* 2004; Sandvik *et al.* 2012). These studies found that the effect of climate was strongest indirectly, mediated by sea temperatures affecting the availability of prey. This is true for the puffin population breeding at Røst in Nordland county, where Durant *et al.* (2003) showed that the fledging success was coupled to sea temperatures affecting the availability of first-year herring, the predominant prey in this area. NAO was also set as a proxy for climate for climate in these studies. In Durant *et al.* (2004) study, they found that timing of breeding was influenced by the NAO winter index; when NAO was high, the puffins generally bred earlier. A clear relationship between breeding success and NAO is, however, not always present. In Sandvik *et al.* (2012) study they show that the relationship between the NAO and breeding and adult survival of seabirds is highly variable, concluding that species with slow life histories (clutches of 1) respond much less to climate.

Since climate change is predicted to continue and accelerate during the next decades (Stocker 2014), resulting in increasing stormy weather and sea temperatures in areas such as the Barents Sea (Gradinger 2015; Ingvaldsen 2015; Sunby 2015), it would be interesting to study the effect these changes have on the population dynamics of Atlantic puffins breeding in this area.

1.1 MY AIMS

In this study I will focus on how climate fluctuations affect the population dynamics of a population of Atlantic puffin breeding at Hjelmsøya in the Barents Sea, a breeding population not previously studied. I will use breeding success data for the past 10 years (2006-2015) as a parameter for population dynamics affecting population size. This is because breeding success has been documented to respond rapidly to short-time variability such as change in availability of prey (Barrett 2002; Piatt *et al.* 2007). Since the NAO index is not the only index which explain variations in climatic and oceanographic conditions (Mesquita *et al.* 2015), this study will also include other teleconnection indices and oceanographic variables to study the relationship between ecological time series of breeding success and climate. Through the analysis of the time-series data I wish to explain which climate and oceanographic conditions best explain the variance in breeding success. My hypotheses are that 1) the short-time variation apparent in breeding success is best explained by climatic conditions in the months leading up to the breeding season, and that 2) this effect will be most apparent indirectly, through the availability of prey.

1.1.1 STUDY QUESTIONS

1) What is the trend for breeding success for the puffin colony breeding at Hjelmsøya?
2) What is the choice of prey fed to the chicks?
    a. Does the diet choice reflect prey availability?
3) How do climate and oceanographic conditions explain the variance in breeding success?
    a. Which climate and oceanographic factors explains most of the variance?
    b. Is the variance best explained by large-scale climate conditions prior to the breeding season or local conditions during the breeding season?
4) How does prey availability explain the variance in breeding success?
    a. Which species/group of prey explains most of the variance?
    b. Does prey availability explain more of the variance than climate and oceanographic conditions?
5) How does climate and oceanographic conditions explain the variance in abundance of prey?
    a. Which climate and oceanographic factors explains most of the variance?
    b. Is this relationship clearer than the effect of climate on breeding success?

2 MATERIALS AND METHODS

2.1 STUDY SPECIES AND AREA

The Atlantic puffins (Fratercula arctica) is one of four puffins belonging to the auk family (Alcidae), and the only puffin that is endemic to the North Atlantic, breeding on both sides of the Atlantic and as far north as there is ice-free land (Figure 1) (Harris & Wanless 2011). The Norwegian population of Atlantic puffins account for 25 % of the global population, with a total of 1.5 million puffins estimated to breed on the Norwegian mainland (excluding Jan Mayen and Svalbard) in 2014 (SEAPOP 2014; Fauchald *et al.* 2015a). The global population trend is decreasing, and the Atlantic puffin listed as Vulnerable, both on *the IUCN* and *Norwegian Red List of Threatened Species* and (IUCN 2015; NBIC 2015).

During the breeding season the puffins congregate in large breeding colonies. They nest underground in burrows, usually on steep hill cliffs where they are less exposed to predation. The burrow is either dug in the ground or in a crevice and the nest itself is a dent in the ground (usually lined) in the far end of the burrow (Harris & Wanless 2011). Puffins show high degree of natal philopatry, returning to their natal breeding colony where they nest in the same burrow, or adjacent burrows, as previous years (Harris & Wanless 2011). The puffins normally do not breed until they are four years old, which is common for long-lived birds (Harris & Wanless 2011). They are socially monogamous, and a pair might stay together all their life (Harris & Wanless 2011). However, “divorce”, where both male and female return to the colony but do not breed together, does occur (Harris & Wanless 2011). The female lay a single egg, and both the

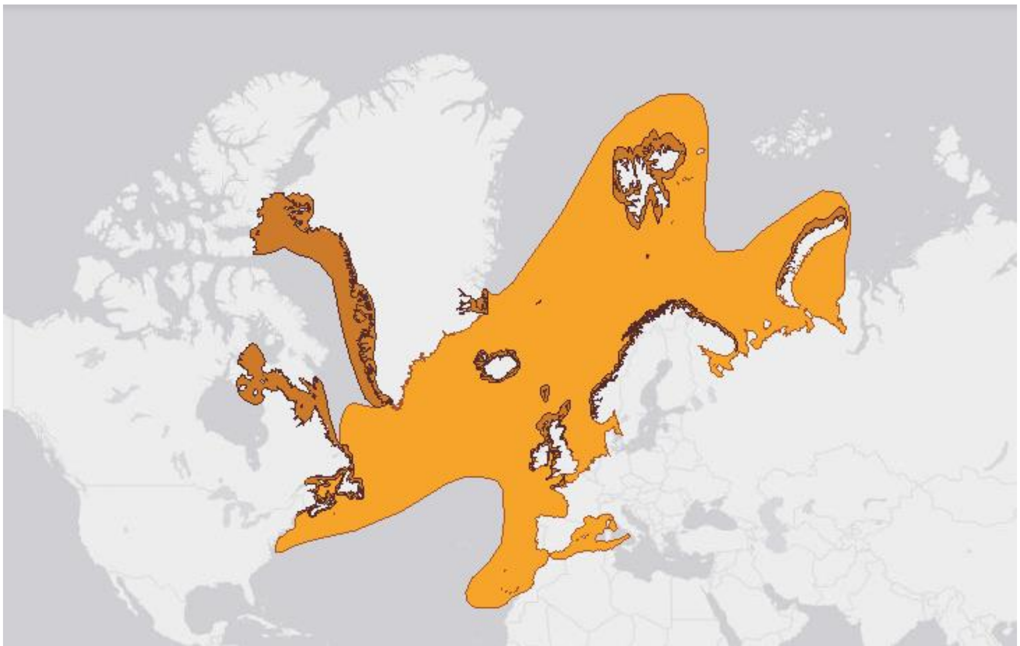


Figure 1. Illustration of the global distribution of the Atlantic puffin. Light orange represent non-breeding distribution and dark orange represents breeding distribution (IUCN 2015).

female and male attend the egg during the incubation period (39 to 43 days) and during chick rearing when the chick is fed on small fish (another 38 to 44 days) (Harris & Wanless 2011).

Puffins are pursuit-diving pelagic seabirds that use their wings as fins for propulsion, flying under water. The puffins feed their chicks on small, lipid-rich fish that they carry in their beak. The colony is dependent on the local area for food, and they usually forage in a distance of a few tens of kilometres from the colony (Harris & Wanless 2011). In Norway, Atlantic puffins usually catch small pelagic fish (30-60 mm in length) such as lesser sandeel (*Ammodytes tobianus*), capelin (*Mallotus villosus*) (all age classes) and younger age classes (0- and 1-group) of Norwegian spring-spawning herring (*Clupea harengus*) or Northeast Atlantic cod (*Gadus morhua*) (hereby referred to as cod and herring) (Barrett 2002). Other, less frequently occurring choice of prey may be gadoids such as north-east Arctic saithe (*Pollachius virens*) and haddock (*Melanogrammus aeglefinus*), in addition to capelin (IMR 2011b, c; 2014b).

The colony of Atlantic puffins in this study is located on Hjelmsøya, an island that lies east in the Barents Sea, on the north tip of Norway in Finmark county (Figure 2). In 2014, an estimated 10 500 pairs were breeding at this colony, which at that time represented about 6 % of the total Norwegian population (1 465 000 pairs), and 10 % of the pairs breeding in the Barents Sea area (90 000 pairs) (SEAPOP 2014).

The Barents Sea is a relatively shallow ocean with a mean depth of 230 meters. It is characterized as a highly productive ocean with high variations in yearly temperatures, ice cover and water transport (Ingvaldsen 2015). The productivity conditions in the Barents Sea depend on the temperature conditions, which are mainly determined by the relatively warm Atlantic Current connected to the continental

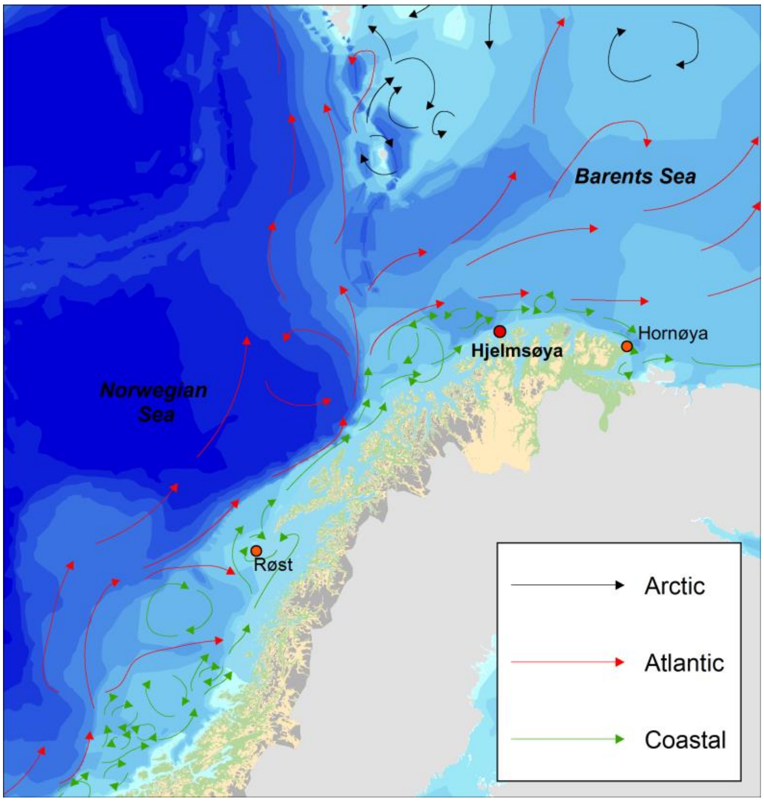


Figure 2. Schematic map showing the oceanic currents affecting the local conditions at Hjelmsøya. The black arrows represent the main conditions of the Arctic Current, the red arrows the Atlantic Current, and the green represents the Costal Currents. The location of seabird the colonies at Hjelmsøya, Røst and Hornøya are presented. Map is revised from a combination of maps presented in Dalpadado *et al.* (2012) and IMR (2014a).

shelf, and the Coastal Current closer to the coast (Figure 2) (Vikebø *et al.* 2010). Temperature conditions in the Barents Sea are thereby affected by the temperature in the Norwegian Sea, as well as the volume of the water transported by the currents (Ingvaldsen 2015). The volume and viscosity of oceanic currents are mainly determined by the wind conditions in the west of the Barents Sea (Ingvaldsen 2015), which may vary considerably from year to year, according to atmospheric pressure (Vikebø 2009; Vikebø *et al.* 2010). Low-pressure systems, which are associated with increasing wind and precipitation, will lead to a larger inflow of water, while high-pressure systems associated with dry and cooler conditions will lead to less inflow (Blindheim *et al.* 2000; Ingvaldsen 2015).

The oceanic and coastal currents not only determines the local temperature conditions, it also supplies the Barents Sea with zooplankton, fish eggs and larvae (Ingvaldsen 2015). Eggs and larvae of herring and cod are transported from their spawning grounds in the Norwegian Sea to their nursing grounds in the Barents Sea (Vikebø *et al.* 2011; Myksvoll *et al.* 2013). The puffins in the Barents Sea are also supplied with local fish stocks of cod and sandeel (*Ammodytes* spp.), which spawn in the area (IMR 2011a, c).

2.2 DATA COLLECTION AND PROCESSING

2.2.1 ECOLOGICAL TIME-SERIES

The ecological time-series from the breeding colony at Hjelmsøya has been established by the SEAPOP program. The time-series I will use from this colony is of breeding success (2006-2015) and diet choice (2009-2015). I collected the data for 2015 during my fieldwork at Hjelmsøya from June 6th to July 20th. This time-period is consistent with the former field work seasons.

The breeding success is determined by monitoring the nest contents of a fixed-sized sample of the breeding colony during the breeding season. We collected the breeding success data on a designated breeding success field on the north facing slope of Laksmannen (71^{0}11.4”N 24^{0}72.7”E). In this field, we marked 120 active nests (burrows) on the 13th and 14th of June. At that time we knew the breeding puffins would have laid their eggs, at the same time as it being well in advance to the expecting hatching date. The burrows marked had to be active, meaning we either (a) found an egg, or (b) found an incubating bird. Some burrows were too deep for us to be able to reach the egg, but where the topography and direction of the burrows allowed it we dug holes to get to the egg. These holes were then “plugged” with vegetation to be reused. The burrows with incubating birds were left alone, and rechecked within the next few days. We then left the field undisturbed until the 23th of June. Then, we started to check for hatching every third day for the rest of the field season (23.06-17.07). The burrows that had pullus on the 17th of July were set as successful, resulting in a binomial time-series of success and failure.

The chick diet is determined by diet sampling. We sampled the diet by taking pictures of the beak content. Digital cameras with high resolution and high optical zoom are used for collection of diet samples. The diet samples were collected at Laksmannen. We sampled the diet by taking pictures of the beak content carried back to their chicks (example is given in Figure 3) using digital Nikon cameras with 200-600mm lenses with built-in image stabilization. When possible, multiple pictures were taken of the same sample, preferably from different angles and both sides of the beak. This made subsequent analysis of the food samples easier.

The time-series for chick diet is composed of proportion data (counts) for different choices of prey (food samples), classified down to species, genus or family for the period 2006-2015. The food samples are categorized in these categories; herring, sandeel (*Ammodytes* spp.), capelin, gadoids (consisting of cod, saithe and haddock). When comparing my food sample with other pictures, I looked for external morphological traits that are possible to detect from a picture. These morphological traits are listed in Table 1. Since the proportion of mass gives a more accurate presentation of the different ratios of prey total mass (g) was calculated for each class of prey. Total mass was estimated from approximate lengths of food items in relation to bill height (measured at gonys), combined with regression estimate functions of measured length and mass of food items collected from puffins and guillemots at Hornøya , provided by Rob Barrett from Hornøya (personal communication, March 2, 2016). The formulas used to estimate mass are presented in Appendix A.

Table 1. List of external morphological traits used to identify food samples at Hjelmsøya.

General shape; elongated/short, thin/fat.
Pigmentation; present/non-present, differentiation between dorsal and ventral side.
The jaw; over- or under bite.
Size and placement of the eye relative to the jaw, prepercular margin and operculae.
Size of the caudal peduncle in relation to caudal fin and body size.
Shape of lateral line.

Figure 3. A puffin holding five sandeels (Ammodytes sp.) in its beak. Photo: Åshild Idsø.

2.2.2 CLIMATE AND OCEANOGRAPHIC TIME-SERIES

As parameters for large scale climatic variation that may affect the breeding population at Hjelmsøya prior to breeding, several teleconnection pattern indices are used in this study (Table 2). The time-period *prior* to the breeding season in this thesis is set to February-April. Other indices associated with the northern hemisphere were dropped due to high correlation with the presented indices (correlation coefficient ≥ 0.5, see Appendix C for R syntax). The different indices represent different atmospheric circulation patterns having different effects on the Barents Sea region. In the Barents Sea region, a positive phase of NAO and BO are associated with higher levels of precipitation, increased temperatures and stormy weather in Northern Europe and Scandinavia (low-pressure system), while the negative phase is associated with lower temperatures and below average precipitation (high-pressure system). The opposite is true for EAWR and SCAND, where the positive phase is associated with dry and cold conditions in Northern Europa (Wallace & Gutzler 1981; Barnston & Livezey 1987; Skeie 2000; Washington *et al.* 2000; Knight *et al.* 2006; CPC 2012a, b, c). Monthly means of NAO, SCAND and EAWR were downloaded from online databases, provided by the National Oceanic and Atmospheric Administration (NOAA) (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/MJO/climwx.shtml). Monthly means of BO were provided by Hans W. Chen, from The Pennsylvania State University (Chen *et al.* 2013). The monthly BO indices from February to March were downloaded from his webpage (http://hanschen.org/bo/#data), while the April to July addition were calculated and sent personally (Chen, H.W., personal communication, December 30, 2015). All indices are normalized using the 1981-2010 base monthly means and standard deviations (Appendix B, Table *iii)*. Annual variation of NAO (2006-2015) prior to the breeding season is presented in Figure 4.

Table 2. List of teleconnection patterns of the Northern Hemisphere used in this study. The name is presented with the acronym.

Teleconnection patterns	Seasonal occurrence	Definition
North Atlantic Oscillation (NAO)	All months.	North-South dipole in SLP between Iceland and the Azores.
East Atlantic-Western Russia (EAWR)	All months.	Dipole in SLP between four main anomaly centres, shifting according to season.
Scandinavia (SCAND) pattern	All months except June to July.	Dipole in pressure systems, with primary circulation centre over Scandinavia.
Barents Oscillation (BO)	December to March.	Anomalous atmospheric circulation pattern, with a primary centre of action located over the Barents region.

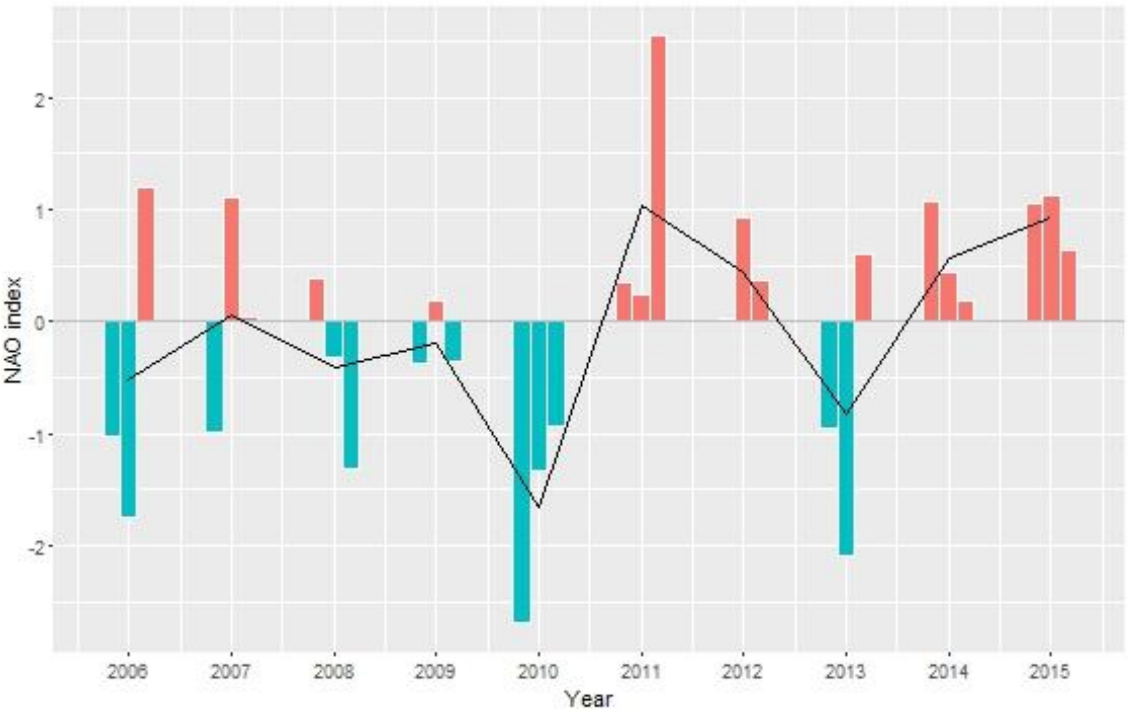


Figure 4. Monthly means of the NAO index (February to April) and local mean sea-level pressure (May to July) (bars). Bars are coloured red and blue to illustrate positive and negative phases of NAO. The black line represents the annual means.

Mean sea surface temperature (SST) and sea-level pressure (SLP) were used as parameters for small scale oceanographic (SST) and climatic (SLP) variation that affect the breeding population directly *during* the breeding season. Both SST and SLP were retrieved from the European Centre of Medium-Range Weather forecasts (ECMWF) Re-Analysis Interim Project (ERA-Interim) (Berrisford *et al.* 2009; Dee *et al.* 2011). The ERA-Interim SST data was compared with data from other sources (NOAA and ICES) prior to the analysis, to verify that they correspond. The ERA-Interim data are assembled from different sources, such as satellite and station data, which are put into a model simulation, which results in a product that is in accordance with observation data and are often used in climatic studies (Dee *et al.* 2011; Mesquita *et al.* 2015).Because puffins are known to forage at a distance of a few ten kilometres from the colony, mean ERA-Interim data on SST and SLP from 2006 to 2015 retrieved from a 15 x 15 km box around Hjelmsøya were used (between 19.4 and 27.6 longitude, and 71.4 and 73.6 latitude). Both SST and SLP were normalized using the monthly means and standard deviations in according to the length of the time-series (see Appendix B, Table i*v*-*v*). A cross-correlation analysis was also conducted with mean SLP and mean SLP, to assess the lagged effect of oceanography on the atmosphere and vice versa.

2.2.3 Biotic time-series

In addition to time-series of breeding success and diet choice, I used time-series of larval drift and fish abundance indices as estimates of prey availability and abundance.

Time-series on larval drift of cod (north of 62^0) were provided by the Institute of Marine Research (IMR). The drift and development of cod are modelled using an individual-based model, where particles representing cod eggs are released at known spawning grounds along the Norwegian coast. Data from ocean models are included in the drift model to calculate how many of the eggs arrive in the area around Hjelmsøya. The ocean models include horizontal resolution of 4 x 4 km of daily averages of oceanic currents, temperatures, turbulence and salinity in the Norwegian and Barents Sea. See Myksvoll *et al.* (2013) for further details. The

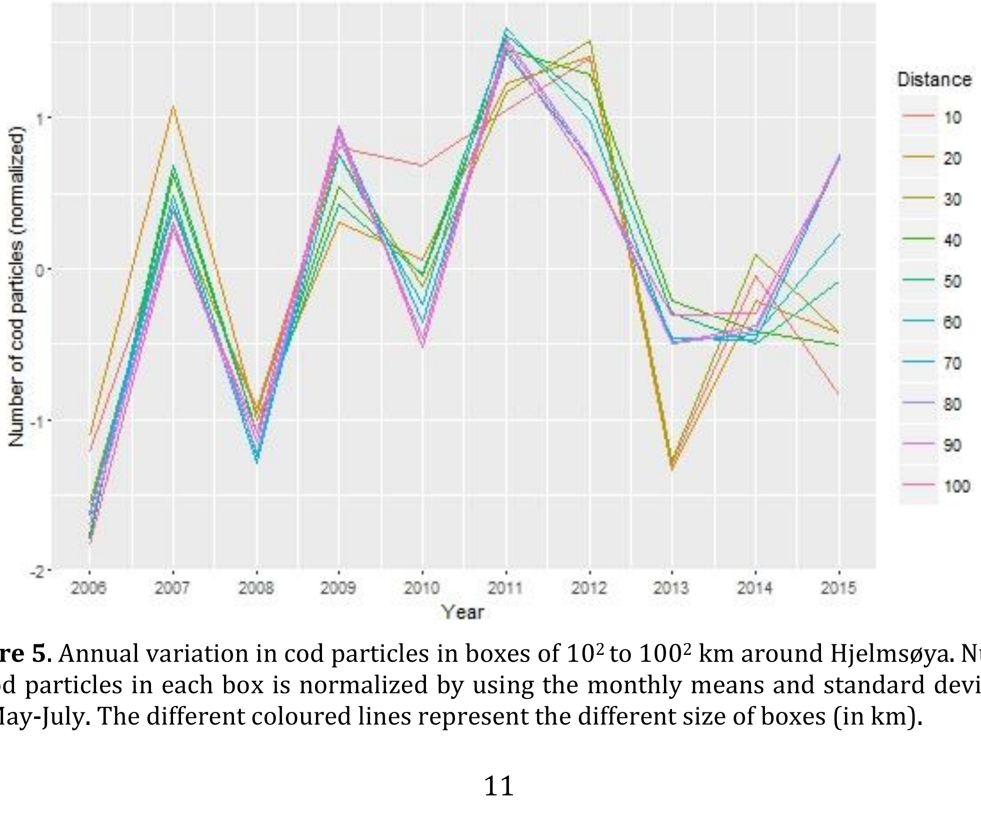


Figure 5. Annual variation in cod particles in boxes of 10^2 to 100^2 km around Hjelmsøya. Number of cod particles in each box is normalized by using the monthly means and standard deviations for May-July. The different coloured lines represent the different size of boxes (in km).

amount of cod particles for areas of 10^2 to 100^2 km around Hjelmsøya is presented in Figure 5. Since 20 km is a reasonable foraging distance for birds feeding young, the number of cod particles within a 20 km box around Hjelmsøya during the breeding season (May-July) was used in this thesis (Appendix B, Table *i*).

Abundance indices of first year classes of cod and herring (0-groups) were obtained from published data from the joint Norwegian-Russian survey in the Barents Sea and Norwegian Sea (ICES Sub-Areas I and II) conducted by IMR and PINRO (Russian Federation) (ICES 2015) . The abundance indices used in this thesis are from 2006-2015 (May-July). They are calculated by the "stratified sample mean" method, first applied by Dingsør (2005), which is based on catch rates (trawl surveys) and echo recordings conducted in August-September (Eriksen *et al.* 2009) (Appendix B, Table *ii*).

2.3 STATISTICAL ANALYSIS

2.3.1 EFFECTS ON BREEDING SUCCESS

To assess which climatic and oceanographic conditions best explain the variation in breeding success, I have included both large-scale climatic variables prior to breeding season (teleconnection indices) and small-scale variables during breeding season (local SST and SLP) as covariates in generalized linear regression models (GLM, n = 10). In addition to SST, modulated cod larval drift was also included as an oceanographic variable, as a parameter for inflow of Atlantic water. As a result of the cross-correlation analysis of local mean SST and SLP, a lagged effect of SST was also included (February to April) (see Appendix C for R-syntax). Due to overdispersion, I used the quasibinomial distribution. Table 3 lists the variables used in all analyses. The normalized values are used for all explanatory variables.

To assess the effect of availability of prey, I did a separate GLM analysis including abundance indices of 0-group cod and herring as covariates (n = 10, family = quasibinomial). Cod larval drift was included as weight to account for the availability of prey, in an area of 20 km from the breeding colony at Hjelmsøya. I then added the biotic parameters of prey abundance and larval drift in the climate analysis, to compare the effects of climate and biotic factors.

I used the forward selecting approach to select the best model. In the first step, I tested the addition of variables to a null model containing only the intercept. The variable that improved the model the most was kept, and the process was repeated in additional steps until there was no improvement. Since neither AIC nor R-squared is attainable from quasibinomial distribution models, the different models were compared and ranked using the residual deviance. This is feasible since all variables are normalized and have identical n.

In addition, a separate GLM analysis was carried out to assess the effect of different ratios of chick diet (gadoids, herring and sandeel) on breeding success from 2009-2015 (family = quasibinomial, n = 7). 2006-2008 was excluded in this analysis due to inadequate diet samples.

Table 3. The explanatory variables examined. For each variable, the expected relationship and reason is provided.

Explanatory variable	**Expected relationship**	**Reason**
NAO, prior to breeding season	Positive	Indirect effect on oceanographic conditions, mediated by the food chain.
SCAND, prior to breeding season	Negative	Same as for NAO
EAWR, prior to breeding season	Negative	Same as for NAO
BO, prior to breeding season	Positive	Same as for NAO
Local mean SST, during breeding season	Positive	Indirect effect, by the effect on productivity conditions
Local mean SST, *prior* to breeding season	Positive	Lagged effect on local conditions through its effect on lower trophic levels early in the season
Local mean SLP, during breeding season	Negative	Same as for NAO
Larval drift (cod particles), during breeding season	Positive	Indirect effect, mediated by food availability
Northeast cod 0-group abundance index, during breeding season	Positive	Main food source
Norwegian herring abundance index, during breeding season	Positive	Main food source

2.3.2 *EFFECTS ON AVAILABILITY OF PREY*

To assess the effect of prey availability on breeding success, I conducted a separate analysis where the abundance index of cod (original values) was set as response variable in a GLM (n= 10, family = quasipoisson). The climatic variables were set as explanatory variables as previously. To include information on how much cod which is actually available at Hjelmsøya, larval drift was included as weights in all the models. The different models were compared and ranked using the residual deviance as in previous analyses.

All analysis are were done in RStudio, Version 0.98.1103 (RStudio Team 2015), which is a part of the statistical environment of R (R Core Team 2015).

3 RESULTS

3.1 ECOLOGICAL TIME-SERIES

The time-series for breeding success for the colony at Hjelmsøya is presented in Figure 6. The colony has experienced annual fluctuations in breeding success in the study period of 2006-2015. From 2006-2010 there was a general decline in breeding success, where 2010 had the lowest registered breeding success. In 2011 the breeding success recovered, increasing by over four times, but has continued to fluctuate. In 2015, the breeding success declined again to only 20 percent of what it was in 2014 (see Appendix D, Table *vi*).

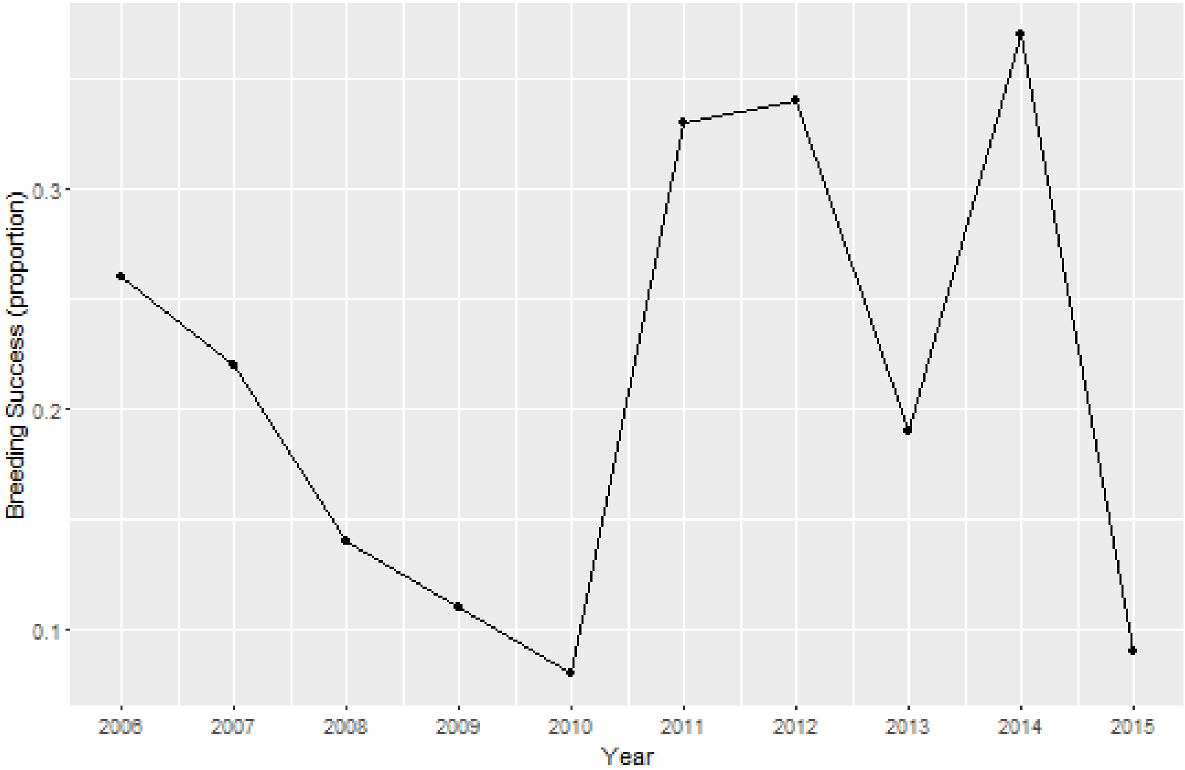


Figure 6. Time-series of annual breeding success for the puffins at Hjelmsøya, illustrating the annual fluctuations in breeding success for this colony.

The chick diet at Hjelmsøya consists mainly of gadoids, herring and sandeel. In term of the number of fish brought in to the chicks, herring is the most abundant choice of prey (see Appendix D, Table *vi* for counts of prey-fish). This is because the puffins usually bring in large numbers of small glass larvae, while larger fish, such as cod, saithe and sandeel are caught in smaller numbers. When calculating the sum of mass (g) of each group of fish, however, gadoids and sandeels represent a larger proportion of the chick diet (Figure 7). Cod represent more than half of the gadoid share (Appendix D, Table *vi*). The ratio of the different groups of prey varies from year to year, with the near disappearance of cod in 2015 being the most apparent. The ratio of the different groups of fish in the chick diet did not explain the variance in breeding success for this colony (see Appendix E for R-syntax).

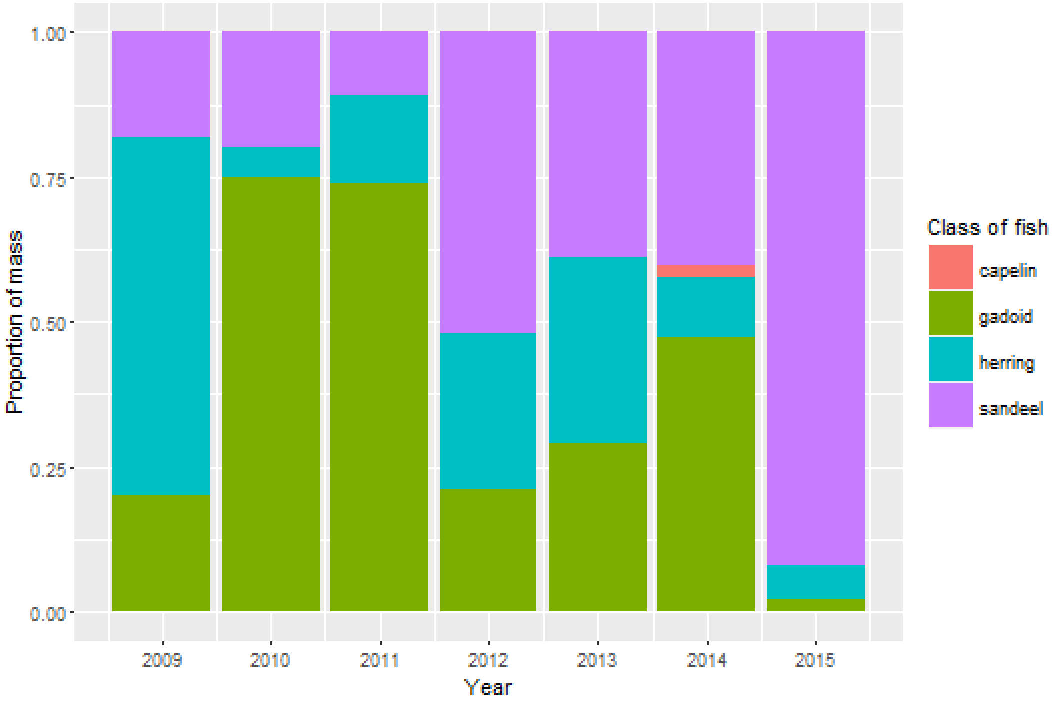


Figure 7. Proportion of the different groups of prey-fish; capelin, gadoid (cod, saithe and haddock), herring and sandeel (*Ammodytes* spp.) given to the chicks at Hjelmsøya from 2009-2015. 2006-2008 was excluded due to inadequate sample size.

3.2 EFFECTS ON BREEDING SUCCESS

Selected effects of climate and oceanographic variables are presented in Table 4. All models are presented in Appendix F, Table *viii.* The simple regression model explaining most of the variation was the model containing the NAO index, which explained 17 % of the variance in breeding success (not significant, $p > 0.05$). This model was then set as the null model for the next step in the forward selection process. The multiple linear model which explained most of the variation in breeding success was the model containing both the NAO index and local mean SLP as covariates. Together, the model containing variables for both large scale climate conditions prior to the breeding season and local conditions during the breeding season was able to explain 14 % more of the variance in breeding success than the null model containing just the NAO index as explanatory variable (not significant, $p > 0.05$). The model with the NAO and SCAND index explained 13 % of the variance. The other models did not have a considerable effect on breeding success, all explaining less than 3 % of the variance, and were therefore omitted. The relationship between breeding success and the strongest environmental variables are presented in Figure 8. In accordance to what was predicted, a positive phase of NAO and a larger displacement of cod particles to Hjelmsøya had a positive effect on breeding success. SLP also demonstrated a positive effect on breeding success, which was opposite to what was predicted.

Table 4. Environmental effects on breeding success of the puffin colony at Hjelmsøya. The best models are shown. The first null model contains only the intercept, the second null model is the best model from previous step. P-values are presented for descriptive reasons (Estimate, β-estimate of the effect ± std. error; P-value, the level of significance; Deviance, residual deviance; Explained deviance, proportion of the difference between the deviance of current model and the null model).

Model	Estimate	P-value	Deviance	Explained deviance proportion
Null model	-1.3 ± 0.2		63.3	0
NAO	+0.35 ± 0.27	0.2	52.7	0.17
SCAND	+0.46 ± 1.01	0.7	61.8	0.02
Local mean sea-level pressure , during breeding season	+0.57 ± 0.66	0.8	58.1	0.08
Cod larval drift	+0.15 ± 0.13	0.3	54.2	0.14
NAO + SCAND	+0.45 ± 0.29 +1.07 ± 1.02	0.3	45.9	0.13
NAO + local mean SLP	+0.38 ± 0.27 +0.64 ± 0.6	0.3	45.5	0.14

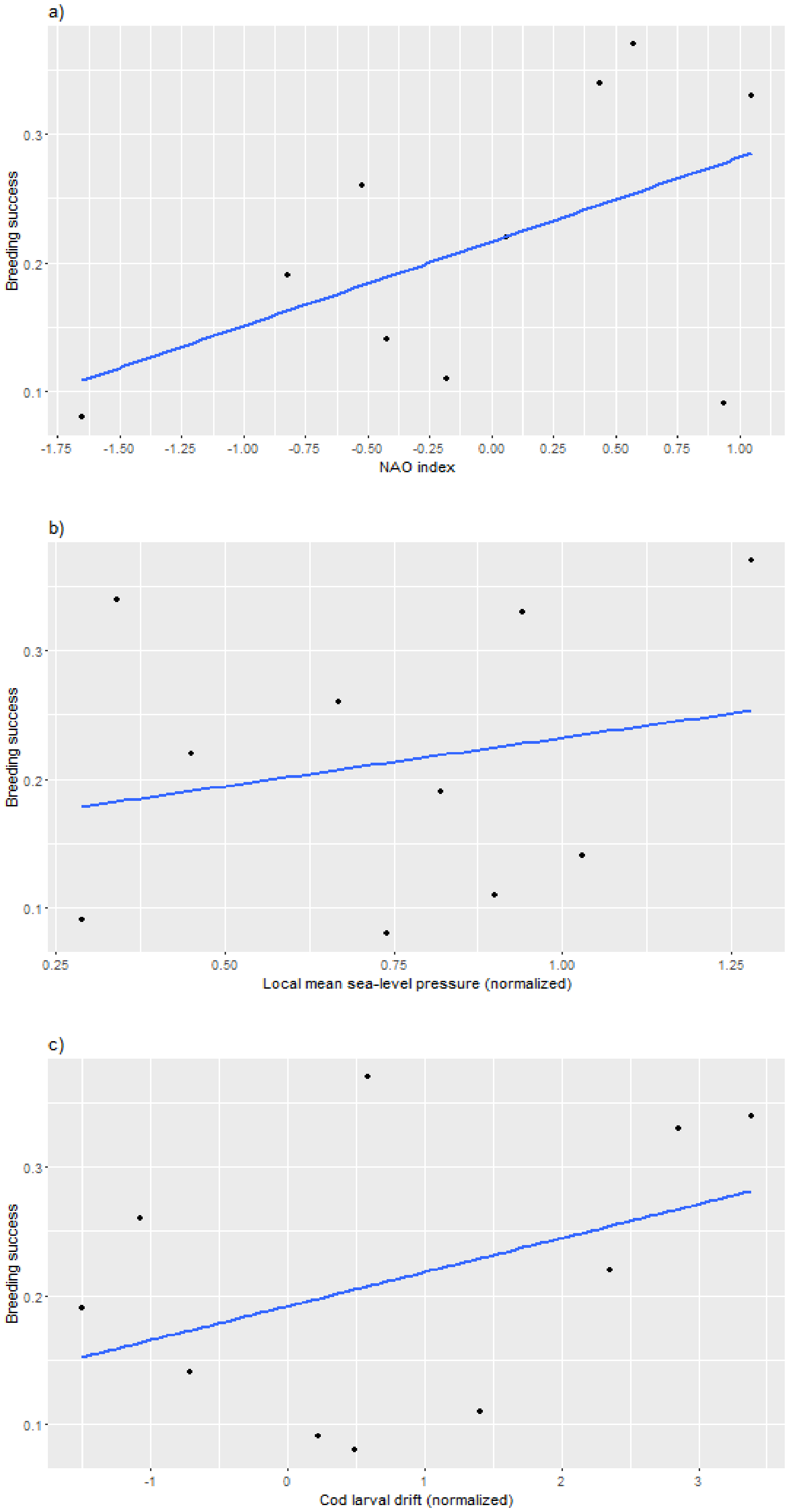


Figure 8. Selected relationships between breeding success of puffins at Hjelmsøya and environmental factors. The factors chosen are the ones which accounted for most of variation in breeding success for this breeding colony. a) show a positive relation between breeding success and the NAO index prior to breeding, b) show a positive relation with local sea-level pressure during breeding season and c) show a positive relation with modulated cod larval drift during breeding season at Hjelmsøya. See Table 4 for estimates of the slopes and explained deviance.

In the biotic models concerning prey abundance, the single effect of cod abundance in the Barents Sea region was the best model, achieving a significant reduction in deviance of 39 % (p = 0.05). This model explained more of the variance in breeding success, both compared to the abundance index of 0-group herring (see Table 5) and the climate model with the NAO index as single explanatory variable (see Appendix F, Table *viii* for all comparisons). The model incorporating herring abundance performed, however, more poorly than the climate model with NAO. Both cod and herring abundance in the Barents Sea had a positive effect on breeding success at Hjelmsøya (Figure 9).

Table 5. Biotic effects on annual breeding success of the puffin colony at Hjelmsøya. The models have modulated cod larval drift as weights. The best models are shown. The first null model contains only the intercept; the second is the best model from the first step (see legend of Table 4 for explanations).

Model	Estimate	P-value	Deviance	Explained deviance proportion
Null model	-0.18 ± 0.2		34801	0
0-group cod abundance index	+0.36 ± 0.16	0.05	21138	0.39
0-group herring abundance index	+0.11 ± 0.74	0.3	29708	0.15
Null model	+0.36 ± 0.16		21138	0
0-group cod + 0-group herring abundance index	+0.32 ± 0.17 +0.09 ± 0.14	0.5	20029	0.05

The effects of adding prey availability data to the best climate models are summarized in Table 6. Adding abundance data on 0-group cod to the model with the NAO index (from Table 4) improved the model by 15 % (not significant, p > 0.05). Although not significant, the model containing NAO, cod abundance and cod larval drift as covariates was the multiple regression model explaining most of the variance in breeding success (33 %).

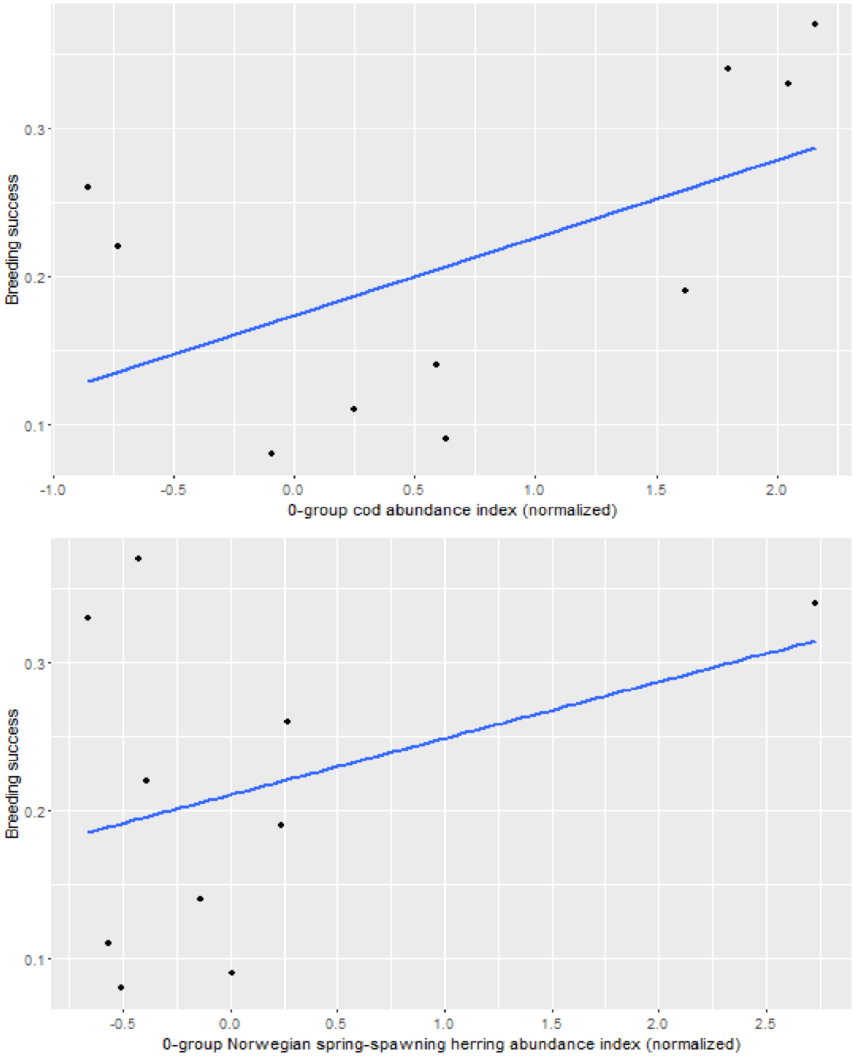


Figure 9. Relationships between breeding success of puffins at Hjelmsøya with abundance index of a) of 0-group cod and b) 0-group herring in the Barents Sea. Both show a positive relationship. See Table 5 for estimates of the slopes and explained deviance.

Table 6. Environmental and biotic effect on breeding success. The first null model is the best model from the first step in Table 4, the second null model is the best model from present first step (see legend of Table 4 for explanations).

Model	Estimate	P-value	Deviance	Explained deviance
Null model	+0.35 ± 0.27		52.7	0
NAO + 0-group cod abundance index	0.19 ± 0.29 +0.23 ± 0.21	0.3	44.704	0.15
NAO + 0-group cod abundance index + cod larval drift	+0.09 ±0.36 +0.24 ± 0.22 +0.1 ± 0.15	0.5	41.654	0.33

3.3 EFFECTS ON AVAILABILITY OF PREY

As for breeding success, the NAO index was the variable that explained most of the variance in the abundance of cod larvae in the Barents Sea, explaining 34 % of the total variance (reduction in deviance close to significant, p = 0.06). The combined effect of the large scale teleconnection patterns NAO and EAWR prior to breeding season was the best climate model, explaining 14 % of the variance in availability of cod. Table 7 lists the best models (see Appendix F, Table *ix* for all models). As with breeding success, the NAO had a positive effect on cod abundance, while the EAWR had a negative effect (Figure 10, see Appendix G, Figure *i-xii* for scatterplots of all relations not presented).

Table 7. Environmental effects on abundance of 0-group cod. Weights = modulated cod larval drift. The best models are shown (see legend of Table 4 for explanations).

Model	Estimate	P-value	Deviance	Explained deviance
Null model	+12.3 ± 0.19		588581836	0
NAO	+0.55 ± 0.27	0.06	385975689	0.34
SCAND	-1.18 ± 0.98	0.3	505241107	0.14
EAWR	-0.41 ± 0.53	0.5	549771960	0.07
Local mean SLP	+0.54 ± 0.63	0.4	546368649	0.07
NAO + EAWR	+0.71 ± 0.29 -0.75 ± 0.43	0.1	262641972	0.32

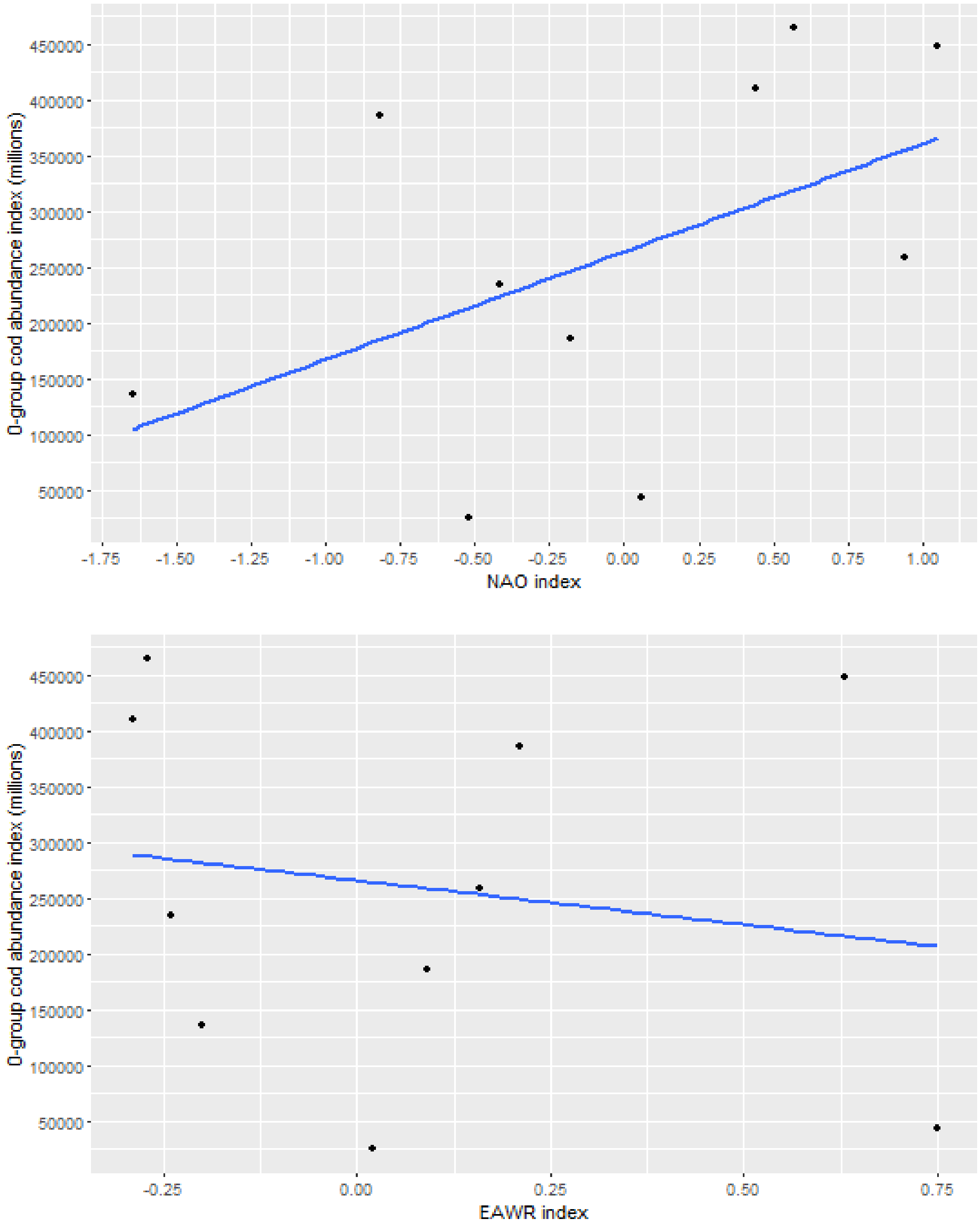


Figure 10. Selected relationships between the abundance of 0-group cod in the Barents Sea and environmental factors. The factors chosen are the ones which accounted for most of variation in abundance. a) show a positive relation between cod abundance and the NAO index prior to breeding, while b) show a negative relation with the EAWR index. See Table 7 for estimates of the slopes and explained deviance.

4 DISCUSSION

Of the climate and oceanographic variables, the single variable that explained the most of the variance in breeding success was the NAO index (explaining 17 %); supporting the hypothesis that short-time variation in breeding success is best explained by conditions prior to the breeding season. This also supports the popular use of NAO as a proxy for climate variability in ecological studies (Durant *et al.* 2003; Durant *et al.* 2004; Sandvik *et al.* 2005; Sandvik *et al.* 2012). The model containing both NAO and local SLP as covariates was able to explain 14 % of the variability in the breeding success, suggesting that both large-scale conditions prior to breeding and local conditions during the breeding season have an effect on breeding success. This is not surprising, since the NAO index represents the difference in atmospheric pressure between the low-pressure system in the north and high-pressure system in the south, influencing small-scale atmospheric conditions in the Barents Sea (Barnston & Livezey 1987; Mesquita *et al.* 2015). The difference in atmospheric pressure is also known to control the strength of the westerly winds in the North Atlantic, which is linked to several environmental variables such as precipitation, wind speed and temperature in this area (Barnston & Livezey 1987; Durant *et al.* 2004). The effect of climatic events such as increase in rainfall and storms may have direct effects on breeding success, as demonstrated for ivory gulls (*Pagophila eburnean*) breeding in North Greenland (Yannic *et al.* 2014). However, for seabirds such as puffins, where the chicks are protected in burrows, the effect of climate on breeding success is most apparent indirectly, through the food chain.

The indirect effect can be seen by the strong effect of cod larvae abundance on breeding success. Of all the variables included in this thesis, this was the single variable that explained the most variance in breeding success, explaining a total of 39 %. In addition, the multiple regression model explaining most of the variance, was the model including NAO, cod larvae abundance and cod larval drift as covariates, which explained 33 % of the variance. This supports the hypothesis that the pathways along which climate is hypothesized to influence the breeding success is indirect, through the availability of prey. Both the abundance of cod and herring had a positive effect on breeding success, though the effect of herring abundance was significantly smaller. This is not surprising, since cod makes up such a large part of the chick diet at Hjelmøya. The strong relationship between abundance of cod larvae and breeding success indicates that breeding success of these seabirds may be good indicators of fish stock in the area, and thereby the status of the marine environment, as documented for the breeding colony at Hornøya, east of Hjelmsøya in the Barents Sea area (Barrett 2002). The relationship between prey availability and breeding success is in accordance with similar studies on puffins breeding at Røst in the Norwegian Sea (Durant *et al.* 2003; Durant *et al.* 2004; Durant *et al.* 2006), where the fledging success and timing of breeding was affected indirectly through the effect of sea temperature and NAO on availability of 0- and 1-group herring, the main prey in this area.

As for breeding success, the NAO index was the single best climate variable, explaining 34 % of the variance in the abundance index of 0-group cod in the Barents Sea, illustrating a much clearer relationship between environmental conditions and fish abundance, than with breeding success. Although the effect of climate and oceanography on recruitment of fish is stated to be complex, it is well documented and supports the hypothesis that the effect of climatic and oceanographic conditions on breeding success is indirect, through the effect on lower trophic levels (Ottersen & Loeng 2000; Sætre *et al.* 2002; Fauchald *et al.* 2015b; Stige *et al.* 2015). A schematic illustration of the pathway along which climate was shown to affect the breeding success of the puffin colony at Hjelmsøya is presented in Figure 11.

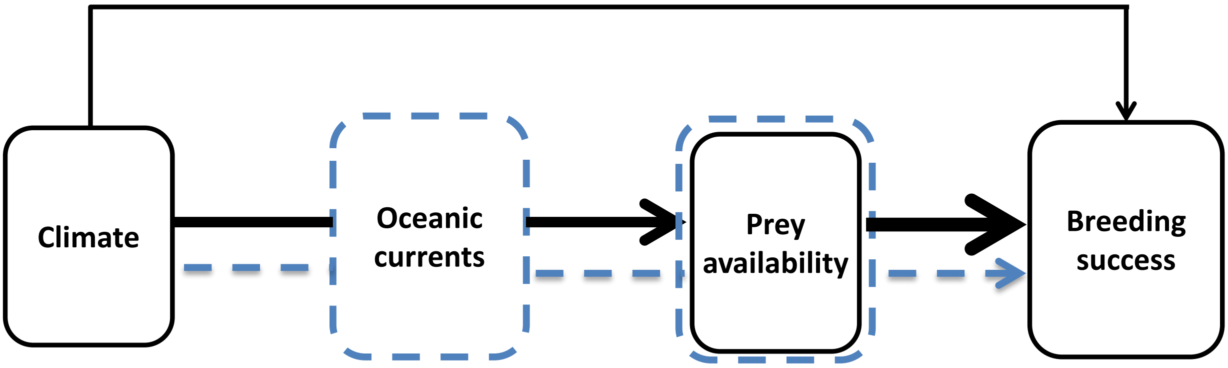


Figure 11. The climate effect pathway. Solid arrows illustrate the direct effect of the single variables tested in this thesis, each represented with the variable that explained most of the variance in breeding success and prey availability and the explanatory variance (%) ("climate", the NAO index; "oceanic currents", cod larval drift; "prey availability", 0-group cod abundance index). "Oceanic currents" is included in a dotted box to illustrate the pathway of which NAO most likely operates. The blue dotted lines represents the best multiple regression model.

Even though NAO was the climate variable that explained the most variance in both breeding success and cod larvae abundance, none of these effects were significant ($p > 0.05$). This is likely due to the small sample size of this study ($n = 10$), which decreases the statistical power of the results, increasing the probability of concluding that there is no effect. Given the small sample size of this study, only very large effects could be statistically significant, and even when significant this must be treated with caution. Other, specific climate indices could also have been included as parameters for climate variability affecting the breeding population at Hjelmsøya. Specific climate indices can be established using point maps, where point correlation and point regression are used to identify hotspots of climate variability that may explain the variability in ecological time-series such for specific areas (Mesquita *et al.* 2015). Climate indices based on hot spot areas may explain more of the variance in breeding success, than widely used proxies such as the NAO. However, when identifying such hot spots, larger time-series is preferable (Mesquita *et al.* 2015). Due to the small sample size, time lags of 1 year and more were also not included in the analysis. When reviewing the literature, time-lags are commonly used to investigate the indirect effects of climate (e.g Durant *et al.* 2004; Sandvik *et al.* 2005; Sandvik *et al.* 2012). A time-lag of 1-3 year is associated with indirect effects of climate, via its effect on the availability of prey in preceding years, while a longer time-lag is associated with the effects on recruitment (equivalent to the age of maturity) (Sandvik *et al.* 2012). Since the puffins breeding at Hjelmsøya predominantly feed their chicks with 0-group of cod and herring, the effects of the availability of prey in preceding years is probably less important. The adults may feed on older year classes of fish, which may be reflected in the body condition of the parents and hence their ability to rear young (Chastel *et al.* 1995; Kitaysky *et al.* 2000). Little specific is documented on the diet of adult puffins, since sampling of adult food choice is difficult (Harris & Wanless 2011), and new methods are needed. Studies on the common guillemot does, however, demonstrate a close relationship between 0-group abundance of cod and adult body condition during the breeding season (Barrett & Erikstad 2013; Erikstad *et al.* 2013). The time-lags equivalent to the age of maturity, and the body condition of the adults prior to breeding, are also most likely to influence the birds' decision to breed, affecting the size of yearly the breeding population, rather than the actual breeding success. While my results underpin the hypothesis that the effect of climatic and oceanographic conditions on breeding success is indirect, through the effect on lower trophic levels based on explained deviance, a larger sample size is required to detect the relative importance of each variable.

Both the NAO index and mean SSTs had a positive effect on breeding success and the abundance of 0-group cod , which indicates that an increase in temperature and westerly winds have a positive impact on the population breeding at Hjelmsøya as well as availability of prey. The positive effect on breeding success is in contrast to similar studies on kittiwakes (*Rissa tridactyla*) breeding both in the UK and Ireland (Carroll *et al.* 2015) and in Norway (including a colony at Hjelmøya) (Sandvik *et al.* 2014). Here, a warmer ocean was related to a decrease in both breeding success and population. A similar response is also true for arctic seabirds, such as the little Auk (*Alle alle*) and the Brünnich's guillemot (*Uria lomvia*) (Moe *et al.* 2009; Fauchald *et al.* 2015b). The arctic is experiencing a change in the spatial distribution of fish communities due to the northward expansion of boreal species (Fauchald *et al.* 2015b; Fossheim *et al.* 2015). However, a northward expansion might be beneficial for seabirds breeding further south in the Barents Sea, where it may improve the availability of prey (Fauchald *et al.* 2015b). Studies have shown how an increase in sea temperatures is favourable for the reproduction and survival of pelagic fish in the Barents Sea (Toresen & Østvedt 2000; Bogstad *et al.* 2013). Fish larva and younger year classes of fish prey on zooplankton. Zooplankton in turn are highly dependent on the phytoplankton bloom in the spring, which is known to fluctuate with SST (Durant *et al.*

2003). An example is the copepod *Calanus finmarchicus*, which has been demonstrated to have a positive influence on breeding success of the Atlantic puffin breeding in the Northeast Atlantic (Frederiksen *et al.* 2013). Knowing the importance of oceanographic conditions on lower trophic levels, a positive relationship between NAO, SST and larval drift on breeding success is coherent with the hypothesis that the effect of climate on breeding success is most apparent indirectly, through the food chain.

In contrast to most studies, e.g. the studies of Durant *et al.* (2003; 2006) at Røst, SST did not constitute a large effect on the breeding success. After NAO, the single variable that explained most of the variance in breeding success was the count of cod particles available at Hjelmsøya. Cod larval drift was included in the model to account for the oceanographic effect of oceanic currents which are incorporated in the models (Myksvoll *et al.* 2013). This is in accordance with Vikebø *et al.* (2010) results from the model simulation showing that although warmer water is favourable for survival, a rapid northwards displacement is more important for herring larvae survival than ambient temperature. According to Blindheim *et al.* (2000), the velocity of the Atlantic current is connected to the NAO index; when the NAO index is low the current can be displaced from the shelf and the velocity decreased, or onto the shelf with a high NAO, thereby increasing the current velocity. The positive effect of larvae drift can therefore be interpreted as the increase in inflow from the oceanic currents having a positive effect on prey availability at Hjelmsøya, and thereby breeding success. This is true for guillemots breeding at Hornøya, west in the Barents Sea area, where Myksvoll *et al.* (2013) showed that the variability in the contribution of cod larvae at Hornøya was positively linked to the inflow of Atlantic water, which had a positive effect on the growth and survival of guillemot chicks in the Hornøya colony.

While the focus in this study was the effect of climate and availability of prey on breeding success, other factors may have implications for breeding success, such as predation pressure (Sandvik *et al.* 2014). This is most likely the case for the puffins breeding at Hjelmsøya, an island which is accessible for e.g. mink (*Neovison vison*) which posed a problem during this year's field season. In fact, predation may have an amplifying negative effect on breeding success during years of low prey availability. During years of low prey availability, the adult puffins are forced to leave the nest more frequently and in longer durations to search for food (Monaghan *et al.* 1994), leaving the eggs and chicks vulnerable to predation. Increased predation from e.g. larger gulls, white-tailed eagle (*Haliaeetus albicilla*) and mink in combination with food shortage may therefore have profound negative consequences for individual breeding populations of seabirds (Finney *et al.* 2003; Hipfner *et al.* 2012; Fauchald *et al.* 2015b). This may have implications for conservation; while there are few management strategies regarding prey availability, measures dealing with the added stressor of predation pressure may mitigate the negative effect of declining prey availability (Fauchald *et al.* 2015b). Further monitoring and development of time-series on predation pressure at Hjelmsøya is needed for further research and development of local management plans.

4.1 CONCLUSIONS

In this thesis, I provide additional insight into the effects of climate on the population trajectories of a population not previously described. I found that the effect of climate on breeding success for the puffin colony at Hjelsmøya was most apparent indirectly, through the availability of cod larvae. The causal pathway by which climate seems to influence breeding success is by its effects on oceanic currents affecting larval drift and thereby the amount of fish larvae available to the puffins breeding at Hjelmsøya. Where earlier studies mainly consider the NAO index as a parameter for climate variability, I have included several other teleconnections to account for other modes of climate variability in the Northern Atlantic. My results show that NAO was the climate variable that explained most of the variance in breeding success and abundance of cod larvae, although significantly weaker than prey abundance. Larval drift was the oceanographic variable that explained most of the variance in breeding success, having a larger explained variance than local SST. While a more rapid displacement of fish larvae to the Barents Sea is shown to have positive effects for the birds breeding in this area, it also indicates a negative effect on breeding success for seabirds breeding further south in the Norwegian Sea. This study demonstrates the importance of further research, to investigate the causal links between climate and oceanographic conditions and breeding success of seabirds breeding in different regions. This may explain the differences in population trends for colonies in the Norwegian Sea and Barents Sea (Fauchald *et al.* 2015b).

APPENDIX A: FORMULAS USED TO ESTIMATE MASS (G) OF THE DIFFERENT CLASS OF PREY AT HJELMSØYA

The formulas are derived from a linear regression of measured length and mass of food items collected from puffins and guillemots at Hornøya (Barrett, R., personal communication, March 2, 2016)

$\mathrm{log10}(\mathrm{Herr\ m}) = -\ 6.346 + 3.542\ \mathrm{log10}(\mathrm{Herr\ l})$

$\mathrm{log10}(\mathrm{See\ m}) = -\ 6.128 + 3.285\ \mathrm{log10}(\mathrm{See\ l})$

$\mathrm{log10}(\mathrm{Cap\ m}) = -\ 6.012 + 3.311\ \mathrm{log10}(\mathrm{Cap\ l})$

$\mathrm{log10}(\mathrm{Gad\ m}) = -\ 5.495 + 3.174\ \mathrm{log10}(\mathrm{Gad\ l})$¨

$\mathrm{log10}(\mathrm{See\ lar\ m}) = -\ 6.130 + 3.286\ \mathrm{log10}(\mathrm{See\ lar\ l})$

$\mathrm{log10}(\mathrm{Herr\ lar\ m}) = -\ 6.605 + 3.699\ \mathrm{log10}(\mathrm{Herr\ larv\ l})$

Herr/See/Cap/Gad/See lar/Herr lar l = length of herring, sandeel, capelin, gadoids, sandeel larvae and herring larvae respectfully.

The length of each group is calculated by multiplying the measure of the length of the food item in relation to bill height with mean bill height ± the standard error (38.17 ± 0.13, n = 276).

Herr/See/Cao/Gad/See lar/Herr lar m = mass (g) of each class of prey.

APPENDIX B: BIOTIC, CLIMATE AND OCEANOGRAPHIC TIME-SERIES

Table *i*. Cod particles in a 20x20 km box around the breeding colony at Hjelmsøya, modelled using an individual-based (particle) model (larval drift).

20km	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
01.mai	281	902	427	811	548	745	836	195	441	643
02.mai	291	860	509	816	508	797	725	168	401	653
03.mai	317	876	518	762	501	890	429	187	397	633
04.mai	422	896	431	792	554	903	728	262	402	605
05.mai	481	883	570	658	484	915	768	179	514	666
06.mai	505	871	632	709	587	877	809	144	515	699
07.mai	527	778	534	805	626	807	1012	166	516	717
08.mai	527	810	333	707	501	849	1106	177	523	699
09.mai	485	727	315	631	475	807	1077	189	521	672
10.mai	465	649	273	573	488	731	576	235	525	662
11.mai	604	640	248	537	488	742	655	205	449	533
12.mai	692	870	308	544	504	772	747	267	460	500
13.mai	608	1085	309	528	522	1019	743	255	520	535
14.mai	710	1055	348	515	513	1067	701	264	534	514
15.mai	520	1050	277	490	490	1021	610	322	520	511
16.mai	498	1054	253	479	465	988	530	245	428	640
17.mai	442	1022	235	476	455	926	517	222	407	696
18.mai	457	1033	217	487	466	872	499	207	392	652
19.mai	499	973	290	620	460	828	562	234	363	672
20.mai	456	978	622	865	454	878	551	242	358	810
21.mai	424	982	690	928	454	727	510	245	399	758
22.mai	376	927	682	988	447	803	557	245	375	741
23.mai	212	928	674	972	440	760	608	234	327	643
24.mai	176	941	686	920	433	712	640	207	508	631
25.mai	179	909	649	898	436	733	653	173	567	715
26.mai	146	895	601	870	466	673	586	147	592	730
27.mai	121	875	377	788	608	616	533	145	576	709
28.mai	105	877	222	707	654	639	528	145	557	708
29.mai	104	831	232	742	650	653	509	145	559	671
30.mai	108	815	217	705	1009	647	540	142	533	656
31.mai	112	882	185	539	939	609	547	168	533	647
01.jun	114	969	162	571	675	543	549	138	546	530
02.jun	114	942	164	572	523	503	532	147	489	639
03.jun	111	805	167	628	525	520	533	121	343	682
04.jun	112	826	166	674	493	524	555	125	331	700
05.jun	132	741	167	675	458	563	1106	131	333	557
06.jun	120	607	156	666	405	575	1404	132	324	423

07.jun	108	544	153	614	347	534	1340	140	335	293
08.jun	101	562	142	546	360	521	1341	124	347	280
09.jun	117	536	145	521	372	493	1333	120	350	266
10.jun	184	554	160	684	371	683	1312	118	355	265
11.jun	209	596	161	622	389	1151	1280	121	358	317
12.jun	201	835	169	493	384	1334	1308	119	368	281
13.jun	152	629	171	468	375	1424	1317	115	274	295
14.jun	113	650	169	467	407	1417	1320	121	261	275
15.jun	127	615	161	493	436	1391	1216	120	254	261
16.jun	163	638	249	602	372	1334	1149	134	272	256
17.jun	156	639	175	1089	359	1191	1110	117	279	278
18.jun	146	607	152	959	339	1122	1135	88	359	228
19.jun	160	625	155	1072	294	1109	1195	81	329	173
20.jun	146	649	161	1086	294	1114	1236	103	367	220
21.jun	140	573	360	1005	300	1106	1229	116	358	249
22.jun	126	599	373	980	301	1106	1248	105	429	245
23.jun	134	595	356	900	337	1114	1272	88	520	232
24.jun	163	623	240	676	317	1184	1208	93	548	230
25.jun	297	644	251	536	329	1184	1263	84	524	215
26.jun	286	723	295	490	370	1232	1292	76	513	167
27.jun	165	581	225	366	350	1269	1234	74	508	174
28.jun	172	864	240	411	352	919	1134	85	568	207
29.jun	138	905	229	426	356	806	1208	78	570	200
30.jun	138	819	198	491	374	737	1284	92	576	205
01.jul	144	743	291	525	360	736	1356	95	589	219
02.jul	140	653	265	500	433	772	1406	84	595	228
03.jul	143	698	233	527	474	841	1422	86	613	259
04.jul	137	635	221	518	504	869	1384	86	632	241
05.jul	142	622	252	399	537	793	1177	112	651	236
06.jul	162	546	240	374	506	852	1273	102	575	246
07.jul	131	568	245	377	433	863	1287	89	767	236
08.jul	128	797	231	377	497	825	878	118	850	369
09.jul	122	981	228	341	426	809	827	334	840	395
10.jul	130	954	207	345	442	788	1147	112	826	394
11.jul	118	766	185	383	445	764	1175	124	718	377
12.jul	115	1003	141	425	436	813	1046	120	603	398
13.jul	116	909	174	626	429	837	972	163	596	393
14.jul	124	788	251	674	429	730	1031	81	614	406
15.jul	152	750	283	762	470	663	1119	82	626	417
16.jul	124	717	293	670	476	716	1105	144	633	423
17.jul	124	730	233	641	480	1075	921	139	606	374
18.jul	119	757	149	587	466	1084	940	129	617	429
19.jul	118	786	164	615	442	692	1071	125	600	472
20.jul	126	763	182	653	541	894	1091	134	611	410

21.jul	123	788	171	646	555	1109	1075	186	582	398
22.jul	116	712	136	645	770	1125	1124	155	597	403
23.jul	90	704	159	633	854	831	1075	144	612	355
24.jul	89	841	162	589	695	815	1053	129	569	391
25.jul	122	868	225	614	661	1009	1034	121	503	377
26.jul	133	874	212	568	602	974	976	117	530	339
27.jul	108	884	300	603	638	1067	936	133	586	350
28.jul	95	1026	284	609	638	1050	894	143	551	329
29.jul	90	1059	286	597	595	1012	936	148	553	329
30.jul	165	1052	259	572	576	918	944	173	534	316
31.jul	180	1012	315	536	598	836	1152	276	520	302

Table *ii*. 0-group abundance indices (in millions) for Northeast Atlantic cod and Norwegian spring-spawning herring with 95 % confidence limits, corrected for catching efficiency.

Year	**0-group cod**			**0-group herring**		
	Abundance index	**Confidence limits**		**Abundance index**	**Confidence limits**	
2006	25061	11469	38653	294649	102788	486511
2007	42628	26652	58605	144002	25099	262905
2008	234144	131081	337208	201046	68778	333313
2009	185457	123375	247540	104233	31009	177458
2010	135355	68199	202511	117087	32045	202129
2011	448005	251499	644511	83051	48024	118078
2012	410757	170242	651273	855742	0	2111493
2013	385430	269640	501219	289391	67718	511064
2014	464124	323330	604919	136305	42164	230447
2015	240309.8			235143.3		

APPENDIX C: R-SYNTAX

CORRELATION TEST OF THE TELECONNECTION INDICES

```
               NAO_s    SCAND_s       PNA_s        EA_s      EAWR_s        AO_s       AMO_s
NAO_s     1.00000000  0.2702577 -0.06606938  0.23759657 -0.28843794  0.71137825  0.12292345
SCAND_s   0.27025771  1.0000000 -0.10036620 -0.51732364 -0.17226214 -0.25408694  0.45265911
PNA_s    -0.06606938 -0.1003662  1.00000000  0.04934311  0.35321729 -0.17461608 -0.59350305
EA_s      0.23759657 -0.5173236  0.04934311  1.00000000  0.03907996  0.74127499 -0.44339320
EAWR_s   -0.28843794 -0.1722621  0.35321729  0.03907996  1.00000000 -0.35909844 -0.58453499
AO_s      0.71137825 -0.2540869 -0.17461608  0.74127499 -0.35909844  1.00000000 -0.06642139
AMO_s     0.12292345  0.4526591 -0.59350305 -0.44339320 -0.58453499 -0.06642139  1.00000000
BO_s      0.53415658  0.0759286 -0.44569912 -0.28618771 -0.36387102  0.17461467  0.56179805
NAO_w    -0.33796046 -0.3735480  0.01764966 -0.22956390  0.37878629 -0.20065297 -0.42060032
SCAND_w   0.45992107  0.3263112  0.23724631 -0.20168012 -0.30428459  0.16637815  0.38105973
PNA_w    -0.14363401 -0.1867890  0.15302860  0.52239660 -0.40033784  0.30178982  0.06576954
EA_w      0.15563309  0.2488775 -0.13973232  0.00553489 -0.30751993  0.08915437  0.11734429
EAWR_w    0.26423771  0.1168550  0.65965291 -0.04554063  0.07662824  0.07619049 -0.50840304
AO_w     -0.49547593 -0.2913254  0.08114745 -0.34289172  0.47781958 -0.43729916 -0.38371317
BO_w     -0.37520312 -0.8067649 -0.04188165  0.44638163  0.19622070  0.15815971 -0.09251937
AMO_w     0.18509415  0.4321622  0.01917501  0.18076925 -0.62746955  0.24264815  0.31728421
                BO_s       NAO_w     SCAND_w       PNA_w        EA_w      EAWR_w
AO_w
NAO_s     0.53415658 -0.33796046  0.45992107 -0.14363401  0.15563309  0.26423771 -
0.49547593
SCAND_s   0.07592860 -0.37354800  0.32631116 -0.18678903  0.24887748  0.11685495 -
0.29132536
PNA_s    -0.44569912  0.01764966  0.23724631  0.15302860 -0.13973232  0.65965291
0.08114745
EA_s     -0.28618771 -0.22956390 -0.20168012  0.52239660  0.00553489 -0.04554063 -
0.34289172
EAWR_s   -0.36387102  0.37878629 -0.30428459 -0.40033784 -0.30751993  0.07662824
0.47781958
AO_s      0.17461467 -0.20065297  0.16637815  0.30178982  0.08915437  0.07619049 -
0.43729916
AMO_s     0.56179805 -0.42060032  0.38105973  0.06576954  0.11734429 -0.50840304 -
0.38371317
BO_s      1.00000000 -0.20473445  0.37078315 -0.37750061  0.01157773 -0.27956917 -
0.27380102
NAO_w    -0.20473445  1.00000000 -0.46665227 -0.55032260 -0.20787784  0.30241893
0.94104975
SCAND_w   0.37078315 -0.46665227  1.00000000  0.26107950  0.21034848 -0.04138703 -
0.56399562
PNA_w    -0.37750061 -0.55032260  0.26107950  1.00000000  0.28936035 -0.25966351 -
0.56915636
EA_w      0.01157773 -0.20787784  0.21034848  0.28936035  1.00000000 -0.18063006 -
0.16598956
EAWR_w   -0.27956917  0.30241893 -0.04138703 -0.25966351 -0.18063006  1.00000000
0.28137584
AO_w     -0.27380102  0.94104975 -0.56399562 -0.56915636 -0.16598956  0.28137584
1.00000000
BO_w     -0.09479478  0.13130009 -0.23394128  0.29514502 -0.51425114 -0.37063730
0.09756628
AMO_w    -0.18072297 -0.64849996  0.14817587  0.54884487  0.02365978  0.16504693 -
0.63925244
```

```
               BO_w      AMO_w
NAO_s   -0.37520312  0.18509415
SCAND_s -0.80676489  0.43216221
PNA_s   -0.04188165  0.01917501
EA_s     0.44638163  0.18076925
EAWR_s   0.19622070 -0.62746955
AO_s     0.15815971  0.24264815
AMO_s   -0.09251937  0.31728421
BO_s    -0.09479478 -0.18072297
NAO_w    0.13130009 -0.64849996
SCAND_w -0.23394128  0.14817587
PNA_w    0.29514502  0.54884487
EA_w    -0.51425114  0.02365978
EAWR_w  -0.37063730  0.16504693
AO_w     0.09756628 -0.63925244
BO_w     1.00000000 -0.22277662
AMO_w   -0.22277662  1.00000000
```

CROSS-CORRELATION ANALYSIS OF LOCAL MEAN SST AND SLP

```
Autocorrelations of series ‘X’, by lag

   -14    -13    -12    -11    -10     -9     -8     -7     -6     -5     -4
-3     -2
-0.012  0.314  0.380  0.044 -0.396 -0.445  0.024  0.356  0.452  0.021 -0.481
-0.539 -0.019
    -1      0      1      2      3      4      5      6      7      8      9
10     11
 0.384  0.544  0.049 -0.511 -0.603 -0.031  0.372  0.584  0.104 -0.436 -0.500
-0.027  0.314
    12     13     14
 0.470  0.073 -0.338
```

APPENDIX D: ECOLOGICAL TIME-SERIES

Table *vi*. Time-series of breeding success/failure for the puffin colony breeding at Hjelmsøya. Data is provided by the SEAPOP program.

Year	Date	Nests	Hatched	Breeding failure (chicks)	Breeding failure	Breeding success (%)	Chick survival
2006	13.06.2007	101	26	26	75	26	0.57
2007	14.07.2007	117	48	26	91	22	0.54
2008	12.07.2008	100	120	14	86	14	0.74
2009	14.07.2009	82	148	9	73	11	0.90
2010	15.07.2010	74	0	6	68	08	0.75
2011	12.07.2011	73	24	24	49	33	1.00
2012	15.07.2012	93	22	32	61	34	1.00
2013	13.07.2013	100	41	19	81	19	0.63
2014	17.07.2014	119	19	44	75	37	0.72
2015	17.07.2015	117	39	10	107	9	0.34

Table *vii*. Count of prey fish in the food samples collected for the colony breeding at Hjelmsøya 2006-2015.

Year	herring	sandeel	capelin	cod	codfish	other	undefined	Grand Total
2006	7	5			3	1	23	39
2007		3					11	14
2008	65	2	1	23	31	1	10	133
2009	331	7		14	12		41	405
2010	26	29	1	65	60		47	228
2011	206	16		100	53		44	419
2012	823	99	1	60	23		47	1053
2013	485	21		75	3	1	48	633
2014	193	50	31	175	33	2	118	602
2015	270	231		1	11		6	519
Grand Total	2406	463	34	513	229	5	395	4045

APPENDIX E: CHICK DIET EFFECT ON BREEDING SUCCESS R-SYNTAX

```
Call:
glm(formula = cbind(success, failure) ~ gadoid + herring + sandeel, 
    family = binomial, data = puffin1)

Deviance Residuals: 
      1        2        3        4        5        6        7  
-2.0542  -3.3590   1.9866   3.6303   0.8374   0.0000  -1.8658  

Coefficients:
            Estimate Std. Error z value Pr(>|z|)    
(Intercept)   24.523      7.942   3.088 0.002017 ** 
gadoid       -25.601      8.068  -3.173 0.001507 ** 
herring      -26.875      7.866  -3.417 0.000633 ***
sandeel      -26.334      8.021  -3.283 0.001027 ** 
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 60.873  on 6  degrees of freedom
Residual deviance: 36.811  on 3  degrees of freedom
AIC: 75.933

Number of Fisher Scoring iterations: 4

> fit.glm<-glm(cbind(success,failure)~gadoid+herring+sandeel, 
data=puffin1, family=quasibinomial)
> summary(fit.glm)

Call:
glm(formula = cbind(success, failure) ~ gadoid + herring + sandeel, 
    family = quasibinomial, data = puffin1)

Deviance Residuals: 
      1        2        3        4        5        6        7  
-2.0542  -3.3590   1.9866   3.6303   0.8374   0.0000  -1.8658  

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)    24.52      27.81   0.882    0.443
gadoid        -25.60      28.25  -0.906    0.432
herring       -26.88      27.54  -0.976    0.401
sandeel       -26.33      28.09  -0.938    0.418
```

```
(Dispersion parameter for quasibinomial family taken to be 12.26056)

    Null deviance: 60.873  on 6  degrees of freedom
Residual deviance: 36.811  on 3  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 4

> anova(fit.glm)
Analysis of Deviance Table

Model: quasibinomial, link: logit

Response: cbind(success, failure)

Terms added sequentially (first to last)


        Df Deviance Resid. Df Resid. Dev
NULL                        6     60.873
gadoid   1   9.4774         5     51.395
herring  1   4.1525         4     47.243
sandeel  1  10.4318         3     36.811
```

APPENDIX F: ALL STATISTICAL MODELS

Table *viii.* All environmental and biotic effects on breeding success for the colony at Hjelmsøya (estimate, β-estimate of the effect ± std. error; Resid.Dev, residual deviance; ΔResid.Dev, difference between the Resid. Dev of the current model and the null model; P-value, significanse level of the reduction in Resid. Dev compared to the null model).

Model	Estimate	P-value	Resid.Dev	ΔResid.Dev	ΔResid.Dev proportion
Environmental effects					
First null model (intercept)	-1.3 ± 0.2		63.3	0.0	0.00
NAO	+0.35 ± 0.27	0.2	52.7	-10.6	0.17
SCAND	+0.46 ± 1.01	0.7	61.8	-1.6	0.02
EAWR	-0.12 ± 0.62	0.9	63.1	-0.3	0.00
BO	-0.09 ± 0.7	0.9	63.2	-0.2	0.00
local mean SST, during breeding season	+0.17 ± 0.71	0.8	62.9	-0.4	0.01
local mean SLP	+0.57 ± 0.66	0.4	58.1	-5.3	0.08
local mean SST, *prior* to breeding season	+0.41 ± 1.65	0.8	62.9	-0.5	0.01
cod larval drift	+0.15 ± 0.13	0.3	54.2	-9.1	0.14
Second null model (NAO)	+0.35 ± 0.27		52.7	0.0	0.00
NAO + SCAND	+0.45 ± 0.29 +1.07 ± 1.02	0.3	45.9	-6.8	0.13
NAO + EAWR	+0.37 ± 0.8 -0.28 ± 0.58	0.6	51.2	-1.6	0.03
NAO + BO	+0.37 ± 0.29 -0.29 ± 0.67	0.7	51.5	-1.3	0.02
NAO + local mean SST, during	+0.34 ± 0.28 +0.15 ± 0.71	0.8	52.4	-0.3	0.01
NAO + local mean SLP	+0.38 ± 0.27 +0.64 ± 0.6	0.3	45.5	-7.2	0.14
NAO + local mean SST, *prior*	+0.36 ± 0.3 -0.25 ± 0.64	0.9	52.6	-0.1	0.00
Third null model (NAO + local mean SLP)	+0.38 ± 0.27 +0.64 ± 0.6		45.5	0.0	0.00
NAO + local mean SLP + SCAND	+0.44 ± 0.3 +0.49 ± 0.66 +0.77 ± 1.11	0.5	42.2	-3.3	0.07
NAO + local mean SLP + EAWR	+0.4 ± 0.3 +0.6 ± 0.67 -0.11 ± 0.64	0.9	45.3	-0.2	0.00
NAO + local mean SLP + BO	+0.36 ± 0.3 +0.84 ± 0.9 +0.32 ± 0.94	0.7	44.7	-0.8	0.02
NAO + local mean SLP + local mean SST	+0.38 ± 0.3 +0.63 ± 0.64 +0.11 ± 0.74	0.9	45.4	-0.2	0.00
NAO + local mean SLP + local mean SST, *prior*	+0.35 ± 0.3 +0.8 ± 0.72 +0.86 ± 1.92	0.7	44.2	-1.3	0.03

Biotic effects (weights = cod larval drift)					
First null model (intercept)	-0.18 ± 0.2		34801	0	0.00
0-group cod abundance index	+0.36 ± 0.16	0.05	21138	-13663	0.39
0-group herring abundance index	+0.11 ± 0.74	0.3	29708	-5093	0.15
Second null model (0-group cod abundance index)	+0.36 ± 0.16			0	0.00
0-group cod + 0-group herring index	+0.32 ± 0.17 +0.09 ± 0.14	0.5	20029	-1109	0.05
Combined environmental and biotic effects					
Second null model (NAO)	+0.35 ± 0.27		52.7	0.0	0.00
NAO + 0-group cod abundance index	+0.19 ± 0.29 +0.23 ± 0.21	0.3	44.7	-8.0	0.15
NAO + 0-group herring abundance index	+0.33 ± 0.28 0.17 ± 0.19	0.4	48.0	-4.7	0.09
NAO + 0-group cod abundance index + cod larval drift	+0.09 ±0.36 +0.24 ± 0.22 +0.1 ± 0.15	0.5	41.7	-11.1	0.33
NAO + mean SLP + 0-group cod abundance index + cod larval drift	+0.13 ± 0.4 +0.58 ± 0.82 +0.14 ± 0.27 +0.14 ± 0.17	0.6	37.7	-7.8	0.17

Table *ix.* All environmental effects on abundance of 0-group Northeast Atlantic cod. Weights = modulated cod larval drift (see legend of Table *viii* for explanations).

Model	**Estimate**	**P-value**	**Resid.Dev**	**ΔResid.Dev**	**ΔResid.Dev proportion**
First null model (intercept)	+12.3 ± 0.19		588581836	0	0.00
NAO	+0.55 ± 0.27	0.06	385975689	-202606147	0.34
SCAND	-1.18 ± 0.98	0.3	505241107	-83340729	0.14
EAWR	-0.41 ± 0.53	0.5	549771960	-38809876	0.07
BO	+0.3 ± 0.6	0.6	573379756	-15202080	0.03
Local mean SST	+0.17 ± 0.92	0.9	586639789	-1942047	0.00
Local mean SLP	+0.54 ± 0.63	0.4	546368649	-42213187	0.07
Second null model (NAO)	+0.55 ± 0.27		385975689	0	0.00
NAO + SCAND	+0.51 ± 0.33 -0.29 ± 1.12	0.8	382827551	-3148138	0.01
NAO + EAWR	+0.71 ± 0.29 -0.75 ± 0.43	0.1	262641972	-123333717	0.32
NAO + BO	+0.55 ± 0.29 +0.21 ± 0.51	0.7	378347093	-7628596	0.02
NAO + local mean SST	+0.57 ± 0.3 -0.25 ± 1.03	0.8	383041712	-2933977	0.01
NAO + local mean SLP	+0.54 ± 0.27 +0.48 ± 0.52	0.4	347806563	-38169126	0.10

NAO + local mean SST, *prior*	+0.56 ± 0.3 +0.46 ± 1.03	0.7	376684730	-9290959	0.02
Third null model (NAO + EAWR)	+0.71 ± 0.29 -0.75 ± 0.43		262641972	0	0.00
NAO + EAWR + SCAND	+0.7 ± 0.34 -0.75 ± 0.46 -0.07 ± 1.02	1	262462590	-179382	0.00
NAO + EAWR + BO	+0.74 ± 0.3 -0.91 ± 0.5 -0.32 ± 0.51	0.6	246709614	-15932358	0.06
NAO + EAWR + local mean SLP	+0.71 ± 0.29 -0.77 ± 0.43 +0.46 ± 0.44	0.3	221994198	-40647774	0.15
NAO + EAWR + local mean SST, prior	+0.79 ± 0.28 -0.24 ± 0.57 -1.49 ± 1.26	0.3	212723502	-49918470	0.19

APPENDIX G – SCATTERPLOTS

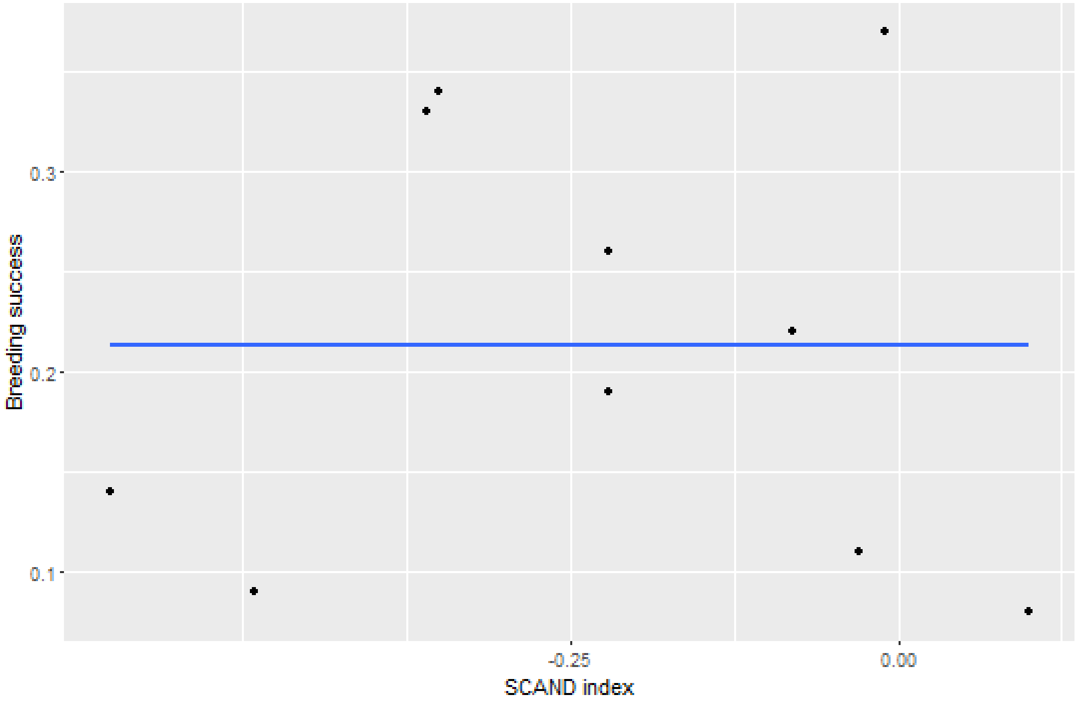
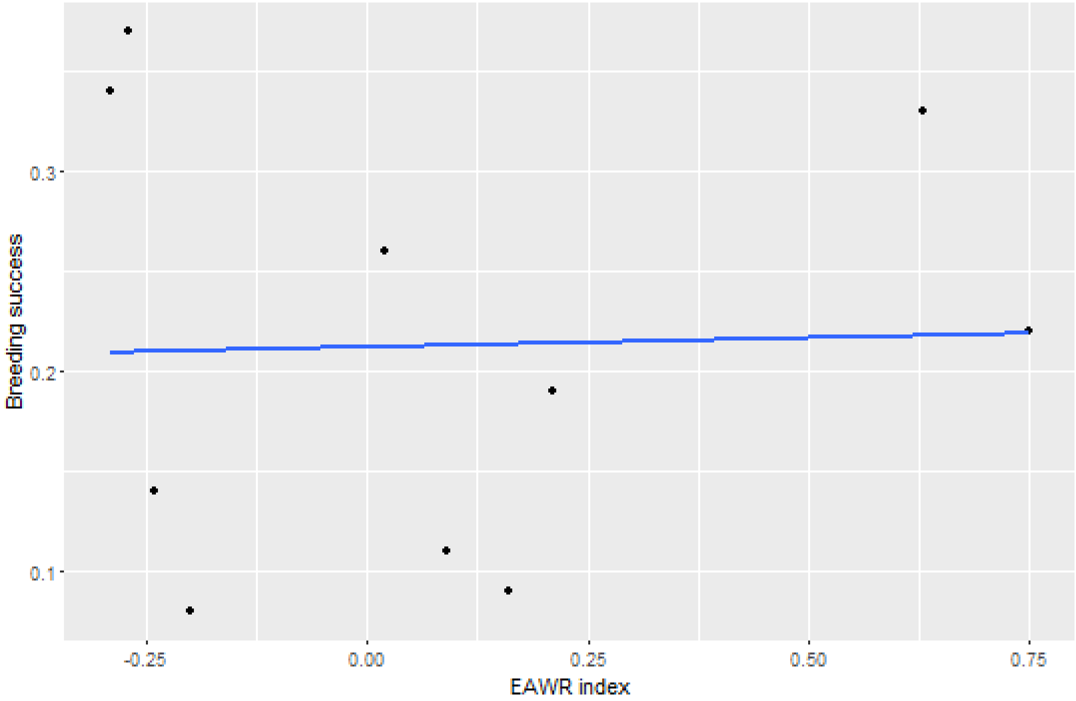


Figure *i*. Relationship between breeding success and the SCAND index.



Figure*ii*. Relationship between breeding success and the EAWR index.

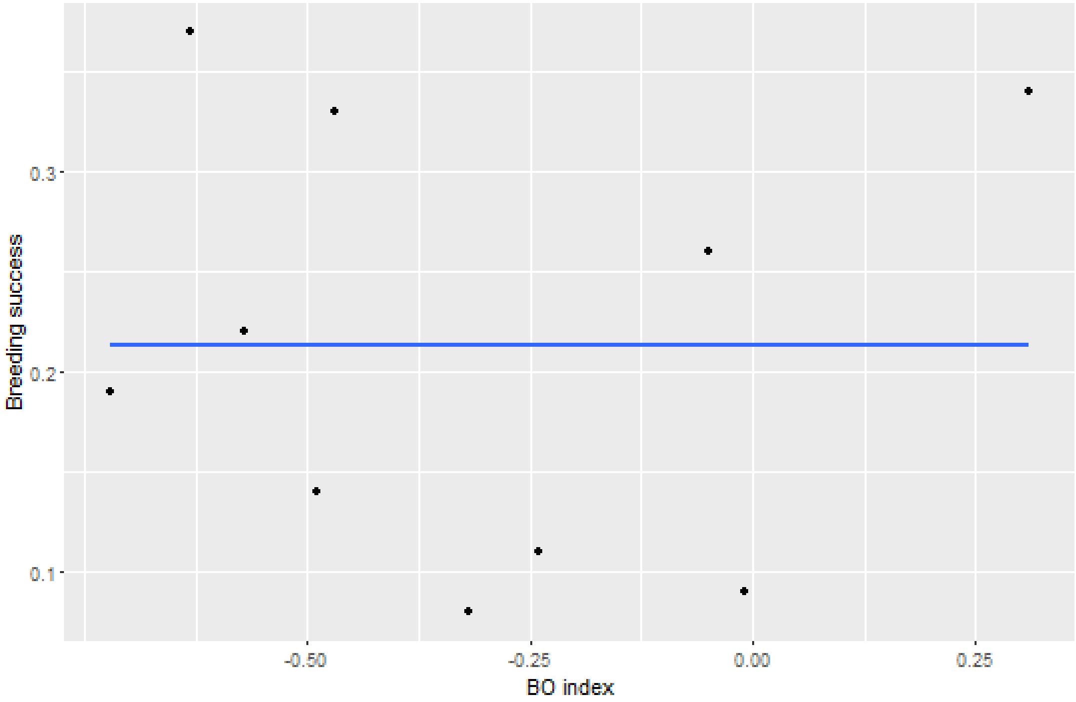


Figure *iii.* Relationship between breeding success and the BO index.

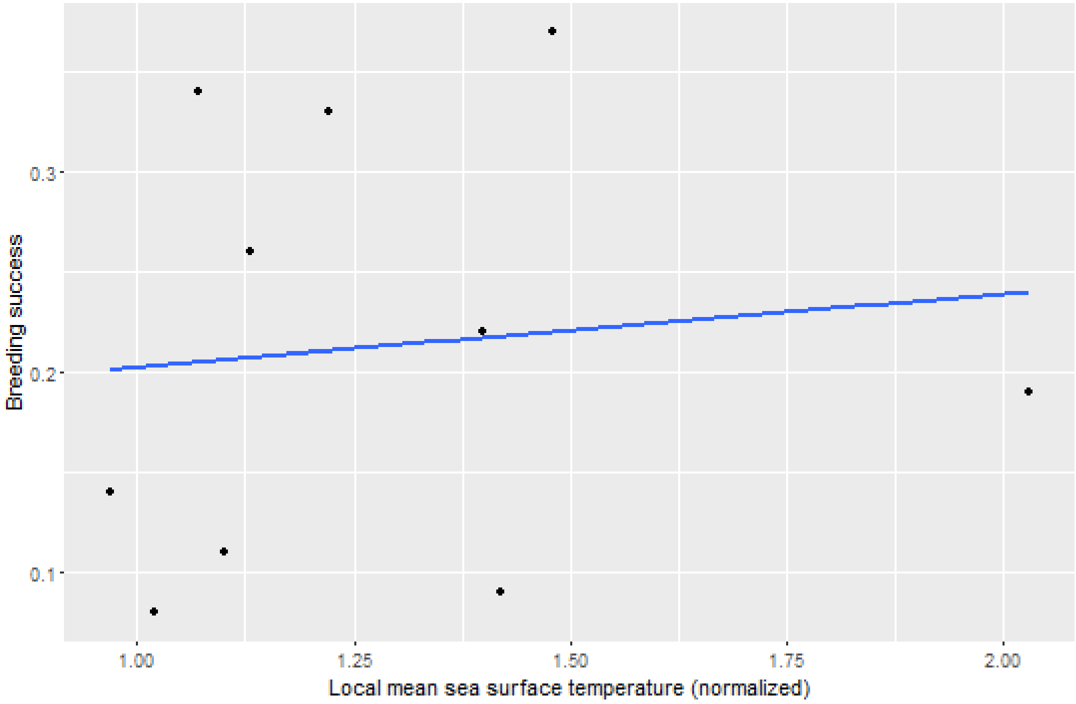


Figure *iv*. Relationship between breeding success and local mean SST (summer).

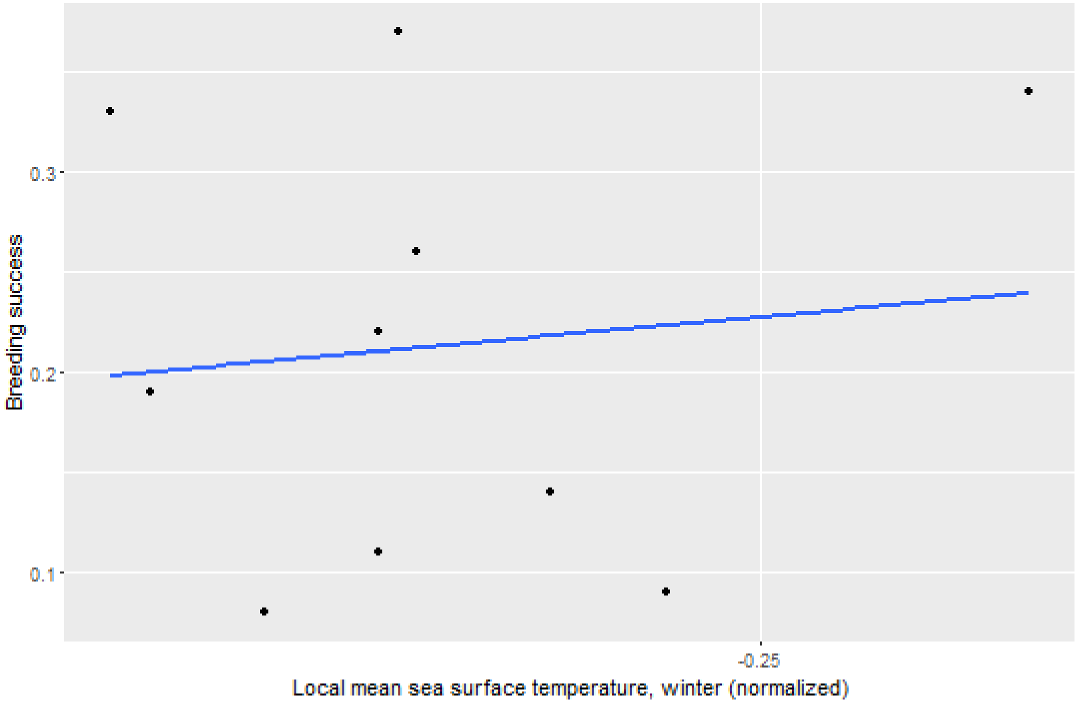


Figure *v.* Relationship between breeding success and local mean SST (winter).

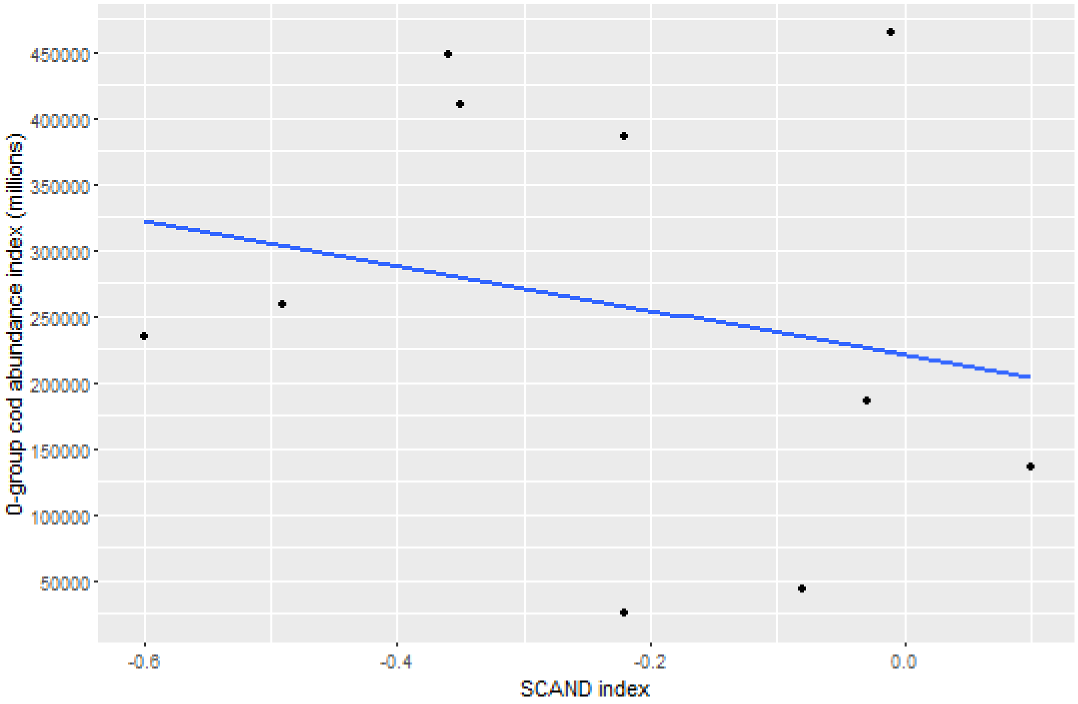


Figure *vi.* Relationship between 0-group cod abundance index and the SCAND index.

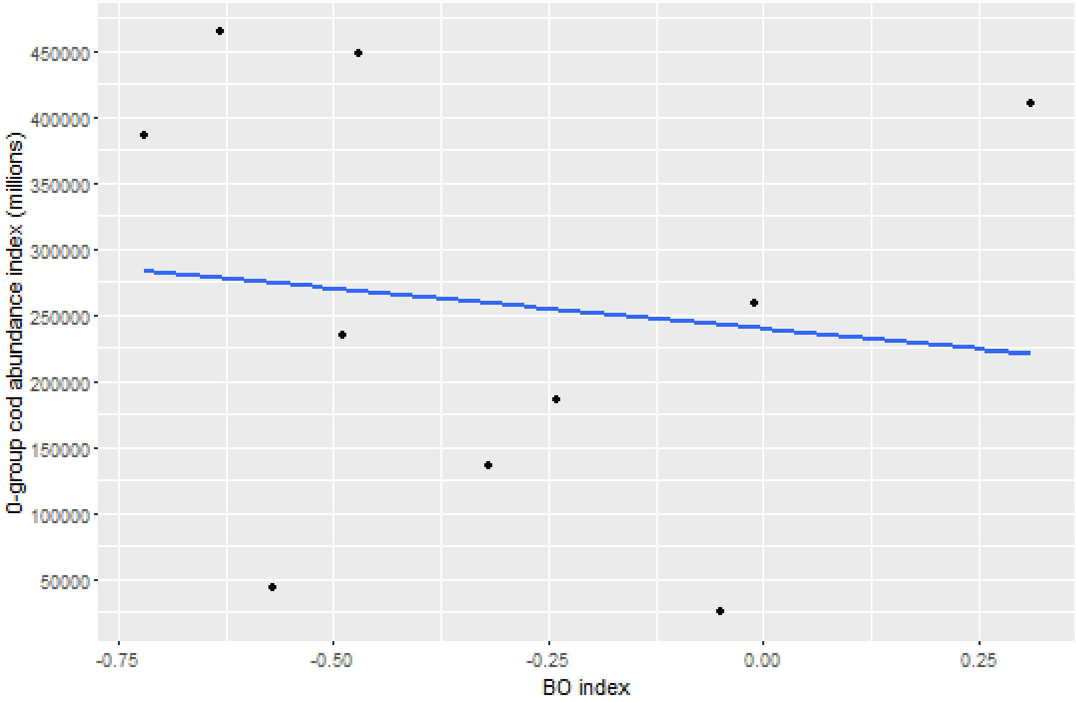


Figure *vii.* Relationship between 0-group cod abundance index and the BO index.

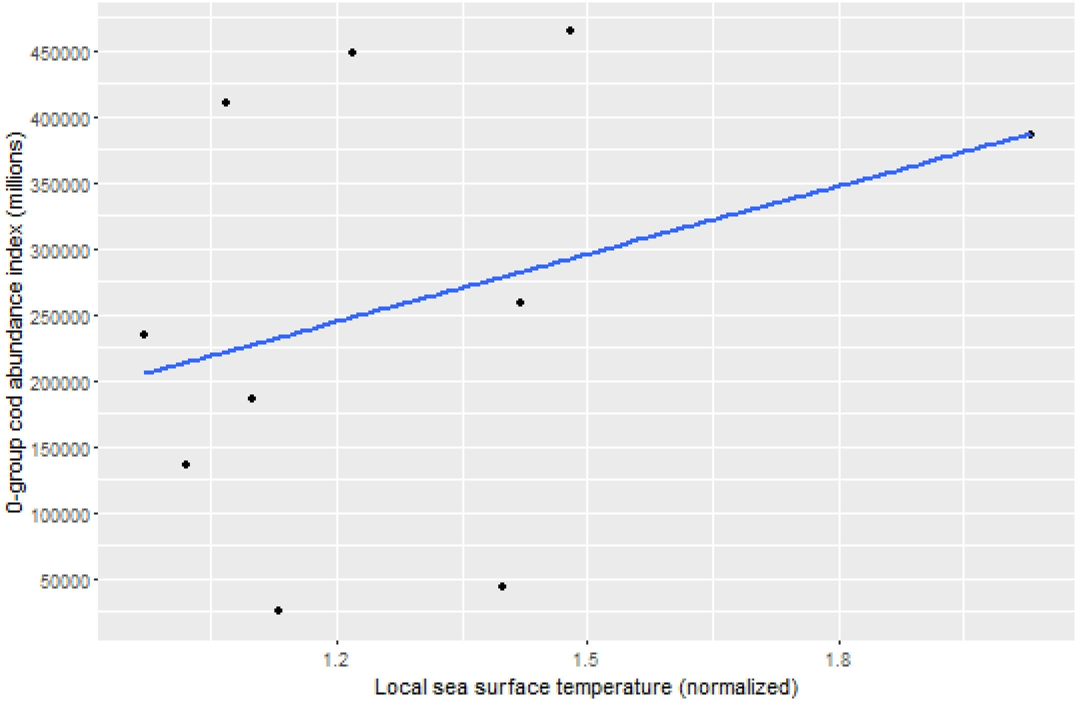


Figure *viii.* Relationship between 0-group cod abundance index and local SST.

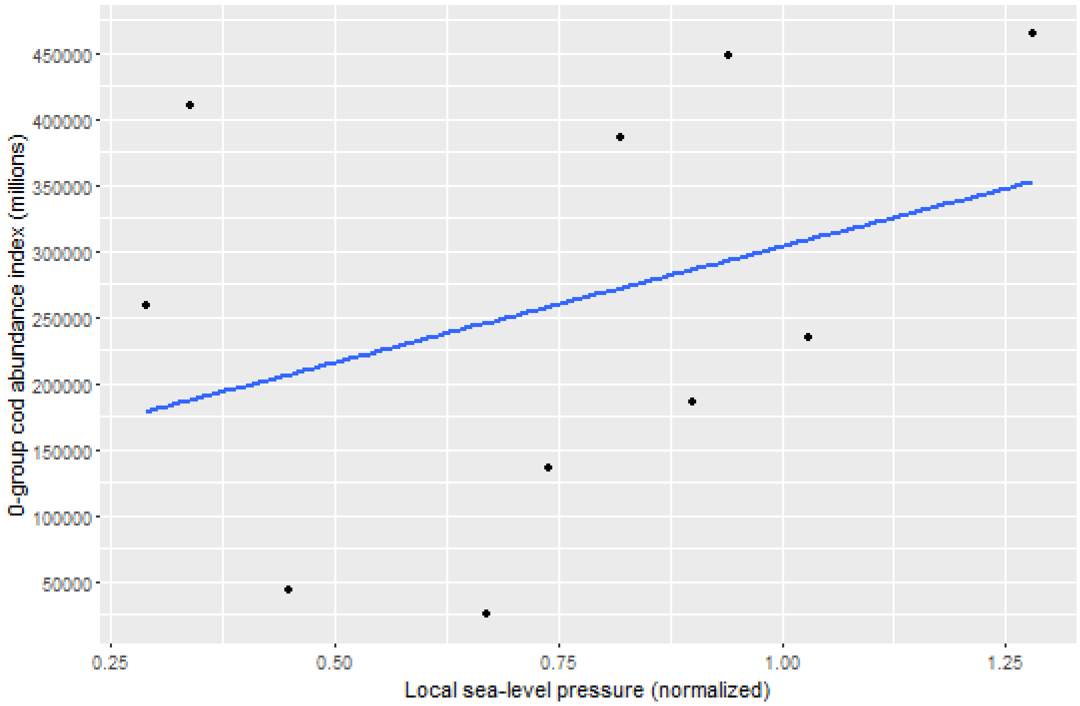


Figure *ix.* Relationship between 0-group cod abundance index and local mean SLP.

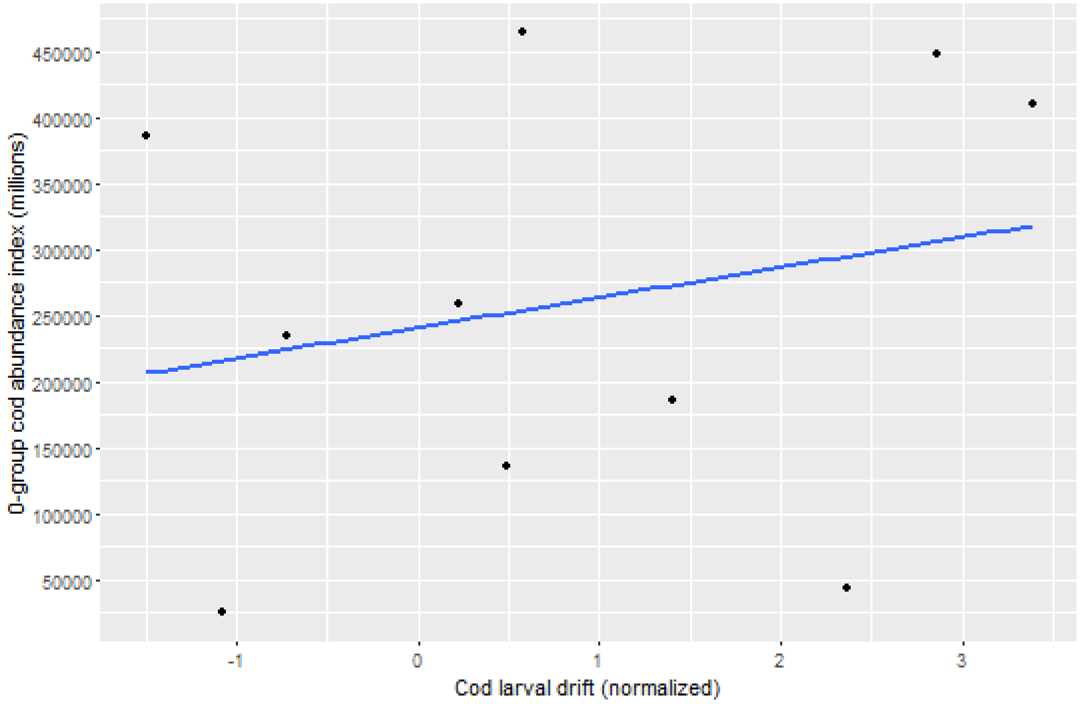


Figure *x.* Relationship between 0-group cod abundance index and cod larval drift.

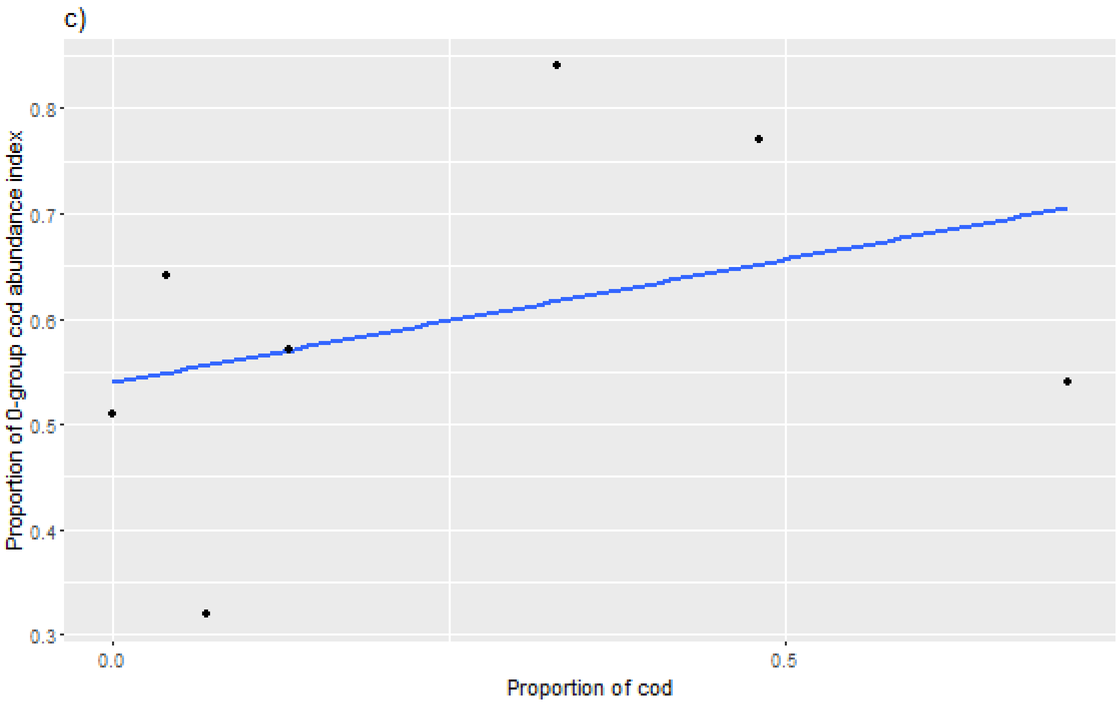


Figure *xi*. Relationship between the ratio of cod in the chick diet and proportion of cod abundance in the Barents Sea (both in relation to herring).

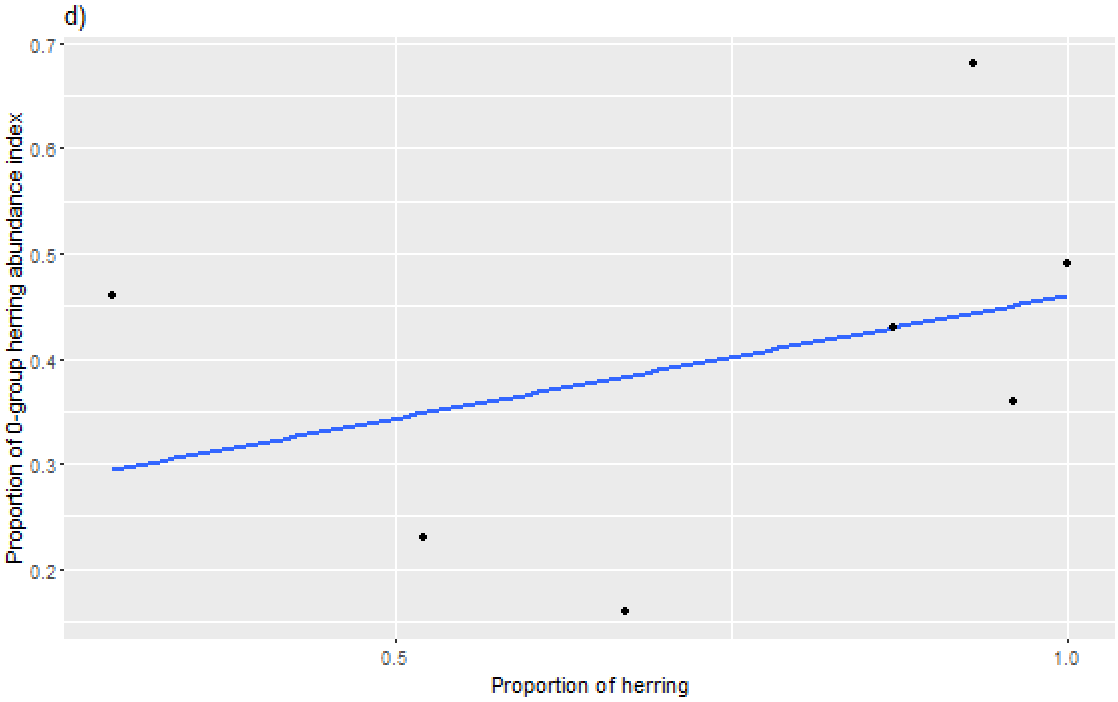


Figure *xii*. Relationship between the ratio of herring in the chick diet and proportion of herring abundance in the Barents Sea (both in relation to cod).

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