Faculty of Biosciences, Fisheries and Economics, Department of Arctic and Marine Biology

Environmental drivers of multi-species synchrony in seabird breeding success

Signe Hjellestad Jørgensen
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Acknowledgements

Abstract

Populations living close together in space are likely to experience more similar environmental fluctuations, and thus may display similar temporal changes in population parameters, in other words synchrony. Interspecific synchrony has implications for ecosystem stability, and highly synchronous populations and communities tend to have a higher risk of extinction. In this thesis, I used long-term data from six seabird species, breeding at Hornøya colony in the Barents Sea, to analyse the degree of synchrony in breeding success. I then investigated potential environmental drivers of inter-specific synchrony, and also asynchrony, in their breeding success. A generalized linear model (GLMs) was fitted to the breeding success data of each species. Pairwise correlations of the model residuals were calculated for all species combinations. Model selection was performed including climate and oceanographic covariates, which were considered to possibly influence breeding success, to identify the best model of breeding success for each species. If a covariate was included in the best-fitting model for multiple species, I tested the extent to which that shared effect led to interspecific synchrony. A higher level of synchrony in breeding success was found between auks and between gulls, than between these groups of birds. Atlantic water-inflow during winter was identified as a driver of breeding success, with potential synchronizing effect for kittiwakes (*Rissa tridactyla*), great black-backed gulls (*Larus marinus*) and herring gulls (*Larus argentatus*). For Atlantic puffins (*Fratercula arctica*) and razorbills (*Alca torda*), a lagged effect of Atlantic water-inflow during winter on breeding success was found. Sea surface temperature was identified as a potentially synchronizing driver of breeding success for great black-backed gulls and herring gulls. The results indicate that climate-induced changes in the Barents Sea ecosystem can have pronounced effects on seabirds breeding on Hornøya.

Keywords: Synchrony, seabirds, breeding success, Hornøya, Atlantic Water-inflow, Sea surface temperature, Arctic oscillation index

Table of Contents

1 Introduction

Population dynamics, i.e., how populations changes in size and structure over time, are the result of changes in demographic rates, such as survival and reproduction. Synchronous dynamics, i.e., when multiple populations display similar changes in population dynamics, can be influenced by a wide range of processes including environmental variation and dispersal (Hansen et al., 2020; Shoemaker et al., 2022). If populations experience the same directional effect of environmental variation, the temporal changes in population dynamics are expected to be correlated, or in other words synchronous (Engen & Sæther, 2005; Hansen et al., 2020). Spatial synchrony in populations' demographic rates can occur between several populations of the same species (intraspecific synchrony) or at the same location between populations of different species (interspecific synchrony). For example populations of snowshoe hare (*Lepus americanus)* in Canada, showed similarities in population fluctuations, i.e., intraspecific synchrony, over large areas (Stenseth et al., 1999). Interspecific synchrony is also a widespread phenomenon, like for example in Finnland where evidence was found for interspecific synchrony between four species of rodents (Huitu et al., 2004).

Highly synchronous populations and communities have a higher extinction risk (Heino et al., 1997). Thus, the hypothesis that correlations in environmental variation synchronizes population dynamics is relevant in the context of climate change, as it suggest that several populations might display similar responses to climate trends (Post & Forchhammer, 2002). Determining the mechanisms behind population synchrony and potential extrinsic drivers of that synchrony can improve our understanding of large-scale ecological outcomes of global climate change, and have implications for conservation and management strategies(Hansen et al., 2020; Sæther et al., 2007; Youngflesh et al., 2021).

When demographic parameters fluctuate similarly for populations of different species living in the same area (i.e., sympatric species), it can be referred to as interspecific demographic synchrony, or simply community synchrony (Youngflesh et al., 2021). Populations that are close together in space are likely to experience more similar environmental fluctuations than populations living in different environments(Robertson et al., 2015). In such a situation where sympatric species experience the same environmental conditions, species that are ecologically similar in terms of breeding and foraging behaviour, may be expected to exhibit more synchronous temporal fluctuations in demographic parameters while more dissimilar species might show less synchrony (Robertson et al., 2015). This suggests that species exploiting the

same resources will be affected in a similar way by environmental variation, and thus display synchronous fluctuations in population dynamics (Loreau & de Mazancourt, 2008; Robinson et al., 2013). For example, synchrony in breeding success may be explained by similarities in diet and foraging range (Robertson et al., 2015). However, overlap in diet or habitat can also lead to asynchrony between species exploiting the same resources, e.g., due to competition (Gonzalez & Loreau, 2009; Loreau & de Mazancourt, 2008). Looking at community synchrony might tell us something about whether there are environmental conditions that could be relevant to the community as a whole, and if the dynamics of one species is indicative of the dynamics of another species (Youngflesh et al., 2021). We need to understand the drivers behind the observed degrees of synchrony if we are to use these patterns to predict for example the consequences of environmental changes.

Seabirds are long-lived, and their life-history is characterized by high adult survival rates, slow maturation, and low lifetime reproductive rates. In addition to producing few offspring per breeding season, seabirds can also skip breeding during years with unfavourable climatic conditions (Jenouvrier, 2013). This life-history strategy has implications for how and why seabird populations sizes fluctuate (Sæther & Engen, 2002). As top predators, seabirds are sensitive to changes at lower trophic levels in the ecosystem (Hazen et al., 2019; Moore & Kuletz, 2019). Seabirds are often used as sentinel species, as it is possible to detect information about changes in the marine environment by studying seabird population dynamics and ecological parameters (Barrett, 2001; Hazen et al., 2019; Moore & Kuletz, 2019). Over 90 % of all seabirds breed in colonies (Barret, 2010), and several big colonies are found along the Norwegian coast (Systad, 2010). The birds usually come back to the same colony, the same partner and even the same nest every year (Barret, 2010). Egg-laying and chick -rearing is very energy demanding, and thus good foraging conditions are important during the breeding season (Barret, 2010; Frederiksen et al., 2005).

Seabirds are declining worldwide (Dias et al., 2019), and the causes of decline are often indirectly affecting breeding performance or survival (Fayet et al., 2021). As breeding success is likely to be connected to prey availability, it likely reflects changes in environmental conditions (Frederiksen et al., 2005; Hazen et al., 2019; Olin et al., 2020). In contrast to seabird population dynamics in general, which can be influenced by climate conditions all year around and over large areas (Reiertsen et al., 2014), reproduction is likely to be influenced by local conditions during the breeding season, because this is what affects the seabirds abilities to bring food to their chicks (Furness & Tasker, 2000). Variation in adult

survival tends to be minimal as this is generally the life-history trait with the highest elasticity in seabirds (Sandvik et al., 2005). Consequently, the effects of climate variation are more likely to act through breeding success or recruitment of immature birds, rather than adult survival (Erikstad et al., 1998).

Most studies on impact of climate variability on seabirds shows an indirect effect of climate conditions through the availability and quality of food (Jenouvrier, 2013). Such indirect effects could also be time-lagged (Hansen et al., 2020), meaning that climate conditions in the years before indirectly affect the food conditions in the year the seabirds breed. One way in which indirect effects of climate change on population dynamics may be mediated is through species interactions, as for example via predator-prey relationships, where climate variability influences the distribution and/or abundance of either prey or predator (Layton-Matthews et al., 2019; Schmidt et al., 2012). Seabirds are largely affected by indirect effects of climate variability, via bottom-up effects on prey availability (e.g.,Jenouvrier et al., 2005; Sandvik et al., 2005). Sea surface temperature (SST) is a commonly used proxy for bottom-up effects of food resources, by altering the distribution of their prey and thereby has implications for seabird breeding success (Fayet et al., 2021). For example, in the Barents Sea, the dynamics of capelin (*Mallotus villosus*), a major component of seabird diet, is influenced by climate (Hjermann et al., 2004). More specifically, increased SST has been shown to lead to a decrease in capelin abundance and a northward displacement of capelin which spawn along the Norwegian coast in spring (Gjøsæter, 1998; Hjermann et al., 2004).

The Barents Sea is a shallow, shelf-sea with a complex ecosystem showing clear bottom-up effects, as well as top-down and climate effects (Durant et al., 2014; Frainera et al., 2017; Johannesen et al., 2012). Hornøya is a seabird colony located in the productive southern Barents Sea. Each spring approximately 100 000 seabirds arrive to the island to breed (https://seapop.no/). In this thesis, using time-series data of breeding success from six seabird species breeding on Hornøya, I explore the degree of inter-specific synchrony in breeding success, and whether some of this synchrony can be explained by climate effects, i.e., related indirectly to foraging conditions around the colony. I will use data on breeding success from three auk species and three gull species, which means that the study species differ in both breeding and foraging behaviour

I investigated four main questions in this thesis:

1) To what extent do the six seabird species display synchrony in breeding success?
2) What environmental factors do best explain the interannual variability in breeding success for each species?
3) Can this same environmental effect be observed in several species simultaneously?
4) And if so, to what extent does the shared environmental effect explain the synchrony between the species in breeding success?

I expected a higher degree of synchrony between species with more similar ecology. Considering that food is a limiting factor for successful breeding, one could expect that a greater overlap in diet leads to higher synchrony. I expected a higher degree of synchrony in breeding success among the three gull species, and among the three auk species, since they are more similar in terms of foraging behaviour, and breeding timing. The gull-species breed earlier than the auks, and in addition the gulls are surface-feeders not able to reach prey at the same depths as the diving auk species.

2 Method

2.1 Study area

The data used in this thesis has been gathered on Hornøya (70° 23′ 15.72″ N, 31° 9′ 19.08″ E), a small island located outside of Vardø in eastern Finnmark (Figure 1). Hornøya has a large and diverse colony of seabirds, with the nutrient rich southern Barents Sea as their foraging area. Through the national monitoring program SEAPOP, demographic data has been gathered since the 1980s for some species. In 2005 Hornøya became one of the key sites of the program, and among the demographic parameters being monitored is reproduction, which will be the focus in this thesis (https://seapop.no/).

Figure 1. Location of the study area, Hornøya, in the municipality of Vardø in Finnmark.

2.2 Study species

In this study I use long-term data on breeding success for six seabird species, three auks and three gulls, all breeding in the same colony on Hornøya: Atlantic puffin (*Fratercula arctica*), Razorbill *(Alca torda),* Common guillemot *(Uria aalge),* Black-legged kittiwake *(Rissa tridactyla),* Great black-backed gull (*Larus marinus*) and Herring gull (*Larus argentatus*).

The seabirds arrive the colony on Hornøya between February and March. Timing for egg laying varies between years. The gulls lay eggs earlier, usually in late April to mid-May, than the auks that lay the eggs in late May and early June (Burr et al., 2016; Hestem, 2019; Kvivesen, 2009). Clutch sizes vary, where gulls lay 1-3 eggs and auks lay one egg (Barret,

2010). Puffins, razorbills, common guillemots and kittiwakes all breed in the steep, cliff-parts of Hornøya, while the herring gull and great black backed gull breed on the ground in the grass dominated, flat and more open habitat of the island (https://seapop.no/). The puffin and razorbill breed in burrows, while the other study species nest in the open. Common guillemot lay their egg directly on the stony cliffs, and the kittiwake breed in small nests in the steep cliff. For seabirds breeding on Hornøya important prey species has been found to be small, pelagic, schooling fish such as capelin (*Mallotus villosus*), sand lance(*Ammodytes* spp), herring (*Clupea harengus*) and small gadids (Barret, 2007; Barrett, 2015; Barrett & Erikstad, 2013; Eilertsen et al., 2008). The auk-species are diving seabirds capable of reaching prey at depths that are not available to the surface-feeding gulls (Barret, 2010).

2.2.1 Puffin

Atlantic puffins (hereon referred to as "Puffins") are medium-sized auks known to breed in large colonies all over the North Atlantic (Gaston & Jones, 1998; Reiertsen & Barrett, 2010). Puffins incubate their egg for around 40 days (Harris, 1984), and the chicks usually hatches in late June. Puffin chicks remain in the burrow until they are capable of flying, and the fledging period varies (Harris, 1984). The chicks are fed by the parents in the colony for as long as necessary, normally around 40-50 days (Harris, 1984). Puffins are, in common with the other auks, considered to be pursuit- divers, and are capable of diving down to 60 meters, but usually forage in more shallow depths(Gaston & Jones, 1998) diving 10-40 meters (Barrett, 2002). There has been a declining trend in many puffin populations, and today it is classified as endangered on the Norwegian red list (Artsdatabanken, 2021; Fauchald et al., 2015).

2.2.2 Razorbill

Razorbills are robust and heavy-billed auks, and are distributed in the sub-Arctic waters of the North Atlantic (Gaston & Jones, 1998). When the razorbill-chicks hatch, they are fed by the parents in the colony for around 21 days, before the chick, not yet able to fly, leaves the breeding ledge to swim offshore (Erikstad et al., 2018). The male parent accompanies and takes care of the chicks as they migrate (swimming migration) to the areas where the chicks are raised to independence(Erikstad et al., 2018). Razorbills have a maximum diving depth of around 120 meter, but most dives seems to be more shallow (Gaston & Jones, 1998). Razorbills are classified as vulnerable on the Norwegian red list (Artsdatabanken, 2021).

2.2.3 Common guillemot

The common guillemot is a large auk with a circumpolar distribution (Gaston & Jones, 1998). Common guillemots start incubating in mid-to late May, and the incubation period normally lasts 32-33 days(Gaston & Jones, 1998). Common guillemots share the unique intermediate departure strategy with razorbills, where the chicks are fed in the colony for around 21 days before they leave for the open sea with the male parent (Erikstad et al., 2018; Gaston & Jones, 1998). The common guillemot can dive to depths of over 150 meters during the non-breeding season, but normal feeding depth is thought to be 20-30 meters (Erikstad, Benjaminsen and Reiertsen unpubl). Common guillemot is classified as critically endangered on the Norwegian red list (Artsdatabanken, 2021).

2.2.4 Kittiwake

The black-legged kittiwake (hereon referred to as "kittiwake") is the most numerous gull species in the world, distributed throughout the northern hemisphere (Coulson, 2011; Hatch, 2012). Kittiwakes are pelagic, surface feeding birds, only capable of capturing food within the top metre of the sea surface (Coulson, 2011). For the kittiwakes the incubation-period lasts around 27 days(Coulson, 2011). Kittiwake chicks are usually able to fly around 36 days after hatching, but they keep coming back to the nest to be fed by their parents for many days, or even weeks after this, before they eventually leave the colony and are independent (Coulson, 2011). Kittiwakes are classified as endangered on the Norwegian red list (Artsdatabanken, 2021).

2.2.5 Great black-backed gull and herring gull

Great black-backed gulls and herring gulls are considered to be coastal species, in contrast to pelagic kittiwakes and auks (Fauchald et al., 2015). Herring gulls are considered to be the second most abundant gull species (Coulson, 2011). The length of incubation period is similar to kittiwakes, and the gull-chicks continue to beg for food several weeks in the colony, also after leaving the nest (Barret, 2010). Herring gulls and great black-backed gulls are both considered opportunistic generalist predators (Robertson et al., 2015) and have a diverse diet. In addition to small fish and invertebrates, the large gulls have also been found to prey on eggs and chicks of the other species breeding on Hornøya (Jenssen, 2008). In 2021 the herring gull was for the first time classified as vulnerable on the Norwegian red list (Artsdatabanken, 2021). Great black-backed gull is the only one of the six study species that is not red listed (Artsdatabanken, 2021).

2.3 Data

2.3.1 Reproductive data

Each year data of mean breeding success has been collected, along with the number of breeding pairs/nests through monitoring studies. In this thesis I used time-series data of breeding success from puffin (1988 – 2017), razorbill (1989 – 2017), common guillemot (2009 – 2017), kittiwake (2005 – 20217), great black-backed gull and herring gull (2007 – 2017) (Table 1). For common guillemot reproductive data is missing for year 2012. For puffin data is missing for 1991,1994 and 1999. For razorbill data is missing for 1991,1994,1995,1998, 2000 and 2001.

As the different species nest in different areas on Hornøya and vary in clutch size, the collection of reproductive data differs slightly. For the kittiwake, great black-backed gull and herring gull, selected nests are marked and monitored throughout the breeding season. It is monitored when and how many eggs hatch per nest, and later the number of chicks is counted at day 10 and 20 after hatching. For puffins and razorbills selected burrows are monitored throughout the season, and from the day the egg hatches the chicks are followed every 5th day until they are 20 days old. Pairs of common guillemots are also followed from the egg hatches until the chicks is 20 days old. This means that for both gulls and auks the estimations for mean breeding success are based on number of large chicks or chicks older than 20 days per pair or nest (Table 1). Large chicks, and chicks that survived to an age older than 20 days, are considered to successfully fledge the nest, and will be referred to as fledglings.

The number of nests/pairs being monitored vary between species and years, generally ranging around 30-40 nests/pairs for the auks and large gulls, and more than 100 nests for kittiwakes.

Table 1. An overview of years with available data on breeding success, and how breeding success was measured, for each species.

Species	Years of data	How reproduction was measured
Puffin	1988-2017	Number of medium chicks per egg
Razorbill	1989-2017	Number of medium chicks per egg
Common guillemot	2009-2017	Number of 20 days old chicks per pair
Kittiwake	2005-2017	Number of 20 days old chicks per nest
Great black-backed gull	2007-2017	Number of large chicks per pair
Herring gull	2007-2017	Number of large chicks per pair

2.3.2 Environmental data

Covariates describing environmental conditions that could affect reproduction during the breeding season were included for the years 1988-2017 (Table 2), to examine whether they could explain the observed variation in seabird breeding success, and potentially act as synchronising agents.

Sea surface temperatures were extracted for the foraging area around Hornøya, based on the Extended Reconstruction SST dataset available on a 2°×2° grid (ERSST v 3b, NOAA 2012; cf. Smith et al. 2008). SSTs were calculated as monthly means of the 2 grid cells adjacent to the colony (Sandvik et al., 2014). SST was included as it could work as an index for a multitude of bottom-up effects in the marine environment (Thayer et al., 2008).

Time-series of a monthly Arctic oscillation index (AO-index) and North Atlantic oscillation index (NAO-index) were downloaded from the website of "National Center for Environmental Information" (http://www.cpc.ncep.noaa.gov). The oscillation refers to movement of atmospheric mass and the oscillation-indexes can be considered a "proxy" for different climatic processes (Sandvik et al., 2005). Fluctuations in AO and NAO between phases (negative and positive) produce large changes in wind direction and speed over the Atlantic and Arctic, as well as heat transport, precipitation and the intensity and frequency of storms(Hurrell et al., 2003; Thompson & Wallace, 1998), which may affect seabirds.

Oscillation indexes are often used in studies investigating climate effects on seabirds (Stenseth et al., 2003).

Finally, monthly values of the inflow of Atlantic Water (AW-inflow) into the Barents Sea has been measured over several decades (https://thredds.met.no/thredds/catalog/nansen-legacy-ocean/https://thredds.met.no/thredds/catalog/nansen-legacy-ocean/SVIM/catalog.html). The climate variability in the Barents Sea is largely determined by the fluctuating inflow of warm and salty Atlantic water (Ingvaldsen et al., 2004; Loeng, 1991). Thus, AW-inflow might indirectly affect seabirds through changes in food availability and abundance (Barrett et al., 2017).

Table 2. An overview of all the covariates entered in the GLMs.

Sea Surface Temperature (SST)	Arctic Oscillation - index (AO-index)	North Atlantic Oscillation-index (NAO-index)	Atlantic water-inflow (AW-inflow)
SST March-April	AO-index February	NAO-index March-April	AW-inflow March
SST March-April 1 year lag	AO-index March	NAO-index May-July	AW-inflow April
	AO-index April		AW-inflow May
SST March-April 2 years lag	AO-index May		AW-inflow June
SST May-July	AO-index June		AW-inflow July
SST May-July 1 year lag	AO-index July		AW-inflow December-February
	AO-index April-May		
SST May-July 2 years lag	AO-index June-July		AW-inflow December-February 1 year lag
	AO-index April-June		AW-inflow December-February 2 years lag

2.4 Statistical analysis

2.4.1 Pairwise synchrony analysis

To examine the extent to which the different species displayed synchrony in breeding success, I calculated the pairwise correlation between all species. This was done by estimating the

residuals of the null GLM model (described in 2.4.2, i.e., without covariate effects) and estimating the correlation between the residuals (i.e., the Pearson's correlation coefficient).

2.4.2 Model selection: Environmental drivers of breeding success

I performed a model selection to find the model that best explained the annual variation in breeding success for each species. A generalized linear model (GLM) was made for each species using the package "lme4".

For razorbills, puffins and common guillemots, which lay only a single egg, I estimated the proportion of fledged chicks per pair (ρ_t) using data of the number of fledged chicks $F(t)$ from a given number of monitored pairs $E(t)$ of birds that attempt breeding in year t, where $F(t)$ has a binomial distribution $Bin(E(t), \rho_t)$ i.e., using a logit link function. The linear predictor is as follows;

$$\text{logit}(\rho(t)) = \alpha + \beta_j \text{cov}_j(t),$$

where α represents mean breeding success and β_j is the slope representing the effect of time-varying covariate j.

For the kittiwake, great black-backed gull and herring gull, which lay multiple egg clutches, I modelled the total number of chicks fledged, $\text{prod}(t)$, as a Poisson distributed response variable (i.e., a log link function), and included the number of pairs as an offset in the GLM;

$$\log(\text{prod}(t)) = \alpha + \beta_j \text{cov}_{j,t} + \log(\text{Npairs}).$$

All covariates (Table 2) were entered to find the best candidate model. Covariates were scaled (mean = 1, SD = 1) and any temporal, linear trend was removed (i.e., detrended) before being entered as explanatory variables in the GLMs.

The candidate models were compared using Akaike's information criterion corrected for small sample sizes (AICc). AICc is a measure of the goodness of fit of a fitted model relative to the model's complexity, where a model with a lower AICc reflects a more parsimonious (i.e., a model which explains the most variance with the fewest parameters) (Burnham, 2002; Zuur, 2009). Here, the model with the lowest AICc-value was considered the best model however, if the difference between models' AICc (Δ) was less than 2 AICc, then I could not draw a conclusion that one model is better than the other. In situations where several models where within Δ2AICc, the model containing the least number of parameters was retained (i.e.,

the most parsimonious). I performed model selection based on a candidate model set which included all combinations of covariates (Table 2), given that a maximum of two covariates could be included in each competing model and only covariates with a correlation of less than 0.4 could be entered in the same model, to avoid substantial collinearity in predictors (Dormann et al., 2013). The 95 % confidence interval was calculated for the estimated slopes in the top model (most parsimonious model) for each species, using the "confint" function in R. Model selection was performed using the "MuMIn" package in R.

I calculated the proportion of variance explained in the response by all covariates in the model (R^2) for each of the best-fitting GLMs and, where relevant, the partial R^2 for each covariate in the model, using the package "rr2" (Zhang, 2017).

I confirmed there was no strong collinearity between the covariates (Zuur, 2009) using the package "car" the variation inflation factor (VIF). For each of selected models the predicted and observed values of breeding success was plotted along with the covariates, using the package "ggeffects".

2.4.3 Synchrony in breeding success and environmental drivers of synchrony

Based on the best-fitting model of breeding success for each species found in 2.4.2, I identified which species had the same covariates included in the best model. I then compared the "total" interspecific correlation in breeding success (calculated in 2.4.1, i.e., residuals from the fitted GLM without covariates included) with the residuals from the GLM including the shared covariate as a predictor (i.e., removing the effect of that covariate from the residuals for both species). The difference in the correlation in annual breeding success between the two focal species, before and after accounting for the effect of the shared covariate, reflects the amount of observed breeding synchrony explained by the focal covariate.

All plots were made using the function ggplot from the package "ggplot2", and statistical analysis were carried out using R version 4.0.3(RCoreTeam, 2021).

3 Results

3.1 Interspecific synchrony in breeding success

The Pearson correlation matrices revealed that breeding success was highly synchronous between some pairs of species (Appendix 1, Table 3). Puffins and razorbills had a high synchrony in breeding success with a correlation of 0.93 (95% CI [0.84, 0.97], p-value < 0.001). A high synchrony in breeding success was also found among the gulls, where the correlation in breeding success between herring gull and great black-backed gull was 0.84(95% CI [0.49, 0.96], p-value<0.001), and the correlation between kittiwakes and herring gulls was 0.70 (95% CI [0.17, 0.92], p-value=0.02). There was overall a low correlation between auks and gulls, and therefore they are plotted separately (Figure 2 and 3). There was also a low correlation between common guillemots and all other species (Appendix 1, Table 3).

Herring gulls, great black-backed gulls and kittiwakes, all show a highly fluctuating breeding success (Figure). Great black-backed gulls and herring gulls had a higher mean breeding success than kittiwakes. Breeding success for herring gulls, great black-backed gulls and kittiwakes fluctuates between 0.14-1.81 (mean=0.75), 0.03-2.26 (mean=0.78) and 0-0.44 (mean=0.17) respectively. For all three gull species 2010 was the year with the highest breeding success during the study period, while 2008 was a year with low breeding success for all three species (Figure 2).
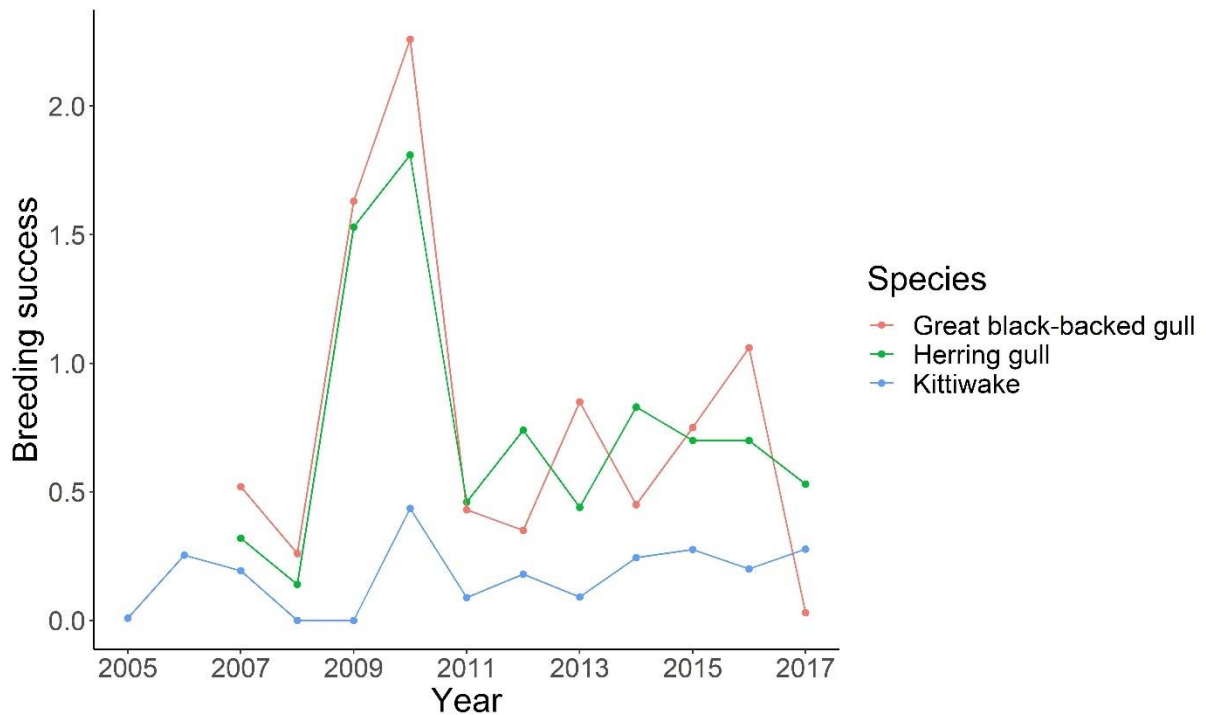
Figure 2. Mean breeding success for great black-backed gull, herring gull and kittiwake from 2005-2017.

In general, all three auk species had a high breeding success (Figure 3). Common guillemot breeding success was overall high ranging between 0.55 - 0.89 (mean=0.78), while puffin and razorbill had larger fluctuations with a breeding success ranging between 0.19 -0.93 (mean=0.72) for puffins, and 0.07 -0.88 (mean=0.68) for razorbills. Both puffins and razorbills had a very stable, high, reproductive success until 2005, when the fluctuations increased. In 2011 and 2012, as well as 2014 and 2015 all auk species, but particularly puffins and razorbills, had a very low breeding success.
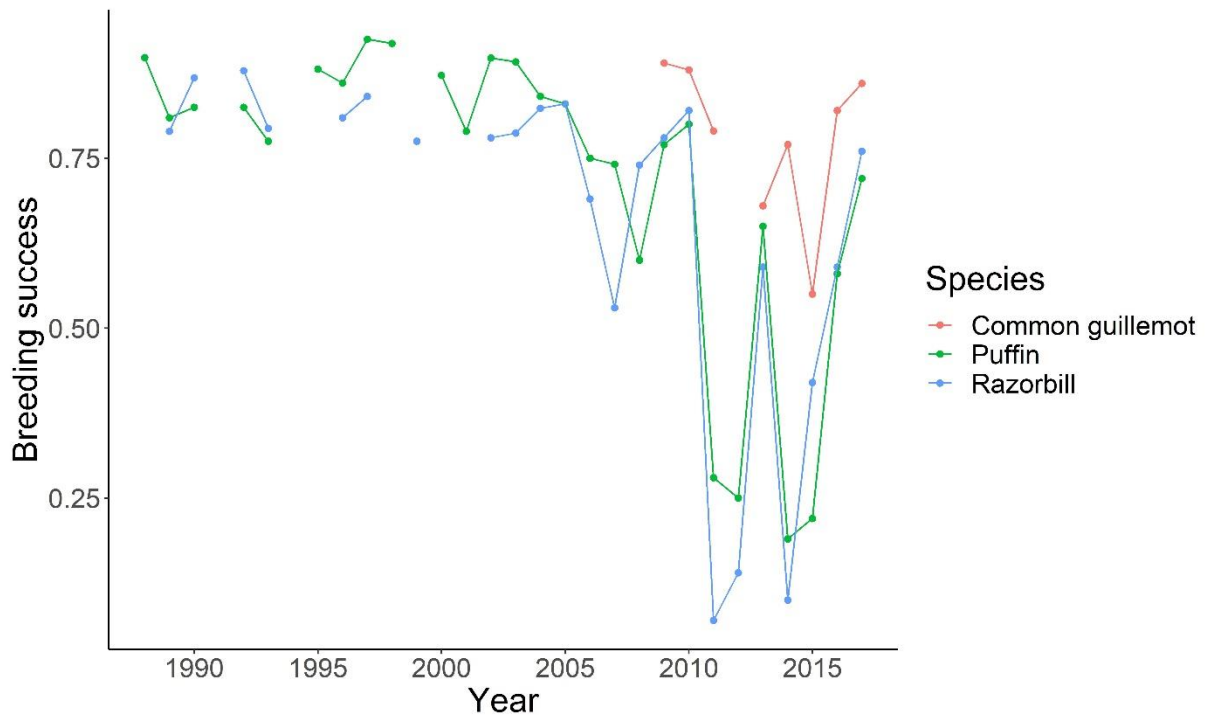
Figure 3. Mean breeding success for puffin, razorbill and common guillemot from 1988-2017.

3.2 Environmental drivers of breeding success

For both puffins and razorbills, the top model with the lowest AICc included a positive effect of Atlantic water-inflow from December -February (Winter AW-inflow) one year prior to breeding, as well as Atlantic water-inflow in June (AW-inflow June). For Puffins the estimated slope of Winter AW-inflow one year earlier was 0.40 (95%CI [0.27, 0.54]), and the estimated slope for AW-inflow June was 0.38 (95%CI [0.24, 0.53]) (Figure 4). For this model the total model R^2 was 0.20 (Appendix 1, Table 4), and the difference in AICc between the top model and the next was more than 7(ΔAICc > 7) (Appendix 2, Table 5). In addition to Winter AW-inflow one year prior to breeding, NAO-index for May-July was present in five of the top ten models. (Appendix 2, Table 5)
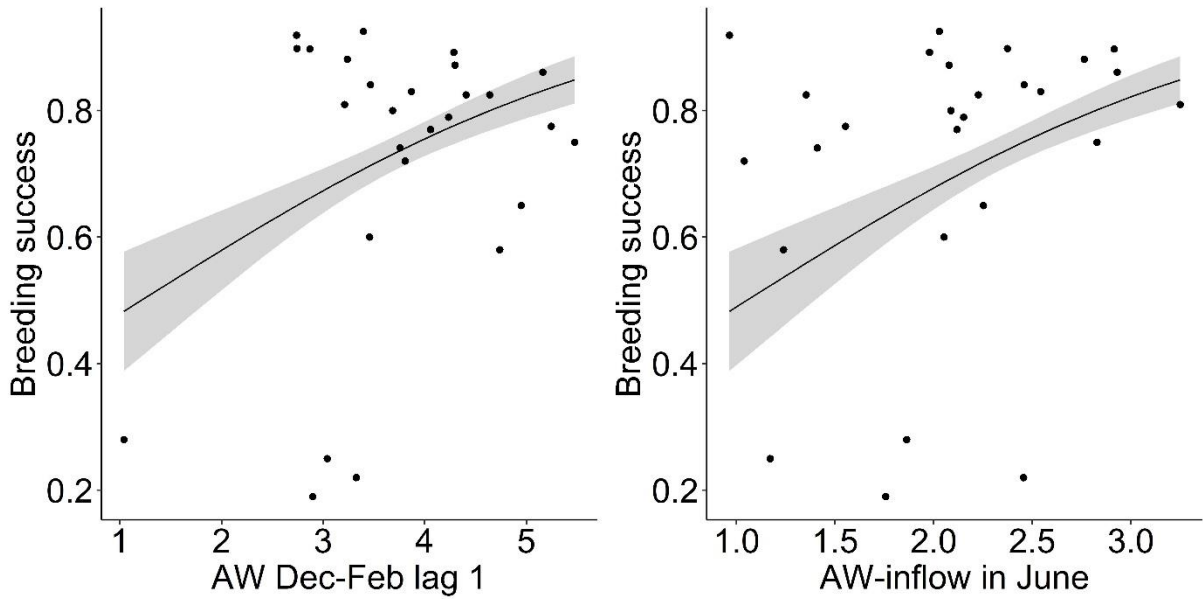
Figure 4. Model predictions for puffins.

For razorbills the estimated slope of Winter AW-inflow one year prior to breeding was 0.70 (0.56, 0.85), and the estimated slope of AW-inflow June was 0.49 (95%CI [0.34, 0.64]) (Figure 5). The total model R^2 was 0.50 (Appendix 1, Table 4), and from the top model to the second-best fitting model $\Delta AICc > 14$ (Appendix 3, Table 6). All top ten models included Winter AW-inflow one year prior to breeding as a covariate, and no other covariate was present in more than one of the top ten models. (Appendix 3, Table 6)
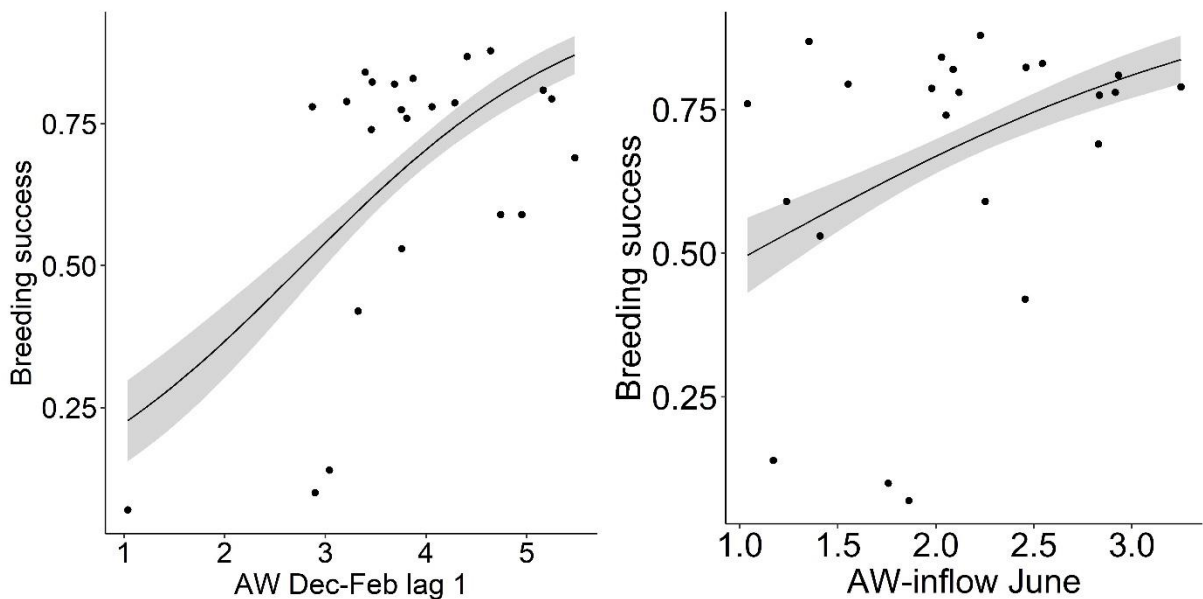

Figure 5. Model predictions for razorbills.

For common guillemot the top five models were within a difference of 2 AICc (Δ2AICc) (Appendix 4, Table 7). As there was no good way to conclude that one of the top five models were a better fitted model, I continued with the top model which had the fewest covariates and the highest weight. The top model included a negative effect of AO-index for April-June (AO April-June) with an estimated slope of -0.61(95% CI [-1.02, -0.23]) (Figure 6), and the total model R^2 was 0.67 (Appendix 1, Table 4). Four out of the five top models included AO-indexes between April and July, while the fifth model included sea surface temperature (SST) in May-July two years prior to breeding. All covariates in the top ten models had a negative effect on common guillemot breeding success (Appendix 4, Table 7).
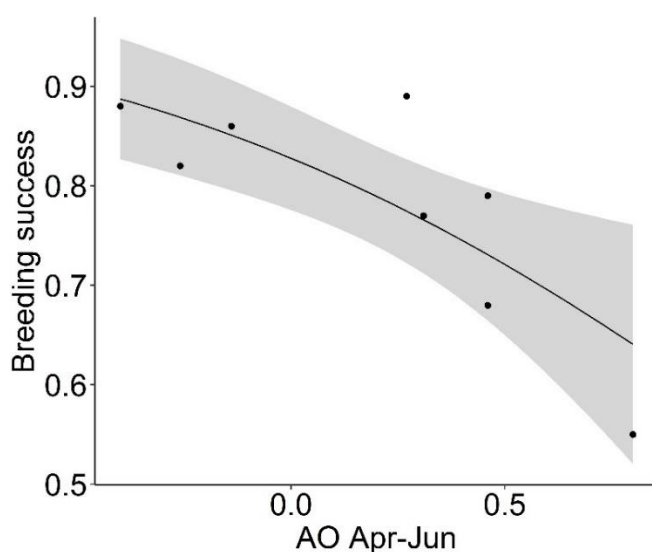
Figure 6. Model predictions for common guillemot.

For both kittiwakes and herring gulls, the model with lowest AICc included a negative of Winter AW-inflow with no lag. The top model for kittiwakes also included a positive effect of SST March-April one year prior to breeding. In the kittiwake top model, the estimated slope of Winter AW-inflow was -0.35(95%CI [-0.44, -0.25]), and the estimated slope of SST March-April was 0.51(95% CI [0.34, 0.69]) (Figure 7), and the total model R^2 was 0.76 (Appendix 1, Table 4). The second top model, also within Δ2AICc, included negative effect of AW-inflow May-July and SST March-April two years prior to breeding. Winter AW-inflow was included in six of the top ten models. (Appendix 5, Table 8)

Figure 7. Model predictions for kittiwakes.

The top models for both great black-backed gulls and herring gulls included a negative effect of SST March-April two years prior to breeding. In addition, the top model for great black-backed gulls included a negative effect of AO-index for February (AO February). For great black-backed gulls the top four models were within $\Delta 2AICc$, and the second model included a negative effect of Winter AW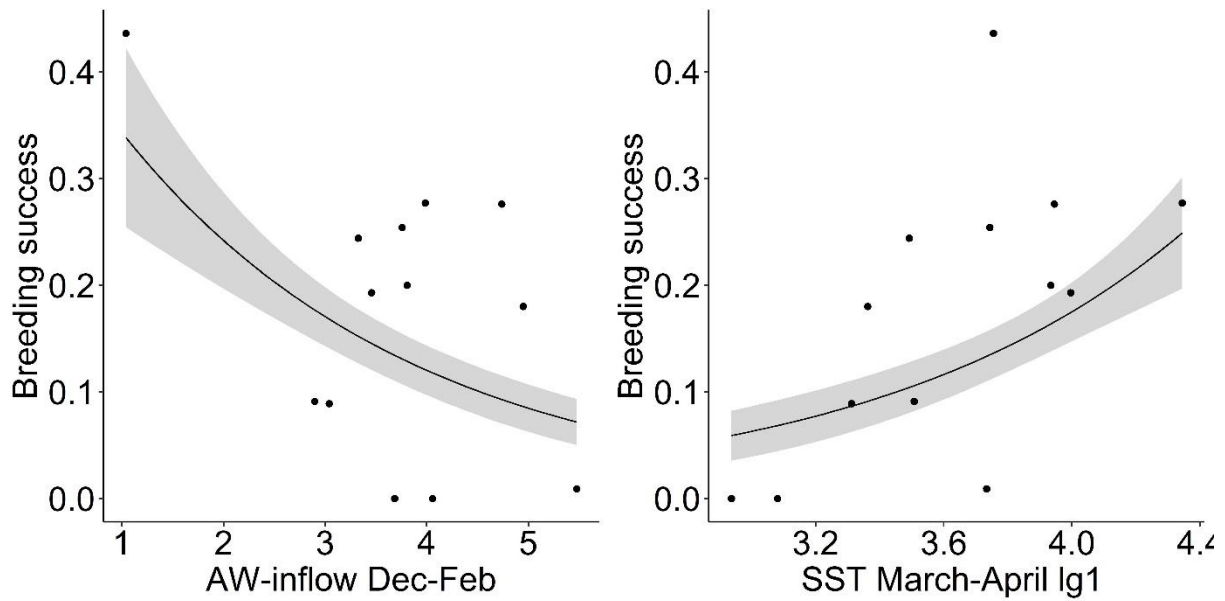-inflow as well as SST March-April two years prior to breeding. The third and fourth model included the negative effect of AO February in addition to AO July and AW-inflow in May. Eight of the top ten models included an effect of SST, and AO February was included in the three of the ten top models, all three being among the four models within $\Delta 2AICc$ (Appendix 6, Table 9). As for kittiwakes and common guillemots there was no good way to decide which model within $\Delta 2AICc$ was better fitted, and thus I continued with the top model as where the estimated slope of SST March-April two years prior to breeding was -0.53 (95% CI [-0.65, -0.39]), and the estimated slope of AO February was -0.24(95%CI [-0.33, -0.14]) (Figure 8). The total model R^2 was 0.90 (Appendix 1, Table 4).

This means that the top model for herring gulls included a negative effect of Winter AW-inflow in common with the kittiwakes and a negative effect of SST March-April two years prior to breeding in common with great black-backed gulls. There was a $\Delta AICc > 3$ between
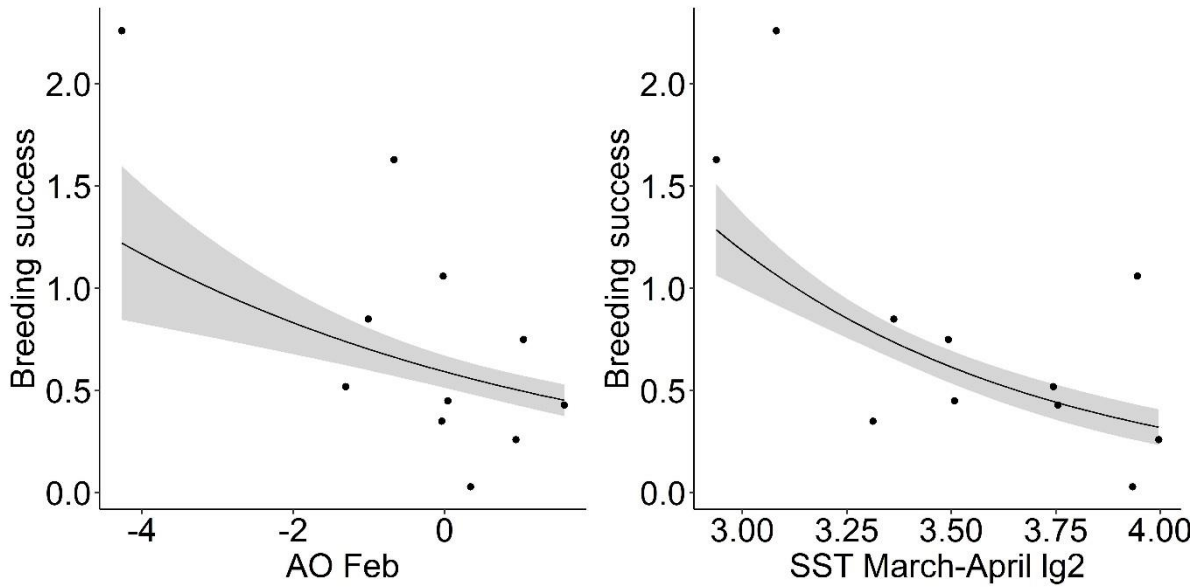
Figure 8. Model predictions for great black-backed gulls.

the top model and the second-best fitting-model (Appendix 7, Table 10). The estimated slope of Winter AW-inflow was -0.13(95% CI [-0.21, -0.06]), and the estimated slope of SST March-April two years prior to breeding was -0.73 (95% CI [-0.85, -0.55]) (Figure 9). The total model R^2 was 0.97 (Appendix 1, Table 4). All top ten models included the negative effect of SST, and no other covariate was included in more than one of the top ten models (Appendix 7, Table 10).
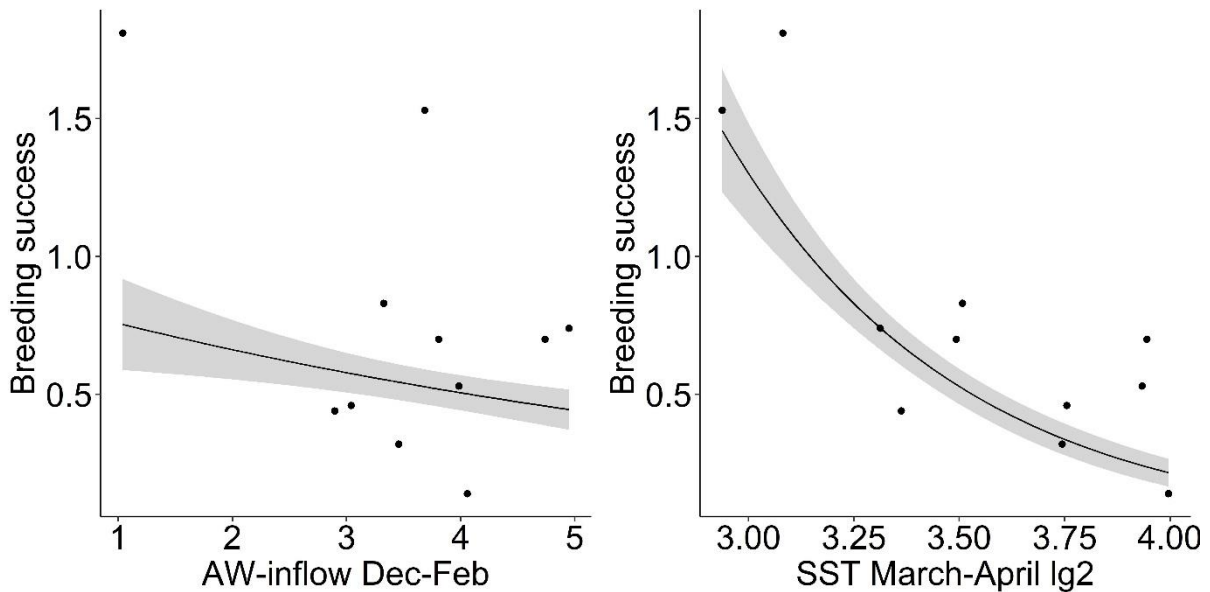
Figure 9. Model predictions for herring gulls

The VIF was close to one for all covariates in all top models, suggesting no collinearity among the parameters (Appendix 1, Table 4).

3.3 Environmental drivers of interspecific synchrony in breeding success

Based on the model selection I found that herring gulls and great black-backed gulls were both negatively affected by SST March-April two years prior to breeding. The correlation in breeding success between the two gulls was 0.84 (95% CI [0.49, 0.96], p-value=0.001) (Figure 10). When removing the effect of SST, the correlation was calculated to be 0.49 (95% CI [-0.15. 0.84], p-value=0.13) (Figure 11).
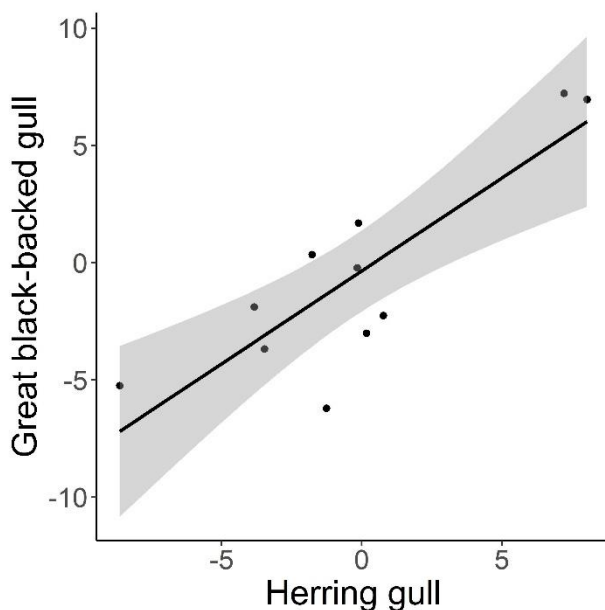
Figure 10. Correlation in breeding success between great black-backed gull and herring gull.
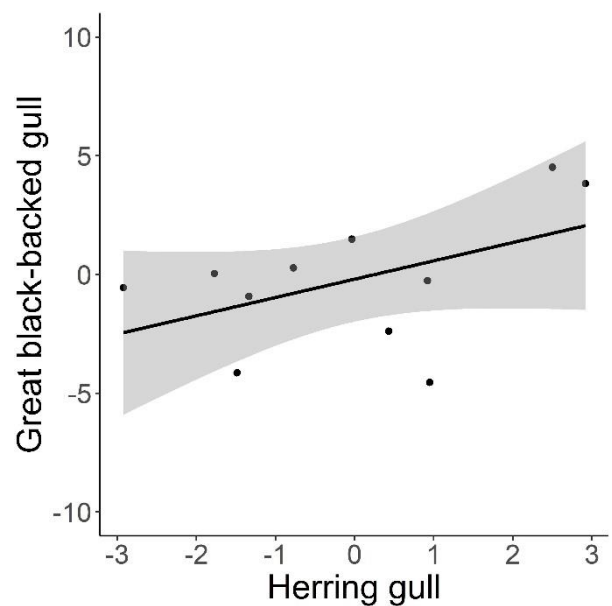
Figure 11. Correlation in breeding success between great black-backed gull and herring gull, after taking out the effect of SST March-April lag 2.

A negative shared negative effect of Winter AW-inflow was found for both kittiwakes and herring gulls. As this effect also was in the second top model (Δ2AICc) for great black-backed gull, I include great black-backed gulls in the synchrony analysis. The correlation between herring gulls and great black-backed gulls without the effect of Winter AW-inflow

was calculated to be 0.79 (95% CI [0.38, 0.95]) (Figure 12). The overall correlation between kittiwakes and great black-backed gulls was 0.40 (95% CI [-0.27, 0.81]), and when the effect of Winter AW-inflow was removed the correlation was calculated to be 0.10 (95% CI [-0.53, 0.67]) (Figure 12). Finally, the overall correlation between herring gulls and kittiwakes was 0.70 (95% CI [0.17, 0.92]), and the correlation without the effect of Winter AW-inflow was 0.53 (95% CI [-0.10, 0.86]) (Figure 12).
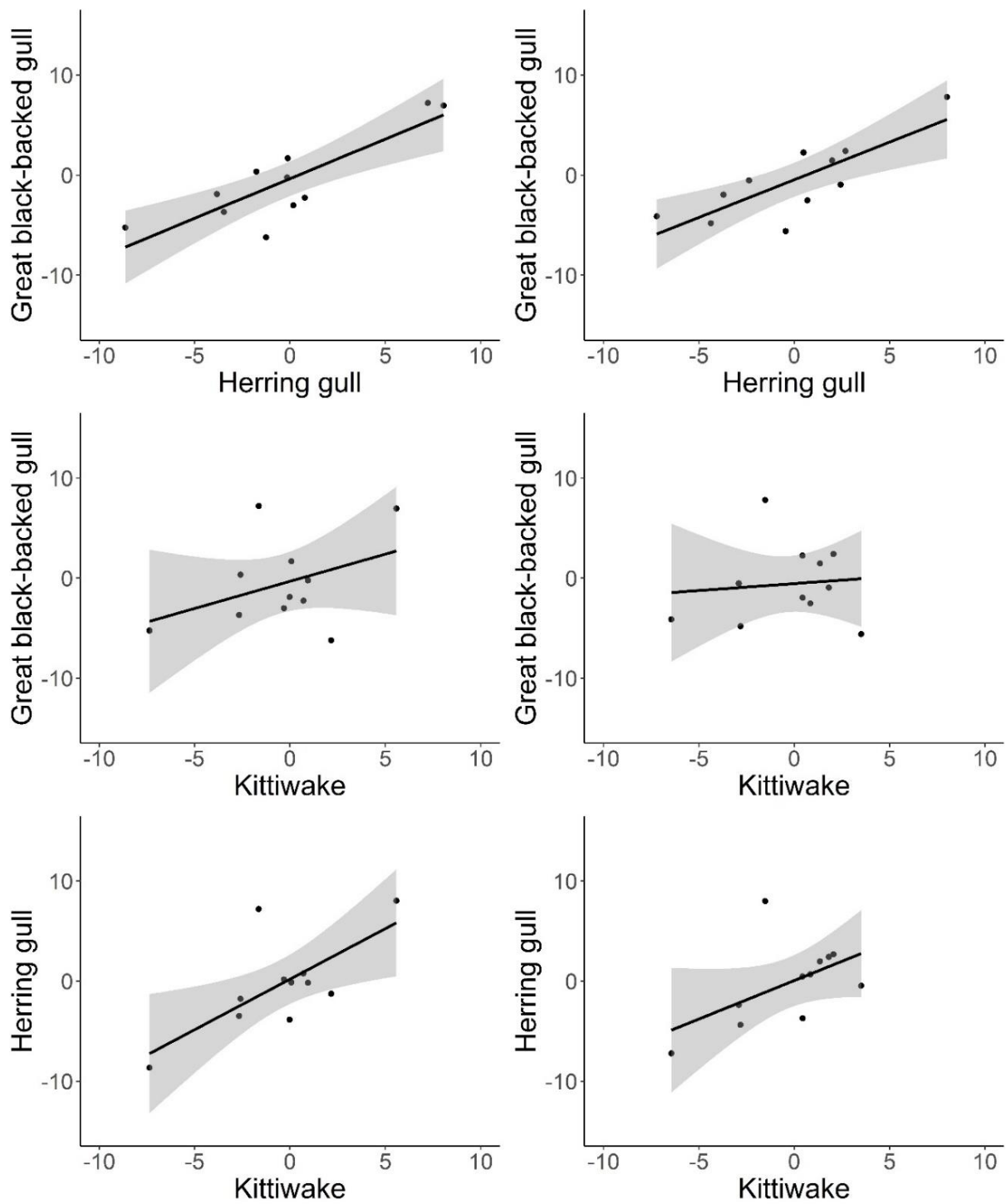
*Figure 12. (**Left column**) The figure shows the overall correlation between the three gull- species and (**right column**) the correlation between them after accounting for the effect of AW-inflow Winter.*

Puffins and razorbills shared a positive effect of both AW-inflow in June and Winter AW-inflow one year prior to breeding. The correlation in breeding success between the two auks was calculated to be 0.93 (0.83. 0.97. p-value < 0.001) (Figure 13) and when removing the effect of Winter AW-inflow one year earlier the correlation was calculated to be 0.87 (0.71. 0.95. p-value< 0.001) (Figure 14). When taking out the effect of AW-inflow June, the correlation was calculated to be 0.90 (0.78. 0.96. p-value< 0.001) (Figure 15).
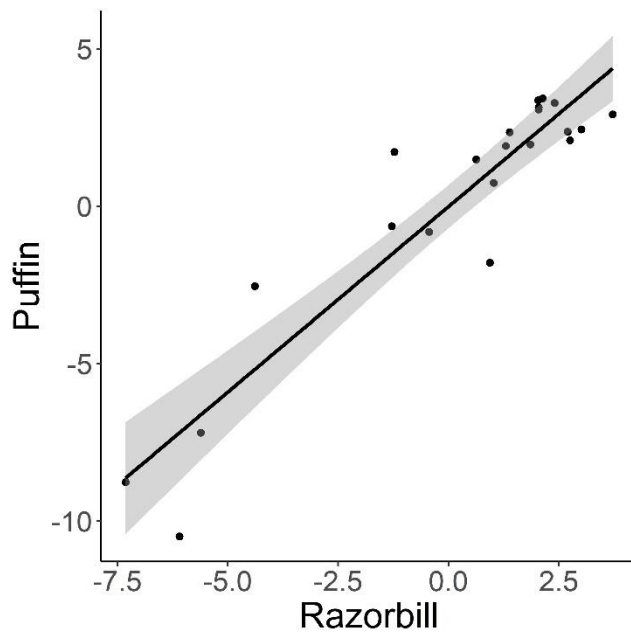
Figure 13. Correlation in breeding success between puffins and razorbills
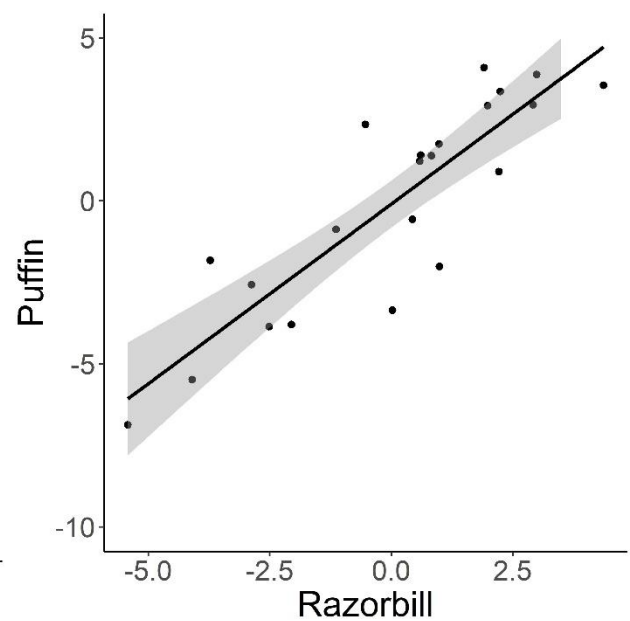
Figure 14. Correlation in breeding success between puffin and razorbill after taking out the effect of winter AW-inflow one year prior to breeding.
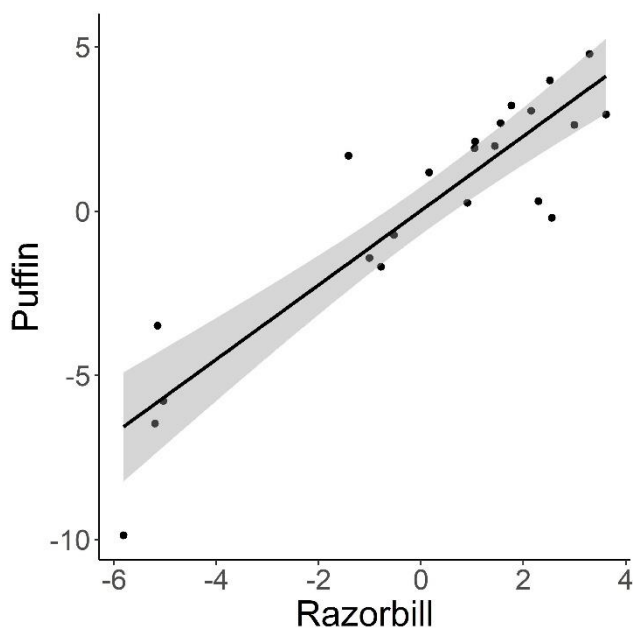
Figure 15. The correlation in breeding success between puffin and razorbill after taking out the effect of AW-inflow June.

4 Discussion

A high degree of synchrony was found between auks and between gulls, respectively. In general, my results show that oceanographic conditions have indirect effects on seabird breeding success. While some environmental factors acted asynchronously and only affected one species, common drivers of breeding success were found for two auk species and three gull species. Atlantic water inflow in December to February (Winter AW-inflow) was identified as a common driver of breeding success for kittiwakes, great black-backed gulls and herring gulls, and had a negative, synchronizing effect. Sea surface temperatures (SST) in March-April two years prior to breeding also had a negative, synchronizing effect on herring gulls and great black-backed gulls. Among the auks, Winter AW-inflow one year prior to breeding was identified as a common driver of breeding success for puffins and razorbills. Arctic-oscillation (AO) index acted asynchronously, affecting only common guillemots (AO April-June) and great black-backed gulls (AO February) during different periods.

As hypothesized, the results suggests that the interspecific synchrony in breeding success on Hornøya is higher among the auks and among the gulls, than between the two groups. One reason for this could be due to similarities in foraging behaviour. As pursuit-divers, auks are capable of reaching prey that is unavailable to surface-feeding gulls (Barret, 2010; Furness & Tasker, 2000). Another factor distinguishing the two groups is their phenology. Gulls generally start breeding earlier than the auks and have shorter incubation periods. Thus, the two bird groups experience different environmental conditions at different stages in the breeding season. Several studies have suggested that observed synchrony in breeding success in multi-species communities can be related to similarities in their diet during chick rearing (Frederiksen et al., 2004; Robertson et al., 2015). For example, Robertson et al (2015) found that terns with more similar foraging and breeding behaviour displayed higher synchrony than species that were less similar (Robertson et al., 2015).

Herring gulls and great black-backed gulls displayed an overall high degree of synchrony. The two species shared a negative effect of SST in March-April two years prior to breeding, and this covariate was found to have a high synchronizing effect. In common with kittiwakes, the large gulls had an exceptionally poor breeding season in 2008. This was likely due to food shortage (Barret & Eriksen, 2009), and the low breeding success also coincided with a very high lagged spring SST.

SST is commonly used as a proxy for indirect prey availability (Thayer et al., 2008) and therefore can be representative of local foraging conditions around Hornøya. In the Barents Sea, young age-classes of Norwegian spring-spawning herring and cod consumes large amounts of small capelin (Hjermann et al., 2004). Increased SST has been found to have a positive correlation with (0-group) cod and herring abundance and consequently a strong negative impact on capelin (Hjermann et al., 2004). This means that climate conditions indirectly influence the population dynamics of capelin by affecting recruitment of cod and herring (Hjermann et al., 2004). Considering this, a negative correlation between breeding success and SST could indicate that seabirds, or their chicks, are more dependent on cold-water species such as capelin as a food resource. Conversely, a positive correlation could be expected if the seabird is dependent on fish-species that prefer warmer water such as herring and cod (Reiertsen et al., 2012). Additionally, Hjermann et al (2004) found that warmer temperatures had a strong negative effect on capelin cohorts two years before spawning (Hjermann et al., 2004), similar to the negative effect of SST March-April two years before breeding for the large gulls. In the Newfoundland-Labrador area large gulls were found to feed capelin to their chicks and in years with delayed arrival of capelin, due to changes in ocean temperatures, gulls delayed breeding (Carscadden et al., 2002), which led to reduced chick survival (Carscadden et al., 2002). Warmer SST is also associated with increased ocean stratification where increased SST has been correlated with poorer breeding success of kittiwake in the UK(Carroll et al., 2015). Thus, climate change may be driving long term declines in gulls productivity (Carroll et al., 2015).

For all species, except common guillemots, breeding success was affected by Atlantic Water-inflow. All the gull-species shared a negative effect of Atlantic water-inflow in December-February (Winter AW-inflow). Winter AW-inflow explained little of the synchrony between herring gulls and great black-backed gulls, but a large proportion of the synchrony between kittiwakes and great black-backed gulls. Synchrony in breeding success between kittiwakes and great black-backed gulls was lower than for the other gulls however, Winter AW-inflow explained a substantial proportion of the estimated synchrony. The overall synchrony between kittiwakes and herring gulls was relatively high of which some was explained by Winter AW-inflow. This indicates that herring gulls and great black-backed gulls are more sensitive to the conditions reflected by SST two years earlier, while Winter AW-inflow is more important for kittiwake breeding success. Kittiwakes differ from the large gulls in their foraging behaviour, where kittiwakes are considered pelagic birds, while herring gulls and great black-backed

gulls forage more along the coastal, or both coastal and pelagic (Fauchald et al., 2015; Systad, 2010)

Puffins and razorbills shared a positive effect of both Winter AW-inflow one year prior to breeding, and Atlantic water-inflow in June (AW-inflow June). The two auk species displayed an overall high degree of synchrony in breeding success, but the synchronizing effect of the covariates they shared was low. Thus, although AW-inflow appears to affect breeding success of puffins and razorbills, it does not explain the high degree of synchrony between them.

The influx of Atlantic water, transported via the Norwegian Atlantic current (NAC) into the Barents Sea, is of major importance for the physical and biological conditions (Ingvaldsen et al., 2004; Loeng, 1991). The inflowing Atlantic current transports nutrients, fish larvae and plankton into the Barents sea (Ingvaldsen, 2003). Furthermore, Atlantic water masses are comparatively warm with high salinity, which influences the distributions and growth rates of zooplankton, fish-larvae and fish populations in the area (Ingvaldsen et al., 2004).

A study by Myksvoll et al (2013) on the effect of AW-inflow in summer on common guillemot chicks from Hornøya, show that the arrival of cod-larvae from more southern spawning grounds had a positive effect on chick size, and that the proportions of these cod-larvae (around Hornøya) correlated with AW-inflow (Myksvoll et al., 2013). Maybe positive effect of AW-inflow in June on puffin and razorbill breeding success could also be related to this.

For puffins and razorbills, a model including Winter AW-inflow had more support than one with AW-inflow June, given that the effect of Winter AW-inflow was present in more of the top candidate models. The maximum inflow of Atlantic water into the Barents Sea occurs in winter (i.e., greatest transport of warmer water masses) (Ingvaldsen et al., 2004). Thus, variation in Winter AW-inflow can be expected to have a larger impact on foraging conditions for seabirds than during other periods (Barrett et al., 2017). Warmer waters positively affects (0-group) cod and herring abundance in the Barents Sea (Hjermann et al., 2004), and therefore, more AW-inflow in winter the year before could lead to more age 1 cod and herring being available for foraging seabirds (Barrett et al., 2017).

Winter AW-inflow had a negative influence on the breeding success of both herring gulls and kittiwakes, and there was some evidence for an effect on great black-backed gulls (a model included Winter AW-inflow was included in the second-best model). Similarly, Barret et al

(2017) found a lagged, negative effect of winter AW-inflow on egg- and clutch-size in kittiwakes (Barrett et al., 2017). Kittiwakes are highly dependent on capelin as a food resource (Reiertsen et al., 2014), and both great black-backed gull and herring gull at Hornøya have been observed feeding on capelin (Furness & Barrett, 1985).

Capelin migrate southwards to spawn off the coast of Finnmark in late winter/early spring (Furness & Barrett, 1985; Gjøsæter, 1998). The location of spawning and nursing grounds varies with oceanic conditions. In years with strong AW-inflow and warmer SST, they are displaced further north and east (Gjøsæter, 1998). Thus, increased AW-inflow during winter, could cause a norward shift in the distribution of capelin, as well as increased predation (on capelin) by cod and herring (Barrett et al., 2017; Hjermann et al., 2004), reducing prey-availability for gulls. There is also evidence that capelin move to greater depths (Gjøsæter, 1998), with potentially severe consequences for surface feeding gulls (Carscadden et al., 2002).

As coexistence of different species and ecosystem stability require some form of niche separation (Loreau & de Mazancourt, 2008), overlap in diet, has the potential to lead to synchrony in demographic parameters, but also to interspecific competition (Gamelon et al., 2019; Schmutz & Laing, 2002). An interesting question whenever discussing multi-species synchrony is whether interspecific competition might desynchronise the population dynamics of sympatric species (Houlahan et al., 2007). When different species coexist, they could show synchronous patterns in population dynamics, or instead, show asynchronous (i.e., compensatory dynamics) where the species would show negative temporal correlation in a demographic rate (Shoemaker et al., 2022; Tredennick et al., 2017). Such compensatory dynamics could occur when species respond differently to environmental fluctuations or due to competitive interactions (Loreau & de Mazancourt, 2008; Shoemaker et al., 2022; Tredennick et al., 2017). However, even though synchronous and asynchronous dynamics reflect opposite correlations between the species (Houlahan et al., 2007), there is a growing understanding of how these dynamics can act in different temporal- (and spatial) scales (Lasky et al., 2016; Shoemaker et al., 2022; Vasseur et al., 2014). Species may, for example, be display synchrony on one timescale and asynchrony on another(Lasky et al., 2016; Vasseur et al., 2014), or they could be synchronous under some environmental conditions and asynchronous under others (Xu et al., 2015). Given that species are thought to differ in sensitivity to prey abundance, where kittiwakes are considered the most sensitive(Furness & Tasker, 2000), it could be that the different birds have different thresholds in terms of when

an effect of change in the environment is observable (Lahoz-Monfort et al., 2013). For example, SST above a certain threshold could potentially act as a synchronizing factor on breeding success for all species.

Even though the study species on Hornøya overlap in diet and foraging area, they employ different foraging strategies and rely on different amounts and sizes of similar prey species (Furness & Barrett, 1985). This could be one reason for why overlapping diets does not cause asynchrony between the puffins and razorbills or between the gull -species, as this suggests that the differences in dietary choice depends on differences in anatomy and behaviour rather than competition and consequential niche partitioning(Furness & Barrett, 1985). Puffins, for example, feed on smaller fish than common guillemot (Furness & Barrett, 1985).

As great black-backed gulls and herring gulls are predators, eating eggs and chicks from the other study species (Jenssen, 2008), this could have implications for community synchrony. In years with little capelin, which exhibits large annual fluctuations stock size, large gulls may predate more on common guillemot and razorbill chicks, this could potential synchrony between all four species, as this predation would exacerbate the negative effect on the auks, while potentially buffering the negative effect on gulls (Carscadden et al., 2002).

The top-model for common guillemots included a negative of Arctic Oscillation-index in April-June. A negative effect of AO-index in February was found in the top model for great black-backed gulls. AO is a large teleconnection pattern in the Northern Hemisphere, associated with NAO (Stenseth et al., 2003; Thompson & Wallace, 1998). An effect of AO-index could indicate that breeding success is influenced by large-scale regional climate conditions. For instance, AO has been shown to affect the breeding success of other Arctic breeding birds (greater snow geese, *Chen caerulescens atlantica*), impacting their brood size and chick survival (Dickey et al., 2008). There is also evidence that Artic Oscillation could also have indirect effects on seabird diet during the breeding season (Renner et al., 2012), thus influencing their breeding success.

For common guillemots the fifth (within Δ2AICc) model included a negative effect of SST in May-July two years prior to breeding. In comparison with the gulls, where the time period of the lagged effect of SST was March-April, an effect of SST later in the season makes sense as the gulls start breeding earlier than the common guillemots. As for the other species, reduced availability of capelin in warm years (Barrett & Erikstad, 2013) could have a negative effect

on common guillemot breeding success. However, common guillemots have been shown to be relatively insensitive to changes in prey, as long as prey sources are available (Burger & Piatt, 1990). Common guillemots have an overall high and stable breeding success during the study period. They have little annual variation with one exceptional year (2015), which gives a high risk of finding spurious covariate effects.

In this thesis I focus on bottom-up effects, but it is no doubt that top-down effects of predation can have a strong synchronizing effect as well (Robertson et al., 2015). In 2010, 2011 and 2014 mink were observed on Hornøya (Reiertsen unpubl), where 2011 and 2014 were among the years with the lowest breeding success for puffins and razorbills however, 2010 was a year with high breeding success overall, thus, the impact of mink on breeding success is unclear.

Considering how environmental factors might have a synchronizing effect on different time scales, it is relevant to note the different in time series length for each species. In particular it would have been interesting to compare the patterns of common guillemot breeding success with the other auks.

Conclusion:

The high degree of interspecific synchrony between auk-species and between gull-species, shows that seabirds with similar foraging behaviour do in fact display synchrony in breeding success. As synchronous fluctuations amplify the extinction risk compared to asynchronous fluctuations, these results could mean that the seabird community on Hornøya is vulnerable to future climate change.

Oceanographic conditions were found to influence breeding success, and even explained a substantial amount of the observed synchrony between species. Increased SST coincided with lower breeding success for two gull-species, having a strong synchronizing effect. An effect of Winter AW-inflow on breeding success was also found for five out of the six study species. Breeding success for herring gulls, great black-backed gulls and kittiwakes was negatively affected by increased winter AW-inflow, while breeding success for puffins and razorbills increased after years of high winter AW-inflow. This opposite effect of winter AW-inflow on auks compared to gulls could indicate differences in responses to climate change and have implications for future development of the two species-groups. The Barents Sea is a hot spot for Arctic climate change (Asbjørnsen et al., 2020), and major changes in the ecosystem are

expected (Aschan et al., 2013). The ongoing "Atlantification" of the Barents Sea, with increasing sea surface temperatures and a movement of more boreal and southern species into the ecosystem (Asbjørnsen et al., 2020; Ingvaldsen et al., 2021), could potentially have pronounced effect on seabirds breeding in the colony on Hornøya.

Further research is required, especially regarding diet, to determine how much "niche overlap" there actually is, and thus to support that the observed interspecific synchrony is in fact due to bottom-up effects rather than other factors like predation, disturbance.

References

Artsdatabanken. (2021, 29.11.2021). *Rødlista - hva, hvem, hvorfor?* Artsdatabanken. Retrieved 14.05, from http://www.artsdatabanken.no/rodlisteforarter2021/Rodlistahvahvemhvorfor

Asbjørnsen, H., Årthun, M., Skagseth, Ø., & Eldevik, T. (2020). Mechanisms Underlying Recent Arctic Atlantification. *Geophysical Research Letters*, *47*(15). https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/2020GL088036

Aschan, M., Fossheim, M., Greenacre, M., & Primicerio, R. (2013). Change in fish community structure in the Barents Sea. *PLoS One*, *8*(4), e62748. https://doi.org/10.1371/journal.pone.0062748

Barret, R., & Eriksen, K. E. (2009). *Keysite monitoring on Hornøya in 2008* (SEAPOP short report-1 2009). Norwegian Institute for Nature Reasearch https://seapop.no/wp-content/uploads/2021/03/seapop-short-report-1-2009.pdf

Barret, R. T. (2007). Food web interactions in the southwestern Barents Sea: black-legged kittiwakesRissa tridactylarespond negatively to an increase in herringClupea harengus. *Marine ecology. Progress series (Halstenbek)*, *349*, 269-276.

Barret, R. T. (2010). Hva er en sjøfugl? *Ottar. Sjøfugl - speiler havets tilstand*, *283*(5), 3-10.

Barrett, R. T. (2001). Monitoring the Atlantic Puffin Fratercula arctica, Common Guillemot Uria aalge and Black-legged Kittiwake Rissa tridactyla breeding populations on Hornøya, notheast Norway, 1980 - 2000. *Fauna norvegica*.

Barrett, R. T. (2002). Atlantic puffin Fratercula arctica and common guillemot Uria aalge chick diet and growth as indicators of fish stocks in the Barents Sea. *Marine ecology. Progress series (Halstenbek)*, *230*, 275-287. https://doi.org/10.3354/meps230275

Barrett, R. T. (2015). The diet, growth and survival of Razorbill Alca torda chicks in the southern Barents Sea. *Norwegian Ornithological Society*, *38*, 25-31.

Barrett, R. T., & Erikstad, K. E. (2013). Environmental variability and fledging body mass of Common Guillemot Uria aalge chicks. *Marine biology*, *160*(5), 1239-1248. https://doi.org/10.1007/s00227-013-2175-y

Barrett, R. T., Erikstad, K. E., & Reiertsen, T. (2017). Ocean climate and egg investment in the black-legged kittiwake Rissa tridactyla. *Marine ecology. Progress series (Halstenbek)*. https://doi.org/10.3354/meps12270

Burger, A. E., & Piatt, J. F. (1990). Flexible time budgets in breeding common murres: Buffers against variable prey abundance. *Studies in Avian Biology*, *14*, 71-83.

Burnham, K. P. (2002). *Model selection and multimodel inference : a practical information-theoretic approach* (2nd ed.). Springer.

Burr, Z. M., Varpe, Ø., Anker-Nilssen, T., Erikstad, K. E., Descamps, S., Barrett, R. T., Bech, C., Christensen-Dalsgaard, S., Lorentsen, S.-H., Moe, B., Reiertsen, T. K., & Strøm, H. (2016). Later at higher latitudes: large-scale variability in seabird breeding timing and synchronicity. *Ecosphere*, *7*(5), e01283. https://doi.org/https://doi.org/10.1002/ecs2.1283

Carroll, M. J., Butler, A., Owen, E., Ewing, S. R., Cole, T., Green, J. A., Soanes, L. M., Arnould, J. P. Y., Newton, S. F., Baer, J., Daunt, F., Wanless, S., Newell, M. A., Robertson, G. S., Mavor, R. A., & Bolton, M. (2015). Effects of sea temperature and stratification changes on seabird breeding success. *Climate research*, *66*(1), 75-89. https://doi.org/10.3354/cr01332

Carscadden, J. E., Montevecchi, W. A., Davoren, G. K., & Nakashima, B. S. (2002). Trophic relationships among capelin (Mallotus villosus) and seabirds in a changing ecosystem. *ICES journal of marine science*, *59*(5), 1027-1031.

Coulson, J. C. (2011). *The kittiwake*. T. & A.D. Poyser.

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., Yates, O., Lascelles, B., Borboroglu, P. G., & Croxall, J. P. (2019). Threats to seabirds: A global assessment. *Biological conservation*, *237*, 525-537. https://doi.org/10.1016/j.biocon.2019.06.033

Dickey, M.-H., Gauthier, G., & Cadieux, M.-C. (2008). Climatic effects on the breeding phenology and reproductive success of an arctic-nesting goose species. *Global change biology*, *14*(9), 1973-1985. https://doi.org/10.1111/j.1365-2486.2008.01622.x

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27-46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Durant, J. M., Skern-Mauritzen, M., Krasnov, Y. V., Nikolaeva, N. G., Lindstrøm, U., & Dolgov, A. (2014). Temporal dynamics of top predators interactions in the Barents Sea. *PLoS One*, *9*(11), e110933-e110933. https://doi.org/10.1371/journal.pone.0110933

Eilertsen, K., Barrett, R. T., & Torstein, P. (2008). Diet, growth and early survival of Atlantic Puffin (Fratercula arctica) chicks in North Norway. *Waterbirds*, *31*(1), 107-114.

Engen, S., & Sæther, B.-E. (2005). Generalizations of the Moran Effect Explaining Spatial Synchrony in Population Fluctuations. *The American naturalist*, *166*(5), 603-612. https://doi.org/10.1086/491690

Erikstad, K. E., Benjaminsen, S., Reiertsen, T. K., Ballestros, M., & Strøm, H. (2018). *Modellering av svømmetrekket til lomvi (Uria aalge) fra Bjørnøya til norskekysten. Utvikling av ny metodikk for bruk av lysloggere (GLS),dykkeloggere (TDR) og sjøtemperaturer (SST) til kartlegging av svømmetrekket hos alkefugl* (NINA report 1546). Norsk Institutt for Naturforskning (NINA).

Erikstad, K. E., Fauchald, P., Tveraa, T., & Steen, H. (1998). On the Cost of Reproduction in Long-Lived Birds: The Influence of Environmental Variability. *Ecology 79*(5), 1781-1788.

Fauchald, P., Anker-Nilssen, T., Barrett, R. T., Bustnes, J. O., Bårdsen, B.-J., Christensen-Dalsgaard, S., Descamps, S., Engen, S., Erikstad, K. E., Hanssen, S. A., Lorentsen, S.-H., Moe, B., Reiertsen, T., Strøm, H., & Systad, G. H. (2015). *The status and trends of seabirds breeding in Norway and Svalbard* (NINA report 1151). Norwegian Institute for Nature Research.

Fayet, A. L., Clucas, G. V., Anker-Nilssen, T., Syposz, M., & Hansen, E. S. (2021). Local prey shortages drive foraging costs and breeding success in a declining seabird, the Atlantic puffin. *Journal of Animal Ecology*, *90*(5), 1152-1164. https://doi.org/10.1111/1365-2656.13442

Frainera, A., Primicerioa, R., Kortscha, S., Auneb, M., Dolgovc, A. V., Fossheimd, M., & Aschana, M. M. (2017). Climate-driven changes in functional biogeography of Arctic marine fish communities. *PNAS*, *114*(46), 12202–12207.

Frederiksen, M., Harris, M. P., Daunt, F., Rothery, P., & Wanless, S. (2004). Scale-dependent climate signals drive breeding phenology of three seabird species. *Global change biology*, *10*(7), 1214-1221. https://doi.org/10.1111/j.1529-8817.2003.00794.x

Frederiksen, M., Wright, P. J., Harris, M. P., Mavor, R. A., Heubeck, M., & Wanless, S. (2005). Regional patterns of kittiwake Rissa tridactyla breeding success are related to variability in sandeel recruitment. *Marine ecology. Progress series (Halstenbek)*, *300*, 201-211. https://doi.org/10.3354/meps300201

Furness, R. W., & Barrett, R. T. (1985). The Food Requirements and Ecological Relationships of a Seabird Community in North Norway. *Ornis Scandinavica*, *16*(4), 305-313. https://doi.org/10.2307/3676695

Furness, R. W., & Tasker, M. L. (2000). Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine ecology. Progress series (Halstenbek)*, *202*, 253-264. https://doi.org/10.3354/meps202253

Gamelon, M., Vriend, S. J. G., Engen, S., Adriaensen, F., Dhondt, A. A., Evans, S. R., Matthysen, E., Sheldon, B. C., & Sæther, B.-E. (2019). Accounting for interspecific competition and age structure in demographic analyses of density dependence improves predictions of fluctuations in population size. *Ecology Letters*, *22*(5), 797-806.

Gaston, A. J., & Jones, I. L. (1998). *The auks : Alcidae*. Oxford University Press.

Gjøsæter, H. (1998). The population biology and exploitation of capelin (Mallotus villosus) in the barents sea. *Sarsia*, *83*(6), 453-496. https://doi.org/10.1080/00364827.1998.10420445

Gonzalez, A., & Loreau, M. (2009). The Causes and Consequences of Compensatory Dynamics in Ecological Communities. *Annual review of ecology, evolution, and systematics*, *40*(1), 393-414. https://doi.org/10.1146/annurev.ecolsys.39.110707.173349

Hansen, B. B., Grøtan, V., Herfindal, I., & Lee, A. M. (2020). The Moran effect revisited: spatial population synchrony under global warming. *Ecography*, *43*(11), 1591-1602. https://doi.org/10.1111/ecog.04962

Harris, M. P. (1984). *The puffin*. Poyser.

Hatch, S. A. (2012). *The KittiwakeThe Kittiwake.—By John C. Coulson . 2011. T & A D Poyser, London. 304 pp. Hardcover: £50.00 (about $80 US). (ISBN: 978-1-4081-0966-3)* (Vol. 35). https://doi.org/10.1675/063.035.0219

Hazen, E. L., Abrahms, B., Brodie, S., Carroll, G., Jacox, M. G., Savoca, M. S., Scales, K. L., Sydeman, W. J., & Bograd, S. J. (2019). Marine top predators as climate and ecosystem sentinels. *Frontiers in ecology and the environment*, *17*(10), 565-574. https://doi.org/10.1002/fee.2125

Heino, M., Kaitala, V., Ranta, E., & Lindstrm, J. (1997). Synchronous dynamics and rates of extinction in spatially structured populations. *Proceedings of the Royal Society. B, Biological sciences*, *264*(1381), 481-486. https://doi.org/10.1098/rspb.1997.0069

Hestem, M. (2019). *Should I Stay or Should I Go? Geolocators reveal different winter home ranges and -foraging patterns in sympatrically breeding razorbills (Alca torda)* [Master thesis, Norwegian University of Life Science].

Hjermann, D. Ø., Stenseth, N. C., & Ottersen, G. (2004). Indirect climatic forcing of the Barents Sea capelin: a cohort effect. *Marine ecology. Progress series (Halstenbek)*, *273*, 229-238. https://doi.org/10.3354/meps273229

Houlahan, J. E., Currie, D. J., Cottenie, K., Cumming, G. S., Ernest, S. K. M., Findlay, C. S., Fuhlendorf, S. D., Gaedke, U., Legendre, P., Magnuson, J. J., McArdle, B. H., Muldavin, E. H., Noble, D., Russell, R., Stevens, R. D., Willis, T. J., Woiwod, I. P., & Wondzell, S. M. (2007). Compensatory dynamics are rare in natural ecological communities. *Proceedings of the National Academy of Sciences*, *104*(9), 3273-3277. https://doi.org/doi:10.1073/pnas.0603798104

Huitu, O., Norrdahl, K., & Korpimäki, E. (2004). Competition, predation and interspecific synchrony in cyclic small mammal communities. *Ecography*, *27*(2), 197-206. https://onlinelibrary.wiley.com/doi/abs/10.1111/j.0906-7590.2003.03684.x

Hurrell, J. W., Kushnir, Y., Ottersen, G., & Visbeck, M. (2003). An Overview of the North Atlantic Oscillation. *Geophysical Monograph-American Geophysical Union*, *134*. https://doi.org/10.1029/GM134

Ingvaldsen, R. B. (2003). *The Atlantic inflow to the Barents Sea* [University of Bergen].

Ingvaldsen, R. B., Asplin, L., & Loeng, H. (2004). The seasonal cycle in the Atlantic transport to the Barents Sea during the years 1997–2001. *Continental shelf research*, *24*(9), 1015-1032. https://doi.org/10.1016/j.csr.2004.02.011

Ingvaldsen, R. B., Assmann, K. M., Primicerio, R., Fossheim, M., Polyakov, I. V., & Dolgov, A. V. (2021). Physical manifestations and ecological implications of Arctic Atlantification. *Nature Reviews Earth & Environment*, *2*(12), 874-889. https://doi.org/10.1038/s43017-021-00228-x

Jenouvrier, S. (2013). Impacts of climate change on avian populations. *Glob Change Biol*, *19*(7), 2036-2057. https://doi.org/10.1111/gcb.12195

Jenouvrier, S., Barbraud, C., & Weimerskirch, H. (2005). Long-Term Contrasted Responses to Climate of Two Antarctic Seabird Species. *Ecology*, *86*(11), 2889-2903. https://doi.org/10.1890/05-0514

Jenssen, T. R. S. (2008). *Kjønnsspesifikk overlevelse av unger hos gråmåke Larus argentatus og svartbak Larus marinus* [University of Tromsø].

Johannesen, E., Ingvaldsen, R. B., Bogstad, B., Dalpadado, P., Eriksen, E., Gjøsæter, H., Knutsen, T., Skern-Mauritzen, M., & Stiansen, J. E. (2012). Changes in Barents Sea ecosystem state, 1970–2009: climate fluctuations, human impact, and trophic interactions. *ICES journal of marine science*, *69*(5), 880-889. https://doi.org/10.1093/icesjms/fss046

Kvivesen, E. R. (2009). *The importance of brood sex ratio on survival of herring gull (larus argentatus) chicks in years with food scarcity* [Master thesis, Norwegian University of Life Science].

Lahoz-Monfort, J. J., Morgan, B. J. T., Harris, M. P., Daunt, F., Wanless, S., & Freeman, S. N. (2013). Breeding together: modeling synchrony in productivity in a seabird community. *Ecology*, *94*(1), 3-10. https://doi.org/10.1890/12-0500.1

Lasky, J. R., Uriarte, M., & Muscarella, R. (2016). Synchrony, compensatory dynamics, and the functional trait basis of phenological diversity in a tropical dry forest tree community: effects of rainfall seasonality. *Environ. Res. Lett*, *11*(11), 115003. https://doi.org/10.1088/1748-9326/11/11/115003

Layton-Matthews, K., Hansen, B. B., Grøtan, V., Fuglei, E., & Loonen, M. J. J. E. (2019). Contrasting consequences of climate change for migratory geese: Predation, density dependence and carryover effects offset benefits of high-arctic warming. *Global Change Biology 12*(2), 642-657.

Loeng, H. (1991). Features of the physical oceanographic conditions of the Barents Sea. *Polar research*, *10*(1), 5-18. https://doi.org/10.3402/polar.v10i1.6723

Loreau, M., & de Mazancourt, C. (2008). Species Synchrony and Its Drivers: Neutral and Nonneutral Community Dynamics in Fluctuating Environments. *The American naturalist*, *172*(2), E48-E66. https://doi.org/10.1086/589746

Moore, S. E., & Kuletz, K. J. (2019). Marine birds and mammals as ecosystem sentinels in and near Distributed Biological Observatory regions: An abbreviated review of published accounts and recommendations for integration to ocean observatories. *Deep-sea research. Part II, Topical studies in oceanography*, *162*, 211-217. https://doi.org/10.1016/j.dsr2.2018.09.004

Myksvoll, M. S., Erikstad, K. E., Barrett, R. T., Sandvik, H., & Vikebø, F. (2013). Climate-driven ichthyoplankton drift model predicts growth of top predator young. *PLoS One*, *8*(11), e79225-e79225. https://doi.org/10.1371/journal.pone.0079225

Olin, A. B., Banas, N. S., Wright, P. J., Heath, M. R., & Nager, R. G. (2020). Spatial synchrony of breeding success in the black-legged kittiwake Rissa tridactyla reflects the spatial dynamics of its sandeel prey. *Marine ecology. Progress series (Halstenbek)*, *638*, 177-190.

Post, E., & Forchhammer, M. C. (2002). Synchronization of animal population dynamics by large-scale climate. *Nature*, *420*(6912), 168-171. https://doi.org/10.1038/nature01064

RCoreTeam. (2021). *R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.* https://www.R-project.org/

Reiertsen, T. K., & Barrett, R. T. (2010). *Sjøfugl - speiler havets tilstand* (Vol. 2010 nr. 5 = Nr. 283). Tromsø museum - Universitetsmuseet.

Reiertsen, T. K., Erikstad, K. E., Anker-Nilssen, T., Barrett, R. T., Boulinier, T., Frederiksen, M., González-Solís, J., Gremillet, D., Johns, D., Moe, B., Ponchon, A., Skern-Mauritzen, M., Sandvik, H., & Yoccoz, N. G. (2014). Prey density in non-breeding areas affects adult survival of black-legged kittiwakes Rissa tridactyla. *Marine ecology. Progress series (Halstenbek)*, *509*, 289-302. https://doi.org/10.3354/meps10825

Reiertsen, T. K., Erikstad, K. E., Barrett, R. T., Sandvik, H., & Yoccoz, N. G. (2012). Climate fluctuations and differential survival of bridled and non-bridled Common Guillemots Uria aalge. *Ecosphere 3*(6), art52-15. https://doi.org/10.1890/ES12-00031R

Renner, H. M., Mueter, F., Drummond, B. A., Warzybok, J. A., & Sinclair, E. H. (2012). Patterns of change in diets of two piscivorous seabird species during 35 years in the Pribilof Islands. *Deep-sea research. Part II, Topical studies in oceanography*, *65-70*, 273-291. https://doi.org/10.1016/j.dsr2.2012.02.014

Robertson, G. S., Bolton, M., Morrison, P., & Monaghan, P. (2015). Variation in Population Synchrony in a Multi-Species Seabird Community: Response to Changes in Predator Abundance. *PLoS One*, *10*(6), e0131543-e0131543. https://doi.org/10.1371/journal.pone.0131543

Robinson, J. P. W., Dornelas, M., & Ojanguren, A. F. (2013). Interspecific synchrony of seabird population growth rate and breeding success. *Ecology and Evolution*, *3*(7), 2013-2019. https://doi.org/10.1002/ece3.592

Sandvik, H., Erikstad, K. E., Barrett, R. T., & Yoccoz, N. G. (2005). The Effect of Climate on Adult Survival in Five Species of North Atlantic Seabirds. *Journal of Animal Ecology*, *74*(5), 817-831. https://doi.org/10.1111/j.1365-2656.2005.00981.x

Sandvik, H., Reiertsen, T. K., Erikstad, K. E., Anker-Nilssen, T., Barrett, R. T., Lorentsen, S.-H., Systad, G. H., & Myksvoll, M. S. (2014). The decline of Norwegian kittiwake populations: modelling the role of ocean warming. *Climate research*, *60*(2), 91-102. https://doi.org/10.3354/cr01227

Schmidt, N. M., Ims, R. A., Høye, T. T., Gilg, O., Hansen, L. H., Hansen, J., Lund, M., Fuglei, E., Forchhammer, M. C., & Sittler, B. (2012). Response of an arctic predator guild to collapsing lemming cycles. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 4417–4422.

Schmutz, J. A., & Laing, K. K. (2002). Variation in Foraging Behavior and Body Mass in Broods of Emperor Geese (Chen Canagica): Evidence for Interspecific Density Dependence. *The Auk*, *119*(4), 996-1009. https://doi.org/10.1093/auk/119.4.996

Shoemaker, L. G., Hallett, L. M., Zhao, L., Reuman, D. C., Wang, S., Cottingham, K. L., Hobbs, R. J., Castorani, M. C. N., Downing, A. L., Dudney, J. C., Fey, S. B., Gherardi, L. A., Lany, N., Portales-Reyes, C., Rypel, A. L., Sheppard, L. W., Walter, J. A., & Suding, K. N. (2022). The long and the short of it: Mechanisms of synchronous and compensatory dynamics across temporal scales. *Ecology*, *103*(4), e3650-n/a. https://doi.org/10.1002/ecy.3650

Stenseth, N. C., Chan, K. S., Hurrell, J. W., Tong, H., Boonstra, R., Boutin, S., Krebs, C. J., Post, E., O'Donoghue, M., Yoccoz, N. G., & Forchhammer, M. C. (1999). Common Dynamic Structure of Canada Lynx Populations Within Three Climatic Regions. *Science*, *285*(5430), 1071-1073. https://doi.org/10.1126/science.285.5430.1071

Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., Chan, K.-S., Yoccoz, N. G., & Ådlandsvik, B. (2003). Review article. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society B-Biological Sciences 270*(1529), 2087-2096. https://doi.org/10.1098/rspb.2003.2415

Systad, G. H. (2010). Sjøfugl i Norge : hvor er de? *Ottar: Sjøfugl - speiler havets tilstand*, 18-27.

Sæther, B.-E., & Engen, S. (2002). Pattern of variation in avian population growth rates. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *357*(1425), 1185–1195.

Sæther, B. E., Engen, S., Grøtan, V., Fiedler, W., Matthysen, E., Visser, M. E., Wright, J., Møller, A. P., Aiaensen, F., van Balen, H., Balmer, D., Mainwaring, M. C., McCleery, R., Pampus, M., & Winkel, W. (2007). The Extended Moran Effect and Large-Scale Synchronous Fluctuations in the Size of Great Tit and Blue Tit Populations. *Journal of Animal Ecology*, *76*(2), 315-325. https://doi.org/10.1111/j.1365-2656.2006.01195.x

Thayer, J. A., Bertram, D. F., Hatch, S. A., Hipfner, M. J., Slater, L., Sydeman, W. J., & Watanuki, Y. (2008). Forage fish of the Pacific Rim as revealed by diet of a piscivorous seabird: synchrony and relationships with sea surface temperature. *Journal canadien des sciences halieutiques et aquatiques*, *65*(8), 1610-1622. https://doi.org/10.1139/F08-076

Thompson, D. W. J., & Wallace, J. M. (1998). The Arctic oscillation signature in the wintertime geopotential height and temperature fields. *Geophysical Research Letters*, *25*(9), 1297-1300. https://doi.org/10.1029/98GL00950

Tredennick, A. T., Mazancourt, C., Loreau, M., & Adler, P. B. (2017). Environmental responses, not species interactions, determine synchrony of dominant species in semiarid grasslands. *Ecology*, *98*(4), 971-981. https://doi.org/10.1002/ecy.1757

Vasseur, D. A., Fox, J. W., Gonzalez, A., Adrian, R., Beisner, B. E., Helmus, M. R., Johnson, C., Kratina, P., Kremer, C., de Mazancourt, C., Miller, E., Nelson, W. A., Paterson, M., Rusak, J. A., Shurin, J. B., & Steiner, C. F. (2014). Synchronous dynamics of zooplankton competitors prevail in temperate lake ecosystems. *Proceedings of the Royal Society. B, Biological sciences*, *281*(1788), 20140633-20140633. https://doi.org/10.1098/rspb.2014.0633

Xu, Z., Ren, H., Li, M. H., Ruijven, v. J., Han, X., Wan, S., Li, H., Yu, Q., Jiang, Y., & Jiang, L. (2015). Environmental changes drive the temporal stability of semi-arid natural grasslands through altering species asynchrony. *The Journal of ecology*, *103*(5), 1308-1316. https://doi.org/10.1111/1365-2745.12441

Youngflesh, C., Li, Y., Lynch, H. J., Delord, K., Barbraud, C., Ji, R., & Jenouvrier, S. (2021). Lack of synchronized breeding success in a seabird community: extreme events, niche separation, and environmental variability. *Oikos*, *130*(11), 1943-1953. https://doi.org/10.1111/oik.08426

Zhang, D. (2017). A Coefficient of Determination for Generalized Linear Models. *The American Statistician*, *71:4*, 310-316.

Zuur, A. F. (2009). *Mixed effects models and extensions in ecology with R*. Springer.

Appendix 1

Table 3. Pairwise correlation in breeding success between the six focal species, shown as the Pearson's product-moment correlation coefficient (with 95% confidence intervals, CIs) and whether that correlation difference significantly from zero based on the calculated p-value

Species *a*	Species *b*	Correlation (95% CIs)	df	P-value
C. guillemot	Puffin	0.60 (-0.18, 0.92)	6	0.12
C. guillemot	Razorbill	0.40 (-0.42,0.86)	6	0.32
C. guillemot	Kittiwake	0.28 (-0.53, 0.82)	6	0.51
C. guillemot	Herring gull	0.54 (-0.26, 0.90)	6	0.16
C. guillemot	Great Black backed	0.32 (-0.49, 0.84)	6	0.43
Puffin	Razorbill	0.93 (0.84, 0.97)	27	<0.001***
Puffin	Kittiwake	0.04 (-0.52, 0.58)	11	0.89
Puffin	Herring gull	0.26 (-0.40, 0.75)	9	0.43
Puffin	Great Black backed	0.45 (-0.20, 0.83)	9	0.16
Razorbill	Kittiwake	0.11 (0.52, 0.67)	9	0.74
Razorbill	Herring gull	0.26 (-0.40, 0.75)	9	0.43
Razorbill	Great Black backed	0.45 (-0.20, 0.83)	9	0.16
Kittiwake	Herring gull	0.70 (0.17, 0.92)	9	0.02*
Kittiwake	Great Black backed	0.40 (-0.27, 0.81)	9	0.16
Herring gull	Great Black backed	0.84 (0.49, 0.96)	9	<0.001***

Table 4. Variation inflation factor and partial R^2 for all covariates included the top model for each species, in addition to the total model R^2 for each top model.

Species	Covariates in top model	Slope (95% confidence intervals)	Variation inflation factor	Partial R^2	Total model R^2
Puffin	AW-inflow December - February lag 1	0.40 (0.27, 0.54)	1.00	0.06	0.20
	AW-inflow June	0.38 (0.24, 0.53)	1.00	0.15	
Razorbill	AW-inflow December-February lag 1	0.70 (0.56, 0.85)	1.00	0.23	0.50
	AW-inflow June	0.49 (0.34, 0.64)	1.00	0.45	
Common guillemot	AO April-June	-0.61(-0.02, -0.23)		0.67	0.67
Kittiwake	AW-inflow December-February	-0.35(-0.44, -0.25)	1.02	0.54	0.85
	SST March-April lag 1	0.51(0.34, 0.69)	1.02	0.71	
Great black-backed gull	SST March-April lag 2	-0.53 (-0.65, -0.39)	1.28	0.36	0.90
	AO February	-0.24(-0.33, -0.14)	1.28	0.76	
Herring gull	SST March-April lag 2	-0.73 (-0.85, -0.55)	1.07	0.96	0.97
	AW-inflow December-February	-0.13(-0.21, -0.06)	1.07	0.96	

Appendix 2

Table 5. Model selection table for puffin.

Intercept	AW Dec-Feb lg 1	AW Dec-Feb lg2	AW Jun	Temp Mar-Apr	NAO May-jul	NAO Mar-Apr	AO Apr-May	AO Apr	AICc	Delta	Weight
1.078	0.40		0.38						292.2	0.00	0.912
1.03			0.46	0.36					299.3	7.03	0.027
1.06	0.40	0.27							299.5	7.25	0.024
1.07				-0.39	0.52				299.9	7.64	0.020
1.03					0.43	-0.35			303.1	10.89	0.004
1.04					0.53		-0.35		303.3	11.02	0.004
1.08	0.36				0.32				303.8	11.56	0.003
1.04	0.40			-0.24					304.9	12.66	0.002
1.02	0.37					-0.25			305.4	13.13	0.001
1.03					0.42			-0.31	306.7	14.4	0.001

Appendix 3

Table 6. Model selection table for razorbill.

Intercept	AW Dec-Feb lg1	AW Dec-Feb lg2	AW Jun	AW Jul	AW Mar-Apr	AW May-Jul	AO Apr-May	AO Apr-Jun	AO May	NAO May-Jul	NAO Mar-Apr	AICc	Delta	Weight
0.78	0.70		0.49									276.4	0.00	0.999
0.78	0.78					0.35						291.2	14.77	0.001
0.77	0.76			0.31								298.5	22.05	0.000
0.79	0.73	0.24										304.6	28.14	0.000
0.76	0.75								-0.24			307.4	31.00	0.000
0.75	0.67					-0.24						308.2	31.82	0.000
0.74	0.71						-0.23					310.1	33.64	0.000
0.77	0.68									0.24		311.2	34.74	0.000
0.74	0.65										-0.18	312.3	35.91	0.000
0.76	0.67				-0.18							313.1	36.67	0.000

Appendix 4

Table 7. Model selection table for common guillemot.

Intercept	AO Apr-Jun	AO Apr-May	AO Apr	AO Jun	AO Jun-Jul	SST May-Jul lg2	SST Mar-Apr lg1	SST May-Jun	AW Apr	AICc	Delta	Weight
1.46	-0.61									40.5	0.00	0.096
1.45		-0.57		-0.58						41.0	0.48	0.076
1.45	-0.63			-0.32						41.0	0.49	0.075
1.47	-0.80				-0.29					41.9	1.35	0.049
1.16						-0.45				42.0	1.45	0.047
1.48	-0.73						-0.36			43.3	2.80	0.024
1.52	-0.62							-0.20		43.7	3.17	0.020
1.45			-0.43	-0.59						43.7	3.18	0.020
1.23						-0.38			-0.38	43.8	3.22	0.019
1.38				-0.38					-0.55	43.8	3.26	0.019

Appendix 5

Table 8. Model selection table for kittiwake.

Intercept	AO Jul	AO Jun-Jul	AW Dec-Feb	AW May-Jul	AW Mar-Apr	AW Jul	AW May	AW Apr	SST Mar-Apr lg1	SST May-Jul lg1	SST Mar-Apr lg2	Temp Mar-Apr	Sst.ma	AICc	Delta	Weight
-2.09			-0.35						0.51					123.9	0.00	0.635
-2.19				-0.68							-0.91			125.4	1.5	0.300
-2.11	0.77							0.53						129.7	5.76	0.036
-2.15							-0.61				-0.81			130.8	6.83	0.021
-1.96			-0.47										0.38	133.8	9.82	0.005
-2.11			-0.54							0.36				134.7	10.75	0.003
-2.02	0.39		-0.25											137.8	13.84	0.001
-1.98		0.3566	-0.29											139.7	15.74	0.000
-2.07			-0.45		-0.38									140.4	16.42	0.000
-1.97	0.69			0.40										140.6	16.65	0.000

Appendix 6

Table 9. Model selection table for great black-backed gull.

Intercept	AO Feb	AO Apr	AO Jul	AW Dec-Feb	Aw Dec-Feb lg1	AW May	NAO Mar-Apr	SST Mar-Apr lg2	SST May-Jul lg1	SST May-Jul	Temp. Mar-Apr	AICc	Delta	Weight
-0.51	-0.24							-0.53				121.8	0.00	0.377
-0.61				-0.23				-0.65				122.8	1.00	0.228
-0.57	-0.55		-0.31									123.3	1.52	0.176
-0.35	-0.49					0.48						123.3	1.57	0.172
-0.48							-0.25	-0.59				127.2	5.44	0.025
-0.63								-0.62	-0.31			127.8	6.03	0.019
-0.55								-0.74			0.23	131.1	9.33	0.0046
-0.54								-0.76		0.17		136.7	14.93	0.000
-0.43					0.18			-0.62				136.7	14.94	0.000
-0.49		-0.14						-0.73				137.8	16.06	0.000

Appendix 7

Table 10. Model selection table for herring gull.

Intercept	SST Mar-Apr lg2	AW Dec-Feb	AO Feb	AO May	AO Apr-May	AO Jul	AO Apr-Jun	AO Jun-Jul	AW May	AW Jun	AICc	Delta	Weight
-0.67	-0.73	-0.13									88.4	0.00	0.662
-0.61	-0.68		-0.12								91.8	3.46	0.117
-0.63	-0.85			-0.13							93.3	4.87	0.058
-0.59	-0.82					0.09					94.0	5.61	0.040
-0.61	-0.79						-0.13				94.9	6.52	0.025
-0.60	-0.81				-0.10						95.6	7.24	0.018
-0.62	-0.79										96.3	7.94	0.013
-0.65	-0.85							-0.14			96.4	7.99	0.012
-0.60	-0.81								0.06		97.6	9.20	0.007
-0.67	-0.82									-0.13	97.8	9.44	0.006