Seabirds, climate and prey.

A population study of two seabird species.

Tone Kristin Reiertsen

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UNIVERSITY OF TROMSØ
Tromsø University Museum
Department of Natural Sciences

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

NORWEGIAN INSTITUTE FOR NATURE RESEARCH
FRAM – High North Research Centre for Climate and the Environment

Supervisors

Rob T. Barrett, Tromsø University Museum, University of Tromsø

Nigel G. Yoccoz, Department of Arctic and Marine Biology, University of Tromsø

Preface

Min tid som doktorgradsstudent ved Tromsø Museum nærmer seg slutten, og det har vært en av de mest givende, morsomme, spennende, strevsomme og utmattende tidsperioder i hele mitt liv. Det er egentlig umulig å beskrive helt og fullt hvordan denne tiden har vært, bortsett fra at den kort oppsummert har vært fantastisk.

Det er mange som skal takkes for at jeg har klart å komme meg gjennom og fullført denne doktorgraden. Først og fremst vil jeg takke mine veiledere Rob Barrett og Nigel Yoccoz. Rob fordi du alltid har hatt døren åpen, og stilt opp både når det gjelder små og store spørsmål. Og i tillegg har det vært en superbonus å ha en veileder med engelsk som sitt morsmål, når jeg med min dårlige skole-engelsk skulle ta fatt på dette store prosjektet. Nigel, du har vært uvurderlig i å sette meg på rett spor hver gang jeg har stått fast med analyser og vanskelige spørsmål. Ikke minst har dere begge vært en uvurderlig støtte i den siste avsluttende fasen hvor dere til og med midt i påskehøytida tok dere tid til å lese gjennom tekst.

Jeg vil også takke alle mine samarbeidspartnere, som har delt av sin kunnskap og erfaring, og ikke minst gitt meg tilgang til data. I den sammenheng må jeg spesielt nevne Thierry Boulinier, Aurore Ponchon, Børge Moe, Mette Skern-Mauritzen, Morten Frederiksen og Tycho Anker-Nilssen for fine diskusjoner og for å ha delt av sin kunnskap. Og ikke minst må jeg få takke Hanno Sandvik for å være min mentor som jeg kunne spørre om alt, og som med sin genuine måte alltid har klart å forklare det vanskelige slik at selv jeg forstod det.

Denne doktorgraden hadde ikke vært mulig uten finansiering fra Universitet i Tromsø og også i den siste fasen fra Norsk Institutt for Naturforskning. I tillegg er jeg svært takknemlig overfor SEAPOP for å ha fått muligheten til å dykke ned i det store tidsserie materialet på sjøfugl som dette programmet har ansvaret for.

Feltarbeidet på Hornøya har vært noe av det jeg har satt mest pris på gjennom hele denne tiden, og mye av det er takket være alle som har vært i felt der sammen med meg. Ditte Lyngbo kristensen, Elisabeth Kvivesen, Signe Dalsgaard-Christensen, Grete Erikstad, Sigurd Benjaminsen, Renate Thorvaldsen og det franske teamet må nevnes spesielt her. I tillegg vil jeg takke Mari Myksvoll som var med meg ei hyggelig uke i felt sist sommer, for å ha gitt meg innblikk i en helt ny verden (for meg) innenfor oseanografi.

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Det er ikke bare faglige kolleger som skal ha æren for at denne doktorgraden endelig kom i mål. Takk til Mari-Ann og Rune Benonisen for alt dere har stilt opp med når det gjelder pass og kjøring av unger, der hvor jeg selv ikke strakk til. Marit Erikstad og Sigurd Benjaminsen – ikke bare er dere en del av min kjæreste familie, men uten dere hadde ikke verden gått rundt i perioder. I tillegg må alle barnevakter som ha hjulpet til med pass av unger både i felt og eller få en takk.

Til sist vil jeg takke hele min store, kjære familie, som alltid er der for meg, og som har gitt meg støtte og styrke til å fullføre dette prosjektet. Spesielt til mine tre barn Emma, Johan og Mathias, og sist men ikke minst min mann Kjell Einar Erikstad. Uten deg hadde jeg gitt opp for lenge siden. Ikke bare har du tatt mer enn din del når det gjelder ungene den siste tiden, men du har vært til en uvurderlig støtte også faglig.

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This thesis is based on the following papers:

Paper 1.

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., Sandvik, H., Skern-Mauritzen, M. and Yoccoz, N.G. Prey density in non-breeding areas affects adult survival of black-legged kittiwakes *Rissa tridactyla* breeding in the southern Barents Sea. (submitted manuscript)

Paper 2.

Reiertsen, T.K., Barrett, R.T. and Erikstad, K.E. Kittiwakes on the cliff edge: a demographic analysis of a steeply declining arctic kittiwake population. (manuscript).

Paper 3.

Erikstad, K.E., Reiertsen, T.K., Barrett, R.T., Vikebø, F. and Sandvik, H. 2013. Seabird–fish interactions: the fall and rise of a common guillemot *Uria aalge* population. Marine Ecology Progress Series 475: 267 - 276.

Paper 4.

Reiertsen, T.K., Erikstad, K.., Barrett, R.obert T., Sandvik, H. and Yoccoz, N. 2012. Climate fluctuations and differential survival of bridled and non-bridled Common Guillemots *Uria aalge*. Ecosphere 3 (6). ISSN 2150-8925 doi:10.1890/ES12-00031R.

Errata

Paper 3 (Erikstad, Reiertsen, Barrett, Vikebø and Sandvik 2013)

In equation (1) of the paper «Seabird – fish interactions: the fall and rise of a common guillemot *Uria aalge* population" has been rendered incorrectly (p. 269) during the publishing process. The correct equation would have been:

$$\lambda_t = \exp\left[r(1 - N_t/K) - \sigma_\mathrm{d}^2/(2N_t) + \sum \beta_i X_{i,t} + \varepsilon_t\right]$$

The equation was originally submitted with a different layout, but **equivalent** meaning:

$$\lambda_t = e^{r(1-N_t/K)-\sigma_\mathrm{d}^2/(2N_t)+\sum \beta_i X_{i,t}+\varepsilon_t}$$

Contents:

Abstract

Many seabird populations have declined dramatically over recent decades, and studying the demography and population dynamic in seabird populations is important to gaining a better understanding of causes and mechanisms lying behind such changes and to identify targets for conservation and management. Climate and prey availability are known to affect demography and population dynamics of seabirds. Climate is now changing and a warming of the ocean may lead to changed availability of prey species and will affect seabirds through their demographic traits and ultimately their abundance and distribution. The main aim of this thesis was to study the impact of climate and prey abundance on seabird demography and population dynamics, using two seabird populations; the black-legged kittiwake *Rissa tridactyla* and the Common guillemot *Uria aalge* breeding on Hornøya in NE Norway whose populations are declining in Norway.

The first question addressed in the thesis was how environmental conditions affect the demography and population variability of kittiwakes and guillemots. The non-breeding distribution of the kittiwakes has recently been documented using year-round light-based geolocators, and we investigated the relationship between environmental conditions in these non-breeding areas and the adult survival of kittiwakes breeding on Hornøya. We found for the kittiwakes that Thecosomata, a group of pteropods (also called sea butterflies), in the Grand Banks/Labrador Sea area in winter and the capelin *Mallotus villosus* stock in Barents Sea in the pre-breeding season together explained as much as 52 % of the yearly variation in adult survival rate. Further we found that the availability of 0-group cod *Gadus morhua* was a much more important factor affecting demography and determining the population dynamics of the common guillemot in the Barents Sea than previously considered.

The second question was which demographic trait drives the population dynamics of the steeply declining kittiwake population on Hornøya. We showed, by using demographic matrix modeling and LTRE analyses, that both the variability in breeding success (and hence the recruitment to the population) and adult survival rate contributed to the steep decline in the kittiwake population on Hornøya. The strong reduction in breeding success (and hence a decline in recruitment to the population) had, however, the highest impact.

The final question was whether populations can adapt to environmental changes through micro-evolutionary processes. This study found that adult survival of the two different genetic colour morphs (bridled and non-bridled morph) of the common guillemot responded differently to yearly variability in sea surface temperatures. Colour dimorphism may, in this case serve as a genetic marker in the guillemot population, and can potentially visualize the direction of selection and micro-evolutionary processes driven by climate.

The studies in this thesis contribute to the understanding of the population dynamic of two declining seabird species which are both on the Norwegian Red List, and to the directions of future studies and conservation targets of both species.

Introduction

The question of why population sizes change over time and the identification of environmental factors that influence these changes is an essential element of population ecology and conservation biology (e.g. Tuljapurkar and Caswell 1997). Population dynamics may vary greatly, with some populations being stable over time while others oscillate regularly or irregularly, and some even dramatically towards possible extinction (see Clutton-Brock et al. 2002). Fluctuations in population sizes are a result of temporal variations in different demographic components, such as survival, fecundity and dispersal rates. Therefore studying demographic traits and what factors influence them provides an important framework in which to explain the causes of population changes.

Seabirds are marine top-predators and their distributions cover vast ranges of the marine environment. They are, as such, considered important indicators of the status and structure of marine ecosystems (Lewison et al. 2012). Most seabirds are long-lived, reach sexual maturity relatively late (4 – 11 years) and have a low reproduction rate. Over the past decades, many seabird populations have experienced dramatic changes and some are still doing so (Lewison et al. 2012) and a comparison of different groups of birds has shown that seabirds comprise the group that is experiencing the most negative change in their status on the international Red List (IUCN) (Birdlife International 2004).

Climate and food availability

The fourth assessment Report (AR4) of the Intergovernmental Panel on Climate Change (IPCC) stated that the warming of the climate is now “unequivocal”(IPCC 2007), and that climate change results in significant changes in populations, species distributions and ecosystems (Hughes 2000, McCarty 2001, Sæther et al. 2004, Stenseth et al. 2005, Parmesan 2006, Visser 2008, Rosenzweig et al. 2008). In marine ecosystems, increasing ocean temperatures lead to changes in oceanographic conditions, such as currents, primary production and the abundance and distribution of key prey species (Behrenfeld et al. 2006, Rickardson and Schoeman 2004, Perry et al. 2005). These changes lead to changed availability of prey species and will affect seabirds through their demographic traits and ultimately their abundance and distribution.

Usually, climate is defined as the mean of a climate parameter over a long time period, however, when referring to climate fluctuations and climate change in this thesis it is important to be aware of that it is the temporal variability of climate conditions that is used here. Predicted future changes in the ocean conditions caused by climate change can affect seabirds both directly, through e.g. increased mortality rates caused by more frequent storms and other extreme weather events, and indirectly through a temporal change in prey availability via changes in prey abundance and/or a shift in the spatial distribution of prey caused by changes in oceanographic conditions (Sandvik et al. 2005, Peron et al. 2010, Lewison et al. 2012).

Among seabirds, fluctuations in food availability have long been hypothesized to play a major role in regulating populations (Lack 1966), and there is strong evidence that fluctuations in prey fish stocks and fisheries are of major importance (reviewed by Furness 2007). In general, seabirds feed on small, pelagic fish species and/or young age classes of demersal fish species, many of which are heavily exploited commercially (reviewed by Croxall & Rothery 1991, Furness 2007). Some seabirds also feed on large zooplankton species (Lydersen et al. 1989, Mehlum and Gabrielsen 1993, Lewis et al. 2001, Karnovsky et al. 2008).

Several seabird studies have documented the effect of climate and food availability on both reproduction and adult survival (e.g. Durant et al. 2004, Frederiksen et al. 2004, Sandvik et al. 2005, Furness et al. 2007, Lee et al. 2007, Le Bohec et al. 2008, Jenouvrier et al. 2005, 2009, 2012). However, even if increasing numbers of studies reveal many of the processes and factors affecting one or a few demographic traits, the relative importance of the different traits affecting the population dynamics is still relatively unexplored (Sandvik et al. 2012), and few studies have integrated these effects into the entire life-cycle (but see Jenouvrier et al. 2009, Barbraud et al. 2010, Hunter et al. 2010). Finding the pathways of the influence of environmental variability on population dynamic is important in our understanding of seabird population dynamics. This isn't, however, always straightforward because environmental effects may operate with different time lags (Post 2004), and some may even affect different demographic traits in opposite directions (Barbraud and Weimerskirch 2001). Furthermore, long-term time series of demographic data that include age specific vital rates and the rate of emigration and immigration are scarce.

Seabird non-breeding distribution

One challenge that has constrained studies of the relationship between demography and environmental conditions for many migrant birds, including pelagic seabirds, is the limited knowledge of their distribution outside the breeding season (Runge and Marra 2005, Ratikainen et al. 2008, Schaub et al. 2011, Smith and Gaston 2012). Recent advances in tracking technology, such as miniaturized year-round light-based tracking devices (GLS loggers or geolocators), has, however, revolutionized our knowledge of the non-breeding ranges of migrant species (e.g. Phillips et al. 2004, Gonzáles-Sólis et al. 2007, Guilford et al. 2009, Egevang et al. 2010, Frederiksen et al. 2012, Smith and Gaston 2012, Seavy et al. 2012). Combining such data with demographical rates now allows us to explore in detail the relationships between environmental conditions, such as climate and prey availability, in both the breeding area and the non-breeding area(s) and important demographic traits, such as adult survival. Although such studies can be very helpful in understanding the mechanisms underlying bird population dynamics, very few have so far investigated such relationships (but see Schaub et al. 2011, Ramos et al 2012, Smith and Gaston 2012). Such knowledge is especially important for the conservation and the management of threatened species (Frederiksen et al. 2012, Croxall et al. 2012, Lewison et al. 2012).

Demography and population fluctuations

Assessing the relative importance of demographic traits on population growth rate represents an essential element of population ecology and conservation biology (e.g. Tuljapurkar and Caswell 1997). Especially for rapid declining populations there is a need to prioritize management strategies based on those demographic traits that are driving the population and the sensitivity of various traits to management actions.

An important question in life history theory and conservation regards the relative importance of environmental influences on population dynamics via offspring production and recruitment on one hand and adult survival on the other (Stearns, 1992; Weimerskirch et al., 2003; Sæther and Engen, 2010). Seabirds are in general long-lived species with delayed maturity, low fecundity and high adult survival. For such species matrix models and sensitivity analyses generally show that the population growth rate is more sensitive to the same proportional change (elasticity) in adult survival than to fecundity (e.g. Sæther and Bakke 2000). Adult survival in long-lived species is therefore suggested to be canalized against temporal environmental variation having a low impact on the variation in population growth rate and instead that variable fecundity and recruitment may be a more important driver (Gaillard et al. 1998, Gaillard and Yoccoz 2003).

However, among seabirds several studies document the effect of climate and food availability on both reproduction and adult survival (e.g. Durant et al. 2004, Frederiksen et al. 2004, Furness et al. 2007, Lee et al. 2007, Le Bohec et al. 2008, Jenouvrier et al. 2009, 2012) and an recent comparative analyses of a large number of species from the north Atlantic suggests that populations are driven both by the variation in reproduction and adult survival (Sandvik et al. 2012). The effect of variability in a life-history trait on the variation of population growth rate, and thus fitness, is a function both of the variability of the trait and its elasticity (Caswell 2001). At the same time, the most elastic life-history trait is predicted to be under the strongest selection pressure against temporal variability (Jonsson and Ebenman, 2001), so that one usually finds a negative correlation between the elasticity of a life-history trait and its variability (Pfister, 1998; Sæther and Bakke, 2000; although this may not be the case for plants (Jongejans et al. 2010)).Thus a prediction of the balance of demographic elasticity versus environmental responsiveness in shaping population dynamics in vertebrates is not straightforward: while a trait must be temporally variable to respond to environmental conditions, it must have a high elasticity if it is to affect the population growth rate.

Environmental variability and micro-evolutionary processes

Another important aspect when studying environmental variability and demography of seabirds is how they adapt to changes in the environment and knowledge of how climate fluctuations affect various life history traits in organisms has greatly improved (e.g., Parmesan 2006, IPCC 2007, Visser 2008). In general, organisms can adapt to a changing environment through shifts in their distribution to more favourable areas and through adjustments of their migration strategies. They may also adapt by phenotypic plasticity and/or micro-evolutionary processes (reviewed in Parmesan 2006, Millien et al. 2006). Surprisingly very little is known as to whether climate change is having evolutionary consequences for bird populations (Sheldon 2010), and a review by Gienapp et al. (2008) of studies of both plants and animals found only three studies that provided evidence for a genetic response over time. More recently also Karell et al. (2011) showed that climate differentially affected the adult survival of two genetically distinct colour morphs of the tawny owl *Strix aluco* resulting in a change in the frequency of the morphs in the population as temperature increased.

In long-lived species, such as seabirds, any effects of climate change on an important demographic trait such as adult survival will, even on a short time scale, exert a strong selective pressure (Gienapp et al. 2008). It is, however, important to detect a genetic marker for such a trait, which responds to climate variability and one such marker could be colour polymorphism. Colour polymorphism, which is the existence of two or more colour variants that differ genetically in a population, can be considered as a phenotypic genetic marker, since it is often related to important fitness-related factors (Roulin 2004). Furthermore, different colour patterns may be adaptive under different environmental conditions by providing behavioural or physiological advantages to their bearers (e.g. Galeotti and Cesaris 1996, Galeotti and Rubolini 2004). Galeotti et al. (2009) also suggested that the equilibrium between gene frequencies could vary under different conditions and habitats if the lifetime fitness of different morphs differed between habitats, and that this equilibrium could be disrupted by climate change through direct and indirect effects on fitness. Thus any differences between morphs in their responses to climatic change and any differences in morph frequencies over time may indicate natural selection.

The common guillemot *Uria aalge* is an example of a species with two colour morphs (bridled and non-bridled morph), with the bridled form being a recessive genetic variant of the normal non-bridled form, carried by a gene on one autosome (Jefferies and Parslow 1976). The frequency of the bridled form is a classic example of a stable ratio-cline polymorphism, with an increase northwards on both sides of the North Atlantic. It has been hypothesized that the bridled morph is better adapted to a colder climate, which is consistent with the increase in frequency of bridling towards the north (Southern 1951, Jefferies and Parslow 1976, Birkhead 1984).

Aim of Thesis

The overall aim of this thesis is to study the impact of environmental conditions on seabird demography and population dynamics, using arctic populations of two species; the black-legged kittiwake *Rissa tridactyla* and the common guillemot. The following questions were examined:

1. How do climate and prey availability affect demography and population variability of kittiwakes and guillemots?
2. Which demographic trait drives the population dynamics?
3. Can populations adapt to environmental changes through micro-evolutionary processes?

These questions were addressed as follows:

1. Analyzing kittiwake and guillemot long-term demographic data using climatic factors and prey densities as covariates (paper 1, 3 and 4).

2. Using demographic matrix modeling to examine the elasticity of adult survival and hatching success (recruitment) on population growth rate (paper 2).

3. Analyzing a demographic trait, the adult survival, and its response to climate within two different genetic colour morphs of the common guillemot (paper 4).

In paper 1 we used recently-gained knowledge of the non-breeding distribution of kittiwakes and linked the environmental conditions in these areas with the adult survival rate in a Barents Sea colony. We explored different potential environmental variables in an attempt to reveal the mechanistic link between the environment and adult survival.

In paper 2, we used demographic modeling to determine which traits drive the population dynamics in the same, strongly decreasing kittiwake population. We used matrix modeling retrospectively to extract the demographic trait that had the highest impact on the population growth rate.

Papers 3 addresses the question of how environmental conditions such as abundance of important prey species, affect population growth rate. The study used a logistic population model, and hence indirectly (via lagged and un-lagged effects of environmental covariates) shows the pathway from environmental conditions to population dynamics.

In paper 4 we investigated whether the adult survival of the different genetic colour morphs (bridled and non-bridled morph) of the common guillemot responded differently to variability in the sea surface temperature. We did this by examining the differences in the adult survival rates of the two morphs and their responses to sea surface temperature. Polymorphism may, in this case, serve as a genetic marker in the guillemot population and has the potential to visualize the direction of selection and micro-evolutionary processes driven by climate.

General Methods

More detailed descriptions of the methods and the analyses used in this thesis can be found in the attached papers.

Study area and study species

The field data used in this thesis were gathered on Hornøya, a seabird colony located in the northeastern part of Norway (70° 22’ N, 31° 10’ E), in the southern Barents Sea. It has a relatively high diversity of breeding seabirds, including black-legged kittiwakes, Brünnich’s *Uria lomvia* and common guillemots, razorbills *Alca torda*, Atlantic puffins *Fratercula arctica*, European shags *Phalacrocorax aristotelis*, herring gulls *Larus argentatus*, great black-backed gulls *L. marinus* and a few pairs of fulmar *Fulmarus glacialis*.

The study species used in this thesis are the black-legged kittiwake (figure 1) and the common guillemot (figure 2), which are both on the Norwegian Red List and categorized as endangered and critically endangered respectively (Kålås et al. 2010). The population sizes of kittiwake and common guillemot on Hornøya have been monitored in study plots since 1980, and since 1988 (common guillemot) and 1990 (kittiwake) breeding adults have been individually marked with coloured or letter-coded rings and re-sighted every year during the breeding season and until present to estimate their survival rate.

Figure 1. The black-legged kittiwake *Rissa tridactyla*.

Figure 2. The common guillemot *Uria aalge,* with the bridled and the non-bridled morph.

The black-legged kittiwake is a small and specialized gull species, and its lifestyle varies greatly through the year (Coulson 2011). It has a circumpolar distribution, and is perhaps the most common gull species in the world. However, the population size is globally decreasing (IUCN 2012), and the Hornøya population has declined by nearly 50 % since the early 1980s (Barrett et al. 2006). They breed in steep coastal cliffs in large single- or mixed-species colonies and breeding occurs from May to July (Coulson 2011). Kittiwakes are migratory birds and disperse after breeding from coastal areas to the open ocean (del Hoyo et al. 1996, Frederiksen et al. 2012), and during their non-breeding season they are highly pelagic.

Like all seabirds, the life-history strategy of kittiwakes is “slow”, which means that they are long-lived, have a low reproduction rate (1-3 eggs per year), high juvenile mortality rate and late maturation (first year of breeding ca 3-4 years) (Coulson 2011).

Kittiwakes cannot dive, and are therefore restricted in finding food on or near the surface of the ocean (surface-feeders). Furthermore, they have a limited capacity to switch prey and they seem to operate at their energetic ceiling (Welcker et al. 2010), all of which makes them sensitive to changes in the marine system (Furness and Tasker 2000).

In the breeding season, kittiwake diet consists mainly of small, energy-rich schooling fish (up to 15-20 cm), of which the composition differs between different ecosystems (Lewis et al. 2001, Carscadden et al. 2002, Barrett 2007). In the non-breeding season, however, less is known of their diet, but some studies have suggested that they feed on both small fish (Erikstad 1990) and a variety of large zooplankton species, e.g. *Calanus* spp., amphipods (Hyperiidea), euphausiids and pteropods (Thecosomata) (Lydersen et al. 1989, Mehlum and Gabrielsen 1993, Lewis et al. 2001, Karnovsky et al. 2008).

The common guillemot is a large auk with a circumpolar distribution. About 3 million pairs breed in the North Atlantic and ca. 15,000 pairs (in 2005) in Norway (Gaston and Jones 1998, Barrett et al. 2006). The Norwegian population has declined by 95% since the 1960s (Barrett et al. 2006) and several mainland colonies are in danger of extinction (Erikstad et al. 2007). A few Norwegian colonies have, however, increased in size since 1988, including the Hornøya population, which has increased from ca 1300 breeding pairs in 1988 to ca 10 000 breeding pairs in 2010 (Barrett unpublished data).

Common guillemot life-history strategy is extremely “slow”. They are long-lived with high adult survival rates, low fecundity (a single egg is laid per year) and poor juvenile survival (which also varies strongly between cohorts) (see Harris et al. 2007), and sexual maturation is at 4–6 years (Birkhead and Hudson 1977). They breed in colonies in high densities, and the single egg is incubated on the bare rock ledge. They have strong nest-site fidelity, and breeding birds normally return to same site each year (Harris and Wanless 1988). Inter-colony movements almost only occur among immature birds (Gaston and Jones 1998, Harris et al. 2007).

Common guillemots are diving birds, and may dive to depths of 150 m, and are thus not constrained to feed in the surface of the ocean as are kittiwakes. They forage at sea, but compared to the kittiwakes they are less agile flyers and may thus be more restricted in their horizontal foraging range when searching for food during the breeding season. The main prey of the Hornøya population during the breeding season are capelin *Mallotus villosus*, herring *Clupea harengus* and young age-classes of cod *Gadus morhua* (Bugge et al. 2011).

One special characteristic of the common guillemot is their colour polymorphism with two colour morphs; a non-bridled morph, with an entirely black or dark brown head, and a bridled morph with a white eye ring and auricular groove sloping back from the eye (figure 2). The bridled morph is a recessive variant of the non-bridled morph, carried by a gene on one autosome (Jefferies and Parslow 1976). The frequency of the bridled form is considered as a classic example of a stable ratio-cline polymorphism with an increase northwards on both sides of the North Atlantic. Along the European cline, the proportion of bridled individuals increases from 0% on the Iberian Peninsula to 50% in the Arctic, whereas in Canada counts in the 1950s indicated a clear cline from 17% in the southern Newfoundland to 71% in northern Labrador (Southern 1962, Birkhead and Lock 1980, Birkhead 1984).

Capture-Mark-Recapture (CMR) Models

The birds used in the CMR analyses in this thesis were captured and marked only once, and then re-sighted the following years. Therefore, the “Recapture-rate” is denoted “re-sighting rate” hereafter in the thesis. In general what we get when re-sighting birds is a return rate for every year which consists of the product of the survival probability and the re-sighting rate. Thus the capture histories result from both observational processes and biological processes, and it is important not to ignore the former because by doing so will produce biased estimates of the latter (Gimenez et al. 2008). Trap-heterogeneity (trap-happiness and trap-shyness) and transience are both observational processes that may occur and create biased estimates of the biological processes. Statistical methods and models have been developed to solve this and help to infer unbiased biological information from CMR analysis. One important component of such statistical analyses is the assessment of “Goodness of Fit” (GOF), which is an assembly of tests that tests for sources of heterogeneity in the dataset. In this thesis, GOF was assessed using the UCARE software (Choquet et al. 2009a).

To analyze adult survival probabilities of the kittiwakes and the guillemots, a capture-mark-recapture (CMR) analysis was used, which is based upon CMR statistical modeling. CMR models are “particular developments of generalized linear models that allow the estimation and modeling of biological and observation processes that generate capture histories” (Grosbois and Gimenez 2010). Such models describe the variation in parameters of interest (e.g. adult survival), and specify their relationships with covariates. They usually involve a link function to get in-range estimates (usually the logit function). The software used to build CMR models in this thesis was ESURGE (Choquet et al. 2009b).

To select the most parsimonious model(s) that described the variation in adult survival rates, the QAICc (Quasi-likelihood Akaike’s Information Criterion corrected for small sample size and overdispersion) was used, where the model with the lowest QAICc-value was considered the best (Burnham and Anderson 2002). The differences between the QAICc of a given model and the QAICc of the best model (ΔQAICc) and the QAICc-weight, which are both derived from information theory, are powerful tools that allow multi-model comparisons and inferences. According to Burnham and Anderson’s (2002) scale of ΔQAICc model interpretation, models with scores of ΔQAICc ≤ 2 are strongly plausible, 4-7 less plausible and ≥ 10 improbable.

A limitation of this kind of model selection is that it can only be used when there is sufficient knowledge of the study system to be able to explain most of the variation in the demographic parameter of interest with only a small set of covariates and models. This is, however, very often not the case, and a larger fraction of the variation cannot be explained by the covariates. In such cases, an analysis of deviance (ANODEV) should be used to assess the statistical relevance of the effect of the covariates (Grosbois et al. 2008, Lebreton et al. 2012).

Modeling the population dynamics

Understanding changes in seabird populations requires modeling tools to estimate the growth rate and to assess what affects the growth rate under different circumstances. Demographic and/or population models are two ways of estimating population growth rate (e.g. Morris and Doak 2002) and there are advantages and disadvantages with both.

Demographic models may help us to make more targeted management decisions (Morris and Doak 2002), and may be a good way to determine which demographic trait has the highest impact on the population growth rate. However, demographic models require long time-series of age-specific adult survival and fecundity rates, some knowledge of population growth rate and emigration and immigration rates. Such detailed data are scarce for most populations. However, when data on some demographic traits exist, it is possible to deduce other demographic rates retrospectively or make assumptions from literature (e.g. Caswell 2001, Munilla et al. 2007, Jenouvrier et al. 2005).

Typically, modeling population dynamics with a demographic modeling approach incorporates matrix models with fecundity and survival probabilities for different stages, sizes or ages depending on how the population’s individuals are classified (Caswell 2001, Morris and Doak 2002). Matrix models are good tools to assess management options by using sensitivity analyses. Sensitivity analyses, which are a collective term of several mathematical methods, investigate how sensitive population growth is to particular demographic changes. They are all used to address how important changes in different matrix elements are to population growth rate. Sensitivity analyses can also be applied to extinction risk and population viability analyses.

Population modeling is based on the annual counts of individuals. In this thesis, such counts were in pre-defined monitoring plots in the colony. For the guillemot population on Hornøya, the only long-term demographical data were adult survival rates. In paper 3 we therefore used a logistic population model (Sæther and Engen 2002) to model the yearly population growth rate as a function of environmental covariates (cf. Jonzén et al. 2002, Woody et al. 2007, Sæther et al. 2009). A logistic population model assumes the growth rate to be larger the further from the carrying capacity the population size is.

If the effect of adult survival on population growth rate is most important, the relevant time lag of prey species abundance on population growth rate would be 0 (assuming a direct effect of prey density) or 1 yr, depending on which time of year is the critical period for survival. Likewise, if the yearly variation in deferred breeding is an important parameter, a lag of 0 or 1 yr might also be expected. If, however, the effect of prey on reproduction is most important, the population dynamics will, for common guillemots, be affected most strongly by prey conditions 4 to 6 yr earlier, a lag that spans the age of recruitment. This follows from the fact that the effect of prey on reproduction will not become evident in the breeding population until the offspring affected have recruited into the population being censused (provided that the signal is not confounded by other factors affecting immature survival).

Results and General Discussion

The effects of climate and prey availability on kittiwake and guillemot demography (papers 1, 3 and 4).

Both climate and prey availability influence demographic traits of seabirds. Climate can have a direct effect on seabirds through e.g. flooding of nests or die-offs caused by storms, but the general consensus is that most effects of climate on seabird demographic traits are indirect through the availability of prey (Frederiksen 2006). How climate change is affecting seabirds is therefore determined by how their preferred prey is affected by changes in temperature, salinity, ocean acidification etc., and whether alternative prey is available. The climatic effects on demography found in this thesis support this pattern. Analyses of adult survival in guillemots revealed a 2-yr lagged effect of the winter sea surface temperature (paper 4), suggesting an indirect effect via prey availability. And for the kittiwakes, prey covariates correlated much more strongly with adult survival than any climate covariates (paper 1). No single environmental factor could explain the large variability in kittiwake adult survival, and prey densities had in general better explanatory power than climatic indices.

Recent tracking data of kittiwakes from Hornøya have revealed that the kittiwakes use three distinct areas in the non-breeding season (González-Solís et al. 2011, Frederiksen et al. 2012). Immediately after the breeding season they move to and stay in a concentrated area east of the Svalbard archipelago, in winter they stay in the Grand Banks/Labrador Sea area, and in the pre-breeding season they are back in the Barents Sea near the colony (Fig 1 a-d in paper 1). This study investigated the relationship between environmental conditions, both climatic factors and prey densities, in these specific areas and the temporal variability of the adult survival rate. The results showed that Thecosomata, a group of pteropods, in the Grand Banks/Labrador Sea area in the wintering season and the capelin in the Barents Sea in the pre-breeding season were together important predictors for the yearly variation in kittiwake adult survival rates. These two prey categories explained as much as 52 % of the yearly variation in adult survival. The adult survival varied greatly over the time period (1990 – 2010), with two severe drops in 1994 and 2003 which coincided with two collapses in the Barents Sea capelin stock.

The effects of prey densities in both the Grand Banks/Labrador Sea and the Barents Sea on kittiwake adult survival demonstrate the complexity of the system and how different factors in different ecosystems can have an impact on kittiwake demography and ultimately population dynamics. Because they wander over vast areas outside the breeding season, kittiwakes are linked to several ecosystems. This was shown here where the effect of the capelin stock in the Barents Sea and the amount of Thecosomata in the Grand Banks/Labrador Sea explained more than half of the variability of the adult survival of kittiwakes. Although a large amount of the variability remains unexplained, any variation in the availability of the capelin stock and/or the Thecosomata density will have a profound impact on the adult survival rate.

Capelin which is one of the most abundant fish species in Barents Sea (Orlova et al. 2010), is known to fluctuate greatly in abundance (Ushakov and Ozhigin 1987), and plays a key role in the pelagic ecosystem of the Barents Sea (Orlova et al. 2010). It is known to follow a characteristic seasonal migration pattern (Gjøsæter et al. 2011) and the kittiwakes' return to the Barents Sea in the pre-breeding season coincides with the capelin spawning migration towards the coast of Norway and Russia in March-April (Gjøsæter et al. 2011), a time when the fish are full of energy-rich gonads (Montevecchi and Piatt 1984). This migration pattern is known to vary both spatially and temporarily between years being dependent on sea surface temperature and other oceanographic conditions (Gjøsæter 1998). Furthermore, in the pre-breeding season, the northern Barents Sea is still covered with ice and primary production is low, such that the seabirds are constrained to feed on mainly pelagic fish such as 1-group herring and capelin (Fauchald et al. 2011). The very high variability of the capelin stock could thus be very critical to the kittiwakes when they return in March-April if no or few alternative prey s available (e.g. paper 3).

Thecosomata is a taxon of pelagic swimming sea snails also called sea butterflies or pteropods. They are rich in lipids, live their whole life in a planktonic form, and can be found in large concentrations in the upper layer of the water. The density of Thecosomata in December declined steeply in the Grand Banks/Labrador Sea between 1990 and 2011 (Fig. 2, paper 1). A possible mechanism for this decline could be ocean acidification, as shown by Lischka et al. (2011) from Svalbard. Thecosomata, such as *Limacina helicina*, have an aragonitic shell, which makes them particularly sensitive to acidification, a process that is expected to be most serious in Arctic oceans (Steinacher et al. 2009, Comeau et al. 2012) and which will be more severe when ocean temperatures increase (Lischka et al. 2011). Kittiwakes from most of the breeding colonies in the north Atlantic spend their winter in Grand Bank/Labrador Sea (Bogdanova et al. 2011, Frederiksen et al. 2012), such that the steep decline in Thecosomata abundances, and factors affecting it, could be an important driver of the overall decline in the North Atlantic kittiwake populations.

Fluctuations in prey availability have long been hypothesized to play a major role in limiting populations (Lack 1966). In paper 3 the aim was to explore whether the variation in fish prey stocks was affecting the variation in population growth rate of the common guillemot. The common guillemot population on Hornøya declined steeply (80%) between 1986 and 1987, coinciding with very low levels of all important prey species such as capelin, herring and cod (Fig 1 and Fig 2, paper 3). Since 1987, the population has steadily increased (i.e. the yearly growth rate was positive or close to zero, and varied between years) (Fig 1, paper 3). Important prey species for the common guillemots on Hornøya are capelin, 1-group herring and 0-group cod. In this study we found that un-lagged 0-group cod could explain much of the temporal variability (40%) in the guillemot population growth rate. Additionally, 0-group cod lagged by 6 yr and capelin lagged by 4 yr (equaling the age of maturation of guillemots) contributed positively, and explained 56% of the variation in population growth rate (paper 3).

Lack of detailed demographic data and not knowing where the guillemots are outside the breeding season constrain our ability to draw conclusions as to which demographic traits are most affected. However, any un-lagged effect of prey on growth rate would suggest an effect via adult survival and/or rate of non-breeding events, whereas a lagged effect would suggest an effect via reproduction, where the lag reflects the age of recruitment. Therefore the un-lagged effect of 0-group cod (paper 3) suggests that it affects population growth rate through a direct effect on either yearly variation in adult survival or deferred breeding. Adult survival has been very high (0.96 ± 0.01, Paper 4) since the 1987 population collapse, and we propose that the availability of 0-group cod is critical for whether birds decide to breed or not. The lagged effect of cod and capelin suggests an effect on reproductive success 4 to 6 years earlier and the recruitment of immature birds to the colony. Since 0-group cod is an important part of the adult diet during the breeding season in the present study population (Bugge et al. 2011), we also utilize a numerical ocean model coupled to an individual-based model (IBM) for early stages of fish to identify mechanisms affecting spatiotemporal prey availability for common guillemots around the colony. The modeled arrival of 0-group cod in areas around Hornøya shows that the different spawning grounds along the Norwegian coast contributed to the supply of prey items for common guillemots at different temporal and quantitative scales. This is particularly relevant as we know that the spawning distribution of northeast Arctic cod varies on a multi-annual scale (Sundby and Nakken 2008). In warm years the spawning distribution tends to shift northwards and in cold years southwards.

The very surprising result of this study was the strong positive relationship between 0-group cod abundance and the variation in guillemot population growth rate. Much focus has previously been put on the capelin stock as being the key prey species for common guillemots in the Barents Sea and playing a significant role in the 1986/87 population crash (Vader et al. 1990, Barrett & Krasnov 2006). The capelin stock has, however, subsequently collapsed twice, in 1994/1995 and 2004/2005 (Fig. 2 paper 3, Gjøsæter et al. 2009), with no apparent effect on the population growth rate of the common guillemot. Although we cannot exclude the possibility that lack of capelin may have contributed to the population collapse in 1987, it is unlikely that it was the sole or major factor, especially since the guillemot population continued to strongly increase through both subsequent periods of low capelin abundance. As such it seems that the availability of 0-group cod may be a much more important factor affecting demography and determining the population dynamics of the common guillemot in the southern Barents Sea than previously considered.

Which demographic trait drives the population dynamics? (Paper 2)

It is not sufficient to know if and how climate and/or prey availability impact demographic traits. The relative importance of environmental influences on population dynamics via offspring production and recruitment on one hand and via adult survival on the other is an important question and an essential element of population ecology and conservation biology (e.g. Tuljapurkar and Caswell 1997). There is a need for a better understanding of this pathway. So far only a few studies have addressed this for seabirds (Jenouvrier et al. 2009, Wolf et al. 2010, Barbraud et al. 2010).

By using demographic matrix modeling and retrospective analyses in paper 2, we show that both adult survival and breeding success and recruitment to the population affect kittiwake population growth rate. We analyzed the population trend in a kittiwake population from 1990 to 2011 when the population was first stable (1990-1999) but later (1999-2012) in steep decline (8.8±3.7 % p.a.). In the early period the mean breeding success was high (0.86 chicks fledged per pair), but in the late period the mean was much lower (0.47 chicks fledged per pair). Adult survival was estimated to 88 % in the first period and 85 % in the late period. Both the variability in breeding success and the adult survival did contribute to the steep decline in the population, but the strong reduction in breeding success, and the reduced recruitment to the population, had the highest impact.

Similar results have also recently been reported in an extensive analysis using 378 time series from 29 seabird species from 187 breeding colonies throughout the North Atlantic (Sandvik et al. 2012). Lack of recruitment in a long-lived species may be a serious problem. As shown by Jenouvrier et al. (2009) for the emperor penguins, even if adult survival improves, lack of recruitment over several years through low breeding success resulted in no population recovery. Therefore, even if adult survival is the trait having the potentially largest impact on the population growth rate, isolating the causes of poor breeding success should be a highly important management target for conservation of seabirds.

Evolutionary adaptations to climate change (Paper 4)

Climate fluctuations and their effects on ecological processes are evident in most areas worldwide but whether such climatic effects are induced phenotypic plasticity or whether animals adapt to the new environment through micro-evolutionary processes are, so far, poorly documented. In paper 4, we investigated whether climate fluctuations have the potential to drive changes in selection, and possibly resulting in micro-evolutionary processes, by analyzing how the adult survival rates of two distinct genetic morphs of the common guillemot were affected by temporal variability of sea surface temperature over a 22 year period.

We found that the two morphs responded differently to variation in the Barents Sea winter sea surface temperature lagged by two years. Although the overall mean survival rate of the two morphs did not differ significantly, the adult survival of the bridled morph was negatively correlated, while the non-bridled adult survival rate was slightly positively correlated to winter sea surface temperature (Fig. 1, paper 4). There were furthermore no significant changes in the frequency of bridling in the population during the study-period (Table 2, paper 4). Over the whole study period, SSTs fluctuated between warm and cold winters and the overall mean survival rates of the two morphs remained similar (96.2% and 95.9% for the bridled and non-bridled morph, respectively). This suggests a balanced selection and a stable dimorphism of the two morphs over this time period. Adult survival is the trait that has the largest potential impact on lifetime fitness in a long-lived species such as the common guillemot and the results of this study suggest that climatic factors, even on a small time scale, are able to exert selection pressure, and hence could induce micro-evolutionary processes for adaptations to a new environment. Further warming of the sea, as predicted by climate models (IPCC 2007), may induce directional changes and alter the frequency of the two morphs.

A main challenge for future studies of climatic effects on population changes would be to study the effect of phenotypic plasticity and micro-evolutionary processes. Such studies are so far scarce (Gienapp et al. 2008, Karell et al. 2011, Franks and Hoffmann 2012, Merila 2012), and there are three conditions that need to be fulfilled in order to demonstrate that a population has responded adaptively to climatic change (reviewed in Parmesan 2006). One is that the selection on a trait related to fitness has to be documented. Second, there should be evidence that this trait is linked to climatic change and third that a genetic change in the trait is demonstrated. Our study gives strong evidence of the first two conditions, and the different responses of the two morphs, which may serve as genetic markers, to climate provide a unique way of visualizing the direction of the selection and how micro-evolutionary processes are driven by climate. Although the frequency of bridling over time shows no trend so far, the predicted warming of the sea may pose directional changes in favour of the non-bridled morph in the years to come.

Conclusions and future prospects

Seabirds are important indicators of the state of marine ecosystems and are relatively easy to monitor compared to other marine organisms (Furness and Camphuysen 1997, Durant et al. 2009). Therefore studying the demography and population biology of seabirds is important not only for a better understanding of a group of birds that are experiencing dramatic changes, but also for a better understanding of the marine ecosystem.

This thesis emphasizes the need for long-term time-series of important demographic traits and detailed knowledge on the migration routes and wintering areas of seabirds for a better understanding of important environmental factors affecting population growth rate. It also highlights the importance of demographic models to understand which demographic traits actually drive the population. However, our knowledge in this respect has huge gaps. Long-term time-series on age specific demographic rates are very scarce and such data needs to be prioritized in the future. In their recent summary of research priorities for seabirds to improve conservation and management in the 21st century, Lewison et al (2012) concluded that the conservation of seabirds is hampered by huge gaps of fundamental knowledge. They highlighted especially a "limited understanding of the interplay between spatio-temporal variability of the environment, notably at large spatial scales, and the demographic, behavioural and ecophysiological responses of populations". They only briefly mention in this extensive review the predicted rise in sea temperature in years to come and how seabirds may respond evolutionarily to such a directional change. Many studies document the effect of climate on important life history traits such as adult survival which is closely linked to fitness but, as shown in the present study, such effects may have the possibility, even on a small time scale, to induce micro-evolutionary processes. Such responses may have fundamental consequences for our understanding of seabird population dynamics and should be a promising avenue of research for the years to come.

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Paper 1

Paper 2

Paper 3

Paper 4

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