Foraging, reproduction and survival of the zooplanktivorous seabird Little Auk (*Alle alle*) in the Arctic in relation to climatic and environmental variability

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Contents

List of original papers

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This thesis is based on the following papers, hereafter referred to in text by their Roman numerals:

I   Hovinen JEH, Welcker J, Rabindranath A, Brown ZW, Hop H, Berge J, Steen H (2014) At-sea distribution of foraging little auks relative to physical factors and food supply. *Marine Ecology Progress Series*, in press (doi:10.3354/meps10740)

II   Hovinen JEH, Wojczulanis-Jakubas K, Jakubas D, Hop H, Berge J, Kidawa D, Karnovsky NJ, Steen H (2014) Fledging success of little auks in the high Arctic: do provisioning rates and the quality of foraging grounds matter? *Polar Biology*, in press (doi:10.1007/s00300-014-1466-1)

III   Hovinen JEH, Welcker J, Descamps S, Strøm H, Jerstad K, Berge J, Steen H (2014) Regional and local variations in climate affect the survival of a high Arctic avian predator. Under review in *Global Change Biology*

Abstract

The ability of individuals to acquire and store energy for life-history traits such as reproduction and survival, is finite. This demands prioritizing some traits at the expense of other traits. Which traits to prioritize, depends on the life-history strategy of a species. 'Slow'-living species, in contrast to 'fast'-living species, mature late, produce small broods, have low extrinsic mortality and high life expectancy. They tend to allocate resources cautiously to current reproduction, thereby enhancing their survival and potential for future reproduction. Many seabird species employ the slow-living life-history strategy. In order to assess the effects of predicted future climate change on seabird populations, it is important to understand how life-history traits, such as reproduction and survival, are influenced by climatic and environmental variability.

The aim of this thesis was to assess the effects of climatic and environmental variability on foraging (i.e. energy acquisition), reproduction and survival of the little auk (*Alle alle*), the most abundant seabird species breeding in the Arctic. It is in the Arctic regions, where the effects of global climate change are expected to be strongest. Data on oceanographic conditions, foraging trip durations, chick provisioning rates, chick diet, chick fledging success and adult survival was collected on Bjørnøya, a small island in the western Barents Sea, and at three colonies (Isfjorden, Kongsfjorden and Magdalenefjorden) on the western coast of Spitsbergen, Svalbard during 2006-2013. The study area is influenced by both warm, Atlantic and cold, Arctic water masses.

The results show that little auk adults preferred to forage in cold water masses at the shelf-sea area, but that oceanographic conditions did not influence their foraging trip durations or chick provisioning rates. On the other hand, the number of good quality prey items delivered daily to a chick correlated negatively with ocean temperature, and both chick fledging success and adult survival was higher when ocean temperature was lower. The higher fledging and survival probabilities were most likely due to higher availability of good quality prey in the little auk's foraging grounds. Indeed, both these life-history traits seemed highly responsive to changes in environment. High sensitivity indicates that in the future, when Arctic warming is expected to continue and favoured Arctic zooplankton is gradually replaced with Atlantic zooplankton, little auk populations are likely to decrease substantially. This in turn may influence the dynamics of the entire Arctic food web, in which little auks play an important role.

1. Introduction

1.1 How to live a life?

The viability of a species depends on its ability to reproduce, grow and survive under variable environmental conditions (e.g. Walther et al. 2002). In maintaining these vital (i.e. life-history) traits, nutrient acquisition and storage plays an important role (Zera & Harshman 2001). However, the ability of individuals to acquire and store nutrients (energy) is finite, and allocating energy to one life-history trait reduces the amount of energy available for other traits. Thus, a 'decision' is needed on which trait to prioritize: should energy be invested more in reproduction than in self-maintenance and survival, or vice-versa (Stearns 1989, Williams et al. 2010). Such prioritizing is referred to as trade-offs, and they depend on the life-history strategy of a species (Williams 1966, Stearns 1992, Zera & Harshman 2001, Williams et al. 2010). 'Fast'-living species mature early, produce many offspring, have high extrinsic mortality, and die young. They tend to prioritize reproduction over survival. 'Slow'-living species, on the other hand, mature late, produce small broods, have low extrinsic mortality, and die old. They rather invest in self-maintenance and survival than in reproduction (Zera & Harshman 2001, Williams et al. 2010). For a long-lived species, even a proportionally small change in adult survival can have a big impact on population growth rate and viability (Charlesworth 1980, Gaillard et al. 1989, Wooller et al. 1992). Consequently, adult survival in a long-lived species is a fitness component that is expected to stand relatively robust against temporal variability, whereas offspring survival is expected to be more sensitive (Sæther & Bakke 2000, Gaillard & Yoccoz 2003).

Employed life-history strategy may be strongly influenced by the environment and the nutrient availability therein (Fabian & Flatt 2012). Higher availability and easier access to nutrients may favour a fast-living strategy, whereas lower availability and harder access may favour a slow-living strategy (Wilbur et al. 1974). Furthermore, if nutrient availability and accessibility is significantly reduced compared to a 'normal' situation, trade-offs characterising either strategy may become more pronounced (Zera & Harshman 2001). Sometimes these reductions can be so significant that individuals fail to maintain each of the life-history traits, in which case the number of individuals is likely to decrease, resulting in population crash (e.g. Barbraud & Weimerskirch 2001). On the other hand, increased nutrient availability and accessibility can either diminish or obviate the need for trade-offs (Kaitala 1987, Zera & Harshman 2001). It

should perhaps be mentioned, for the sake of completion, that also intraspecific differences in the life-history strategies occur, e.g. certain slow-living species may also commit to trade-offs typically associated to fast-living species if environmental conditions are favourable (Suryan et al. 2009, Fabian & Flatt 2012). The life-history strategies and trade-offs are presented in Figure 1.
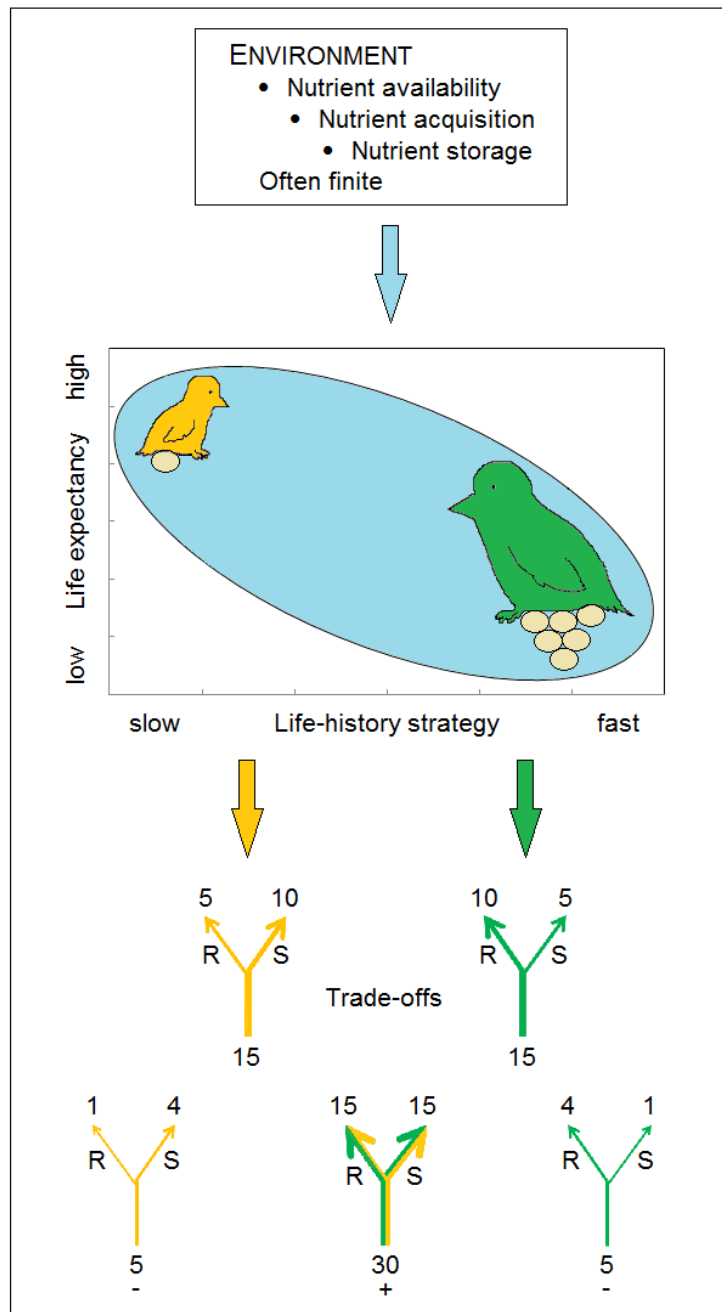
Figure 1 Schematic illustration of life-history strategies and the most common trade-offs. The amount of nutrient input (acquisition + storage) is the number at the base of each 'Y allocation tree'. The proportion of nutrient allocation is presented by the numbers at the tips of the branches. R = reproduction, S = self-maintenance. The aggravating effect of decreased nutrient input on a trade-off is denoted with '-', and the obviating effect of increased nutrient input on a trade-off is denoted with '+' at the base of the trees. After Zera & Harshman (2001) and Williams et al. (2010)

1.2 Hard life of a seabird

Breeding seabirds are central-place foragers; they need to regularly return to a nest-site to feed the offspring (Orians & Pearson 1979). Their food resources are often patchily and scarcely distributed, with unpredictable fluctuations in availability, and they may have to forage at great distance from their breeding site (Lack 1968, Ashmole 1971). The energy consumption of seabirds is especially high during chick rearing, as they should then find a sufficient amount of profitable prey both for themselves and for the offspring (Ricklefs 1983). Also, seabirds should avoid storing too much surplus energy, as an additional body mass may substantially increase energy expenditure during flight (Witter & Cuthill 1993). Consequently, food availability and acquisition are major factors in shaping the life-history strategies of seabirds (Ricklefs 1983, Martin 1987).

Seabirds are typically long-lived, and many of them have adopted a single-egg strategy; it may be difficult enough to provide for a single offspring in a marine environment where food resources are patchily distributed and often unpredictable, and energy expenditure is high (Lack 1968, Ricklefs 1983). Under stressful conditions, for example during a food shortage, seabirds may be expected to refrain from breeding, decrease chick provisioning, or even to abandon the chick altogether, rather than to put their own survival at risk (Chastel et al. 1995, Phillips et al. 1996, Erikstad et al. 1998, Zera & Harshman 2001). Due to their long life expectancy, they have a potential to reproduce several times during a life-time, something which may compensate for the effect of poor breeding success under stressful conditions and thereby help to maintain population stability (Stearns 1992).

However, some seabirds are more flexible in allocating their resources: in times of hardship they may increase their parental effort in order to protect offspring from deteriorating food supply – as long as this does not jeopardize their own survival or reduce their fecundity in later years (e.g. Erikstad et al. 2009). In some cases, seabird parents may invest in their current breeding effort even at the expense of their own survival (Jacobsen et al. 1995, Golet et al. 2004). This flexibility is possibly governed, at least partly, by the level of endogenous energy reserves and by the survival prospects of an offspring. If these reserves are high and offspring is likely to reach breeding age, parents are probably more willing to increase their parental effort under stressful conditions (Erikstad et al. 1998, Chaurand & Weimerskirch 1994, Tveraa et al. 1998).

Some seabirds may also relocate their breeding site or alter their foraging distance if local food supplies are not satisfactory (Furness & Camphuysen 1997). A change in the diet may also occur, at least in species that are not highly specialized on certain prey types (e.g. Schwemmer & Garthe 2008).

In general, seabirds are predicted to respond to a reduction in prey availability sequentially (Cairns 1988): First, they alter their foraging effort (e.g. time spent on foraging). Secondly, chick provisioning, chick growth rates and fledging success would be influenced. Thirdly, the mortality risk of adults increases. Thus, only during a severe food shortage would adult survival decrease. Furthermore, seabirds with a short foraging range and specialized diet are likely to be more sensitive and vulnerable to changes in the food supply (e.g. Furness & Ainley 1984).

1.2.1 To ease a life: a bimodal foraging strategy

Foragers with offspring to provide should forage in a way which i) maximizes the amount of energy delivered to offspring (in order to enhance their growth, fledging success, and post-fledging survival), and ii) keeps their own energy budget balanced so that their survival is not at risk. Thus, in general, a forager should spend some extra time during each foraging trip to replenish the energy spent foraging, and thereby to maintain its own body condition (Ydenberg 1994). It may however be challenging for a seabird to maintain its own energy balance while trying to frequently provisioning the offspring, due to its exposure to often unpredictable and patchy distribution of food resources (Ricklefs 1983).

In response to this challenge, some seabird species employ a foraging strategy which alternates foraging trips of bimodal length: parents self-feed and store energy during long trips, and subsequently spend this energy gathering food for their offspring during short trips (Grandeiro et al. 1998, Weimerskirch et al. 2003a, Welcker et al. 2012). In this way parents can provide regular food supplies both for their offspring and for themselves with lower risk of losing body condition than they would have if trying to manage both tasks during a single trip (Weimerskirch et al. 1994). Furthermore, bimodal foragers may efficiently adjust their foraging effort under stressful conditions by altering the length, duration and frequency of both trip types (e.g. Duriez et al. 2000, Welcker et al. 2009a).

1.4 Life in the Arctic and the climate change

The Arctic is a harsh environment: only species highly adapted to low temperatures and strong seasonality in light conditions, extent and thickness of sea ice cover, primary production and food availability, can thrive there (Blix 2005). It may seem that the Arctic is best suited for a slow life-history strategy – maintaining a slow growth rate may help an animal to adjust to seasonal or temporal shortages in food supply, thereby enhancing its survival (e.g. Johnston 1990, Poltermann 2000, Bell 2012). Many animals visit the area only for shorter periods. This typically happens during the summer, when, for example, thousands of seabirds migrate from further south to feed and reproduce, fully utilizing the brief and blossoming biological production (ACIA 2005).

Warm and saline Atlantic water is the main source of water and heat for the Arctic (Saloranta & Svendsen 2001, Carton et al. 2011). Recently, its temperature as well as its inflow into the Arctic region has increased (Walczowski & Piechura 2006, Carton et al. 2011). This has resulted in dramatic changes, especially in the Arctic marine ecosystem: higher sea-temperatures have been accompanied by a decrease in the extent and thickness of sea ice cover (Perovich & Richter-Menge 2009) and increased stratification, leading to a reduced upward transfer of deep water nutrients which in turn limits the phytoplankton growth (Behrenfeld et al. 2006). These changes are predicted to continue and even to strengthen in the future due to the ongoing climate change, whose effects are predicted to be strongest in the Arctic (IPCC 2013). Higher sea-temperatures and reduced sea ice cover may restrict ice-algae production, advance the onset of phytoplankton bloom, shorten the blooms, and thereby significantly influence zooplankton production and species depending on zooplankton (e.g. zooplanktivorous seabirds) (Søreide et al. 2010, Drinkwater 2011, Usov et al. 2013, Durbin & Casas 2013). Also, higher inflow of Atlantic water may facilitate the northward expansion of boreal marine species and suppress the distribution of the Arctic marine species (Loeng & Drinkwater 2007, Falk-Petersen et al. 2007).

A good example of a species whose reproduction and growth benefit from low sea-temperatures, sea ice and ice-algal blooms, and abundant phytoplankton blooms, is *Calanus glacialis*, a big Calanoid copepod inhabiting cold, Arctic water masses (Søreide et al. 2010, Leu et al. 2011, Durbin & Casas 2013, Pasternak et al. 2013). It stores high amounts of lipids in order to survive the long Arctic winter (Scott et al. 2000, Falk-Petersen et al. 2009), and is thus favoured as a

food by many important Arctic predators, such as the little auk *Alle alle* (Karnovsky et al. 2003) and the bowhead whale *Balaena mysticetus* (Rogachev et al. 2008). Arctic warming may threaten the viability of *C. glacialis*, reduce its abundance, and thereby negatively influence the species feeding upon it (Falk-Petersen et al. 2007).

1.5 The little auk

Figure 2 The little auk *Alle alle* is the most abundant seabird species in the Arctic. © Norwegian Polar Institute

The little auk (Figure 2) is a small (body weight ~ 160 g), zooplanktivorous seabird with a presumably strong mate- and breeding site fidelity (Norderhaug 1968, Stempniewicz 2001, Montevecchi & Stenhouse 2002, Wojczulanis-Jakubas et al. 2014). It is a colonial breeder, and the most abundant seabird species breeding in the high Arctic (> 100×10^6 birds; Barrett et al. 2006). The little auk's breeding range extends from 60°N (south Greenland) to 82°N (Franz Josef Land) and from 67°W (eastern Baffin Island) to 98°W (Severnaya Zemlya). The largest colonies are found in Thule District in north-west Greenland, Scoresby Sound in east Greenland, and in Spitsbergen (Stempniewicz 2001). The age of sexual maturity or longevity of little auks is not known, but based on the information available for closely related alcids (e.g. common murre *Uria aalge* and razorbill *Alca torda*; Friesen et al. 1996) little auks may be expected to live > 20 years and to start reproducing at the age of 4 years (Ralph et al. 1995). Little auks lay a single-egg clutch in a rocky crevice in the talus slope (Stempniewicz 1981). Both sexes incubate the egg and feed the chick, but prior to fledging only males are left to take care of the chick (Harding et al. 2004, Wojczulanis-Jakubas & Jakubas 2012). The chick departs the colony together with its father, who provides extra care at sea until the chick is self-reliant (Stempniewicz 2001). Nestling period is short in the Arctic: parents have 20-31 d to get the chick ready and out of the nest (Harding et al. 2004, Wojczulanis-Jakubas & Jakubas 2012).

Little auks have small, stiff wings that are well suited for underwater propulsion during prey capture, but less so for flying. Energy expenditure associated to flying is high (Gabrielsen et al. 1991, Elliot et al. 2013). As extra body weight would greatly increase flight costs (Witter & Cuthill 1993), little auks should keep their stored energy reserves as small as possible. Recently, little auk parents have been shown to employ a bimodal foraging strategy: they alternate a single long trip with several subsequent short trips (3-5) daily, in order to provide adequate energy for themselves and for the chick (Steen et al. 2007, Welcker et al. 2009a, Brown et al. 2012). Little auks forage, at maximum, within a ~ 200 km distance from their respective colonies (Welcker et al. 2009a, Brown et al. 2012). The food for the chick is brought fresh and undigested in a specialized gular pouch below the beak.

The summer diet of little auks consists mainly of Calanoid copepods (Figure 3). Preferably those found in cold, Arctic water masses (such as *C. glacialis* and *C. hyperboreus*) – due to their high lipid content (Scott et al. 2000). Lipid-rich food helps to compensate the high energy expenditure

of little auks during the breeding season (Gabrielsen et al. 1991, Karnovsky et al. 2003, Harding et al. 2009, Kwasniewski et al. 2010, Jakubas et al. 2012). Atlantic water associated Calanoid copepods (such as *C. finmarchicus*) contain 25% less lipid per milligram of dry weight (Scott et al. 2000), and are therefore not as suited to satisfy the energy requirements of little auks. Little auks harvest up to one fourth of the local zooplankton production within their breeding areas, and therefore have a significant role in the Arctic food web (Karnovsky & Hunt 2002, Barrett et al. 2006). During winter, other prey items, such as krill and amphipods, become the dominant food source (Rosing-Asvid et al. 2013), mainly because copepods hibernate at depths below the maximum diving depth of little auks (~ 35 m) (Karnovsky et al. 2011, Brown et al. 2012, Arendt et al. 2013).
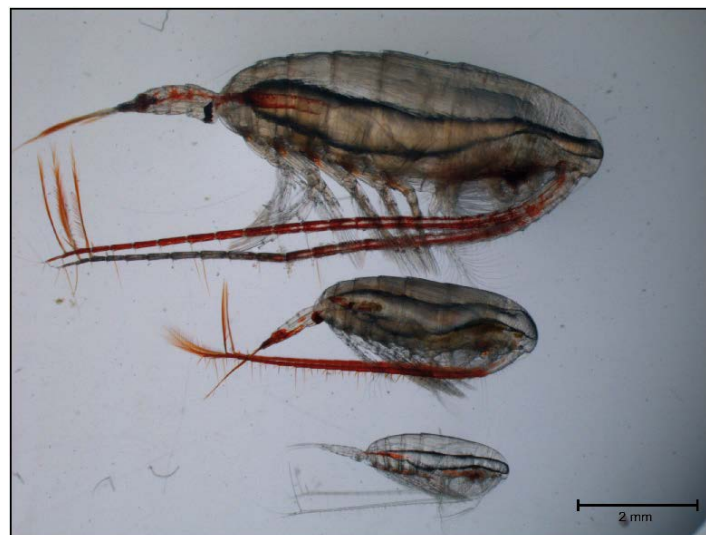

Figure 3 The three Calanoid copepod species in the Arctic: *Calanus finmarchicus* (lowermost), *C. glacialis* (middle), and *C. hyperboreus* (highermost). © Malin Daase

2. Aims of the thesis

Understanding how life-history traits are influenced by climatic and environmental variability is important for assessing the effects of climate change on animal populations (Caswell 2001). The general aim of this thesis was to assess the effects of climatic and environmental variability on foraging, reproduction and survival of the Arctic-breeding little auk. The little auk's specialized diet (Arctic *Calanus* copepods) and low trophic position in the food web suggest both a close link to primary productivity and a sensitivity to any change in prey abundance and/or availability.

More specifically, the aims were:

1. To establish which physical and biological (food supply) factors determine the at-sea distribution of foraging little auks (Paper I)

2. To test whether varying oceanographic conditions with their associated prey affect foraging trip durations, chick provisioning rates and the probability of a little auk chick to fledge (Paper II)

3. To assess the effects of regional and local climatic variability on the adult survival of little auks (Paper III)

Since the little auks are long-lived, have low fecundity and should avoid storing surplus energy as far as possible, it was expected that they would prioritize survival over reproduction. This was predicted to be seen as a decreased investment in reproduction, an increased emphasis on self-maintenance, lower fledging success, and relatively stable survival rates, when facing poor foraging conditions.
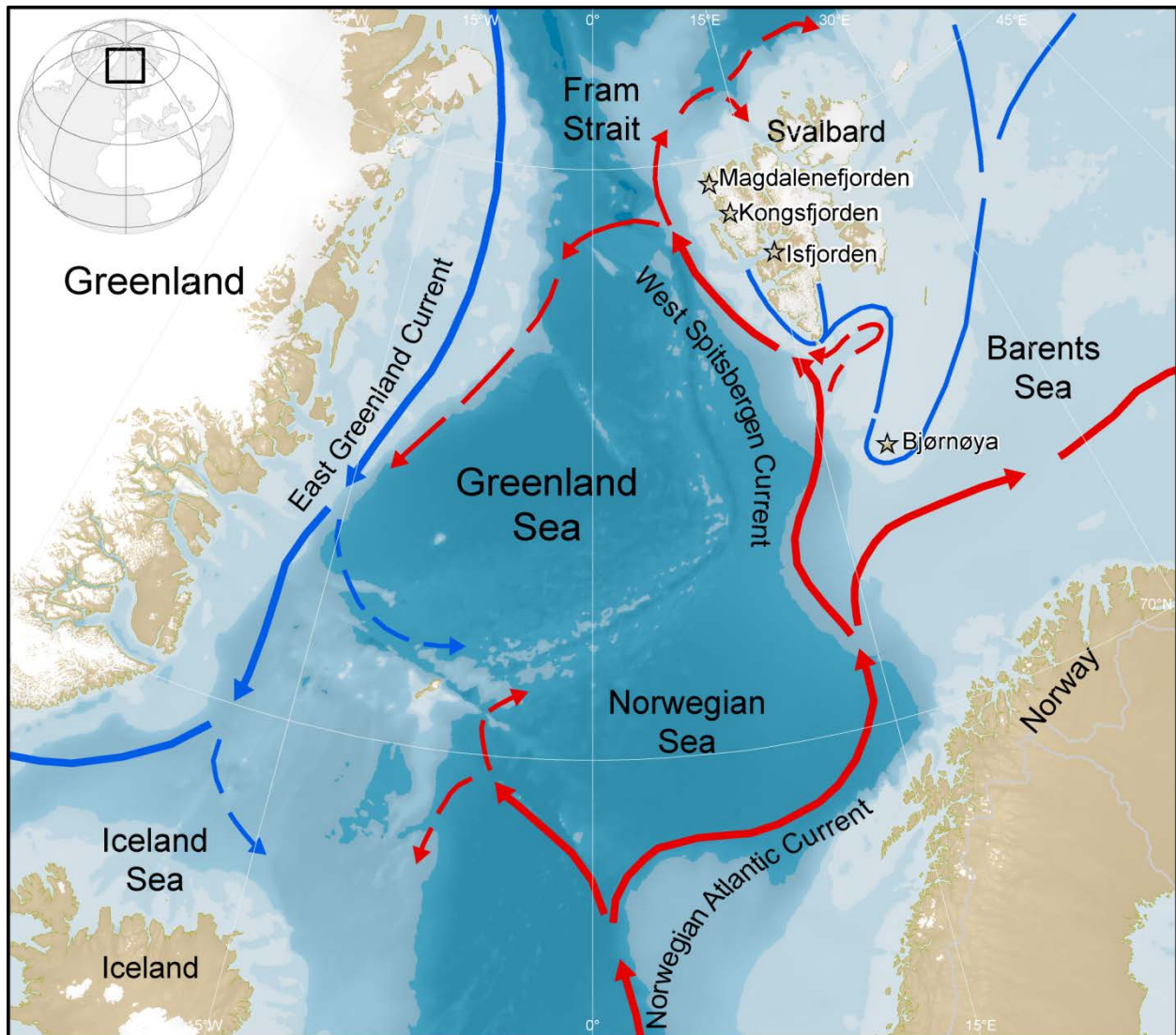
3. Material and methods

3.1 Study area

Figure 4 Study area with the little auk colonies (stars) and the main water currents. Atlantic water is brought into the area by the West Spitsbergen Current (WSC), and Arctic water by the South Cape Current (blue line next to the WSC) © Bernt Bye

Data for this thesis was collected during several field campaigns, both on land and at sea, during 2006-2013. Study area included parts of the coastline of western Spitsbergen, Svalbard, and adjacent sea-area (Figure 4). Little auk colonies in Isfjorden (78°12ʹN, 15°20ʹE) (Papers II and III), Kongsfjorden (79°01ʹN, 12°25ʹE) (Paper III) and Magdalenefjorden (79°35ʹN, 11°05ʹE) (Paper II) were used as study bases on land (Figure 4). Data was also collected on Bjørnøya, further south (74°31ʹN, 19°01ʹE) (Paper III, Figure 4).

The study area is characterized by a presence of both warm, saline Atlantic water (T > 3°C, PSU > 34.95) masses and cold, less saline Arctic water (T < 0°C, PSU: 34.3-34.8) masses. Atlantic water originates from the Northern Atlantic and the Norwegian Sea, and is transported into the region along the steep continental shelf break by the West Spitsbergen Current. Arctic water originates from the north-western Barents Sea, and is carried into the area over the continental shelf by the South Cape Current. These two water masses are separated by a front that varies in strength and tends to break down during summer. When this happens, Atlantic water is able to cross the front and, mixed with Arctic shelf water, may enter the open fjords in western Spitsbergen (Saloranta & Svendsen 2001, Hop et al. 2006, Cottier et al. 2007, Walkusz et al. 2009).

As Atlantic and Arctic water masses contain different zooplankton species, with *Calanus finmarchicus* being associated with Atlantic water and *C. glacialis* with Arctic water, the distribution of these two water masses considerably influences the quality of little auks' foraging grounds (Willis et al. 2006, Kwasniewski et al. 2012, Stempniewicz et al. 2013). The inter-annual variation in the inflow and temperature of Atlantic water into the Arctic can be high, and has recently increased (Carton et al. 2011, Walczowski et al. 2012).

3.2 Data collection

Little auks at sea (Paper I)

Birds were counted throughout the day from the ship's bridge whenever the ship was moving at a constant speed of ~ 9 nm h^{-1} during the surveys at sea. All little auks seen within an arc of 300 m from the bow to 90° abeam of the ship were registered (Tasker et al. 1984) and assigned a time

and spatial positioning from the ship's global positioning system (GPS). Only birds swimming or emerging from water were included into later analyses as they probably were about to forage, or had just been foraging (Hunt et al. 1996). GPS data was later used to assign different environmental variables (see sections below) to count data.

Zooplankton abundance and distribution (Paper I)

In order to estimate abundance and spatial distribution of little auks' prey, a Simrad EK60 echo-sounder operating at frequencies of 38 kHz and 120 kHz and a ping rate of 0.5 pings s^{-1} was used to gather backscatter information from the water column (surface to near seabed). This data was logged simultaneously with little auk counts, and included time and spatial position from the ship's GPS. Noise spikes and bubble occlusions caused by the ship's engine and impacts with ice was removed from the acoustic data in post-processing. Only data from the upper 30 m of the water column was considered, as this coincides with the average and maximum diving depths of little auks (~ 10 m and ~ 35 m, respectively; Falk et al. 2000, Harding et al. 2009, Karnovsky et al. 2011, Brown et al. 2012). The surface layer of 0-10 m was omitted due to excess noise caused by the draft of the ship's hull. However, the amount of prey there was assumed to be reflected by the prey in the 20-30 m layer because of the unsynchronized diel vertical migration performed by zooplankton under midnight-sun conditions (Cottier et al. 2006, Wallace et al. 2013).

Acoustic data was used to calculate a 'Mean Volume Backscattering Strength' (MVBS), which was then partitioned to different echo size-classes defining meso- and macrozooplankton and nekton. This partitioning was based on the length measurements of zooplankton body sizes. Zooplankton were collected with a WP-2 net (mouth opening 0.25 m^2, mesh size 500 µm) from the top 50 m of the water column. MVBS values were further converted to 'volume backscattering co-efficient' values, which were used as a proxy for zooplankton abundance.

Little auks on land (Papers II and III)

Foraging trips and chick provisioning rates (Paper II) Adult birds were caught with mist-nets or noose-carpets during late incubation or early chick rearing period. Each bird was marked with a stainless steel ring and a unique combination of three plastic colour rings (Figure 5). Later during the chick rearing period (chick age: 8-17 d), marked birds were observed non-stop for 48 h. Observation areas were chosen such that they included a sufficient number of nests with visible entrances, and such that they minimized potential disturbance caused by observers. Departure and arrival times of marked birds were marked down, and only birds that returned to the colony with food for their chick (noticeable by their bulging gular pouch; Figure 5) were registered. Trip duration was taken as the time between departure and arrival. A feeding event was logged whenever a bird left the nest with an empty gular pouch after first having entered the nest with a filled one.

Figure 5 Little auk with leg-rings used for identification, and a gular pouch filled with food for the chick. © Benjamin Merkel

Chick food samples (Paper II) Gular pouch samples were collected from birds caught with mist-nets or noose-carpets during the chick rearing period. Samples were procured by gently scooping

out the content from the gular pouch. A bird was sampled only once in order to avoid malnutrition of its chick. Samples were transferred to 4% formaldehyde solution, and later analysed in the lab.

Chick fledging success (Paper II) Nests containing an egg were located and marked during the late incubation period. They were monitored every 2-3 d during the hatching period in order to detect the hatching date. During the chick rearing period nests were monitored every 4-5 d in order to record chick survival. The frequency of the nest checks was increased to every 2-3 d when chicks started to fledge. Presence of an egg or a chick in the nest was confirmed with the use of flashlights or light-scopes (Moritex Europe Ltd, Cambridge, UK). The chick was considered fledged if it disappeared from the nest at the age of ≥ 20 days (Harding et al. 2004, Wojczulanis-Jakubas & Jakubas 2012).

Adult survival (Paper III) Birds were caught and marked as mentioned above, but only individuals known to breed at the time of marking were included into survival analyses. Breeding status was confirmed by the presence of a brood patch or a full gular pouch at capture. These birds were then observed during each breeding season, in order to estimate annual survival rates.

Environmental variables (Papers I, II and III)

Sea-surface temperature (SST, °C) (Papers I, II and III) In the study area, a strong connection has been found between summer SST and the species composition of local zooplankton communities, with large lipid-rich Calanoid copepods inhabiting colder water (Karnovsky et al. 2010). Therefore, SST was used as a proxy for the quality of little auk's summer foraging grounds. Satellite based SST data was acquired from the Moderate Resolution Imaging Spectroradiometer (MODIS/aqua).

The North Atlantic Oscillation (NAO) (Paper III) The NAO was used as a proxy for weather conditions outside the breeding season, and for food availability and abundance during and outside the breeding season. The NAO is defined as the difference in atmospheric sea level pressure between Stykkisholmur/Reykjavik, Iceland and Ponta Delgada, the Azores; it is the

main driving force behind climatic and oceanographic variability in the middle and high latitudes of the Northern Hemisphere (Hurrell 1995). A positive NAO increases storm activity across the Atlantic. This causes a greater inflow of Atlantic water into the Arctic, resulting in higher sea temperatures there. A negative NAO has the opposite effect (Visbeck et al. 2001, Drinkwater 2011). As the noise ratio of NAO is strongest during winter months, with far-reaching repercussions on the dynamics and composition of phyto- and zooplankton communities in the subsequent spring and summer season (e.g. Ottersen et al. 2001, Hurrell et al. 2003), it was the winter NAO (December through March) which was used as a proxy for weather conditions and for food availability and abundance.

4. Main results and discussion

4.1 Foraging (Papers I and II)

Little auks at sea (Paper I)

The energy consumption of seabirds is especially high during the chick rearing period (Drent & Daan 1980). To be able to provision both themselves and the offspring, a sufficient amount of good quality prey has to be found. This task may be complicated by the fluctuating and patchy distribution of prey in the ocean (Lack 1968, Hunt et al. 1998). However, seabirds' ability to detect suitable foraging grounds may be improved by different oceanographic features and processes that aggregate prey into easily located patches (e.g. continental shelf break; Certain et al. 2007).

The results in Paper I show that the number of little auks at sea was negatively correlated with the SST. Also, the shelf-sea area attracted more little auks than the off-shelf waters (defined as the shelf break and deep-ocean areas). In addition, the foraging little auks tended to favour areas with a flat sea-bed. The explanation for these findings could be that Arctic-water associated prey is more likely to be found on the shelf than off the shelf, as Arctic water is brought into the study area by the South Cape Current which flows along the shelf (Saloranta & Svendsen 2001). Also, a flat sea-bed may generate less upwelling of warm and dense Atlantic water from below the cold and lighter Arctic water than sea-bed with a pronounced gradient, since the interaction between sea-bed and currents is reduced (Svendsen et al. 2002, Cottier et al. 2005).

Furthermore, the number of little auks at-sea was positively correlated with the amount of macrozooplankton (e.g. krill and amphipods), but did not correlate with the amount of mesozooplankton, which includes what is assumed to be the main prey of little auks (*Calanus* spp.) during breeding season. Several explanations may apply to this finding: 1) The at-sea distribution of mesozooplankton was less heterogenous than that of macrozooplankton. A more homogenously distributed, sufficient amount of prey may reduce the need for searching out dense prey aggregations (Pianka 1986); 2) The bigger sized macrozooplankton may be easier for little auks to detect, and its presence may also imply the presence of mesozooplankton, for example because macrozooplankton feed on the same phytoplankton source as mesozooplankton

(e.g. Hansen et al. 1994); 3) The little auks feed on macrozooplankton more than what is generally assumed also during summer, and hence seek out the macrozooplankton patches.

Foraging trips, chick provisioning rates and food received by chicks (Paper II)

During poor foraging conditions, the long-lived little auks were predicted to increase self-maintenance at the expense of chick-maintenance. The results in Paper II show that little auks indeed seemed to prioritize self-maintenance: they adjusted the duration of long foraging trips but not the duration of short foraging trips, and provisioned their chicks at a lower rate when the duration of long foraging trips increased. These adjustments, however, were independent of a change in SST, which, as previously mentioned, was used to define foraging conditions (low SST would in general indicate better foraging conditions than high SST; Karnovsky et al. 2010).

It may be a bit surprising that SST did not influence trip durations and provisioning rates of little auks, since the little auks are known to forage preferably in colder water masses (e.g. Karnovsky et al. 2003, Jakubas et al. 2012, Paper I). Indeed, one could expect that more time is required in order to find suitable prey when the SST increases, and vice versa (Duriez et al. 2000). The following reasons may apply for why such an effect was not detected: 1) The little auks were very efficient in seeking and finding pockets of cold water in their foraging area – even when foraging conditions were not optimal; 2) The little auks may have foraged in areas which contain a high amount of good quality prey not influenced by the SST: for example, the marginal ice zone and frontal systems delineating different water masses are known to accumulate phyto- and zooplankton (e.g. Smith et al. 1990, Fauchald 2009). Hence, variations in the spatial location of the marginal ice zone and/or frontal systems may have caused adjustments in trip durations and chick provisioning rates of the little auks.

However, even though the SST did not influence trip durations and provisioning rates in little auks, it did seem to influence the number of prey items delivered to chicks: the number of prey items received by a chick was negatively correlated with SST. Also, the number of Arctic-water associated, lipid-rich prey in the chick food was higher when SST was lower. Provisioning rates *per se* did not influence the number of prey delivered to chicks.

4.2 Reproduction (Paper II)

Increased self-maintenance and decreased investment in chick maintenance during poor foraging conditions may lower the probability of a chick to survive (Zera & Harshman 2001); decreased chick provisioning rate and, hence, a potentially smaller amount of prey and energy delivered to a chick may increase chick mortality (Schaffner 1990). However, the results in Paper II show that provisioning rates neither influenced the number of prey items delivered to chicks nor the probability of a little auk chick to fledge. Instead, the SST had a strong effect on the fledging probability, which increased when SST decreased. The influence of SST on fledging probability was likely related to prey availability and quality – little auk chicks received a higher amount of good quality prey when SST was lower (as mentioned above).

These results suggest that foraging conditions indeed had a strong influence on the fledging probability of a little auk chick. However, this influence was not mediated through the actual chick provisioning rates but rather through the number of prey delivered to a chick, which again was determined by the quality of the foraging grounds (SST).

4.3 Survival (Paper III)

Even though adult survival in a long-lived species is expected to stand relatively robust against temporal variability (Gaillard & Yoccoz 2003), this does of course not mean that adults are completely insensitive to changes in their environment (Gaston & Jones 1998). For example, a food shortage may significantly reduce the energy available for all life-history traits, including self-maintenance, and, hence, may decrease adult body condition, thereby increasing the mortality rate of adults (e.g. Barbraud & Weimerskirch 2001, Welcker et al. 2009b, Harding et al. 2011). The results in Paper III suggest that little auk adults were influenced by climatic and oceanographic variability: adult survival rates were negatively correlated both with the summer SST at the breeding grounds and with the winter NAO, with a time-lag of one and two years, respectively. As seen from the delayed response of adults to both winter NAO and summer SST, their effects were likely mediated through the food chain.

In ice-covered areas, the preferred prey of little auks, cold Arctic water associated *Calanus* copepods, utilize high quality ice-algae to produce eggs during early spring, so that the resulting offspring can utilize the phytoplankton bloom two months later. In ice-free areas, *Calanus* females employ a capital breeding strategy, and time the growth and development of offspring to coincide with the phytoplankton bloom (Daase et al. 2013). Both these strategies result in a *Calanus* stock to be preyed upon by the little auks 2-3 years later – the time it takes to complete a life cycle for Arctic *Calanus* (Falk-Petersen et al. 2009), and thus become old copepodites, which are the most rich in lipid and therefore preferred by the little auks (Scott et al. 2000, Karnovsky et al. 2003, Jakubas et al. 2011). Sea-temperature has a major effect on the extent and thickness of the seasonal sea ice cover in the Arctic, and on the onset and duration of spring phytoplankton bloom (Arrigo et al. 2008, Mann & Lazier 2006). It is strongly influenced by the NAO (Ingvaldsen 2005, Drinkwater 2011): an increase in the NAO, with associated increments in sea-temperature, reduces the amount of sea-ice, which in turn results in a decreased ice-algal production and may also initiate an earlier but possibly shorter lasting spring bloom (Arrigo et al. 2008, Drinkwater 2011). Furthermore, higher summer SST may shorten the reproductive period of Arctic *Calanus* females which are able to maintain egg production as long as temperature in the upper water layer stays below 5°C (Hirche & Kwasniewski 1997). Thus an increased NAO as well as higher summer SST could negatively influence the Arctic *Calanus* stock size (Søreide et al. 2010, Leu et al. 2011, Durbin & Casas 2013, Pasternak et al. 2013, Usov et al. 2013), and thereby also the little auks preying upon it.

Also macrozooplankton (e.g. krill and amphipods) are fed upon by the little auks, especially during the winter months (Rosing-Asvid et al. 2013). However, little auks may feed on macrozooplankton to a larger extent than previously assumed also during the summer (Paper I). Macrozooplankton too may take advantage of sea-ice, ice-algal blooms, and detrital lumps on the underside of sea-ice (Dalpadado et al. 2001, Poltermann 2001, Pinchuk & Hopcroft 2007, Lessard et al. 2010). In general, their numbers correlate negatively with sea-temperature (Coyle et al. 2011). Hence, an increased NAO may result in a reduced abundance and availability of macrozooplankton, which may in turn negatively influence the adult survival of little auks.

5. Conclusions and further perspectives

The little auk inhabits the area that is undergoing the most severe environmental changes due to the ongoing global climate change – the Arctic. For the little auks to adapt to the changing conditions, their life-history traits should show a high resilience to change. Adult survival in particular should stand robust against climatic variability, since it is the fitness component that most strongly influences the population growth rate in a long-lived species (Wooller et al. 1992, Gaillard & Yoccoz 2003). In light of this, the little auks should allocate resources cautiously to current reproduction, in order to secure survival and, hence, the potential for future reproduction (Stearns 1992). A bimodal foraging strategy may help to simultaneously maintain competing life-history traits (e.g. reproduction, self-maintenance and survival), diminishing the need for trade-offs. It may offer some flexibility to parent seabirds in allocating resources to competing life-history traits (Weimerskirch et al. 1994, Duriez et al. 2000).

Nevertheless, the findings of this thesis suggest that changes in the climate and environment did influence both chick- and adult survival in little auks, and that the influence was similar for both life-history traits: poorer foraging conditions decreased the survival probability of chicks and adults, whereas better foraging conditions had the opposite effect. Thus, both traits seemed susceptible to changes in environment. The strong positive correlation between chick- and adult survival is shown in Figure 6. It should be pointed out, however, that adult survival rates were on average higher (0.89) than the chick survival rates (0.84) (Figure 6), which indicates that the little auks prioritized self-maintenance over chick-maintenance.

Cairns (1988) predicted that reduced prey availability influences sequentially the life-history traits in seabirds, with an increase in adult mortality to be expected only when prey is extremely scarce. As both chick- and adult survival were affected in little auks, does this mean that the changes in prey availability have been extreme in the Arctic during the past 8 years? Or could it be that little auks, with their presumably high rate of breeding site fidelity (Wojczulanis-Jakubas et al. 2014), relatively short foraging range (~200 km; Welcker et al. 2009a, Brown et al. 2012) and specialized diet (Arctic zooplankton), in particular during summer months, are rather vulnerable even to minor changes in prey availability (see e.g. Furness & Ainley 1984)? Indeed, many seabirds have been shown to remain faithful to their breeding sites year after year, even

during poor foraging conditions, something which may negatively influence their ability to adapt to environmental changes (Grémillet & Boulinier 2009).
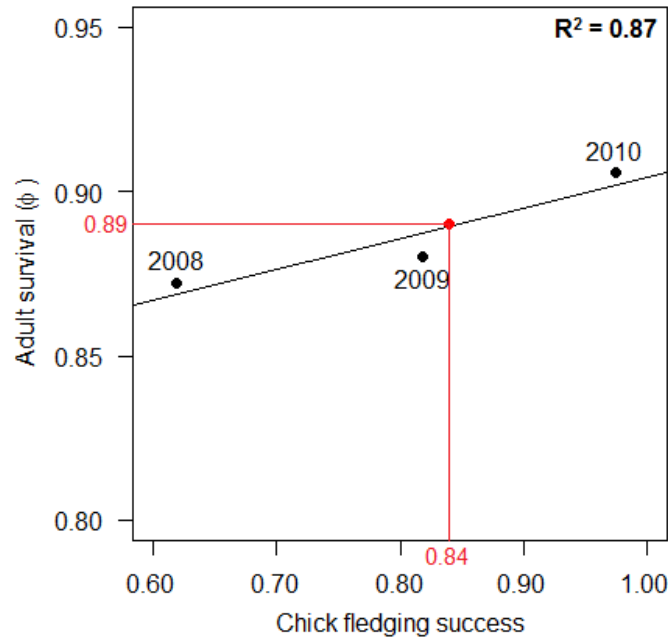

Figure 6 Chick fledging success and adult survival of little auks in Isfjorden 2008-2010 (this is the only period for which data on both traits in the same colony was available). For adults, each year in the figure represents survival interval between that year and the next year; e.g. 2008 = survival interval 2008-2009. Strong positive correlation (R^2 = 0.98) is shown between the two life-history traits. Adult survival is on average higher than chick fledging success (0.89 vs. 0.84; marked in red)

The high sensitivity of little auk chick- and adult survival to climatic and environmental variability suggests that in the future, when Arctic warming continues and favoured Arctic zooplankton is expected to be gradually replaced with Atlantic zooplankton, the number of little auks may substantially decrease, as happened for example in Iceland during the earlier warming period between 1870 and 1930 (Gudmundsson 1951). During the last decades, the little auks have almost completely disappeared from Iceland: the main reason for this decline is supposedly a warming of the climate (Bardarson 1986). Although it is not known whether the climate has influenced the Icelandic decline indirectly through prey availability or directly through

physiological processes (Astthorsson et al. 2007), the results of this thesis (i.e. little auk's preference for cold Arctic water and thereby Arctic water associated prey [Paper I], negative correlation between both the fledging success and adult survival, and the quality of foraging grounds [Paper II, III]) support the former, or at the very least that prey availability has been a partial reason for the decline.

Although the results of this thesis imply that little auks suffer from a warming of the climate, and benefit from the opposite, it is not that straightforward to estimate and/or predict the decline (or increase) in the number of little auks. For example, also the recruitment of new breeders to a seabird population has a big influence on the seabird population dynamics (Sandvik et al. 2012), and juvenile survival may potentially be very sensitive to climatic variability (Gaillard & Yoccoz 2003). Thus, in order to fully evaluate how climatic and environmental variability impacts the little auks, the recruitment probability should be studied too: how big proportion of the little auk chicks that have successfully fledged survive until sexually mature and start breeding, and how is this ratio influenced by climatic and environmental changes? This branch has not yet been investigated in little auks. Furthermore, the age at which little auks reach sexual maturity, as well as how old they get, is not known for sure and only estimates can be given at the moment (4 and >20 years, respectively; Ralph et al. 1995). Neither is it known at which age little auks cease to breed. Due to these uncertainties, and a lack of information on post-fledging survival and recruitment, it is hard to construct a meaningful life-history model or predictions for the future. What can be said is that based on chick- and adult survival and their relation to environmental and climatic variability, the Arctic warming is likely to decrease the amount of little auks, but to what extent is uncertain.

Naturally, there have been several studies on little auks previous to this thesis, and some of them have looked at topics investigated in this thesis as well, such as: Where do little auks forage (e.g. Welcker et al. 2009a, Karnovsky et al. 2003, 2010, Jakubas et al. 2012)? Are their chicks influenced by foraging conditions (e.g. Grémillet et al. 2012, Jakubas et al. 2011, 2013)? Can adults maintain their survival rate despite a deterioration in foraging conditions (e.g. Grémillet et al. 2012)? Their results agree with those of this thesis on little auks foraging preferably in cold Arctic water masses (e.g. Karnovsky et al. 2003), but they disagree on the climatic and environmental influence on chicks and adults: it has been claimed that chick fledging is

insensitive to foraging conditions (e.g. Jakubas et al. 2013), and that adults withstand the impact of the current Arctic climate change (Grémillet et al. 2012). The reason why these studies did not find a connection between foraging conditions and chick- and adult survival, as found in this thesis, may be due to the following: the above mentioned studies concentrated more on so called 'quality'-colonies and/or were perhaps run for too short a time period; results based on a few data points (i.e. years), or on colonies that are influenced more by Arctic than Atlantic water masses, should be considered with caution.

In addition to the little auks, also other zooplanktivorous alcids have shown similar responses in their life-history traits to climate and environmental change: for example, the reproductive success of crested (*Aethia cristatella*), least (*Aethia pusilla*), parakeet (*Aethia psittacula*), whiskered (*Aethia pygmaea*) and Cassin's (*Ptychoramphus aleuticus*) auklets, all inhabiting the north Pacific region, seem to correlate negatively with an increase in sea temperature – which influences the quality of their prey (e.g. Kitaysky & Golubova 2000, Wolf et al. 2010, Bond et al. 2011). Furthermore, the adult survival of least auklets and Cassin's auklets is negatively influenced by a high sea temperature and low food availability, but is in general still higher than the chick survival (e.g. Jones et al. 2002, Wolf et al. 2010). Also, many piscivorous alcids, such as Atlantic puffin (*Fratercula arctica*), common guillemot, and razorbill, have been shown to respond negatively to an increase in sea temperature and an associated decrease in the amount of their preferred prey (e.g. capelin *Mallotus villosus*) (Sandvik et al. 2005). On the other hand, other seabird species have been reported to benefit from the changing climate: for example, tufted (*Lunda cirrhata*) and horned (*Fratercula corniculata*) puffins reproduce more successfully in warm years with a higher proportion of 1+ age sand lance in their foraging area (Kitaysky & Golubova 2000). In the Southern Ocean, increased wind speeds have enabled wandering albatrosses (*Diomedea exulans*) to shorten their foraging trips and incubation shifts, something which has resulted in higher breeding success (Weimerskirch et al. 2012). The number of wandering albatrosses has however decreased, most likely due to increased sea temperatures, reduced ice cover and lower krill abundance that in turn may have influenced the recruitment probability (e.g. Weimerskirch et al. 2003b).

Contrasting trends in chick- and adult survival of different seabird species in relation to climatic and environmental variability shows that while some species may benefit from the climate

warming, others will suffer from it. Little auks seem to belong in the latter category. As mentioned previously, adult survival rate is crucial to the viability of a long-lived species, and we have seen in this thesis that the adult survival rate of little auks is negatively influenced by the climate warming. Indeed, this thesis has provided some new knowledge on how little auk chicks and adults respond to climatic and environmental variability: it has shown that prey associated with cold, Arctic water masses play an important role in foraging, reproduction, and survival of little auks. However, the effects of environmental variability on other life-history traits, such as recruitment and juvenile survival, should also be studied – in order to fully assess the little auk's ability to cope with changes in climate and environment.

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7. Original papers

Paper I

Hovinen JEH, Welcker J, Rabindranath A, Brown ZW, Hop H, Berge J, Steen H (2014) At-sea distribution of foraging little auks relative to physical factors and food supply

Marine Ecology Progress Series, in press (doi:10.3354/meps10740)

Paper II

Hovinen JEH, Wojczulanis-Jakubas K, Jakubas D, Hop H, Berge J, Kidawa D, Karnovsky NJ, Steen H (2014) Fledging success of little auks in the high Arctic: do provisioning rates and the quality of foraging grounds matter?

Polar Biology, in press (doi:10.1007/s00300-014-1466-1)

Paper III

Hovinen JEH, Welcker J, Descamps S, Strøm H, Jerstad K, Berge J, Steen H (2014) Regional and local variations in climate affect the survival of a high Arctic avian predator

Global Change Biology, under review