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seasonal structure in space and environment across species, populations and individuals

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Benjamin Merkel
A dissertation for the degree of Philosophiae Doctor – April 2019
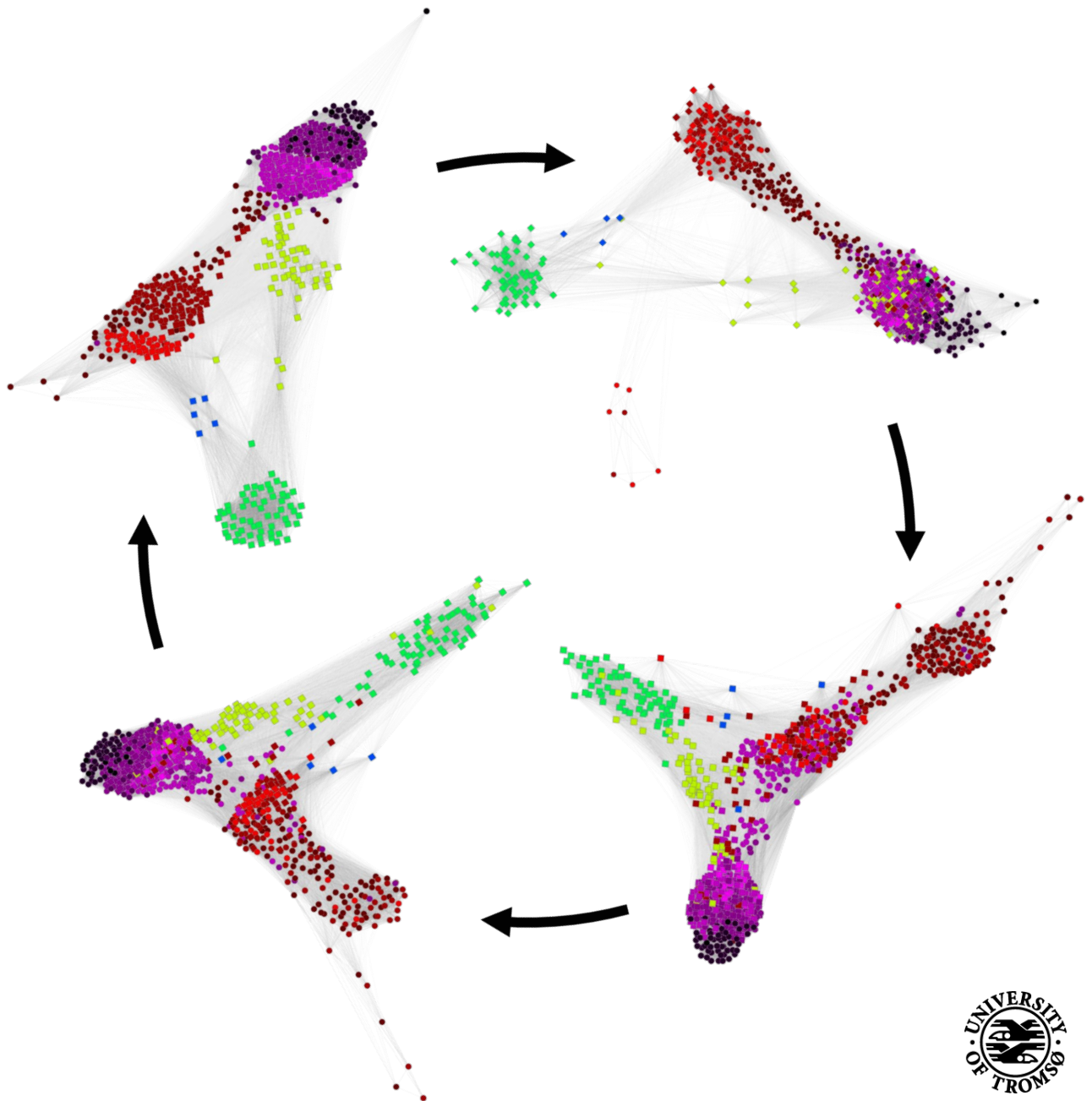
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Table of content

Summary

Identifying drivers of population trends in migratory species is difficult, as they can face many stressors while moving through different areas and environments during the annual cycle. Their population response to environmental change may in addition be affected by consistent differences in individual behaviour, which are widespread in free-living populations. An understanding of the structure of migration in space and time across species, populations and individuals is necessary to identify potential plasticity and constraints for migratory species in a rapidly transforming physical and biological environment. This thesis uses two congeneric long-distance migrants of the genus *Uria*, the common (*Uria aalge*) and Brünnich's guillemot (*Uria lomvia*) to address these questions. To this end, I utilized a large light-level geolocator tracking dataset of 887 individual guillemots breeding at 16 colonies across the Northeast Atlantic, tracked over 10 years resulting in 1740 annual tracks.

Through the development of a novel method to estimate locations from twilight timings, I was able to correct biased estimates for part of my dataset, which made the overall dataset comparable. Further, with the inclusion of information about the species' biology as well as several spatial masks, the method was able to estimate locations also during times of equinox. This in turn made it possible to investigate migratory connectivity (i.e. the connection between breeding and no-breeding regions) and individual migration strategy fidelity (i.e. consistency of individual migratory behaviour) throughout the non-breeding period.

Both guillemot species are comprised of space use specialists selecting for specific sites rather than habitats. They breed in colonies displaying strong migratory connectivity, within and between species. This was apparent through a combination of colony-specific seasonal space use and occupied environmental niches, grouping Northeast Atlantic Brünnich's guillemot populations into two and common guillemot populations into five previously undescribed spatiotemporal movement clusters. Remarkably, common guillemot populations clustered in accordance with the variable population trends exhibited by the species, while Brünnich's guillemot populations are all declining where their trends are known. Colony-specificity was also visible in the exhibited temporal variations of individual migratory movements due to the species breeding biology. Birds were flightless during their autumn moult constricting their movement. Likewise, individuals were constricted to quasi central place foraging during spring prior to egg-laying after arrival back at their colony. These two periods were visible as constricted space and environmental use and often lack of individual specific behaviour. Arrival dates back at the colony were highly variable between species and colonies and

could be best explained by colony size. Unlike timing of egg-laying, arrival date advanced considerably in recent years across the study area in both species, demonstrating that different events in seabird phenology can show different temporal trends.

Migratory behaviour is likely shaped by a combination of the physical properties of the occupied environment, energetic constraints faced due to the animal's physiology and foraging adaptations, inter- and intra-specific competition for food resources as well as nest sites, and conservative migratory behaviour. These traits might leave migrants vulnerable to large-scale perturbations of their environments, which occur at an ever increasing rate, while the compartmentalised annual distribution allows for the potential extinction of an entire population by regional threats, anthropogenic or otherwise.

List of papers

I. **Merkel B**, Phillips RA, Descamps S, Yoccoz NG, Moe B, Strøm H. (2016). A probabilistic algorithm to process geolocation data. *Movement Ecology*

II. **Merkel B**, Descamps S, Yoccoz NG, Grémillet D, Fauchald P, Danielsen J, Daunt F, Erikstad KE, Ezhov AV, Harris MP, Gavrilo M, Lorentsen SH, Reiertsen TK, Systad GH, Þórarinsson ÞL, Wanless S, Strøm H. (20XX). Strong migratory connectivity across meta-populations of sympatric North Atlantic seabirds. *Manuscript*

III. **Merkel B**, Descamps S, Yoccoz NG, Grémillet D, Daunt F, Erikstad KE, Ezhov AV, Harris MP, Gavrilo M, Lorentsen SH, Reiertsen TK, Steen H, Systad GH, Þórarinsson ÞL, Wanless S, Strøm H. (20XX). Individual migration site fidelity but no habitat specialization in two congeneric seabirds. *under review in Journal of Biogeography*

IV. **Merkel B**, Descamps S, Yoccoz NG, Danielsen J, Daunt F, Erikstad KE, Ezhov AV, Harris MP, Gavrilo M, Grémillet D, Lorentsen SH, Reiertsen TK, Steen H, Systad GH, Þórarinsson ÞL, Wanless S, Strøm H. (20XX). Earlier arrival despite constant breeding phenology in two congeneric seabirds. *Manuscript*

Contributions

All work in this thesis is primarily my own. 19 other people co-authored one or more of the papers herein and their contributions are as follows (in no particular order):

	Paper I	Paper II	Paper III	Paper IV
Concept and idea	BMe	BMe, HStr, PF, SD	BMe, HStr, NGY, SD	BMe, HStr, NGY, SD
Study design and methods	BMe, NGY, SD, RAP	BMe, NGY, PF	BMe, NGY	BMe, NGY, SD
Data gathering	RAP	HStr, SD, FD, JD, KEE, AVE, MPH, MG, DG, SHL, TKR, GHS, ÞLÞ, SW	HStr, SD, FD, KEE, AVE, MPH, MG, DG, SHL, TKR, GHS, HSte, ÞLÞ, SW	HStr, SD, FD, JD, KEE, AVE, MPH, MG, DG, SHL, TKR, GHS, HSte, ÞLÞ, SW
Manuscript preparation	BMe, NGY, SD, RAP, HStr, BMo	BMe, HStr, PF, NGY, SD, DG	BMe, HStr, NGY, SD, DG	BMe, HStr, NGY, SD
Comments and input to manuscript		FD, JD, KEE, AVE, MPH, MG, SHL, TKR, GHS, ÞLÞ, SW	FD, KEE, AVE, MPH, MG, SHL, TKR, GHS, HSte, ÞLÞ, SW	FD, JD, KEE, AVE, MPH, MG, DG, SHL, TKR, GHS, HSte, ÞLÞ, SW

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1 INTRODUCTION

Migration, the regular seasonal movement of individuals, between discrete locations often from a breeding location to a nonbreeding location and back, is a common phenomenon in nature across many taxa (Dingle and Drake 2007; Newton 2008; Dingle 2014). It is a response to spatial and temporal fluctuations in resource availability during different phases of the annual cycle (Alerstam and Enckell 1979; Alerstam et al. 2003; Dingle and Drake 2007; Somveille et al. 2015). Thereby migrants take advantage of temporary niches of food availability spaced widely apart and in the extreme case on opposite sides of the globe (Egevang et al. 2010) in order to maximise their fitness (Alerstam and Hedenström 1998). These niches can be divided into two periods, one in which reproduction occurs (breeding) and another focused on survival to be able to reproduce in the future (non-breeding). Many migrants, such as seabirds (Schreiber and Burger 2001), are long-lived species. Hence, their overall population growth rate is sensitive to changes in adult survival (Lebreton and Clobert 1991; Sæther and Bakke 2000). This likely depends on their migration behaviour and condition experienced during the non-breeding period (e.g. Alves et al. 2013; Kramer et al. 2018; Patchett et al. 2018). Additionally, reproductive success can also be affected by conditions experienced during the previous non-breeding period (Norris 2005; Alves et al. 2013; Catry et al. 2013; Bogdanova et al. 2017).

Migratory animals face specific challenges in a rapidly changing world, such as loss of habitat, new physical barriers, overexploitation of seasonal food resources, and climate change impacts (Wilcove and Wikelski 2008; Robinson et al. 2009). Many of those are encountered by migrants outside their breeding season and have the potential to affect population trends through an effect on individual survival (Webster et al. 2002; Gaston and Powell 2003). Hence, assessing the response of migratory species or populations to perturbations requires an understanding of migratory connectivity (Taylor and Norris 2010), which is the connection of different areas used by different populations during the annual cycle via migration strategies of individual migrants (Box 1). Conditions faced during the non-breeding period can drive population trends in migratory species exhibiting strong migratory connectivity, i.e. distinct and population specific non-breeding distributions (Gilroy et al. 2016; Taylor and Stutchbury 2016; Kramer et al. 2018).

Populations are composed of individuals and it is increasingly recognized that consistent differences in individual behaviour are common in free-living populations (Bolnick et al. 2003; Piper 2011; Dall et al. 2012). Site fidelity - an animal's tendency to repeatedly use the same geographic area - is a common form of individual behavioural consistency (Switzer 1993) and in migrants takes the form of individual migration strategy fidelity (IMSF) during the non-breeding period. It has been shown to be exhibited in many marine migrants (Hunter et al. 2003; Broderick et al. 2007; Fifield et al. 2014; Fayet et al. 2016), although flexibility in migration routes has also been reported (Dias et al. 2011; Müller et al. 2014; Van Bemmelen et al. 2017). Rapid environmental changes have the potential to favour individuals with flexible migration strategies (Switzer 1993; Abrahms et al. 2018), while IMSF could constrain the ability of a populations to track habitat changes (Wiens 1985; Keith and Bull 2017).

In addition to the spatial aspects of migration it is also important to consider its seasonal dynamics, i.e. not only *which* sites are used, but also *when* they are used. This varies widely between species, but also populations, and even sex and age groups (Newton 2011). Timing differences can have manifold consequences on individual fitness (e.g. through decreasing body condition or transmission of pathogens) and therefore population dynamics (Bauer et al. 2016; Eyres et al. 2017; La Sorte et al. 2018). This not only includes temporal variation during the non-breeding period, but also variability in migratory timing back to the colony for the next breeding cycle. Breeding phenology is a key adaptation with direct consequences on reproductive success and population dynamics (McLean et al. 2016; Youngflesh et al. 2017). Yet, breeding success is also influenced by the pre-laying period, the time between arrival at the colony and egg-laying. This period allows birds to establish and defend nest sites (Kokko et al. 2004), build up body condition (Joël Bêty et al. 2003; Sénéchal et al. 2011) and mate (Birkhead et al. 1985), which often starts months before egg-laying (Harris et al. 2006; Quillfeldt et al. 2019).

Box 1. Migratory connectivity

The concept of migratory connectivity (also termed migratory diversity) was first coined by Webster et al. (2002) and is defined as the connection of different areas used by different populations during the annual cycle via migration strategies of individual migrants. It is measured on a scale from *"weak"* or diffuse to *"strong"*, depending on the degree to which individuals from different non-breeding areas mix during the breeding period (figure 1.1).

The concept can be divided into two spatial components: population spread and inter-population mixing (Finch et al. 2017). Population spread is a population-level trait that refers to the size of the geographic areas occupied during different parts of the annual cycle, while inter-population mixing is a multi-population-level trait describing the extent to which individuals from a given breeding population mix with other populations (i.e. use the same

Figure 1.1. Schematic illustration of the two extreme cases of migratory connectivity

areas) during the non-breeding period (Gilroy et al. 2016; Finch et al. 2017). Generally, higher population spread is associated with enhanced inter-population mixing (i.e. *"weak"* migratory connectivity) while lower population spread reduces inter-population mixing (i.e. *"strong"* migratory connectivity). Moreover, in addition to the spatial aspects of migratory connectivity it is also important to consider its seasonal dynamics, i.e. not only *which* sites are used, but also *when* they are used (Bauer et al. 2016).

Methods to measure migratory connectivity include direct estimates of a species geographic distribution throughout the annual cycle via marking and resighting of known individuals (e.g. Cohen et al. 2018) or tracking of individuals with bio-telemetric or bio-logging devices (e.g. PAPER II; Kramer et al. 2018). Indirect methods also exist using genetic techniques (e.g. Ruegg et al. 2014; Ruegg et al. 2017), or ratios of stable isotopes (e.g. Rundel et al. 2013) to infer migratory connectivity. To quantify the strength of migratory connectivity several methods have been developed using Mantel correlation analyses (Ambrosini et al. 2009; Cohen et al. 2018) as well as network theory (PAPER II; Taylor and Norris 2010; Knight et al. 2018).
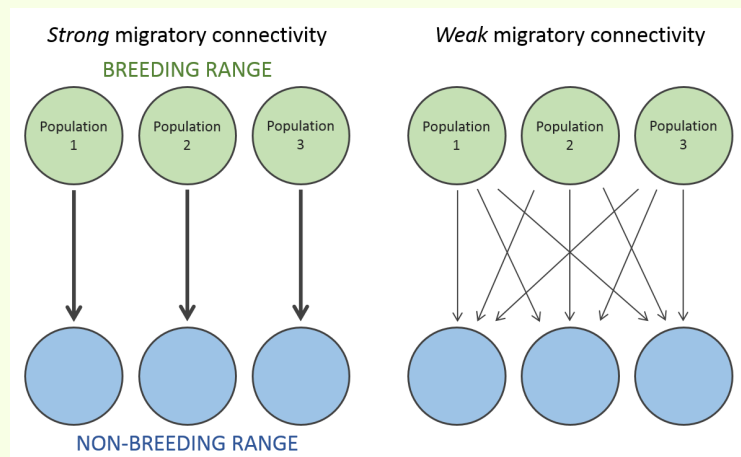
2 OBJECTIVES

The overall objectives of this thesis were; (1) to answer the simple questions "Where do birds go when they are not breeding?", "What is their annual schedule?" and "How is this structured among species, populations and individuals"; (2) to assess migration behaviour of two long-distance migrants in multiple dimensions (space, time and environmental niche) in order to evaluate limitations and potential for adaptations for migratory species in the light of rapid climate change. More specifically, the aims were:

- To establish a methodology to make the available light-level geolocator dataset comparable irrespective of logger model used and to be able to estimate locations, including during the times of equinox, in order to investigate migration strategies throughout the non-breeding period (PAPER I).

- To investigate migratory connectivity both in terms of space use and the environment occupied throughout the annual cycle and its possible link to displayed populations trends (PAPER II).

- To investigate whether individuals of both species across their range employ individual-specific migration strategies or alternatively generalist migratory behaviour outside the breeding period (PAPER III).

- To assess if individual migratory behaviour throughout the non-breeding period is a consequence of site familiarity (fidelity to specific sites) or habitat specialization (fidelity to specific habitats) (PAPER III).

- To examine temporal flexibility in migration strategies throughout the non-breeding period (PAPER II & III) including the early breeding period (PAPER IV).

3 MATERIAL & METHODS

Study species & area

The two species studied in this thesis are the two auks of the genus *Uria*, the common guillemot (*Uria aalge*, also known as common murre) and the Brünnich's guillemot (*Uria lomvia*, also known as thick-billed murre). These morphologically similar species (figure 2), are large (~1kg), deep diving (up to ~200m), long lived (current record is 42 years, Fransson et al. 2010), colonial seabirds that generally do not breed before 4-5 years old and have high adult survival, high breeding philopatry, high breeding synchrony and low annual fecundity (Nettleship and Birkhead 1985; Gaston and Jones 1998; Benowitz-Fredericks and Kitaysky 2005). They have a circumpolar, breeding distribution constrained to the northern hemisphere, with Brünnich's guillemots exhibiting a more arctic distribution than common guillemots (figure 1, Irons et al. 2008). However, the two species are observed to breed sympatrically at many sites throughout their range. Global population sizes are estimated at 7.3 - 7.4 million common guillemot and 4.0 - 7.5 million Brünnich's guillemot breeding pairs (Mitchell et al. 2004).

Figure 1. Distribution and size of Thick-billed (*aka* Brünnich's guillemot) and Common Murre (*aka* Common guillemot) colonies in the northern hemisphere (figure from Irons et al. 2008).

Guillemots are pursuit-diving predators. Due to their excellent swimming and diving abilities (with concomitantly low energetic costs), their flight costs are among the highest ever recorded for vertebrates (Elliott et al. 2013). Hence, guillemots are more sensitive to horizontal changes in prey abundance than vertical changes in prey depth.

Figure 2. A Common (front) and a Brünnich's guillemot (back) on Bjørnøya where they breed sympatrically.

They feed on various schooling fish species such as Atlantic cod (*Gadus morhua*), capelin (*Mallotus villosus*), polar cod (*Boreogadus saida*), herring (*Clupea harengus*), redfish (*Sebastes* spp.), sand lance (*Ammodytes* spp.) and sprat (*Sprattus sprattus*) (Nettleship and Birkhead 1985; Gaston and Jones 1998). Brünnich's guillemots are more generalist predators than common guillemots and feed not only on a wide variety of schooling fish, but also euphausiids (e.g. *Thysanoessa* spp.), amphipods (e.g. *Themisto libellula* and *Gammarus wilkitzkii*) and squid (e.g. *Gonatus* sp.) (Gaston and Jones 1998;

Gabrielsen 2009), which is supported by slight differences in bill morphology between these species (Bédard 1969). At sympatric breeding sites both species rely most likely on similar prey when resources are plenty but display dietary segregation during times of scarcity (Barrett et al. 1997; Barger and Kitaysky 2012). However, prey species composition in guillemot diets differs throughout their range in accordance to locally available resources. For example, Brünnich's guillemots feed mainly on polar cod off Newfoundland (Elliot et al. 1990), on Atlantic cod in the Barents Sea (Erikstad 1990; Erikstad et al. 2013) and on capelin and crustaceans in western Greenland (Falk and Durinck 1993). However, most of the data on guillemot diet has been collected during the breeding period (Barrett et al. 2007) and it is often biased towards hard bodied prey items due to the observation methods used (often visual inspections). Only limited data are available regarding potential seasonal diet shifts outside the breeding period with Elliot et al. (1990) reporting a shift from schooling fish to crustaceans as the winter progresses for Brünnich's guillemots near Newfoundland. Guillemot non-breeding diet information is often anecdotal and patchy. As direct assessments of non-breeding diet are generally difficult in seabirds due to the habitat they occupy, stable isotope studies have been used in recent years to help identify the trophic level at which these species feed (e.g. Ramos et al. 2009; Fort et al. 2010; Hinke et al. 2015). But, diet studies based on stable isotopes have their own challenges such as spatially shifting levels of nitrogen and carbon isotope ratios across seas and oceans (i.e. isoscapes, Graham et al. 2010; Trueman et al. 2017).

The annual cycle of guillemots can be divided into several seasons based on their biology (figure 3). Timing of breeding is thought to occur as close as possible to the seasonal peak in local food availability (Nettleship and Birkhead 1985). Hence, generally breeding occurs later at higher latitudes (Laidre et al. 2008; Burr et al. 2016). Timing of egg-laying within a colony is rather synchronous and the incubation period has a median duration of 33 days for both species (Nettleship and Birkhead 1985). Chick rearing length on the other hand is more variable, ranging from 15 to 30 days with the variability observed between colonies dependent on chick growth rate (Gaston and Nettleship 1981; Nettleship and Birkhead 1985). Chicks leave the colony before being able to fly. After leaving the colony, successful males stay with their flightless chicks for at least a month after colony departure (Harris and Wanless 1990; Elliott and Gaston 2014; Elliott et al. 2017). Further, guillemots moult their primaries and secondaries during one to two months in the autumn post-breeding which renders them flightless during this time period (Birkhead and Taylor 1977; Thompson et al. 1998; Bridge 2004; Elliott and Gaston 2014). Both species display periodic synchronized attendances at their breeding colonies starting up to several months prior to egg-laying (Birkhead 1978; Gaston and Nettleship 1981; Hatchwell 1988; Wilhelm and Storey 2002; Harris et al. 2006), which in effect restricts them to central place foraging during this period (figure 3). Hence, adult guillemots are only

able to move without constraints for extended periods of time after they have renewed their flight feathers and before arrival back at the colony.
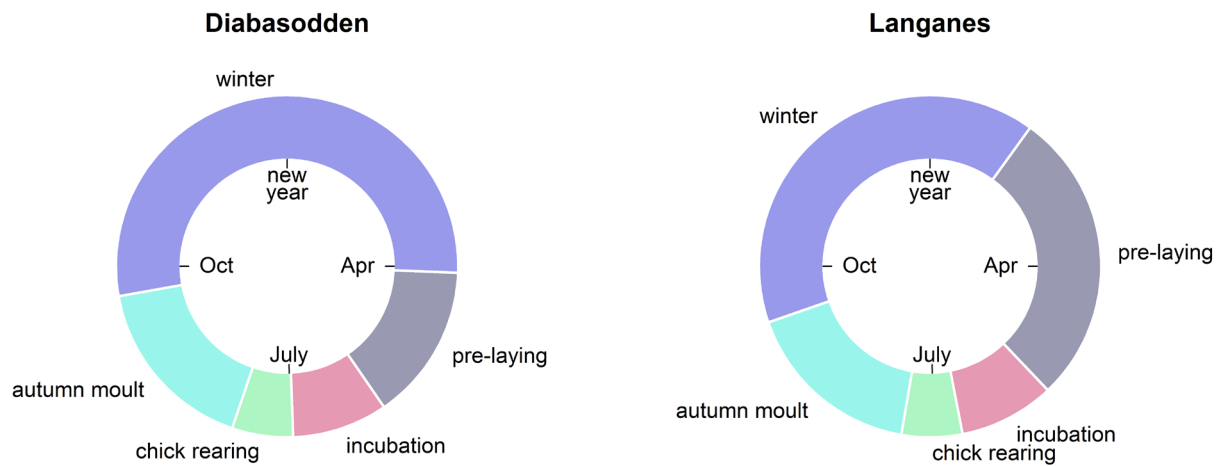
Diabasodden

Langanes

Figure 3. Two examples of the annual cycle of guillemots illustrating exhibited variability among colonies and species: a Brünnich's guillemot colony in the high Arctic (Diabasodden, Svalbard) and a common guillemot colony in Northeast Iceland (Langanes).

In this dissertation I studied common and Brünnich's guillemots in the North Atlantic and its adjacent seas (figure 4). This ocean is characterized by several water masses and ecoregions ranging from temperate latitudes to the high Arctic and from productive shelf seas to the deep ocean (Skjoldal et al. 2013). Notable features are the major currents; (1) the warm and saline Gulf Stream, which crosses the Atlantic from west to east and flows as the North Atlantic Current (NAC) along the eastern shelf edge of Ireland, the UK and Norway into the Barents Sea, as the West Spitsbergen Current (WSC) into the Arctic Ocean through Fram Strait and as the Irminger Current (IC) south of Iceland and into the Irminger Sea; (2) the cold and fresh East Greenland Current (EGC), which flows south out of the Arctic Ocean through Fram Strait and follows the eastern Greenland shelf edge through the Denmark Strait and into the Irminger Sea and branches north of Iceland into the Iceland Sea; (3) the West Greenland Current (WGC), which flows out of the Irminger Sea around the southern tip of Greenland and into Davis Strait and Baffin Bay; and (4) the cold Labrador Current (LC), which flows out of Baffin Bay and along the Canadian shelf edge towards the Grand Banks (Hansen and Østerhus 2000; Hátún et al. 2005; Belkin et al. 2009; Drinkwater et al. 2013; Trenkel et al. 2014; Hunt Jr et al. 2016). The northern edge of the study area is characterized by seasonally changing arctic sea ice (figure 4). Due to the presence of several water masses, currents, shelf edges as well as sea ice edges, several productive upwelling and frontal systems can be found in the North Atlantic such as (1) the marginal sea ice zones in the Northeast Atlantic (Kara, Barents and Greenland Seas) and Northwest Atlantic (Baffin Bay, Davis Strait and the Labrador Sea); (2) the Polar Front in the Barents

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Sea dividing the Atlantic southern Barents Sea and the Arctic northern Barents Sea; (3) the West Greenland and (4) East Greenland fronts, following their respective currents as well as the marginal sea ice zone; (5) the Norwegian Sea Arctic Front, dividing the Norwegian Sea from the Iceland and Greenland Seas; and (6) the Norwegian Coastal Current Front, following the Norwegian shelf edge into Fram Strait (Wassmann et al. 2015). Regarding shelf seas, some of the most productive are the Barents Sea, the North Sea as well as the Grand Banks. Another important feature in the North Atlantic is the cold and low-saline subpolar gyre, an important nutrient and zooplankton source, which is situated in the Irminger and Labrador Seas south of Greenland (Heath et al. 2008; Hátún et al. 2016).
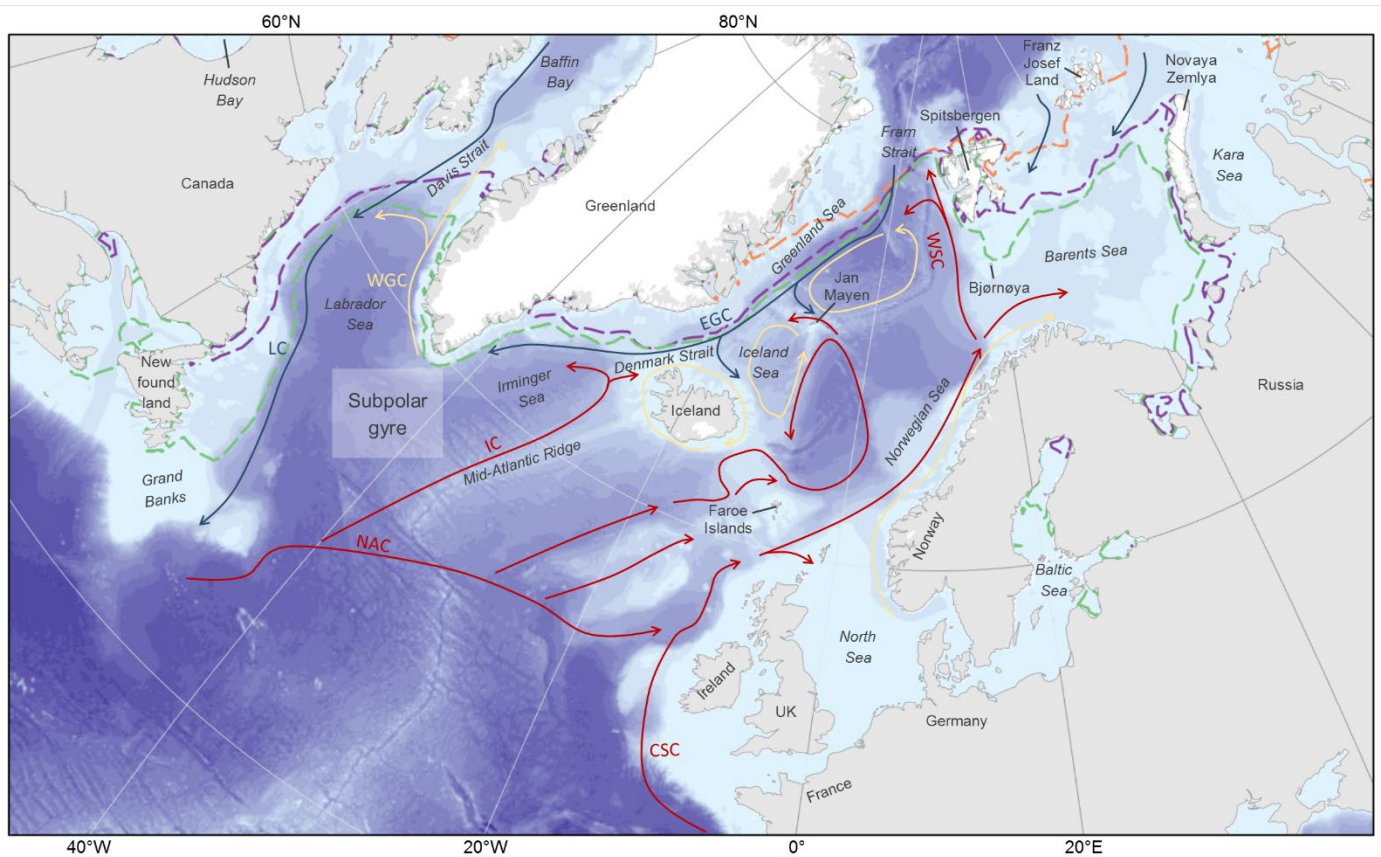

Figure 4. Map of the study area, the North Atlantic and its marginal seas including its bathymetry (Amante and Eakins 2009; Jakobsson et al. 2012), major currents and seasonal average sea ice extent (as area covered by ≥ 15 % average sea ice concentration between 2014 - 2017, Reynolds et al. 2007) during autumn (August - October, orange), winter (November - January, purple), spring (February - April, green). Coloured arrows illustrate major surface currents: North Atlantic Current (NAC), Irminger Current (IC), Continental Slope Current (CSC), West Spitsbergen Current (WSC), East Greenland Current (EGC), West Greenland Current (WGC), and Labrador Current (LC). Red and blue arrows show flow of Atlantic and Arctic water masses, respectively, while yellow arrows indicate flow of other water masses.

Data for PAPER II, III and IV were collected at 16 seabird colonies spanning 56°N to 80°N and 16°W to 68°E in the Northeast Atlantic (table 1, figure 5). Common and Brünnich's guillemots breed sympatrically at six of these sites. I had the opportunity to utilize a large tracking dataset collected

through several projects with varying temporal and spatial coverage with the first birds being tracked already in 2007. Hence, the dataset is rather heterogeneous not only with regards to the amount of data collected at each colony but also regarding the time period over which data was collected at each colony (figure 5). The majority of data however, was collected during the SEATRACK project (www.seapop.no/en/seatrack) which started deployments in 2014 and is to date still ongoing. In total 1740 annual tracks (882 and 858 for common and Brünnich's guillemots, respectively) were available from 887 individual guillemots (438 and 449 common and Brünnich's guillemots, respectively) tracked over 10 years.

Table 1. Study colonies, their location in the Northeast Atlantic as well as corresponding colony sizes and trends when known. Colony sizes and trends are based on counts and estimates conducted during the last 20 years. Also included is available geolocator tracking data for each colony and species and their temporal coverage.

| colony | acronym | colony location | Common guillemot | | | | | Brünnich's guillemot | | | | |
			colony size [pairs]	colony trend	tracking years	annual tracks	unique birds	colony size [pairs]	colony trend	tracking years	annual tracks	unique birds
Isle of May	IM	56.18°N, 2.58°W	16 000	↗	2011-17	97	51	0	-			
Faroe Islands (Lonin)	FA	61.95°N, 6.80°W	100 000	↘	2015	5	5	0	-			
Sklinna	SK	65.22°N, 10.97°E	1 100	↗	2011-17	129	66	0	-			
Langanes	LA	66.18°N, 15.99°W	27 300	↘	2014-17	38	27	2 500	↘	2014-17	25	17
Grimsey	GR	66.53°N, 17.99°W	67 300	↘	2015-16	25	9	4 000	↘	2014-17	32	15
Jan Mayen	JM	71.02°N, 8.52°W	1 000	↘	2011-17	115	57	50 000	↘	2011-17	172	77
Hjelmsøya	HJ	71.07°N, 24.72°E	3 100	↗	2011-17	58	38	50	↘			
Hornøya	HO	70.38°N, 31.15°E	20 000	↗	2011-17	174	83	200	↘	2009-17	150	71
Cape Gorodetskiy	CG	69.58°N, 32.94°E	2 400	?	2014-17	16	9	80	?	2014-17	23	15
Bjørnøya	BI	74.50°N, 18.96°E	132 000	↗	2007-17	225	93	95 000	↘	2007-17	176	71
Diabasodden	DO	78.25°N, 15.51°E	0	-				900	↘	2008-16	93	55
Ossian Sarsfjellet	OF	78.94°N, 12.49°E	0	-				700	↘	2007-10	16	15
John Scottfjellet	JS	79.15°N, 11.96°E	0	-				200	?	2008-09	14	14
Alkefjellet	AL	79.59°N, 18.46°E	0	-				48 000	(↗)[a]	2015-17	49	30
Kara Gate	KG	70.59°N, 55.02°E	0	-				?	?	2015-17	82	48
Oranskie islands	OI	77.07°N, 67.64°E	0	-				?	?	2016-17	26	21

[a] based on only 4 years of data (S. Descamps unpublished data)

In the Northeast Atlantic common guillemots occur in the British Isles, the Faroe Islands, Iceland, Norway, Jan Mayen, Svalbard and Russia (figure 5). But, small colonies (< 2 000 pairs) also exist in Germany, France and in the Baltic Sea. The total breeding population in the Northeast Atlantic is estimated at ~2.5 million breeding pairs, with the majority breeding in the UK and on Iceland (Hüppop 1996; Mitchell et al. 2004; Krasnov et al. 2007; Frederiksen 2010; Peterz and Blomqvist

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2010; Cadiou et al. 2015; Fauchald et al. 2015; JNCC 2016; Skarphéðinsson et al. 2017). Brünnich's guillemots occur in the Northeast Atlantic in Greenland, Iceland, the Norwegian and Russian Barents Sea coast, Jan Mayen, Svalbard, Franz Josef Land and Novaya Zemlya (figure 5). Its total breeding population in the Northeast Atlantic is estimated at ~1.7 million breeding pairs (Merkel et al. 2014; Fauchald et al. 2015; Skarphéðinsson et al. 2017), with the majority breeding in the eastern and northern Barents Sea and on Iceland (Frederiksen et al. 2016).

Common guillemot populations in the UK and in Norway are increasing (Fauchald et al. 2015; JNCC 2016; Anker-Nilssen et al. 2017), while Icelandic and Faroese populations are in decline (Frederiksen 2010; Garðarsson et al. 2019) and Northwest Atlantic colonies seem to be stable (Gaston et al. 2009). Population declines may be attributable to reduced adult survival outside the breeding season, as well as low breeding success in some colonies (Garðarsson et al. 2019). Conversely, population increases may represent a recovery from recent dramatic population declines rather than net increases (Erikstad et al. 2013; Birkhead 2016). Contrastingly, all Brünnich's guillemot populations in the Northeast Atlantic that have available monitoring data appear to be declining significantly (with the possible exception of populations in eastern Spitsbergen, e.g. Alkefjellet, table 1), while populations in the Northwest Atlantic seem to be stable (Frederiksen et al. 2016; Garðarsson et al. 2019). Both species are red listed in Norway (Artsdatabanken 2018) and Iceland (Icelandic Institute for Natural History 2018) and categorized as least concern by the IUCN Red list (BirdLife International 2018).

The Northeast Atlantic breeding population of guillemot spp. consumes in the order of 1.2 - 2 million tonnes wet food annually based on a back of the envelope calculation using published energy requirements for Brünnich's guillemots (Fort et al. 2009). When put in relation to the total landing of Atlantic cod, sprat, herring, Northern shrimp (*Pandalus borealis*), sand lance, redfish (*Sebastes marinus* & *Sebastes mentella*) and capelin in the Northeast Atlantic in 2017 (~3.5 million tonnes) (ICES 2019), it becomes clear that these congeneric seabird species are significant consumers of marine resources in the Northeast Atlantic (Barrett et al. 2006). Seabirds in general consume large quantities of available prey biomass (Cury et al. 2011).
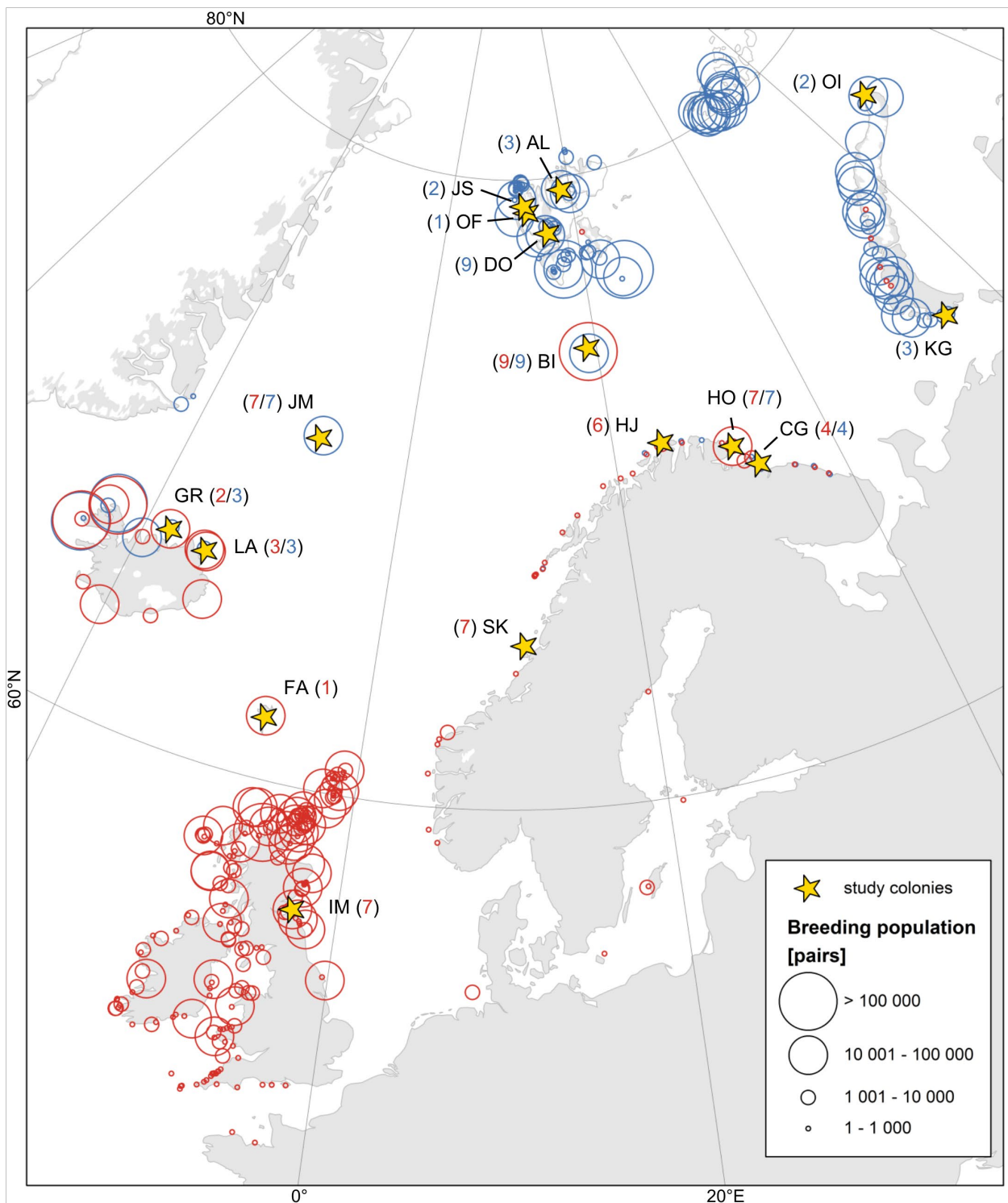
Figure 5. Map of the Northeast Atlantic displaying all guillemot breeding populations (circles) as well as all study colonies (stars, labels detailed in table 1). Values in brackets display number of years with tracking data available for the two species at each colony. Red and blue circles indicate presence of a common or Brünnich's guillemot colony, respectively, while their size denotes population size.

Tracking migration

Most of the data presented in this thesis were collected using geolocators (also called light-level data logger, Global Location Sensors or GLS loggers). These small, lightweight and cheap devices have been used to track animals since the early 1990s (Wilson et al. 1992). Unlike Argos and GPS (global positioning system) devices, which estimate locations using the Doppler effect and/or triangulation, the fundamental underlying principle used by geolocators is to record ambient light and time in order to estimate a series of locations for an individual over the time it carries the device (Hill 1994). An often unrecognized challenge is the translation of recorded light levels and time into geographic locations. Several methods have been developed to calculate geographic locations from light levels (reviewed in PAPER I). All methods rely on identifying twilight events as the transition between the illuminated (day) to the non-illuminated (night) part of the planet and vice versa. Using these transition periods, various methods either use the threshold or curve-fitting (aka template-fit) approach to derive locations. Threshold methods use two consecutive twilight events to calculate day length (or night length) as a proxy for latitude and timing of noon (or midnight) as proxy of longitude. Furthermore, latitude depends on the sun elevation angle below the horizon at which the threshold is crossed (Hill 1994). This sun elevation angle, which is affected by shading during the twilight events and latitude (Lisovski et al. 2012), has to be calibrated, and for practical purposes, is generally assumed to stay constant during the entire deployment period. In contrast, curve-fitting methods derive a location based on a single twilight event using not only its timing, but also the rate of change in light levels (Ekstrom 2004). Overall, variability and ambiguity in light data highly affects location uncertainty for both approaches. These can have a variety of causes such as weather, habitat, the animal's behaviour and the time of the year (PAPER I, Phillips et al. 2004; Fudickar et al. 2012; Lisovski et al. 2012; Rakhimberdiev et al. 2016).

Geolocators used in this thesis were produced and distributed by several companies with different sensors, settings, as well as sensor resolutions and accuracies (Box 2). The settings and sensor resolutions are comparable between most models with the notable exception of loggers from Lotek (St. John's, Newfoundland, Canada), which comprise about 20 % of the dataset. These do not store raw light intensities, but rather estimate twilight times and threshold- as well as template-fit-based locations with an on-board algorithm. All other logger models used in this study stored raw light intensities. Frederiksen et al. (2016) showed that the on-board algorithm for threshold-method derived locations in Lotek loggers uses a hard coded sun elevation angle rather than calibrating it, which results in seasonally changing biases for estimated latitudes (i.e. on the order of 100s to 1000s of kilometres, Lisovski et al. 2012, figure 5). As this was not discovered until recently, faulty conclusions about guillemot distribution have been drawn in the past such as Fort et al. (2013)

placing Brünnich's guillemots from Bjørnøya south of Iceland on either side of the mid-Atlantic ridge during winter, while they more likely utilize areas north and east of Iceland instead (PAPER II). Because Lotek loggers do not store raw light intensities and employ a faulty algorithm to derive locations, I developed a methodology to make this part of the dataset comparable to the rest of the data based on the threshold approach (PAPER I).

Analytical approaches

I have used a variety of analytical approaches to address the objectives specified in this thesis. As detailed earlier, guillemots face different restrictions on their movement throughout the annual cycle, which I needed to address in order to estimate the genus' migratory connectivity and individual migration strategy fidelity (IMSF). Using my algorithm to estimate locations from geolocators (PAPER I), I was able to derive approximate locations also during times of equinox which filled large non-random gaps in my dataset. However, I was unable to derive a robust solution for estimating locations during times without twilight events (i.e. polar night and midnight sun) despite my best efforts. This presented an unsolved limitation to my dataset, which I dealt with to some extent in PAPER II (migratory connectivity) by making assumptions for these time periods based on other information such as last known location, colony location and salt water immersion as well as temperature data recorded by the loggers. In paper III (individual fidelity), I could only acknowledge the existence of these data gaps and discuss the limitations they posed.

Another challenge when assessing migratory connectivity and fidelity in seabirds, compared to for example passerines (e.g. Finch et al. 2017; Knight et al. 2018), is the high spatiotemporal variability in movements between colonies and individuals throughout the year and often the lack of any clearly defined stationary period. After several initial attempts using various methods (hidden Markov models (e.g. Whoriskey et al. 2017), first passage time (Fauchald and Tveraa 2003), time spent in area (Sumner 2016), 2 week displacement, net square displacement (Bunnefeld et al. 2011) as well as a forward moving sliding window algorithm determining stationary periods based on kernel utilization distribution (UD) overlaps using Bhattacharyya's affinity (Fieberg and Kochanny 2005)) to identify individual stationary periods, I opted to use a simplistic compromise for PAPER II. I defined overall stationary periods based on results of many previous approaches applied across the dataset as well as from information on the species' biology (e.g. timing of moulting and pre laying colony attendance). Some of the reasons for this decision included the spatiotemporal uneven error structure associated with estimated locations and the uneven gaps in the dataset. Contrastingly, in

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PAPER III I made no such inferences about stationary periods, as I rather estimate fidelity at constant intervals throughout the non-breeding period.
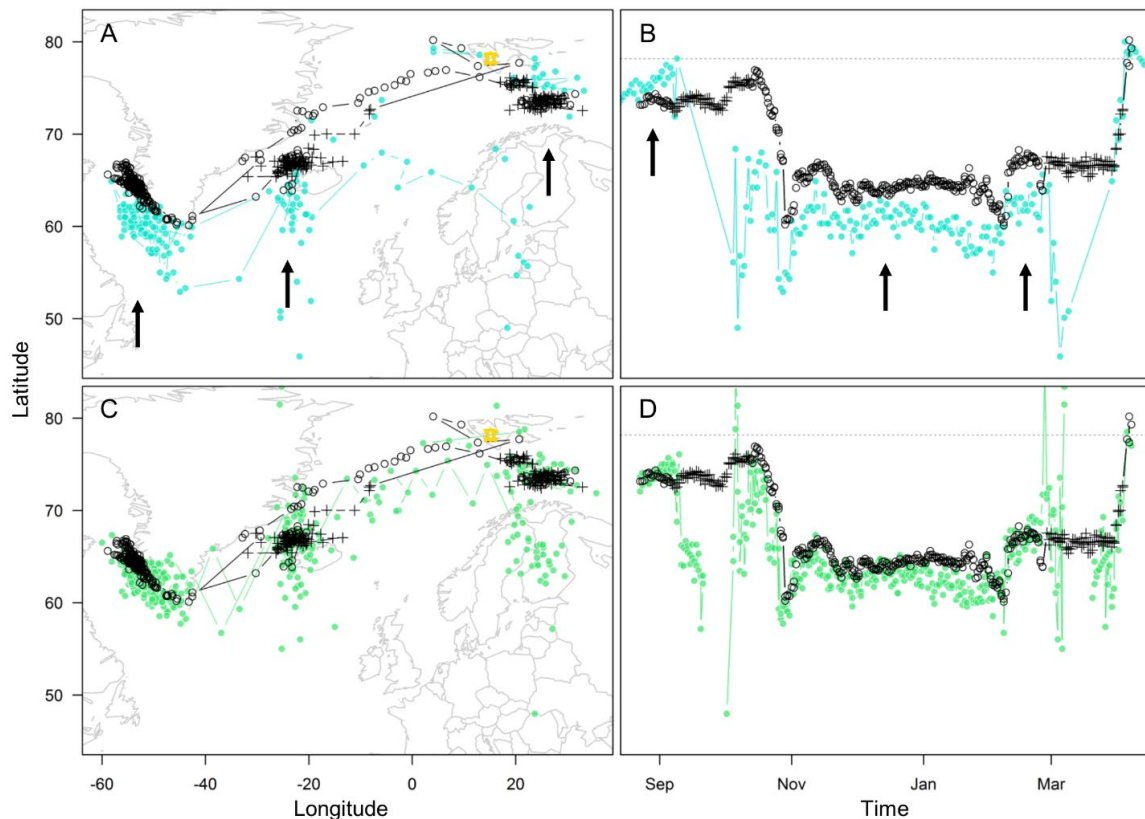

Figure 6. Example track of a Brünnich's guillemot from Diabasodden (yellow star in panel A and C) tracked using a Lotek L250A logger. Panel A and C display estimated locations in longitude and latitude while B and D show estimated latitudes throughout the non-breeding period (grey line denotes colony latitude). Black locations in all panels correspond to `probGLS` calculated positions (crosses are estimates around times of equinox), while blue locations in panel A and B were estimated with a hard coded solar angle of -3.44° (i.e. threshold location output provided by the internal logger algorithm). Green locations in panel C and D are estimated with a more likely solar angle of -4.9°. Arrows in panel A and B indicate stationary periods with over or underestimated latitudes (depending on time of year) due to a wrongly used solar angle.

In order to make inferences about the habitats occupied by guillemots, I chose to adopt the concept of environmental space put forward by Broennimann et al. (2012) in the context of comparing species distributions. The advantage of this method is that environmental niches can be compared quantitatively as a whole rather than each environmental parameter separately as done in previous studies (reviewed in Phillips et al. 2017). Briefly, environmental space is the two dimensional representation of the multidimensional space (as the first two axes of a principle component analysis or PCA; more dimensions could be used but two dimensions are often sufficient to summarize the environmental variation) set by the combination of the selected environmental parameters sampled throughout the entire study area and the entire study period (figure 7). Broennimann et al. (2012)

suggested that "the best practice is to use variables thought to be crucial (i.e. eco-physiologically meaningful) for the biology of the species". Therefore, I selected eight parameters (three sea surface temperature variables (SST; absolute, distance to fronts, predictability), two sea surface height variables (SSH; absolute, distance to meso-scale eddies), surface air temperature, distance to the marginal sea ice zone and bathymetry) in order to describe the above detailed water masses, fronts and shelf seas in the North Atlantic as well as the subpolar gyre as proxies for different habitats and prey availability (Hátún et al. 2009; Scales et al. 2014a; Scales et al. 2014b). Furthermore, I included distance to meso-scale eddies as an identifier of spatially dynamic sources of upwelling and predictability of SST as an identifier of spatially variable SST features across seasons and years (e.g. persistent frontal systems, Scales et al. 2014a; Scales et al. 2014b). I also added surface air temperature in addition to SST as both have been shown to heavily influence energy requirements in guillemots (Fort et al. 2009). Although estimates of Chlorophyll α and net primary production are available, I chose not to include these based on three arguments: (1) I wanted to restrict my definition of environmental space to abiotic parameters; (2) these variables are based on ocean colour, for which estimates during large parts of the winter north of 60°N are unavailable due to a lack of sufficient light; and (3) it has been shown previously that ocean colour is unable to detect subsurface chlorophyll α maxima (e.g. Arrigo et al. 2011 and references therein), which most likely are of high importance for deep diving auks.

Figure 7. Schematic illustrating the concept of environmental space applied to the North Atlantic. The chosen environmental parameters are sampled within the defined study area over the entire study period. The resulting multidimensional space is projected onto two dimensions using the first two principal components of a PCA. Habitat occupied by individuals is then projected onto this surface.
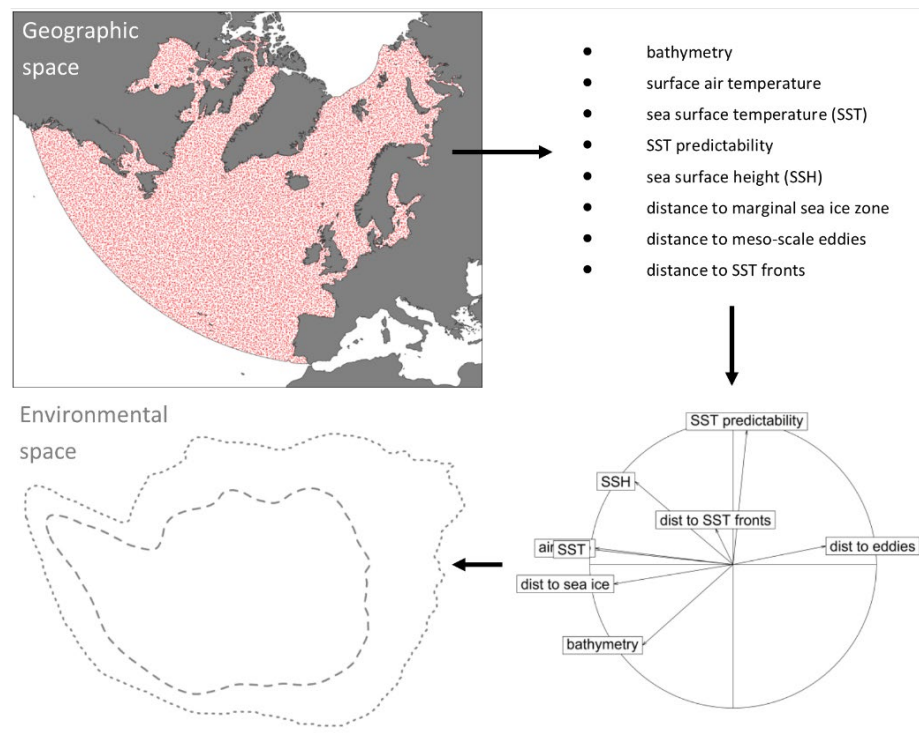
As detailed in box 1, several methods are available to quantify migratory connectivity (PAPER II). Mantel correlation tests provide an estimate of the strength of migratory connectivity in the considered population (Ambrosini et al. 2009; Cohen et al. 2018), while network analyses also provide an estimate of potential groupings among migratory populations (Taylor and Norris 2010; Knight et al. 2018). In this thesis I quantified migratory connectivity on two different scales; (1) large-scale as spatiotemporal movements between large marine ecoregions (Skjoldal et al. 2013) using network theory, and (2) meso-scale as spatiotemporal movements within ecoregions using a randomization procedure of individual kernel UD overlap. Furthermore, I adopted the method of environmental similarity (Warren et al. 2008) to estimate connectivity also in occupied environmental niches.

My work on individual consistency in spatiotemporal migratory movements (PAPER III) is based on the combination of several approaches. Guilford et al. (2011) introduced nearest neighbour distance (NND) as a metric to assess migratory route differences between individuals. I combined NND on varying temporal scales in Cartesian as well as environmental space with a randomization procedure detailed in Wakefield et al. (2015) to quantify individual fidelity to migration strategies in space and environment. Patrick and Weimerskirch (2017) introduced a methodology to assess the relative fidelity of individuals to sites or environmental niches, which I combined with NND to assess the roles of site familiarity and habitat specialization. To assess long-term consistency in IMSF, I used an approach based on linear mixed effect models with year as predictor, similarly to Wakefield et al. (2015).

PAPER IV relies to a great extent on salt water immersion data (also called "wet/dry" or activity data) recorded by geolocators. Counts of "wet" are only recorded if loggers are submerged in salt water (i.e. ion concentration over 64 ppm). I used this metric to determine arrival dates back at the colony for breeding as has been done in previous seabird studies (e.g. McFarlane Tranquilla et al. 2014; Takahashi et al. 2015; Kubo et al. 2018). Unlike in these other studies, I estimated colony-wide arrival dates rather than individual specific dates. This is because the between-individual variability in recorded wet/dry data is high and dependent on multiple factors such as individual differences in leg-tucking behaviour and which foot an individual prefers (Linnebjerg et al. 2014; Burke et al. 2015; Fayet et al. 2016). Nonetheless, I tested various approaches (e.g. various change point analyses as well as simple cut-offs), to identify individual arrival dates in a robust and consistent way but was unable to derive satisfactory results. As guillemots exhibit synchronized attendance at their colonies prior to egg-laying (Gaston and Nettleship 1981; Hatchwell 1988), identification of colony-wide arrival times is more feasible than in other species as the data signal will be stronger. This paper

relies, in addition to logger-derived data, on hatching phenology and breeding success data collected through independent monitoring programs at the different study sites.

Box 2. Light-level geolocator models used in this dissertation and their specifications.

L250A (Lotek) 35 x 8 x 8 mm, 3.6 g, 1-2 years

LIGHT	- Raw data not stored. Internal algorithm determines twilight times.
WET/DRY	- State obtained every 5 min.
TEMP	- Recorded every 5 min. Accuracy: ±0.5°C. Resolution: 0.05°C

MK3006 (Biotrack)/MK15 (BAS) 16 x 14 x 6 mm, 2.5 g, 3-5 years

LIGHT	- Maximum value recorded every 10 min. Clipped range.
WET/DRY	- State obtained every 3 sec, recorded in 10 min bins (0:200).
TEMP	- Recorded after 20 min continuously wet and thereafter with 20 min intervals until dry > 3 sec. Accuracy: ±0.5°C. Resolution: 0.125°C (MK15: 0.5°C)

C250/C330 (Migrate Technology) 17 x 18/19 x 6/8 mm, 2.6 g/3.3 g, 5 years, mode 6

LIGHT	- Clipped range, sampled every minute, max value recorded every 5 min.
WET/DRY	- State obtained every 30 sec, recorded in 10 min bins (0:20).
TEMP	- Measured continuously after 20 minute submersion, max, min and mean recorded every 4 hours. Accuracy: ±0.5°C. Resolution: 0.125°C

F100/C65 super (Migrate Technology) 14 x 8 x 6 mm, 1.0 g, 1-2 years, mode 6

LIGHT	- Clipped range, sampled every minute, max value recorded every 5 min.
WET/DRY	- State obtained every 30 sec. Recorded in 10 min bins (0:20)
TEMP	- Measured continuously after 20 min submersion, max, min and mean recorded every 8 hours. Accuracy: ±0.5°C. Resolution: 0.125°C

MK4083 (Biotrack) 17 x 10 x 6,5 mm, 1.9 g, 3 years

LIGHT	- Maximum value recorded every 10 min. Clipped range.
WET/DRY	- State obtained every 3 sec, recorded in 10 min bins (0:200).
TEMP	- Not recorded.

C65/W65 (Migrate Technology) 14 x 8 x 6 mm, 1.0 g, 1-2 years, mode 6

LIGHT	- Clipped range, sampled every minute, max value recorded every 5 min.
WET/DRY	- State obtained every 30 sec, recorded in 10 min bins (0:20).
TEMP	- Not recorded.

4 MAIN FINDINGS

Estimating and refining locations based on light-level geolocation (PAPER I)

The developed method uses an intuitive and time-efficient algorithm with iterative probability sampling to estimate numerous trajectories based on threshold-based twilight events and additional inputs such as the twilight error, movement speed in different mediums (air or water), and spatial masks (binary e.g. land masks and continuous e.g. remote-sensed sea surface temperature). These can be used to derive a most likely track and location-specific uncertainties. Using a black-browed albatross (*Thalassarche melanophris*) and a wandering albatross (*Diomedea exulans*) tracking dataset from Bird Island, South Georgia, I showed that location error could be reduced compared to standard geolocator methods and kept at constant levels also during times of equinox. However, uncertainty estimates from geolocator locations always have to be viewed with caution as it depends on many spatially and temporally changing factors such as latitude, time of year, weather and the animal's behaviour. The developed method is available within the R open-source software (R Development Core Team 2018) in the `probGLS` package (available at https://github.com/benjamin-merkel/probGLS).

This method enabled me to correct the biased estimates provided by Lotek loggers and made the overall dataset comparable, which was an important aspect, in particular with regards to inter-annual variation. With the inclusion of information about the species' biology (e.g. land avoidance and speed thresholds) as well as remote sensed sea surface temperature, the method was also able to estimate locations during times of equinox. This made it possible to investigate migratory connectivity and fidelity throughout the non-breeding period.

It is likely that geolocator use will decrease in the future as GPS tracking devices become smaller and cheaper. But, studies like this thesis, building on large multi-colony and multi-species tracking efforts, are currently ongoing or in the planning phase and will need to rely at least in part on cheap, durable and long-lasting geolocators. Therefore, deriving approximate locations based on light and time will still be needed in the next decade(s).

Spatial and environmental aspects of migration (PAPER II & III)

When assessing annual space use structure and inter-population mixing of species at the population level, it becomes apparent that both guillemot species are comprised of populations exhibiting strong migratory connectivity both on large- (i.e. between ecoregions) and on meso-scales (i.e. within ecoregions, PAPER II, figure 8A). Hence, guillemots can be considered to consist of meta-populations, defined as spatially discrete populations connected by dispersal (Levins 1970; Taylor and Hall 2011), although very few data and information exist to quantify dispersal in guillemots. Tigano et al. (2015) and Tigano et al. (2017) found that little genetic structure exists within the Atlantic Brünnich's guillemot meta-population. Conversely, common guillemot show significant East-West structuring among Atlantic colonies, but little structuring in the Northeast Atlantic (Riffaut et al. 2005; Morris-Pocock et al. 2008). Thus, substantial genetic mixing, possibly due to dispersal, between breeding sites studied herein must exist, preventing genetic differentiation of the groups identified (PAPER II). Population trends in common guillemots breeding in the North Atlantic were correlated with the spatial structure exhibited by the different colonies. More specifically, colonies in the Northeast Atlantic structured into five different groups based on their population trends and space use; (1) the Barents Sea (increasing trend), (2) around Iceland and the Irminger Sea (decreasing trend) which was also shown for Icelandic colonies in Linnebjerg et al. (2018), (3) the North Sea(increasing trend), (4) along the Norwegian coast (increasing trend), and (5) around the Faroes and the Mid-Atlantic Ridge (decreasing trend). McFarlane Tranquilla et al. (2013), described an additional group of common guillemots breeding in the Northwest Atlantic and utilizing the Grand Banks. No correlation between population trends and annual space use could be found in Brünnich's guillemots breeding in the Northeast Atlantic, mainly because all colonies display the same population trend. Frederiksen et al. (2016) showed that winter space use of populations breeding in the Northwest and Northeast Atlantic is correlated with their population trends and data from eastern Spitsbergen (i.e. Alkefjellet) suggests a possible increase of the population utilizing the Barents Sea. Brünnich's guillemots group into at least three populations based on their population trends and space use, two of which have been identified due to the work detailed in PAPER II. From west to east in the North Atlantic, these groups are distributed in (1) the Hudson and Baffin Bay and Davis Strait, along the Labrador shelf and on the Grand Banks (McFarlane Tranquilla et al. 2013) (no trend), (2) along western and eastern Greenland, as well as in the Irminger, Iceland, Greenland and Norwegian Seas (decreasing trend), and (3) in the Barents and Kara Sea (possibly increasing trend?).

Linking the identified spatial structure with the environmental niches occupied by individuals from different colonies helped explain the segregation between the two species across their range even if they displayed similar space use patterns (PAPER II). This has also been found for these two species breeding in the Northwest Atlantic (Linnebjerg et al. 2013; McFarlane Tranquilla et al. 2015). Additionally, it highlighted that the displayed spatial structure could be translated to some extent into the environment occupied (figure 8B), with the notable difference that populations utilizing vast areas did not necessarily utilize more varied environments, but rather spread out more within similar habitats (e.g. within the Subpolar gyre). Contrastingly, populations exhibiting less varied space use nonetheless might be occupying very varied environments (e.g. Brünnich's guillemots breeding at different colonies in the Barents Sea).
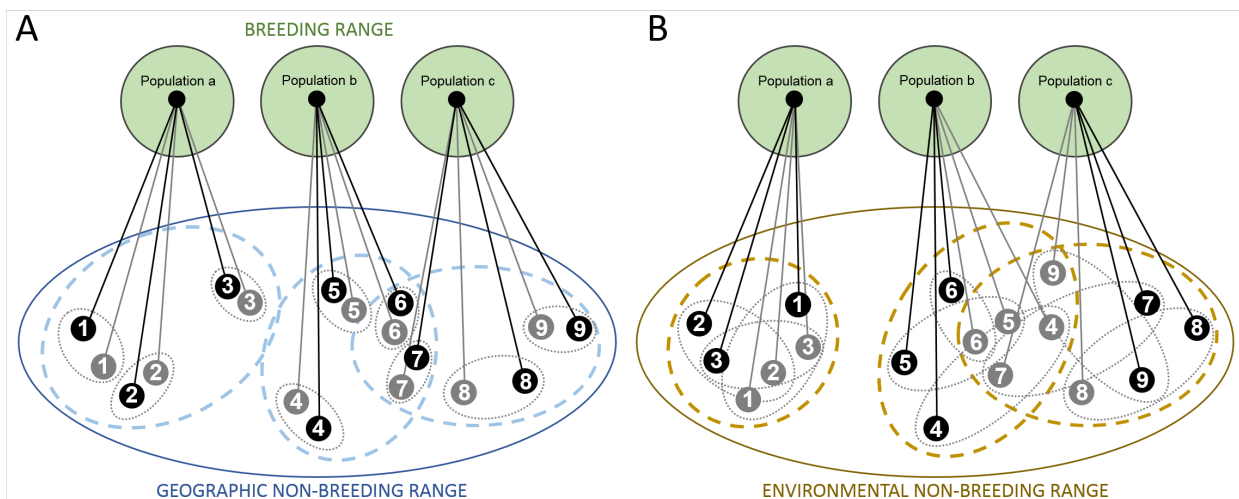

Figure 8. Schematic illustration of geographic (A) and environmental space (B) use of different populations and individuals during different years. Black and grey symbols represent two years from the same individuals (labelled 1, 2 … 9).

The spread of common and Brünnich's guillemot species and populations in space and environment throughout the year reinforces the above conclusion that birds from different populations and species are specialized in both their space and environmental use, utilizing only a fraction of the potential species-wide and genus-wide range. Notably, extensive variability in population spread exists in both species, which is also mirrored in the number of displayed large-scale migration strategies by individuals of different colonies (PAPER II). Interestingly, the "Arctic" species (Brünnich's guillemot) occupies more variable environments than the "temperate" species (common guillemot), similar to findings from the Northwest Atlantic (McFarlane Tranquilla et al. 2015).

On the individual-level, both species in all colonies seem to be comprised of birds following individually-specific migration strategies (i.e. exhibit individual migration strategy fidelity (IMSF), PAPER III, figure 8A). These individual strategies did not change with time suggesting that the exhibited strategies are rather fixed (Senner et al. 2015). This result contrasts with that found for Brünnich's guillemots breeding in the Northwest Atlantic (McFarlane Tranquilla et al. 2014), which reported behavioural flexibility in Brünnich's guillemot mid-winter spatial distribution (defined in their study as January). PAPER III illustrated that, particularly during late winter (February/March) IMSF was more variable, but could be explained by timing differences. Meaning individuals occupied similar areas, but not always at the same time in different years. This result could also explain the reported flexibility by McFarlane Tranquilla et al. (2014). Site familiarity (fidelity to specific sites, figure 8B) explained IMSF across years better than habitat specialisation (fidelity to specific habitats) in both species and across the entire study area.

In summary, guillemot populations are comprised of individuals that are space use specialists selecting for specific sites rather than habitats. They breed in colonies where all individuals are specialised to a specific sub-region of the distributional range and habitat of the entire species (figure 8).

Seasonal aspects of migration (PAPER II, III & IV)

There is a clear seasonality in the temporal structure of guillemot migration across species, populations and individuals. Large parts of this seasonality can be explained by the species' breeding biology as explained in chapter 3. After leaving the colony birds from all colonies occupy rather defined, often colony-specific, areas that are frequently located downstream from their colonies. This pattern is most likely due the autumn moult and the birds being unable to fly (PAPER II, McFarlane Tranquilla 2014; Frederiksen et al. 2016), which increases their dependency towards surface currents. Additionally, successful males accompany flightless chicks for at least a month after leaving the colony, further restricting their movements (Elliott et al. 2017). This is also apparent as a lack of IMSF, particularly in males, in both species across the study area during the autumn (PAPER III). Due to their restricted movement capabilities, individuals do not show individualistic spatial behaviour and all birds from a colony exhibit the same movement patterns (at least on the scale that can be investigated with geolocators). In contrast, females from some colonies, not being constrained by flightless chicks, first migrated to different autumn staging areas before becoming flightless during their autumn moult. Reported variability in the duration of moulting (Birkhead and Taylor 1977; Thompson et al. 1998; Bridge 2004) seems to depend on the bird's physiology and food

availability during the moulting period (Thompson et al. 1998). Consequently, little variability in space and time is exhibited during the autumn (PAPER II & III, figure 9).

The most variability in occupied space and environment is displayed during winter after the autumn moult is finished and individuals are able to fly again (and their chick fledged in the case of males), and before the colony attendance begins for the next breeding season (figure 9). Winter duration can differ markedly as investigated in PAPER IV and exemplified in figure 3. Furthermore, it is during this period that individuals from both species and sexes, across the study area, show IMSF (PAPER III), although this is only the case when individuals from the respective colony use more than one large-scale migration strategy (PAPER II). During this period individuals are also able to exhibit most temporal flexibility, such as moving between different staging areas (e.g. east and west of Greenland, PAPER II & III, figure 9). Note that this flexibility in timing of movements was only displayed if the individual utilized more than one staging area. Hence, a bird staying in the southern Barents Sea throughout the year did not show detectable flexibility in movement or timing.

As guillemots exhibit synchronized attendance at their colonies prior to egg-laying (Birkhead 1978; Gaston and Nettleship 1981; Hatchwell 1988), little flexibility in timing on the individual-level is displayed during this period. Arrival timing seems to depend on the size of the colony and timing of egg-laying (PAPER IV, figure 9). These results are contrary to those for timing of egg-laying, which in seabirds has been shown to be determined by latitude as a proxy for seasonal peaks in food abundance around the breeding sites (Conklin et al. 2010; Burr et al. 2016; Keogan et al. 2018). Also, timing of egg-laying has been shown to not exhibit any trend over time (Keogan et al. 2018). Intriguingly, arrival date at the colony advanced considerably (on average 1.5 days/year) in both species and all study colonies during 2009 – 2018. This suggests that the potential cue used by guillemots to time their arrival is changing (PAPER IV). Such a cue could be relative change in temperature at their wintering site or changes in light regimes during winter and spring due to an increased cloudiness.

In summary, most stages of the annual cycle depend at least in part on the timing of egg-laying (arrival at colony, chick hatching, chick jumping, and autumn moult), which most likely depends on the (expected) timing of peak food abundance at the colony. The only period identified where flexibility in space and time is displayed by individuals is during winter, and only when an individual utilizes more than one staging area (figure 9).

Figure 9. Schematic illustration of the guillemot annual cycle and its flexibility in timing for different stages. Flexibility between different staging areas during winter is only exhibited if the individual used more than one staging area.
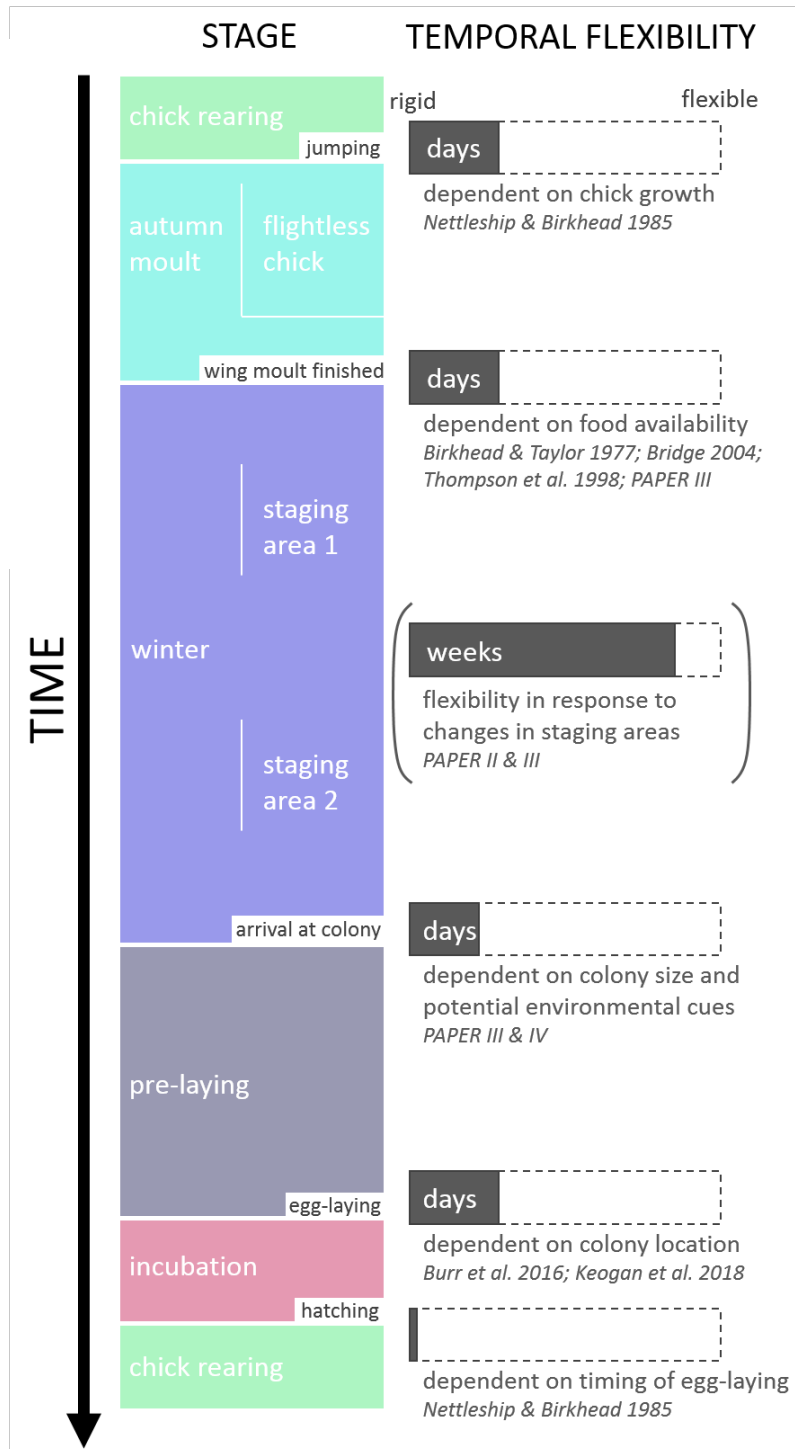
5 LIMITATIONS

Tracking method

Due to the nature of the tracking method used, estimated locations are quite uncertain (median error of 185 km and 145 km for solstice and equinox periods, respectively; PAPER I). Hence, inferences on individual movements can only be made on meso- and large-scales. Location estimations around the solstices at high latitudes (i.e. north of 66°N) was not possible due to the lack of twilight events. This resulted in data gaps particularly for the northernmost colonies. Another limitation of the used tracking method is that the devices need to be retrieved in order to collect their data. Consequently, only surviving adult breeders can be tracked as they return to the colony and can be recaptured. No inference can be made for the immature non-breeding part of the population and individuals not surviving the non-breeding period (i.e. not returning to the colony). Migratory behaviour of adults skipping breeding can also not be assessed for the most part, unless loggers can be retrieved in subsequent years. So, results presented in this thesis only represent a subset of the total population at each colony.

Effect of tagging

Despite their small size and low weight (Box 2), an effect of geolocators (or any other tag or device for that matter) on wild animals is unavoidable, but can range from negligible to substantial (McIntyre 2015). Effects need to be minimized in order to not bias the gathered data (and hence rendering it less useful or useless) as well as for ethical reasons. Different species are affected differently by tracking devices depending on their size, mode of transport (flying/swimming/walking …), the capture method used, the duration of deployment, the size, drag and weight of the device used, the attachment method and the positioning of the device on the animal (Walker et al. 2012; Costantini and Møller 2015; Weiser et al. 2016; Bodey et al. 2018; Brlík et al. 2019; Geen et al. 2019; Omeyer et al. 2019). Studies have found that a device's drag might be more crucial than its weight, in particular for marine species (Bowlin et al. 2010b; Vandenabeele et al. 2012). Generally, loggers have been documented to effect the behaviour (Vandenabeele et al. 2015), physiology (Elliott et al. 2012;

Quillfeldt et al. 2012; Heggøy et al. 2015) as well as survival and reproductive success (Weiser et al. 2016; Bodey et al. 2018; Brlík et al. 2019) of equipped individuals. Results from tracking studies thus need to be interpreted with these limitations in mind. However, most effects have been documented for short term deployments of heavier devices such as GPS loggers as well as for long term deployments of geolocators on smaller species such as waders or passerines (Weiser et al. 2016; Brlík et al. 2019). Tagging effects in seabirds have mainly been found for short term deployments of larger devices (e.g. GPS loggers or accelerometers), rather than long term deployments of small devices such as geolocators (Costantini and Møller 2015; Geen et al. 2019). In guillemots the only known effect of geolocators is elevated corticosterone levels in individuals carrying loggers (Elliott et al. 2012).

Capture methodology

In many colonies, individuals deployed with geolocators were chosen opportunistically often among birds breeding on cliff ledges on the landward edge of the colony. In many cases these individuals have been caught in relatively close proximity to each other in order to increase the potential to resight and retrieve loggers in subsequent years. An argument could be made that logger-tracked individuals represent a non-random sample as only individuals that could be caught have been equipped (biased against "shy" individuals). Also, inferences made in this thesis could be biased if areas in which loggers have been deployed differ from the majority of the colony in terms of individual personality, breeding experience, age structure, or nest site quality and if any of these factors would affect individual behaviour, in particular outside the breeding period. One possibility could be that individuals caught in close proximity to each other (e.g. on the same ledge) could be closely related due to initial settlement strategies (Kokko and Ekman 2002). Such a neighbourhood effect on kinship has been documented for the small population of Brünnich's guillemots breeding on Hornøya (Friesen et al. 1996), but could not be documented to the same extent for the same species breeding in a much larger colony on Coats Island in Nunavut, Canada (Ibarguchi et al. 2011). Even if kinship would bias exhibited migration strategy diversity within a colony, migration strategies documented between colonies would still constitute a random sample. To my knowledge, no information exists on the effect of kinship or individual personality on exhibited migration strategies in guillemots. Hence, I cannot make inferences as to their potential impact on the conclusions reached in this thesis.

Definition of environmental niche

Using the concept of environmental space allowed me to assess the environmental niches occupied by the different species, populations and individuals. However, it is important to remember that the abiotic variables selected to describe the available habitat, although ecologically relevant for the study species', are only proxies, and not actual measures, to describe prey availability as well as guillemot foraging habitat (Grémillet et al. 2008). The spatial scale at which individual birds operate could not be assessed as the environmental variables used are quite coarse and the tracking method has a large inherent uncertainty (Fauchald 2009). Although I estimated temporal changes in migratory behaviour, I did not directly assess changes in the environment and their correlation with migration strategies. A limitation of all satellite derived parameters used is that they only reflect surface water conditions, while guillemots are deep diving foragers. Combining spatiotemporal tracking with time depth-recorders (Elliott et al. 2008), cameras (Watanabe and Takahashi 2013), 3D ocean models and information on spatiotemporal prey abundance (in addition to knowledge about prey species) could help to provide a more holistic image of seabird movement decisions and their consequences (Reiertsen et al. 2014).

Length of time series

Although the tracking dataset available covered up to 10 years, it ranged from 1 - 10 years of available data depending on the population considered. The maximum period an individual was tracked was 9 years, which only covers a part of the lifetime of these long-lived species. Hence, inferences made on population- and individual-level between-year migration strategy consistency and flexibility - even though valid and based on a rather unique dataset - need to be viewed with caution. All data collection has been conducted within the same marine pelagic regime in the North Atlantic (Beaugrand et al. 2015) and started after the unpredicted collapse of sea ice in the Barents Sea in 2006 which has persisted to the present (Lind et al. 2018). Thus, no inferences can be drawn on the rigidity of migratory connectivity and identified consistency in space and time under different regimes.

6   CONCLUSION AND PERSPECTIVE

This thesis provides new insights into the migration of pelagic seabirds and its seasonal structure in space and environment across species, populations and individuals. It also highlights potential constraints migrants might have in adapting to rapid environmental change. In this chapter I will put my main findings into perspective and discuss aspects of migration which are more speculative based on the knowledge gained through this thesis. Topics discussed include potential causes for the exhibited migration structure, ontogeny of migration strategies and the role of learning, potential consequences for migratory species in a rapidly changing biological and physical environment, as well as implications for conservation.

Guillemot migration structure

In this thesis I established that both guillemot species consistently display colony-specific space and environmental niche use in the non-breeding period across the study area and that they cluster into distinct groups (PAPER II). Potential causes for the exhibited patterns include: (1) patchy food availability across the North Atlantic, (2) inter- and intra-specific competition, (3) energetic costs, (4) locations and flow directions of North Atlantic surface currents, and (5) specialisation in individual migratory behaviour.

The North Atlantic has a complex physical oceanography (as described above), resulting in seasonally shifting, patchy and predictable food resources. Hence, it is not surprising that higher trophic predators such as guillemots aggregate in specific areas and are not evenly distributed across their range, although I cannot make any inferences regarding total biomass or species composition of available prey for guillemots in the different parts of the North Atlantic.

Competition is often thought to explain differences in observed migration patterns between populations (reviewed in Greenberg 1986; Alerstam and Hedenström 1998; Alerstam et al. 2003; Svanbäck and Bolnick 2007). Intra- and inter-colony competition for food resources could drive in part the identified migration patterns. For example, thanks to extensive tracking effort of Brünnich's

guillemots in the Russian part of the Barents Sea as well as eastern Spitsbergen, I gained new insights into the non-breeding distributions of (at least parts of) these large populations (figure 5) and could ascertain that they utilize the Barents (and Kara) Sea year round. Hence, the population overwintering in this productive shelf sea is much larger than previously thought (Frederiksen et al. 2016) and it could be density-dependent competition-avoidance that made individuals breeding along its western edge (i.e. on Bjørnøya and western Spitsbergen) migrate towards Icelandic and Greenlandic waters. Competition avoidance might not only drive individual- and often colony-specific space use, but also niche partitioning among individuals and populations. Each population occupies only a subset of the species wide environmental niche, which only partially and unequally overlaps with niches of other populations in most cases. This pattern can be observed both within and between the two sympatric species throughout the non-breeding period (with the possible exception of the pre-laying period). Similar results have been found for the two *Uria* species breeding in the Northwest Atlantic (Linnebjerg et al. 2013; McFarlane Tranquilla et al. 2015). Here, I could confirm that Brünnich's guillemot populations utilize a wider environmental niche than common guillemot populations in the Northeast Atlantic, as has already been shown by McFarlane Tranquilla et al. (2015) for the two species breeding in the Northwest Atlantic. This niche expansion might have originated due to competition between these two species, resulting in segregated space and environmental use. A different aspect of competition shaping migratory movements is the likely need to defend one's nest site in order to be able to breed in the coming summer, which seems to depend on the size of the breeding colony (PAPER IV). Hence, individuals from larger colonies need to return earlier to their nest sites than birds from smaller colonies due to competition for nest sites and potential mating opportunities (Birkhead et al. 1985).

Optimal foraging and optimal migration theory (reviewed in Alerstam 2011) have been essential in understanding the mechanisms behind migratory movements. Migratory species need to balance their energy gain in staging areas with their energy requirements. Thus, they are limited by their energyscape, which is defined as the variation in the energy requirements of an organism across geographical space as a function of environmental conditions (Wilson et al. 2012; Shepard et al. 2013). One aspect of this is the energetic cost of movement. Guillemots, due to adaptations yielding excellent swimming and diving abilities, have extremely high flight costs (Elliott et al. 2013). This results in a theoretical maximum migratory range of ~3400 km from their respective breeding sites (Watanabe 2016). Consequently, unlike soaring seabirds, guillemots are unable to traverse the entire North Atlantic during their non-breeding period and return with sufficient body condition for the next breeding season. This means that due to the great distance, individuals breeding in Canada cannot utilize food resources in the Barents Sea and vice versa. This might in part explain the

apparent migratory divide (with some few individuals that migrate to the Grand Banks from the Northeast Atlantic being the exception to the rule) observed between these populations in both guillemot species. The environmental conditions experienced by migrants and the energy expenditure they incur is another aspect of the energyscape. Especially during winter, guillemots operate on their theoretical limit to sustain energy expenditure, due to the harsh environmental conditions faced (Fort et al. 2009; Burke and Montevecchi 2018). This can result in only individuals with sufficient body size being able to forage in energetically costly, but productive areas as shown for Brünnich's guillemots in the Pacific (Orben et al. 2015). The combination of movement costs and environmentally induced energy expenditures shapes a species energyscape which restricts individuals from different colonies to different subareas of the North Atlantic. This mechanism could be another reason for the displayed strong migratory connectivity and clustering apparent particular among Icelandic colonies as well as within the Barents Sea in both species.

The relative location of colonies to prevailing surface currents (Sandvik et al. 2016) is another factor likely influencing migration strategies in guillemots (figure 4), especially during autumn when both sexes are flightless and successfully breeding males accompany flightless chicks (Frederiksen et al. 2016). Swimming migration away from the colony towards autumn staging sites is known to occur at some guillemot colonies, while individuals at other colonies stay within the general area during their autumn moult. Many autumn staging areas identified for both guillemot species in this thesis occur downstream from their respective colonies, strengthening this hypothesis. These include all Norwegian common guillemot colonies and in particular individuals breeding on Sklinna which potentially utilize the Norwegian Coastal Current as well as the North Atlantic Current to reach the Barents Sea after the breeding season. Also, Brünnich's guillemot populations breeding on western Spitsbergen and Jan Mayen might take advantage of the East Greenland Current to arrive at their autumn staging areas off east Greenland.

Individual specialisation in migratory behaviour (PAPER III) potentially drives the exhibited migratory structure (Bolnick et al. 2003) and particularly the strong migratory connectivity visible in guillemots (PAPER II). This conservative individual behaviour combined with low migration strategy diversity within populations and concomitantly large diversity in migration strategies exhibited between populations (PAPER II) results in compartmentalisation of staging areas, and strong migratory connectivity. Potential reasons for this conservative migration strategies are detailed below.

In summary, annual space use structure of migratory species is likely shaped by the relative location of their breeding sites, the physical properties of their environment, which also influences prey availability, and competition both between and within species from the same and different breeding

sites. Other factors influencing migratory behaviour which are not detailed here include predation pressure and disease as well as parasite avoidance (Alerstam and Hedenström 1998). Although predators for these study species have been documented (e.g. great skuas, *Stercorarius skua*, Glaucous gulls, *Larus hyperboreus*, Bald Eagles, *Haliaeetus leucocephalus*, Common ravens, *Corvus corax*, and artic foxes, *Vulpes lagopus*), these mainly prey on their eggs and chicks during the breeding period. Similarly, parasitism has been observed in low numbers, but might play a more important role in the future due to a warming climate (Descamps 2013).

Ontogeny of migration strategies and the role of learning

Genetic control of migration strategies and routes is well documented in small, short-lived migrants such as passerines (e.g. Berthold et al. 1992; Pulido 2007; Liedvogel et al. 2011), while the mechanisms controlling migration strategies in long-lived animals such as seabirds are less understood (Bowlin et al. 2010a; Scott et al. 2014). The former will repeat their migratory journey only a few times, while the latter will utilize migration strategies for up to several decades. Annual movement strategies might be learned either through experience (i.e. trial and error, Guilford et al. 2011) or culturally (Chernetsov et al. 2004; Grémillet et al. 2004), via 'information acquired from conspecifics through some form of social learning' (Rendell and Whitehead 2001) as has been shown in long lived animals such as turtles (Scott et al. 2014), ungulates (Jesmer et al. 2018) and marine mammals (Abrahms et al. 2019). Thereby, it is important to distinguish between vertical (i.e. inter-generational, e.g. between parents and offspring) and horizontal (between conspecifics of the same generation) transmission of knowledge (Keith and Bull 2017). Vertical transmission of knowledge might encourage conservative movement strategies constraining the ability of a species to respond to rapid changes (Keith and Bull 2017). The low diversity of migration strategies within breeding populations and strong migratory connectivity for both guillemot species across the study area shown herein (PAPER II) as well as the consistently exhibited IMSF selecting for sites and not habitat (PAPER III) could be an indication of conservative behaviour and vertical transmission of knowledge about seasonal staging sites. This could possibly occur between parent and offspring, especially as fathers in these species accompany their young for at least a month after leaving the colony (Elliott et al. 2017). High route fidelity has also been shown in many marine migrants (Hunter et al. 2003; Broderick et al. 2007; Fifield et al. 2014; Fayet et al. 2016), although flexibility in migration routes has also been reported (Dias et al. 2011; Müller et al. 2014; Van Bemmelen et al. 2017). I would argue that this flexibility in routes, which often takes the form of an individual using an alternative migration strategy one year and switching back to the other in the next year, is further evidence for

the role of learning and experience in long-lived migrants. The individuals observed to switch strategies may have been the ones with the knowledge of an alternative strategy and the reason for switching might be due to their personal experience in previous years (e.g. failed breeding due to low body conditions from unfavourable conditions during the winter, i.e. "win-stay lose-switch" rule; Switzer 1993). Migration strategies most likely shaped by expected conditions in non-breeding areas, based on previously experienced historic conditions, as actual conditions must be considered unknown for the individuals at the time of movement due to the large distances covered (Piper 2011; Van Moorter et al. 2016; Thorup et al. 2017). Acquired knowledge or the lack thereof of different historically adequate staging areas during different seasons coupled with high flight costs (Elliott et al. 2013) and a maximum migration range (Watanabe 2016) could drive annual movements in the long-lived species studied herein. Knowledge about suitable migration routes and staging areas might be acquired during the juvenile phase, through vertical transmission of culture (e.g. from their parent or conspecifics of the same colony) or trial and error, when immatures do not yet invest energy and time into breeding and are freer to roam and explore (Riotte-Lambert and Weimerskirch 2013) unlike adult breeders as detailed above. In order to test this hypothesis, it seems essential to acquire information about movement patterns of juveniles and their parents, and to enhance knowledge about potential genetic exchange between breeding sites.

Migration in a rapidly changing environment

Changes in the environment encountered by migrants outside their breeding season have the potential to affect population trends through multiple ways, such as through individual survival (Webster et al. 2002; Gaston and Powell 2003; Møller et al. 2008). We know climate change is happening (IPCC 2013; Franzke 2014; Blunden et al. 2018) and the scientific literature on its effects on physical and biological systems is ever increasing. Within the North Atlantic and the Arctic, numerous changes have been already observed and many more are predicted to happen in this century. These could have numerous consequences both negative and positive for the species' energyscape, food availability and competition. Among those changes, and of relevance for guillemots in particular and marine migrants within the North Atlantic in general are; the Atlantification of the Barents Sea (Fossheim et al. 2015; Lind et al. 2018); the rapid decline of Arctic sea ice (e.g. Stroeve et al. 2007); the uncertainty apparent in climate models regarding the fate of the North Atlantic subpolar gyre (Sgubin et al. 2017) which is an important nutrient and zooplankton source (Heath et al. 2008; Hátún et al. 2016); the shift in spatial distributions of potential prey species (e.g. capelin, *Mallotus villosus*, Carscadden et al. 2013) as well as spatiotemporal shifts of ecosystem distributions and compositions within the changing North Atlantic (Perry et al. 2005;

Wassmann et al. 2011; Frederiksen et al. 2013; Pinsky et al. 2013; Post et al. 2013; Henson et al. 2017; Beaugrand and Kirby 2018).

In general, migratory plasticity is predicted to buffer populations against perturbations at local and regional scales (Cresswell 2014; Betini et al. 2015; Gilroy et al. 2016). The observed variability in diet of guillemots in different parts of the North Atlantic, coupled with the strong migratory connectivity in space and environment found in both species (PAPER II), indicates that individuals from different populations most likely feed on different prey which in turn may be influenced differently by changes in oceanographic systems (e.g. the North Atlantic subpolar gyre, Descamps et al. 2013; Fluhr et al. 2017; Hátún et al. 2017). Hence, different populations will be affected differently by changing environmental conditions, depending on their annual use of different areas (Grémillet and Boulinier 2009). Species such as guillemots, with excellent swimming and diving abilities (with concomitantly low energetic cost) and the highest flight costs ever recorded for vertebrates (Elliott et al. 2013), are less sensitive to changes in prey depth, but more sensitive to horizontal changes in their prey abundance. The evidence that individual guillemots show fidelity to specific sites and not habitats (PAPER III), suggests that these species do not have much capability to adapt to spatially (and possibly temporal) changing distributions of their prey (e.g. shifting or shrinking distributions, Finch et al. 2017, figure 10). In particular, if migration strategies are determined during the first years of life (through genetic determination or learning) and adults do not have much capacity to shift or adapt strategies (Senner et al. 2015), then responses to shifting habitats and spatial distributions of prey species might come with a lag equal to the amount of time a new cohort needs to recruit into the breeding population (i.e. 4-5 years in guillemots). As the speed of change is increasing, this lag might make it unlikely for such long-lived and slowly reproducing species to adapt.

Putting aside the apparent constraints and potential conservative behaviour, shifting habitats and prey distributions also entail other costs and limitations for migrants. New habitats might cause extra energetic costs for migrants due to shifts in their spatial distributions resulting potentially in increased travel distance, which could exceed the maximum migration range for flapping flight migrants such as guillemots (Watanabe 2016). Alternatively, travel costs could decrease if habitats shift closer to their breeding sites. Migrants sustain high energy expenditure during winter, due to harsh environmental conditions faced (Fort et al. 2009; Burke and Montevecchi 2018). Thus, these species are also limited by their energyscape, which of course is highly sensitive to climatic conditions, although this might pose less of a problem in the future in certain areas of a migrants distributional range in the context of climate change (Amélineau et al. 2018). The success of a possible range expansion in migrants can also be negatively affected by new competitors, predators as well as parasites entering the system (Alerstam et al. 2003). Additionally, for visual predators such

as guillemots availability of light to forage seems to be a limiting factor (Ballard et al. 2010), although Brünnich's guillemots have been observed with stomach content in total darkness at 79°N during January (Berge et al. 2015), potentially feeding on bioluminescent prey (Berge et al. 2012). Hence, these predators might be unable to adapt to a shifting prey distribution if their prey moves outside suitable foraging habitat as defined by light availability (into areas of polar night north of 66°N).
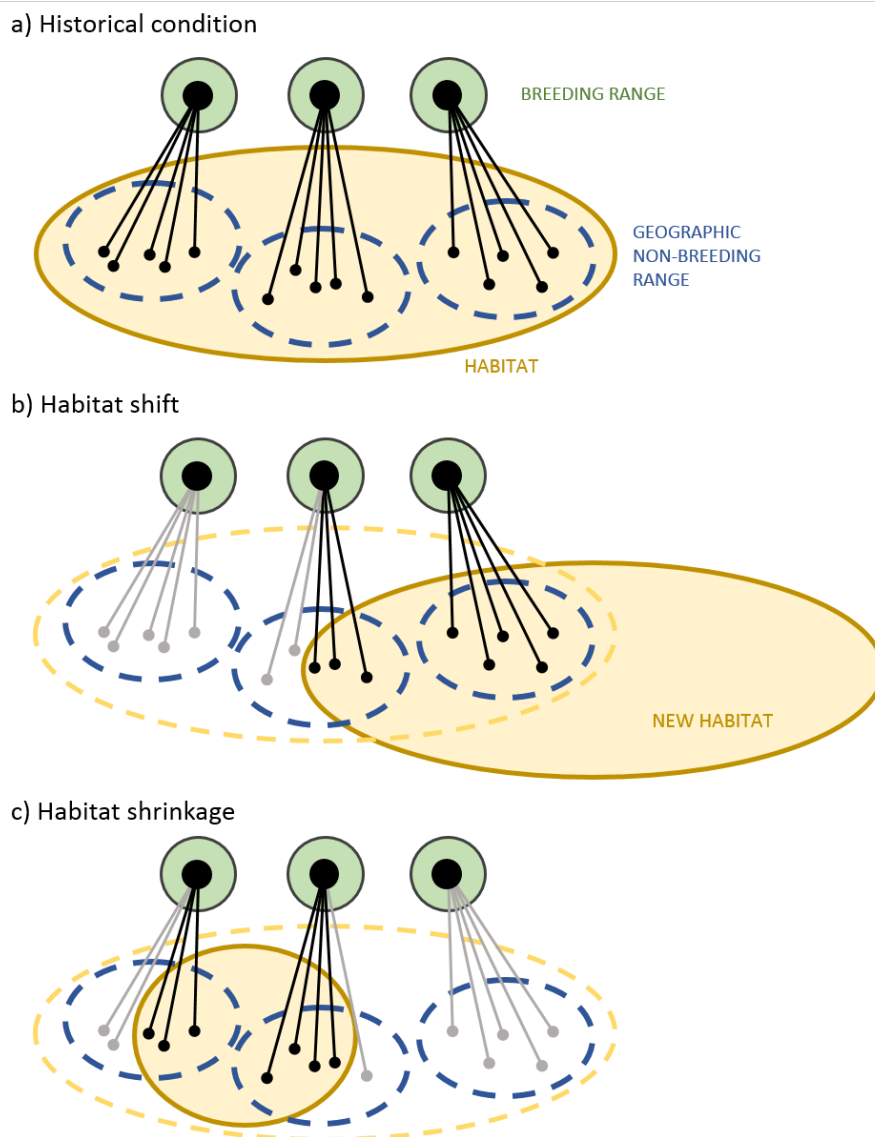

Figure 10. Historical conditions display the connection between non-breeding distributions of different populations and their habitat (a). Panels b and c illustrate potential consequences (mismatch of space use and habitat, grey lines) of spatially shifting (b) of shrinking habitat (c), due to climate change, on a migratory species structured according to results obtained for guillemots (PAPER II & III), i.e. strong migratory connectivity in space and environment with high individual migration strategy fidelity. This figure was modified after Finch et al. (2017).

In both study species space use was most confined during autumn and spring, with concomitantly low variability in environmental characteristics (PAPER II). This suggests critically low capacity to adjust to perturbations during these periods, under the constraints of life-history traits set by the breeding cycle (Dias et al. 2011). Moreover, the timing of both autumn moult (Thompson et al. 1998) as well as pre-laying colony attendance (PAPER IV) seems to depend, at least in part, on timing of egg-laying and colony size. Hence, these migrants might have only limited capacities to adjust to temporally shifting food resources (figure 11, Taylor et al. 2016), especially as timing of egg-laying seems to be insensitive to changing climatic conditions (Keogan et al. 2018). Adult male guillemots are more restricted in their autumn movements compared to other seabirds, due to guillemot breeding strategy in which chicks leave the colony before being able to fly and have to be accompanied by a parent for some time afterwards (Harris and Wanless 1990; Elliott and Gaston 2014; Elliott et al. 2017). In other seabirds and possibly female guillemots, timing if not duration of moulting seems to be more adaptable to changing conditions (Grissot et al. 2019).
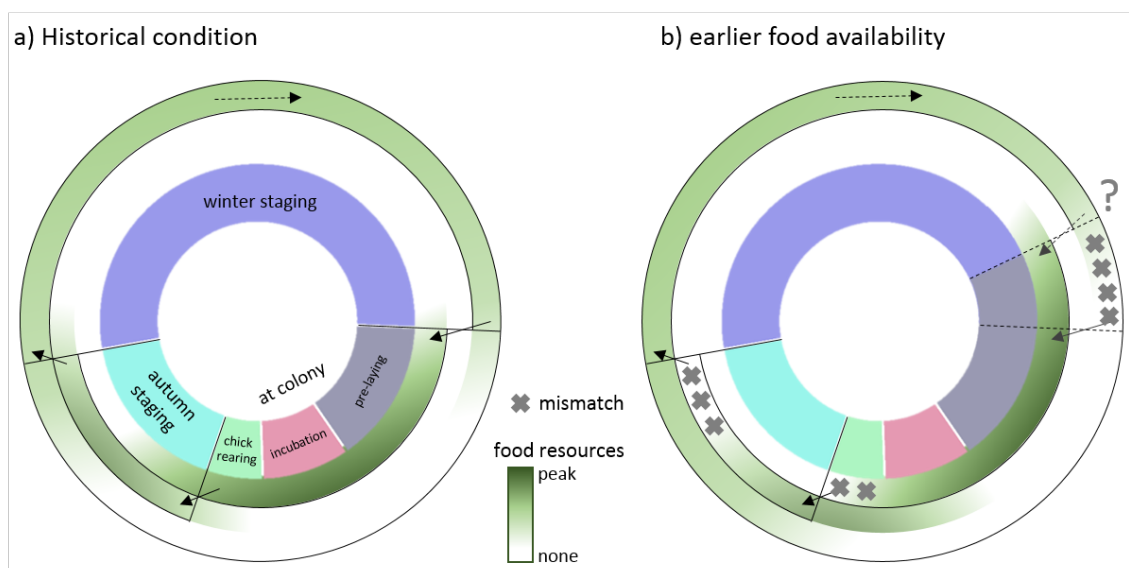

Figure 11. Historical conditions display the adaptation of a seabird's annual cycle to hypothetical seasonal food resources available in different areas. Arrows depict migratory movements between often spatial distinct areas (with potential movements between different winter staging areas; dashed arrow during winter). (a). Panel b illustrates a possible future scenario where temporal mismatch during different parts of the annual cycle occurs due to an earlier peak in prey abundance and little exhibited temporal flexibility in a seabird's annual schedule (figure 9) including potential sensitivity in arrival date at the colony (PAPER IV).

Implications for conservation

Seabirds face numerous other anthropogenic threats next to climate change, including, but not restricted to, hunting, overfishing, bycatch, pollutants (including plastics), increased marine traffic (including oiling events and light pollution), and offshore energy developments (Croxall et al. 2012; Lewison et al. 2012; Frederiksen et al. 2016). Measures have already been taken to protect seabirds during the breeding season, with for example the establishment of protected areas around their colonies or seasonal hunting restrictions to minimize human disturbance. However, protecting seabirds at sea, in particular during the non-breeding period is more challenging both politically and scientifically. Politically, as seabirds, similar to many other marine migrants, travel vast distances and in doing so experience varying levels of protection while crossing multiple countries' jurisdictions (Harrison et al. 2018). Scientifically, as important areas and migration routes still need to be identified for many species and populations and these areas may move in space and time between years (Lewison et al. 2012).

Although this thesis was not motivated by conservation, its results and the method developed in PAPER I are nonetheless valuable for making inferences about potential risk scenarios faced by the two guillemot species. The spatial and environmental segregation between species, colonies (PAPER II), and individuals (PAPER III) suggests that different parts of the (breeding) population will be impacted by different anthropogenic threats (e.g. hunting) and catastrophes (e.g. oil spills) faced in different parts of their distributional range. Furthermore, due to their rather rigid, but colony specific, annual schedule (PAPER II, III & IV) certain areas are more at risk during specific periods of the year and should receive temporally changing protection when these species are more vulnerable (e.g. during the autumn moult and pre-laying period). The knowledge gained through this thesis can help guide management decisions with regards to industry developments and hunting quotas among other measures in different parts of the North Atlantic. However, regarding the potentially biggest anthropogenic threat - climate change - it will be vital to not just focus on conserving current habitat important for these species, but also the genetic and cultural diversity in migration strategies in order to increase the potential adaptability of the species (Keith and Bull 2017) as migratory plasticity is predicted to buffer populations against perturbations (Cresswell 2014; Betini et al. 2015; Gilroy et al. 2016).

In addition, the method I developed to estimate positions from light-data (PAPER I) can be used to identify timing of migration in seabirds and marine animals in general as well as identification of important migration routes, due to the possibility to also estimate locations during times of equinox, which is often a time of migration in seabirds.

Concluding remarks

Through this work I established that the genus *Uria* is comprised of space use specialists selecting for specific sites rather than habitats with colony-specific temporally varying movement restrictions driven by their breeding biology. Guillemots display strong migratory connectivity, both within and between species, which was apparent through a combination of seasonal space use and occupied environmental niches. Their migratory behaviour is likely shaped by a combination of the physical properties of their environments, energetic constraints faced due to their physiology and foraging adaptations, inter- and intra-specific competition for food resources and nest sites and conservative migratory behaviour possible due to learning coupled with incomplete knowledge of available habitat. These traits might leave these migrants vulnerable to large-scale perturbations of their environments, which occur at an ever increasing rate, while their compartmentalised annual distribution allows for the potential extinction of an entire population by regional threats.

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