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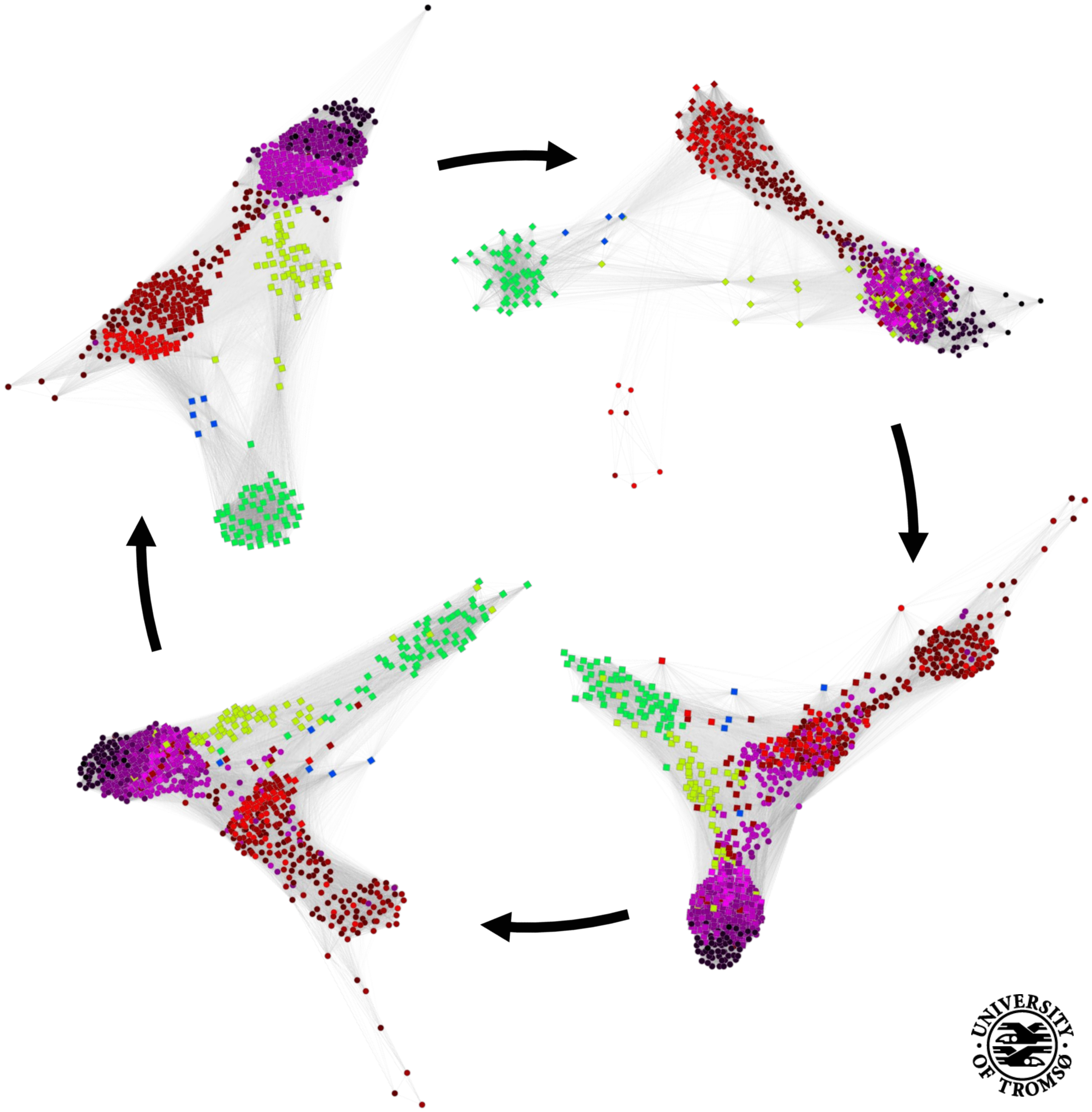
Migration in seabirds: seasonal structure in space and environment across species, populations and individuals

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



Cover image represents the guillemot spp. annual cycle as seasonal geographic similarity networks of the two study species during autumn (top right), early-winter, late-winter and spring.
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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 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).

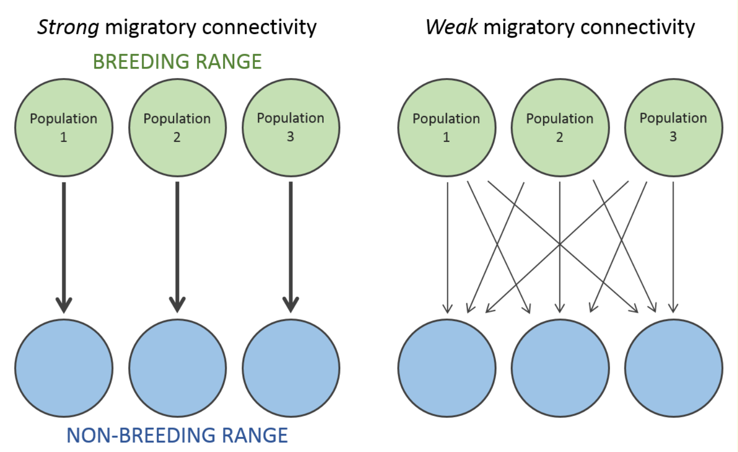


Figure 1.1. Schematic illustration of the two extreme cases of migratory connectivity

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).

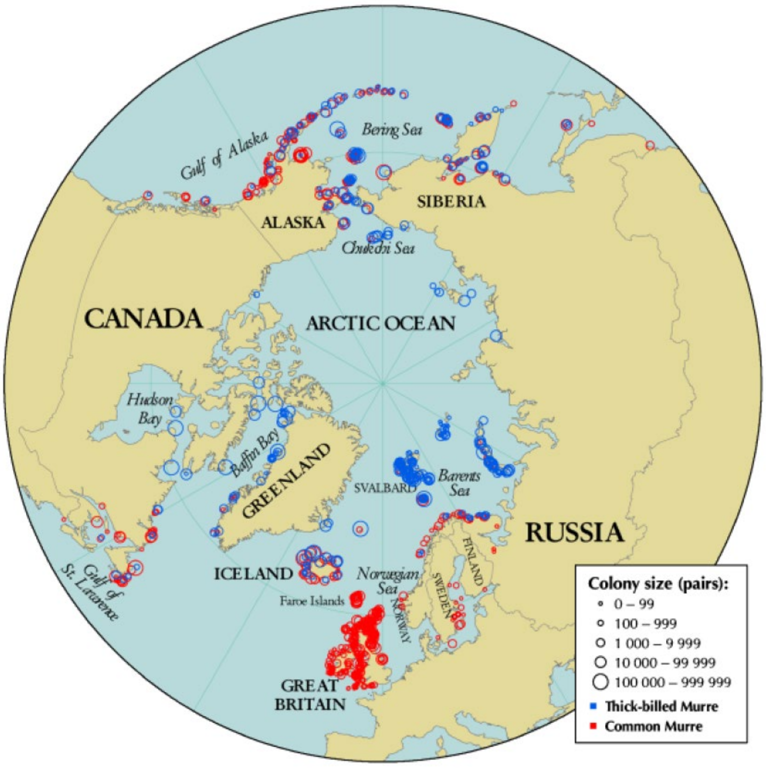


Figure 1. Distribution and size of Thick-billed (*aka* Brünnich's guillemot) and Common Murre (*aka* Common guillemot) colonies in the northern hemisphere (figure from Irons et al. 2008).

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.

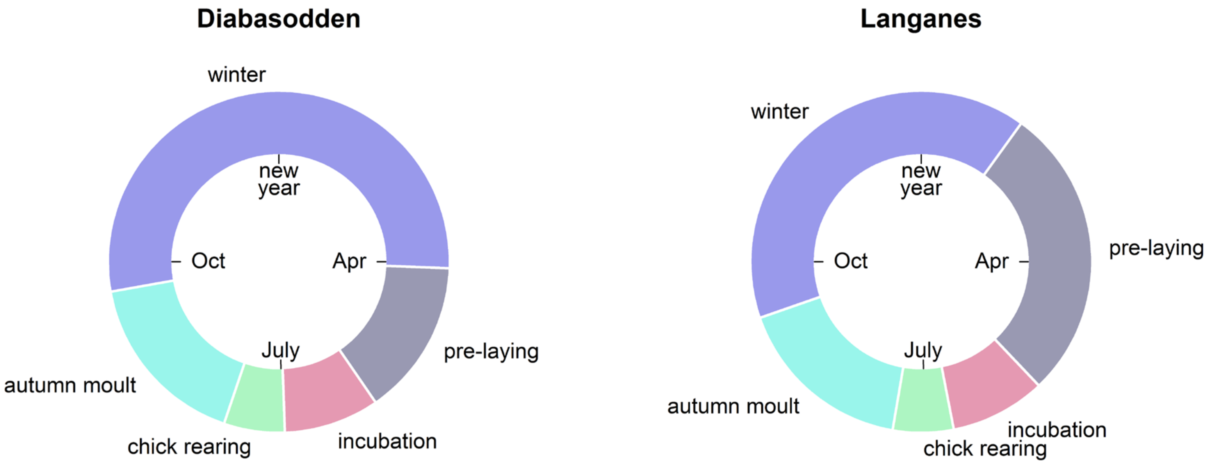


Figure 3. Two examples of the annual cycle of guillemots illustrating exhibited variability among colonies and species: a Brünnich's guillemot colony in the high Arctic (Diabasodden, Svalbard) and a common guillemot colony in Northeast Iceland (Langanes).

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

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).

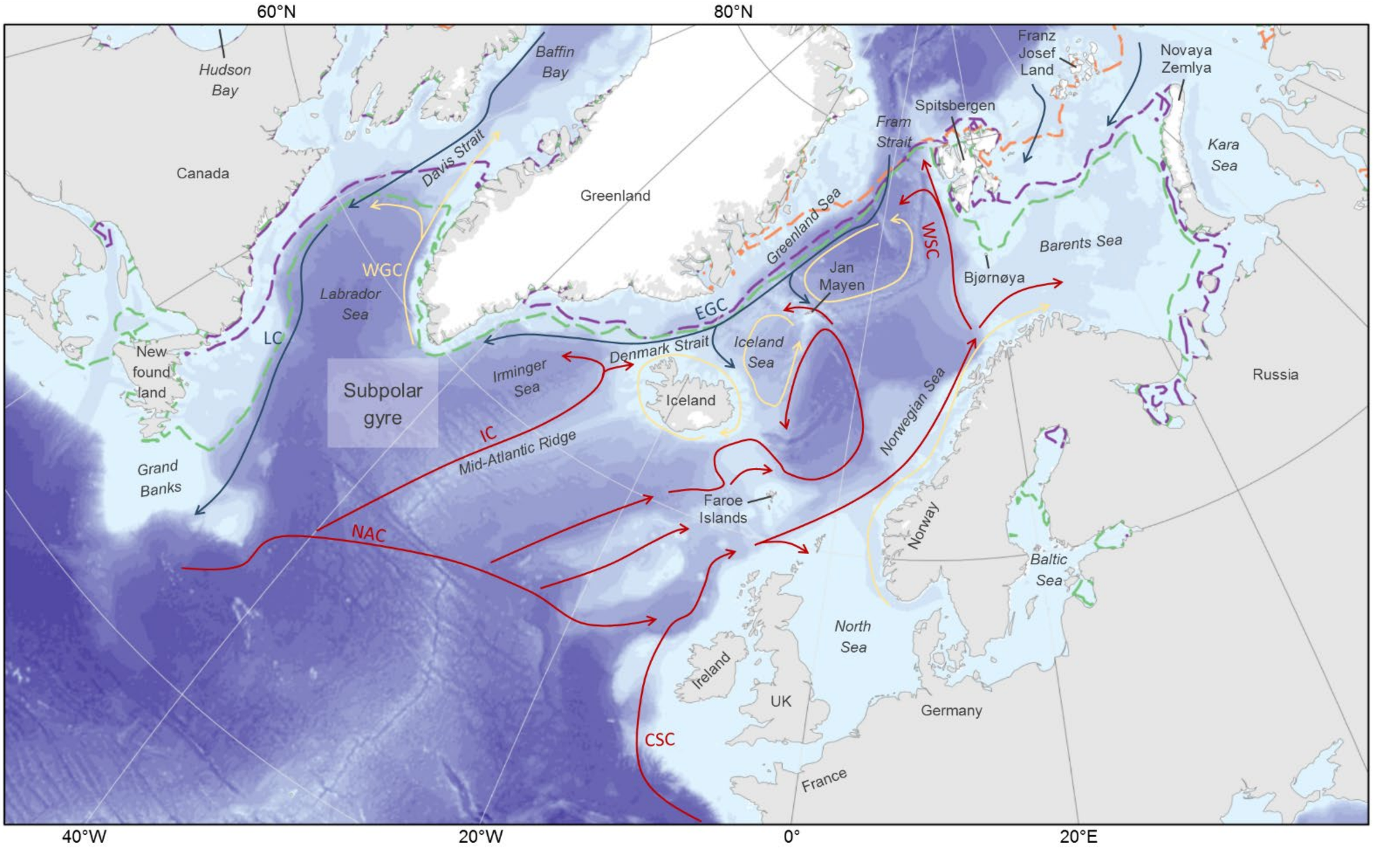


Figure 4. Map of the study area, the North Atlantic and its marginal seas including its bathymetry (Amante and Eakins 2009; Jakobsson et al. 2012), major currents and seasonal average sea ice extent (as area covered by ≥ 15 % average sea ice concentration between 2014 - 2017, Reynolds et al. 2007) during 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

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).

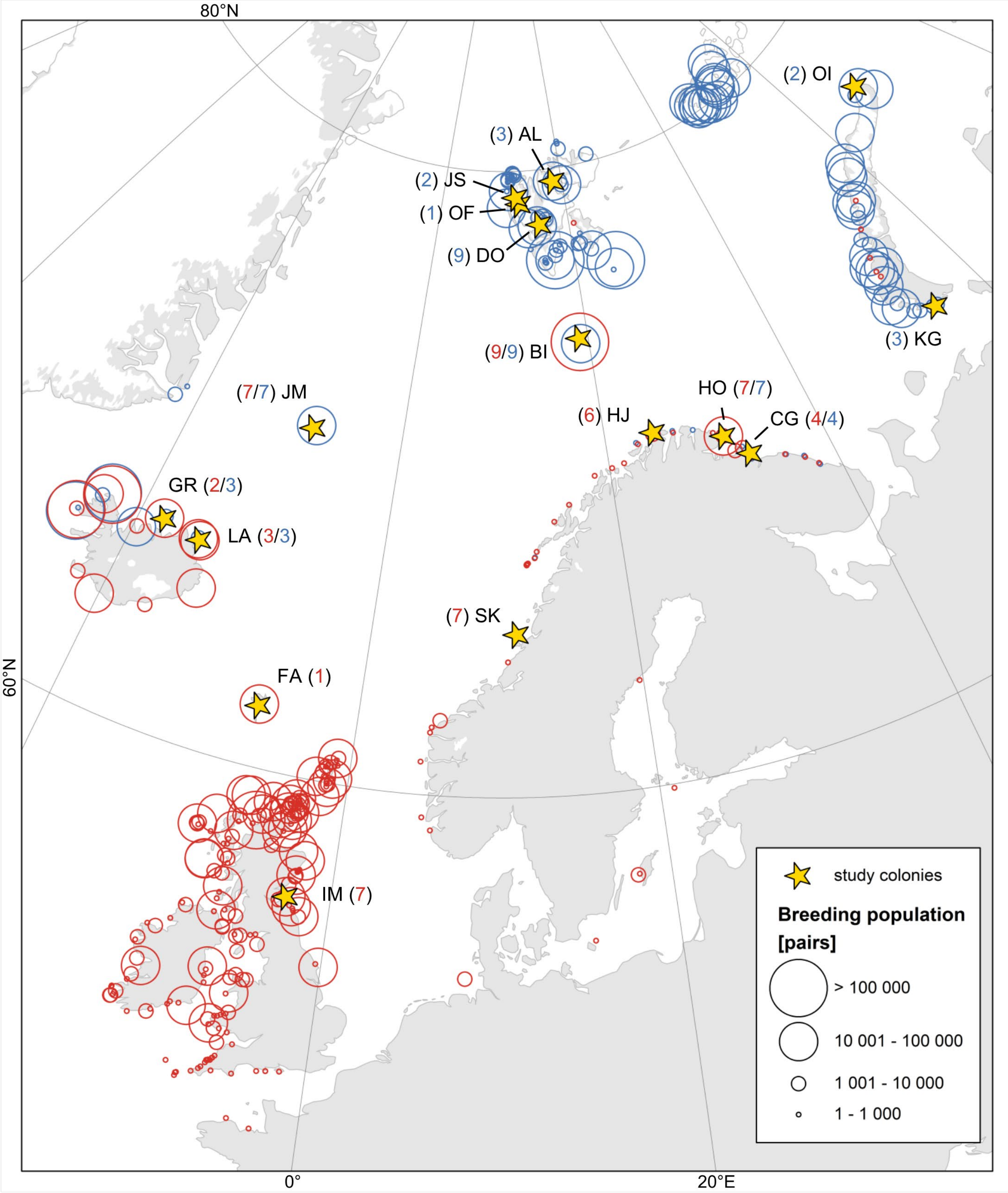


Figure 5. Map of the Northeast Atlantic displaying all guillemot breeding populations (circles) as well as all study colonies (stars, labels detailed in table 1). Values in brackets display number of years with tracking data available for the two species at each colony. Red and blue circles indicate 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

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

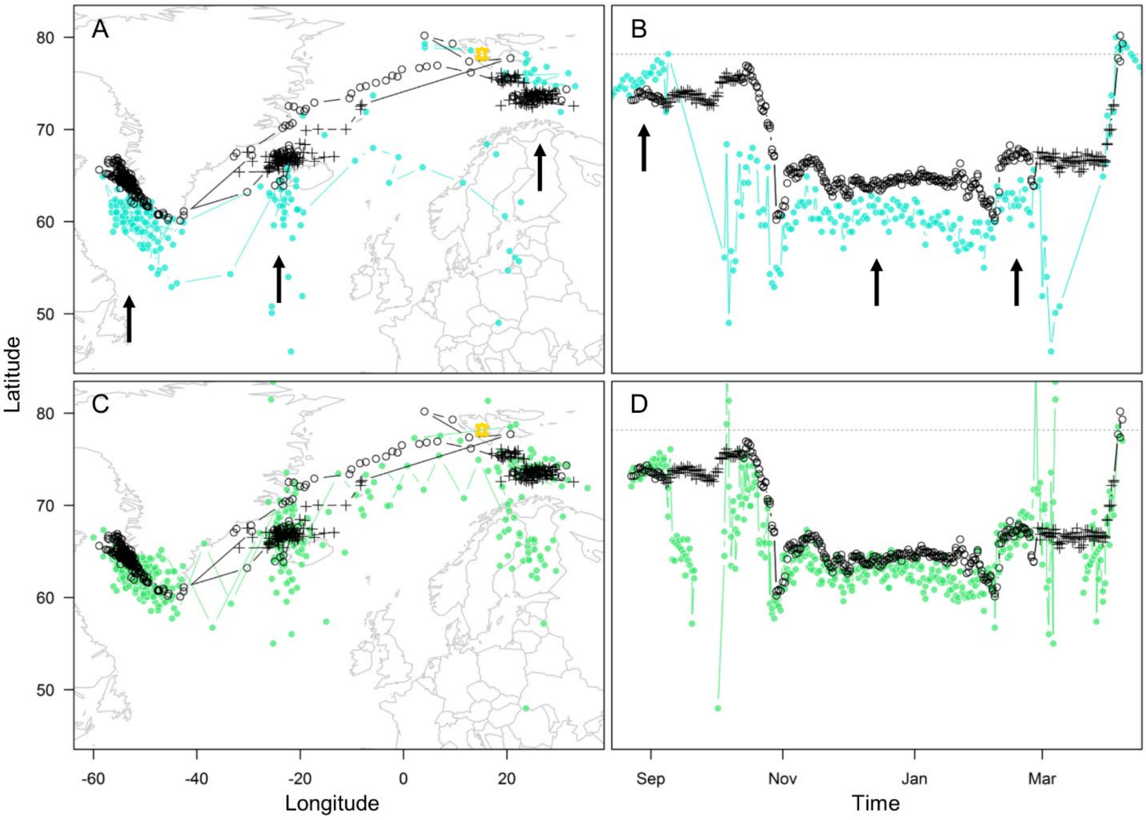


Figure 6. Example track of a Brünnich's guillemot from Diabasodden (yellow star in panel A and C) tracked using a Lotek L250A logger. Panel A and C display estimated locations in longitude and latitude while B and D show estimated latitudes throughout the non-breeding period (grey line denotes colony 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.

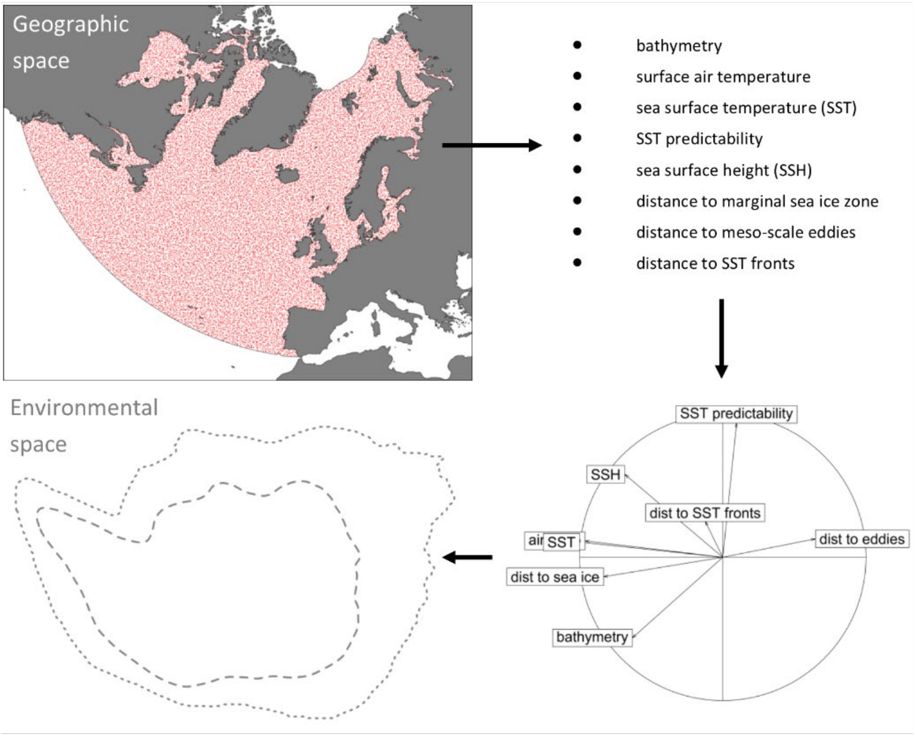


Figure 7. Schematic illustrating the concept of environmental space applied to the North Atlantic. The chosen environmental parameters are sampled within the defined study area over the entire study period. The resulting multidimensional space is projected onto two dimensions using the first two principal 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).

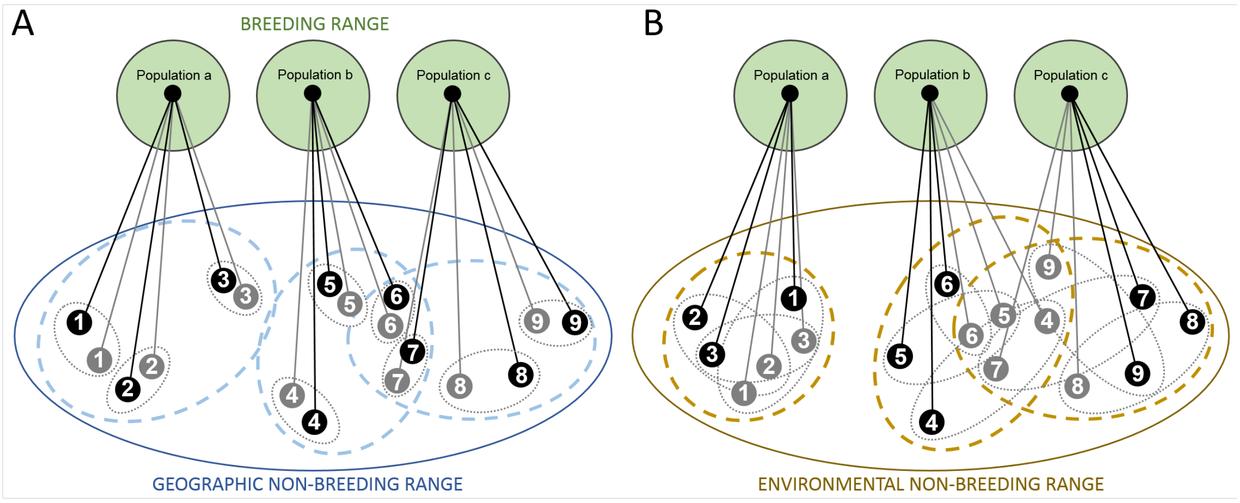


Figure 8. Schematic illustration of geographic (A) and environmental space (B) use of different populations and individuals during different years. Black and grey symbols represent two years from the same individuals (labelled 1, 2 … 9).

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)

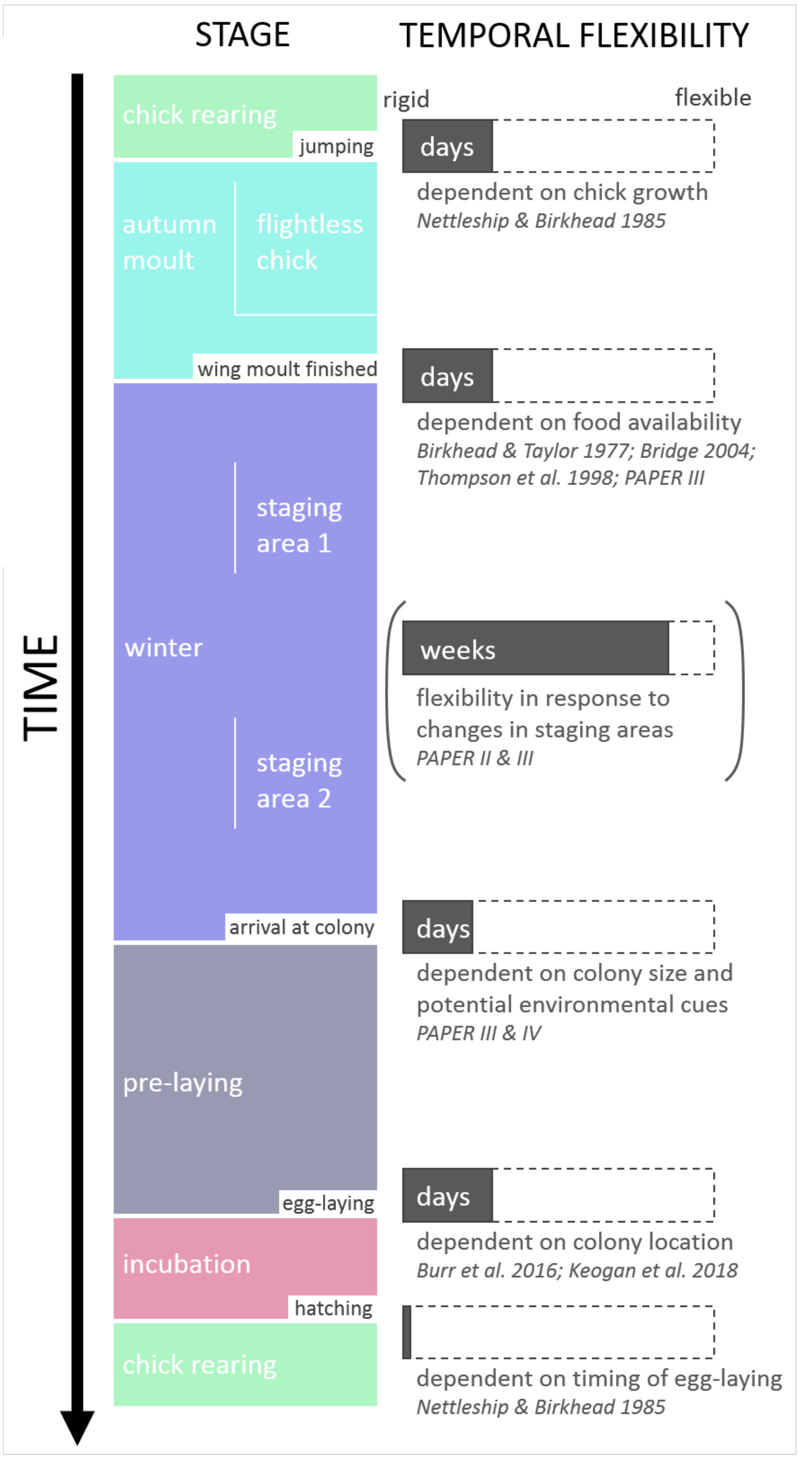
There is a clear seasonality in the temporal structure of guillemot migration across species, populations and individuals. Large parts of this seasonality can be explained by the species' breeding biology as explained in chapter 3. After leaving the colony birds from all colonies occupy rather defined, 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).

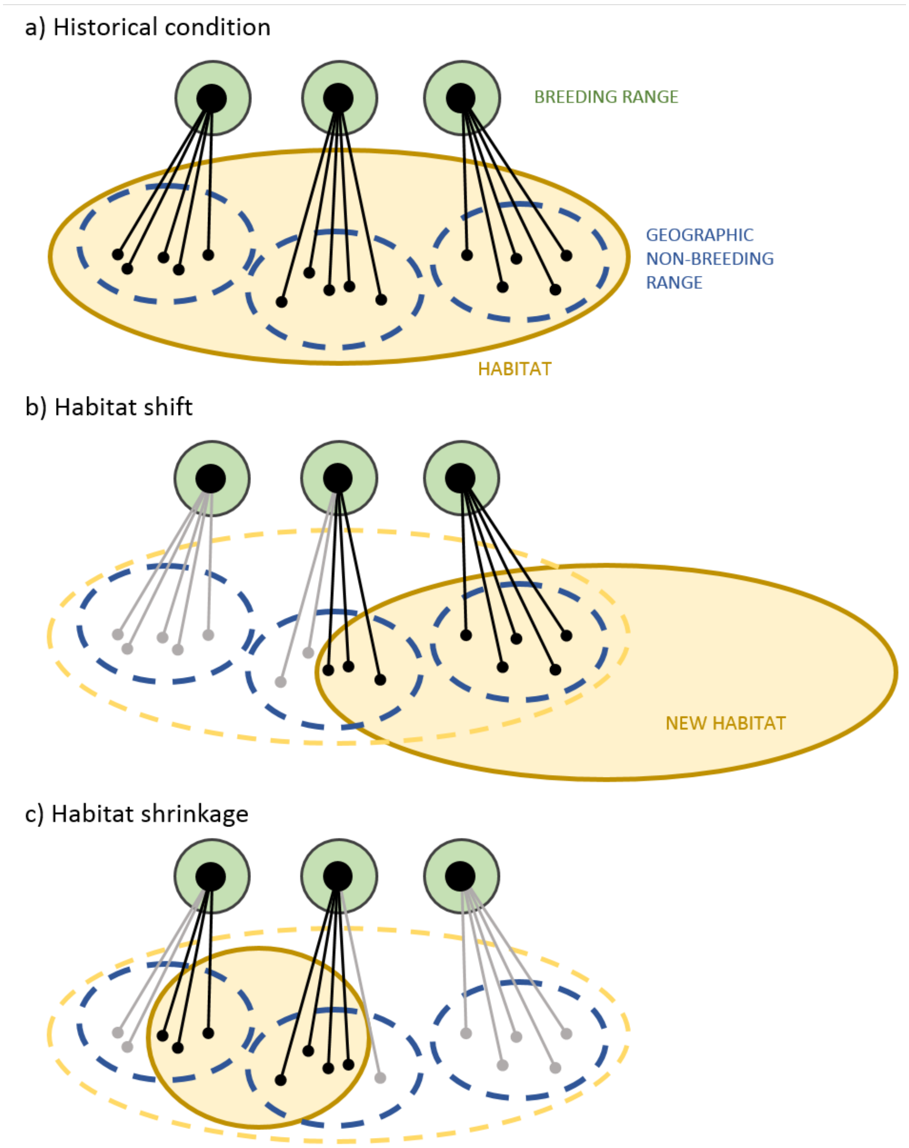


Figure 10. Historical conditions display the connection between non-breeding distributions of different populations and their habitat (a). Panels b and c illustrate potential consequences (mismatch of space use and habitat, grey lines) of spatially shifting (b) of shrinking habitat (c), due to climate 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).

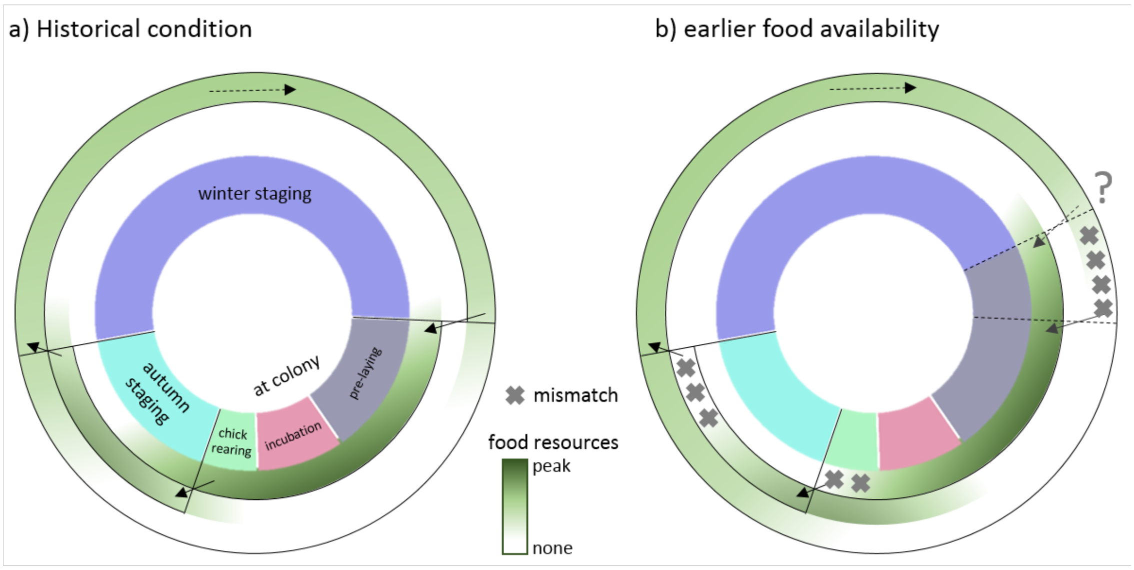


Figure 11. Historical conditions display the adaptation of a seabird's annual cycle to hypothetical seasonal food resources available in different areas. Arrows depict migratory movements between often spatial distinct areas (with potential movements between different winter staging areas; dashed arrow 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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Movement Ecology

METHODOLOGY ARTICLE Open Access

A probabilistic algorithm to process geolocation data

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Abstract

Background: The use of light level loggers (geolocators) to understand movements and distributions in terrestrial and marine vertebrates, particularly during the non-breeding period, has increased dramatically in recent years. However, inferring positions from light data is not straightforward, often relies on assumptions that are difficult to test, or includes an element of subjectivity.

Results: We present an intuitive framework to compute locations from twilight events collected by geolocators from different manufacturers. The procedure uses an iterative forward step selection, weighting each possible position using a set of parameters that can be specifically selected for each analysis.
The approach was tested on data from two wide-ranging seabird species - black-browed albatross *Thalassarche melanophris* and wandering albatross *Diomedea exulans* – tracked at Bird Island, South Georgia, during the two most contrasting periods of the year in terms of light regimes (solstice and equinox). Using additional information on travel speed, sea surface temperature and land avoidance, our approach was considerably more accurate than the traditional threshold method (errors reduced to medians of 185 km and 145 km for solstice and equinox periods, respectively).

Conclusions: The algorithm computes stable results with uncertainty estimates, including around the equinoxes, and does not require calibration of solar angles. Accuracy can be increased by assimilating information on travel speed and behaviour, as well as environmental data. This framework is available through the open source R package `probGLS`, and can be applied in a wide range of biologging studies.

Keywords: Animal tracking, Global Location Sensors, GLS, Method assessment, Sea surface temperature, Probability sampling, `probGLS`, Threshold method

Background

The ability to track animals across large distances in space and time has revolutionized our understanding of their movements during the breeding and nonbreeding seasons [1, 2]. Thanks to the development of light-level data loggers (geolocators; also termed Global Location Sensor or GLS loggers) [3], we are now able to track small animals which cannot carry heavy satellite-transmitters or GPS ('global positioning system') loggers (e.g. [4, 5]). Indeed, geolocators are used very frequently on nonbreeding seabirds, because long-term deployment of satellite or GPS devices using harnesses is a major welfare concern (e.g. [6]) and also on other marine organisms, including fish, that rarely, if ever, are at the sea surface and so cannot be tracked using radio wave technology. Currently, miniaturized GPS loggers in the same weight range as geolocators record few locations throughout the deployment period; thus, the data are unsuitable for answering ecological questions on finer temporal scales.

Geolocators record ambient light intensities and elapsed time, from which longitude and latitude can be estimated [3, 7]. They can record data for up to a year or longer, and cover one or several annual migration cycles [8, 9]. Their small size and mass (to <1 g) allow a wide range of species to be tracked, and because of the relatively low cost (compared with miniaturized GPS

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devices), they can be used to track many individuals for multi-population studies (e.g. [10–13]).

A number of methods have been developed to estimate locations from light data (Table 1), and to filter the resulting outputs in various ways [14–17]. These are mainly based on either a threshold [7, 18] or template-fit approach [19]. In the former, longitude is computed from the timing of local noon, and latitude from day length, based on the timing of twilight events (i.e. dusk and dawn) which are determined using a pre-defined light intensity threshold. Further, latitude depends on the solar angle below the horizon at which the threshold is crossed [7]. This sun elevation angle, which is affected by shading during the twilight period (related to behaviour and activity patterns as well as weather), and latitude [20], has to be calibrated, and for practical purposes, is generally assumed to stay constant during the entire deployment period. In contrast, the template-fit method involves fitting a simplified geophysical model for various latitudes (i.e. the template) to recorded light intensities for each day at a longitude estimated in the same way as in the threshold method [21].

Unlike other tracking methods, locations derived from light data lack a constant spatial error structure. Latitudes are most accurate (i.e. least affected by shading) where the timing of twilight events is most distinct, i.e., during solstices and at high latitudes [7]. However, within the Arctic or Antarctic circles, position estimates are impossible around the solstices due to the lack of twilight events (i.e. polar night and midnight sun). In contrast, the error in latitude (due to shading) is highest during the equinoxes where day length is the same around the globe, and around the equator where there is little variation in day length [7].

Given the wide range of alternative methods and potential observer-specific biases, there would clearly be advantages in determining a common method for analysing all geolocation data. Any method that requires raw light values and not just timing of twilight events (Table 1) cannot be applied to data from all brands of geolocators. For instance, Lotek geolocators (Lotek Wireless Inc., Ontario, Canada) do not store these data by default and have been deployed in many studies of marine organisms. The aim of this paper is to propose an intuitive, probabilistic algorithm, implemented in R [22] through the new package `probGLS`, that can be used on data from all existing geolocator brands. Our method is relatively simple, easy to implement, fast to compute (compared to other more complex methods), does not require the use of a constant solar angle (as needed in the `GeoLight` package [23]), provides uncertainty estimates, can incorporate additional information to increase accuracy (e.g. land avoidance for marine organisms), and greatly reduces location error around the equinoxes (if additional information is available) without making assumptions about behavioural states as in state space models (SSM, e.g. [24–27]). Here we validate the approach for two open landscape species (flying seabirds), but its usability would need to be confirmed for other organisms, particular those that dive or live in closed terrestrial habitats (e.g. forests).

Methods

Method principle

The method is an iterative forward step selection based on [28]. The algorithm uses twilight events (Panel A, Fig. 1) identified using a range of brand-specific software for analysing light data (e.g. TransEdit2, British Antarctic Survey (BAS), Cambridge, UK), the `twilightCalc` function (`GeoLight` package; also incorporated into IntiProc, Migrate Technology, Cambridge, UK), or in the case of Lotek loggers by back-calculating twilight thresholds from computed locations as implemented in the `lotek_to_dataframe` function (`probGLS` package, this study). The framework can incorporate various sources of uncertainty (e.g. uncertainty in solar angle) as well as knowledge of the behaviour and habitat use of the study species (e.g. travel speed), by defining associated parameter values a priori (Table 3). The main steps are described below:

1. The algorithm assumes that the first position at time t_1 is known without error (i.e. release location), regardless of the time difference between t_1 and the first twilight event.
2. The next available pair of twilight events (dusk/dawn or dawn/dusk) is replicated x times with an additional twilight error term (from a log-normal distribution N, μ and σ on the log scale = user-defined, See Additional file 1 for information about setting these parameters) and a random solar angle (from a user-defined range) applied to each twilight before a location is calculated (Panel B, Fig. 1).
3. Using the threshold method and the twilight events computed in step 2, a cloud of positions (i.e. particles) at t_i is calculated. To make computations more robust, all particles outside a defined boundary box (based on known range) are removed. Further, latitudes are unreliable for a variable period around the equinoxes. For these periods (user-defined), random latitudes (with uniform distribution) within the boundary box are added to each computed longitude estimate.
4. Each particle can be weighted (i.e. given a probability of selection) according to behaviour (e.g. maximum possible speed) or environmental characteristics (e.g. sea surface temperature; Panel C, Fig. 1).

Table 1 Comparison of available methods to process geolocation data

	Hill 1994 [7], Hill & Braun 2001 [18]	Teo et al. 2004 [32]	Domeier et al. 2005 [33]	Royer et al. 2005 [34]	Ekstrom 2007 [21]	Nielsen et al. 2006 [24], Lam et al. 2008 [35]	Tremblay et al. 2009 [28]	Sumner et al. 2009 [26]	Nielsen & Sibert 2007 [25], Lam et al. 2010 [36]	Rakhimberdiev et al. 2015 [27]	this study
Principle to infer locations from light data	threshold	threshold (only longitude)	threshold (only longitude)	-	template fit	threshold	-	curve model	template fit	template fit	threshold
Data needed for method	twilight events	twilight events	twilight events	"raw" locations	full light range data	twilight events	"raw" locations	clipped light range data	full light range data	clipped light range data	twilight events
R package	**`GeoLight`** [23]					**`Ukfsst`**		**`SGAT, Trip Estimation`**	**`Trackit`**	**`FlightR`**	**`probGLS`**
Account for difference in shading					+			+		+	+
Account for movement between twilight events								+	+	+	
Estimated locations during equinox		+	+		+	+		+	+	+	+
Uncertainty estimates				+	+	+	+	+	+	+	+
Spatial error structure			constant	constant	estimated through the geolocation process	ad hoc parametric model	constant	estimated through the geolocation process	estimated through the geolocation process	estimated through the geolocation process	estimated through the geolocation process
State space model				+		+		+	+	+	
Optimisation		best match for latitude	least cost track	particle filter	least squares	unscented Kalman filter	probability sampling	MCMC (block update)	unscented Kalman filter	particle filter	probability sampling
Land scape mask		+		+			+	+		+	+
Optional/ mandatory environmental characteristics		/SST	/SST	/SST, depth		SST, depth/	SST/	SST/	SST, depth/	possible to implement/	SST, depth, sea ice …/
Optional/ mandatory speed input		+/	/+	/+				/+		+/	+/
Developed mainly for	all organisms	fish	fish	fish	all organisms	fish	marine organisms	marine organisms	fish	terrestrial birds	marine organisms

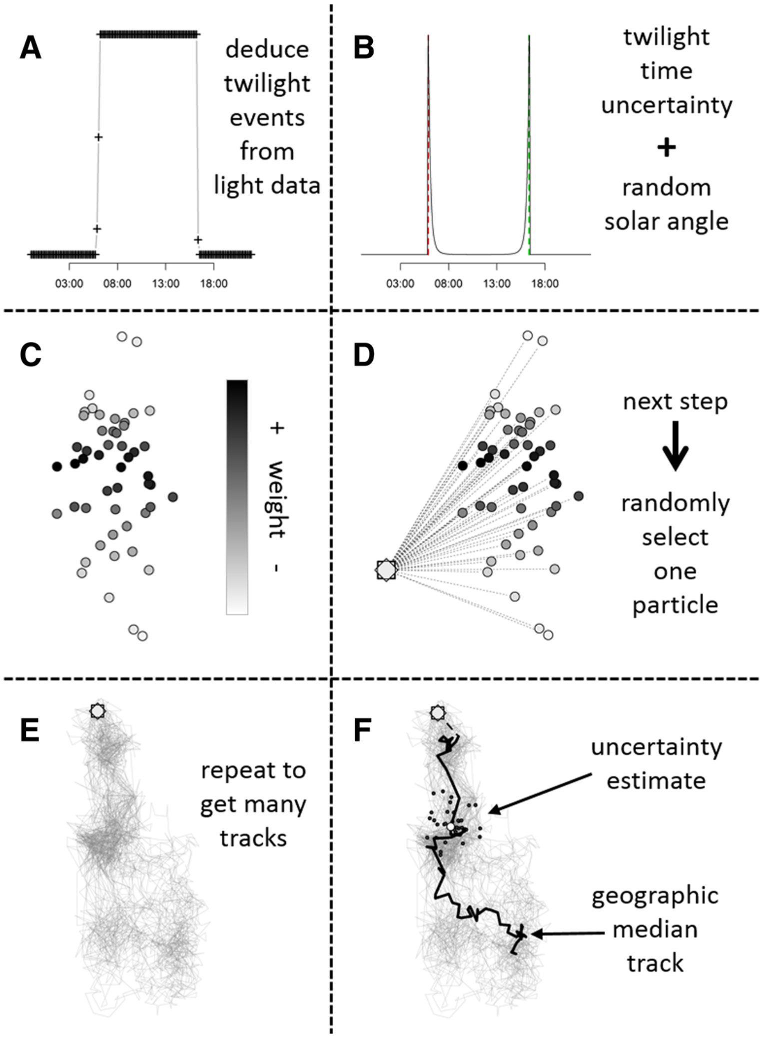

Fig. 1 Description of the probabilistic algorithm. Timing of twilight events are either deduced from raw light data or extracted from logger specific software (**a**). Each set of twilight events is replicated by the number of particles and an uncertainty as well as a random solar angle are added to compute a cloud of possible locations (**b**). These calculated particle locations for a set of twilight events are weighted by any other chosen parameter (**c**). For each step one random particle based on their weights is chosen (**d**) and this process is repeated (**e**). The geographic median track is computed as most likely track and each modelled location has an estimated uncertainty based on all iterated tracks (**f**). This figure is modified after Figure 1 in [28]

5. Then, one particle is randomly selected following a distribution based on the assigned weights (Panel D, Fig. 1). If all particles in a given cloud have a weight of 0, the entire cloud is considered unlikely and discarded.
6. The algorithm moves one time step forward to t_{i+1} and steps 2 to 5 are repeated until t_n (n being the last set of twilight events).
7. Steps 1 to 6 are iterated a set number of times to construct several probable movement paths (Panel E, Fig. 1).
8. The most likely movement path is computed as the geographic median (Additional file 2) for each computed location cloud; the variation in positions of all computed paths denotes the uncertainty at each step in time (Panel F, Fig. 1).

Tremblay et al. [28] defined their particle clouds based on "raw" locations as the geographic average with a spatial error structure. This is the case for locations derived using satellite-transmitters. However, locations estimated from light data using the threshold method can only be assumed to be the geographic average if the correct solar angle for each day is selected, shading was similar both at dawn and dusk, and the animal only moved a short distance between twilight events. If any of these conditions is violated the position could be strongly biased. Therefore, we based our method on the timing of twilight events, incorporating uncertainty and unknown solar angle (steps 2 & 3). This allows uncertainties to be incorporated that are related to differences in behaviour and weather patterns, as well as dynamic latitudinal uncertainty, which reflects the season and latitude-specific uncertainty of the geolocation method. Uncertainty in twilight events is assumed to follow a log-normal distribution. This skewed distribution takes into account that a sunrise may falsely appear to occur later, due to shading, while it is improbable that light is falsely detected prior to sunrise (and the inverse is true for sunsets). The error parameters for this uncertainty can be generated using `twilight_error_estimation` (package `probGLS`, this study). It is important that the error distribution mirrors the actual behaviour of the animal. This should be done using calibration data (i.e. ~2 weeks of data recorded on the individual at a known location). Solar angles do not have to be calibrated or assumed to be constant, but rather a reasonable range of possible angles can be defined (step 2). Also, due to the above mentioned pitfalls regarding use of "raw" locations and unknown latitude and time specific error distributions, we do not interpolate between positions to utilize the higher frequency of temperature measurements by the loggers as described by [28]. Steps 4 to 8 are in principle equivalent to [28]. However, we do not include weighted distributions of individual speeds computed using the next x particles in the record, but rather use a defined speed distribution. This is because there are no specific locations on which to base these distributions; instead, there is a cloud of possible locations. Moreover, we do not consider the geographic average track to be the most probable track, but the geographic median defined as the position with the minimum sum of all distances to all other iterated locations. Therefore the selected position will always be a computed location. In contrast, the average geographic position might, for example, be on land if the cloud of points is around a land mass, even if this is unrealistic for the study species (Additional file 2).

Method assessment

The framework was tested using data from black-browed (*Thalassarche melanophris*) and wandering (*Diomedea exulans*) albatrosses (Table 2) tracked in December-January (incubation) and March-April (brood-guard), respectively, in 2015 from Bird Island, South Georgia (54°00' S, 38°03' W). All individuals were equipped with an i-gotU GPS logger (Mobile Action Technology Inc., New Taipei City, Taiwan) taped to back feathers and programmed to log a position every 10 min, and an Intigeo C250 geolocator (Migrate Technology Ltd, Cambridge, UK) attached by cable-tie to a plastic leg ring, which measured light in the range 1.1 to 74418 lux (maximum recorded at 5 min intervals) and temperature every 20 min of continuous wet (maximum, minimum and mean saved every 4 h), and tested for saltwater immersion every 6 s.

Twilight events from raw light intensities were computed with `twilightCalc` (light threshold of 2; loggers calibrated on Bird Island). To increase precision we included sea surface temperature (SST) and land avoidance. The daily median water temperature encountered by each bird was computed from temperature data collected every 4 h by the loggers. The daily mean satellite-derived SST and mean SST error was extracted from the NOAA optimally-interpolated, high resolution SST dataset at 0.25° resolution [29]. Each movement path incorporated parameter values based on the ecology of the species and information extracted from GPS data (Table 3, and Additional file 3).

To compare GPS tracks to locations estimated from geolocator data, we calculated the average GPS location between two twilight events. Deviation for each geographic median, and nearest location (both derived from geolocator data) from the average GPS positions was computed as the great-circle distance [14]. Additionally, each average GPS position was compared to locations estimated using the classical threshold method with a fixed solar angle of -5.0° and -5.8° for black-browed and wandering albatross data, respectively. These angles give the smallest average deviation of the estimated locations from the corresponding average GPS location in a range of -1° to -7°. In addition, all positions outside the boundary box were removed (Table 2). Finally, we ran sensitivity analyses to assess how many particles (1 – 10 000) and track iterations (1 – 200) were necessary to obtain a stable and reliable track output (see R script in Additional file 4) as well as how changes in the uncertainty distribution of twilight events changes accuracy.

Results

Combined geolocator and GPS data were obtained for 33 and 27 black-browed and wandering albatrosses,

Table 2 Summary of tracking data available for method assessment

Species	# of individuals	# of tracks	mean ± sd (min – max) trip duration [days]	mean ± sd (min – max) # of locations per track	Deployment period
black-browed albatross	33	33	9 ± 4 (3–17)	15 ± 7 (5–31)	10 Dec 2014 to 6 Jan 2015
wandering albatross	27	32	3 ± 1 (1–7)	4 ± 2 (2–9)	14 Mar 2015 to 3 Apr 2015

Table 3 Algorithm parameters used to compute locations for both assessment data sets

Model parameter	Description	Value used
`particle.number`	number of particles computed for each point cloud	10 000
`iteration.number`	number of track iterations	200
`sunrise.sd` & `sunset.sd`	shape, scale and delay values describing the assumed uncertainty structure for each twilight event following a log normal distribution	2.49/ 0.94/ 0[a]
`range.solar`	range of solar angles used	-7° to -1°
`boundary.box`	the range of longitudes and latitudes likely to be used by tracked individuals	120 W to 40 E 90 S to 0
`day.around.spring.equinox` & `days.around.fall.equinox`	number of days before and after an equinox event in which a random latitude will be assigned	includes the entire wandering albatross tracking period
`speed.dry`	fastest most likely speed, speed standard deviation (sd) and maximum speed allowed when the logger is not submerged in sea water	12/ 6/ 45 m/s for black-browed albatross[b] & 12/ 7/ 70 m/s for wandering albatross[b]
`speed.wet`	fastest most likely speed, speed sd and maximum speed allowed when the logger is submerged in sea water	1/ 1.3/ 5 m/s[c]
`sst.sd`	logger-derived sea surface temperature (SST) sd	0.5 °C[d]
`max.sst.diff`	maximum tolerance in SST variation	3 °C
`east.west.comp`	compute longitudinal movement compensation for each set of twilight event [37]	used

[a] The resulting uncertainty structure for both twilight events is illustrated in Additional file 1. These parameters are chosen as they resemble the twilight error structure of open habitat species in [20]

[b] inferred from GPS tracks (see Additional file 3 for details)

[c] Antarctic circumpolar current speed up to fast current speeds (i.e. Malvinas current) [38] as the tagged animal is assumed to not actively move when the logger is immerged in seawater

[d] logger temperature accuracy

respectively, in two contrasting periods characterized by minimal (solstice) and maximal (equinox) uncertainty in latitude estimation using light data (Table 2). Examples for a black-browed albatross track during the summer solstice and a wandering albatross track during the fall equinox showing both processed geolocator and GPS locations are illustrated in Fig. 2. The overall median distance between the most probable geolocator and mean GPS locations was 185 km (range 5 to 2740 km) and 145 km (range 8 to 493 km) for tracks during the summer solstice and fall equinox, respectively (Table 4, Additional file 5). The median closest distance of each iterated location cloud to the mean GPS location was 19 km and 17 km during the summer solstice and fall equinox, respectively. Using the threshold approach with a constant solar angle of -5.0° and -5.8° resulted in median distances to average GPS locations of 226 km (22% lower accuracy than the new method) and 662 km (357% lower accuracy) for the black-browed albatross data during the summer solstice and wandering albatross data during the fall equinox, respectively. Moreover, only 54% of positions could be calculated using the threshold method with the `GeoLight` package and a constant angle of -5.8° during the fall equinox compared to our new approach (Table 3).

The relationship between number of particles used, number of iterations and median minimum distance of each point cloud to the average GPS locations for both time periods is illustrated in Fig. 3. Accuracy increases with increasing iterations and particles numbers, reaching an asymptote at around 60 iterations, and 300 and 800 particles during the solstice and equinox periods, respectively. Varying the shape parameter (μ) for the assumed twilight uncertainty distribution for both twilight events simultaneously from 1 to 4 and thereby increasing the possible range of error from ~8 min to ~2 h, while keeping the maximum probability at the input twilight timing, did not seem to affect the accuracy of the results for either time period (Additional file 6).

Discussion

By comparing locations calculated from light and temperature data to concurrent GPS positions during two contrasting times of the year (close to the solstice and equinox), we demonstrated that our new method provides consistently high accuracy throughout the year, similar to the minimum uncertainty of the standard threshold method (i.e. during solstices at high latitudes; Table 4) [14, 30]. Tracks from two fast moving seabird species, black-browed and wandering albatrosses, could be reconstructed using this approach by incorporating

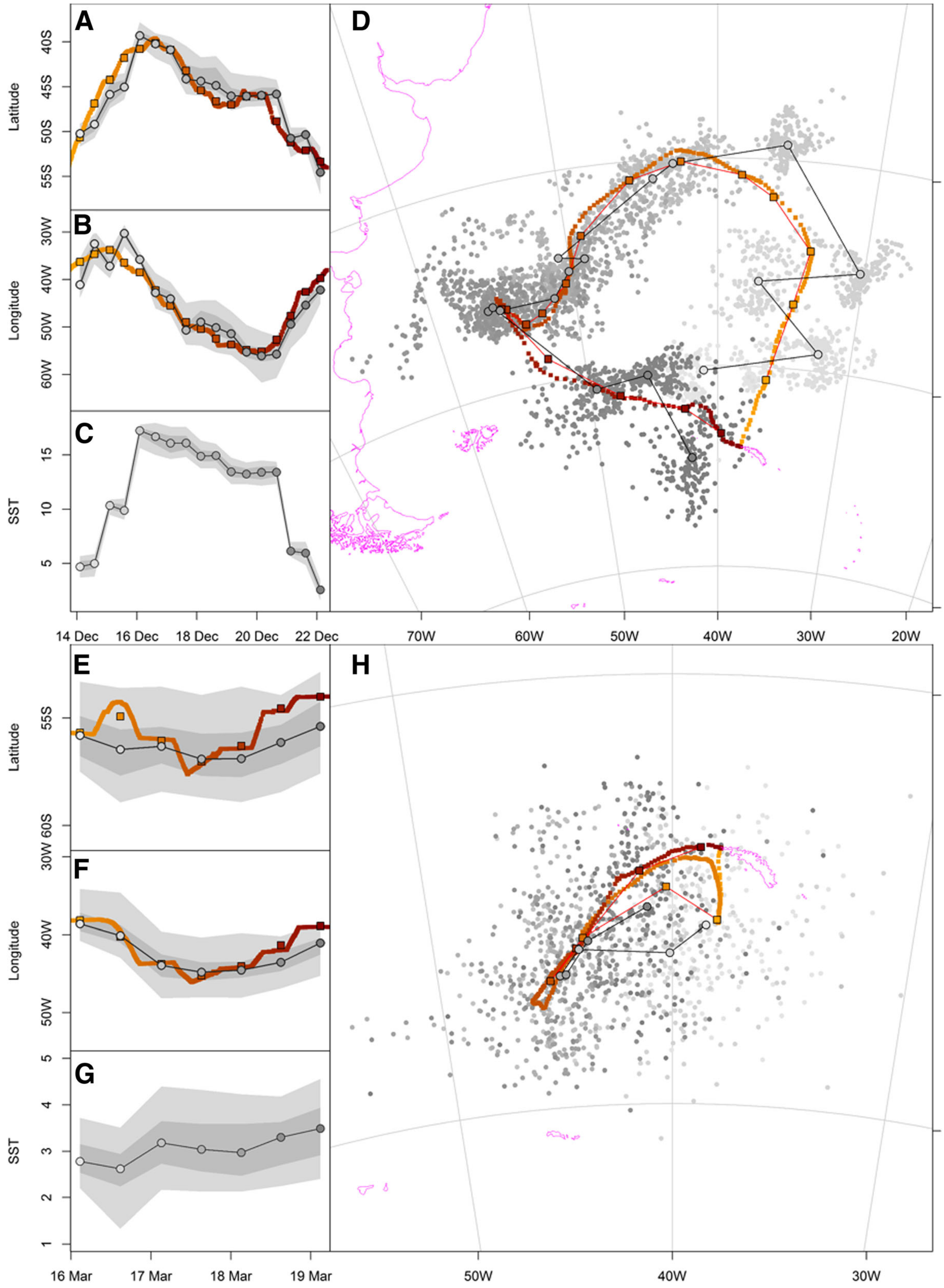

Fig. 2 (See legend on next page.)

(See figure on previous page.)
Fig. 2 Examples trips from a black-browed albatross during the summer solstice (**a**-**d**) and a wandering albatross during the fall equinox (**e**-**h**). (**a** to **c & e** to **g**) show the change in latitude, longitude and encountered sea surface temperature (SST) with time while (**d & h**) represent the tracks. Grey scale positions show all processed geolocator locations; black framed grey positions represent median geographic geolocator locations; red symbols represent 10 min resolution GPS locations; black framed red squares are daily average GPS locations; track direction from light to dark. Shaded grey areas in (**a**) to (**c**) represents 95 and 50% uncertainty

additional environmental data (notably SST). In addition to providing positions around the equinox, this method provides an uncertainty associated with each computed position. This uncertainty could be used, for example, to build more realistic models of the measurement component of SSM for further behavioural analysis to account for the complex error structure of geolocations.

Our method for estimating locations from light-level data offers a simple, fast and intuitive approach accessible via the R package `probGLS`. This method is not Baysian or based on Kalman filter in contrast to the other statistically-advanced methods that are currently available (such as the R packages `Trackit` [25], `SGAT/tripEstimation` [26], and `FlightR` [27], Table 1) and we hope it will be less of a “black box” for many ecologists, with assumptions being more transparent at the expense of a mathematically rigorous framework. As with `FlightR`, our method generates a cloud of possible particles for each location, but uses probability sampling to construct a path rather than a particle filter. Further, the current implementation of `probGLS` takes about 30 min for a 1 year track (2000 particles, 100 iterations; Intel Core i7-3540 M 3 GHz, 16 GB RAM). This is to our knowledge faster than any SSM method (Table 1). With a run time per track of less than an hour it is feasible to run sensitivity analyses on input parameters (as in this study). Unlike the R packages based on SSM, `probGLS` cannot account for movement of the study animal between consecutive twilight events, which can reduce certainty in location estimation for certain taxa. However, it does not require the assumption or calibration of a constant solar angle throughout the year [20, 31], unlike the classical threshold method. The reason is that the added uncertainty around each twilight event as well as the range of solar angles accounts for different behaviour and levels of sensor shading around sunrise and sunset during the tracking period.

Twilight events for both albatross species computed by `twilightCalc` were not inspected manually for false or low-confidence transitions (reflecting interruptions to light records), and only outliers outside the defined boundary box (Table 3) were removed during processing. The range in accuracy, in particular for black-browed albatross data (Table 4), shows that the method was unable to correct twilight events which are far from the correct time (i.e. falsely assigned). These result in unreliable location clouds which the algorithm will attempt to fit into the movement path. However, most of these outliers were removed subsequently in the algorithm based on the assumed speed distribution, as well as land avoidance and SST weighting (steps 4 & 5). Accuracy could be improved if twilight events are either edited manually, filters such as `loessFilter` (`GeoLight` package) are applied, or the extent of the boundary box reduced before running the new method.

The number of particles needed for computation depends on the range of latitudes set in the parameter `boundary.box` (i.e. assumed latitudinal range during the equinox) as well as the longitudes defined through the parameters `sunrise.sd` and `sunset.sd`. We let latitude during the equinox vary by 90° (Table 3) as we did not expect the tracked individuals to cross the equator, whereas longitudinal uncertainty was assumed to vary over ~35 min to

Table 4 Summary of number of locations estimated and distance to average GPS position using two methods of light level location estimation

Species and time period	Method	# of locations	Median distance to GPS location [km]	Mean ± sd (min – max) distance to GPS location [km]
black-browed albatross during solstice	- 5.0° sun elevation	504	226	347 ± 448 (13 – 4170)
	geographic median particle	482	185	235 ± 218 (5 – 2740)
	particle cloud	482	19	66 ± 168 (0 – 2380)
wandering albatross during equinox	- 5.8° sun elevation	79	662	1225 ± 1478 (80 – 5925)
	geographic median particle	148	145	155 ± 82 (8 – 493)
	particle cloud	148	17	25 ± 24 (1 – 133)

Geographic median particle refers to the calculated most probable movement track, and particle cloud refers to the minimum distance of the iterated particle cloud from the GPS location (see Methods for details). Black-browed albatrosses were tracked around the solstice and wandering albatrosses around the equinox

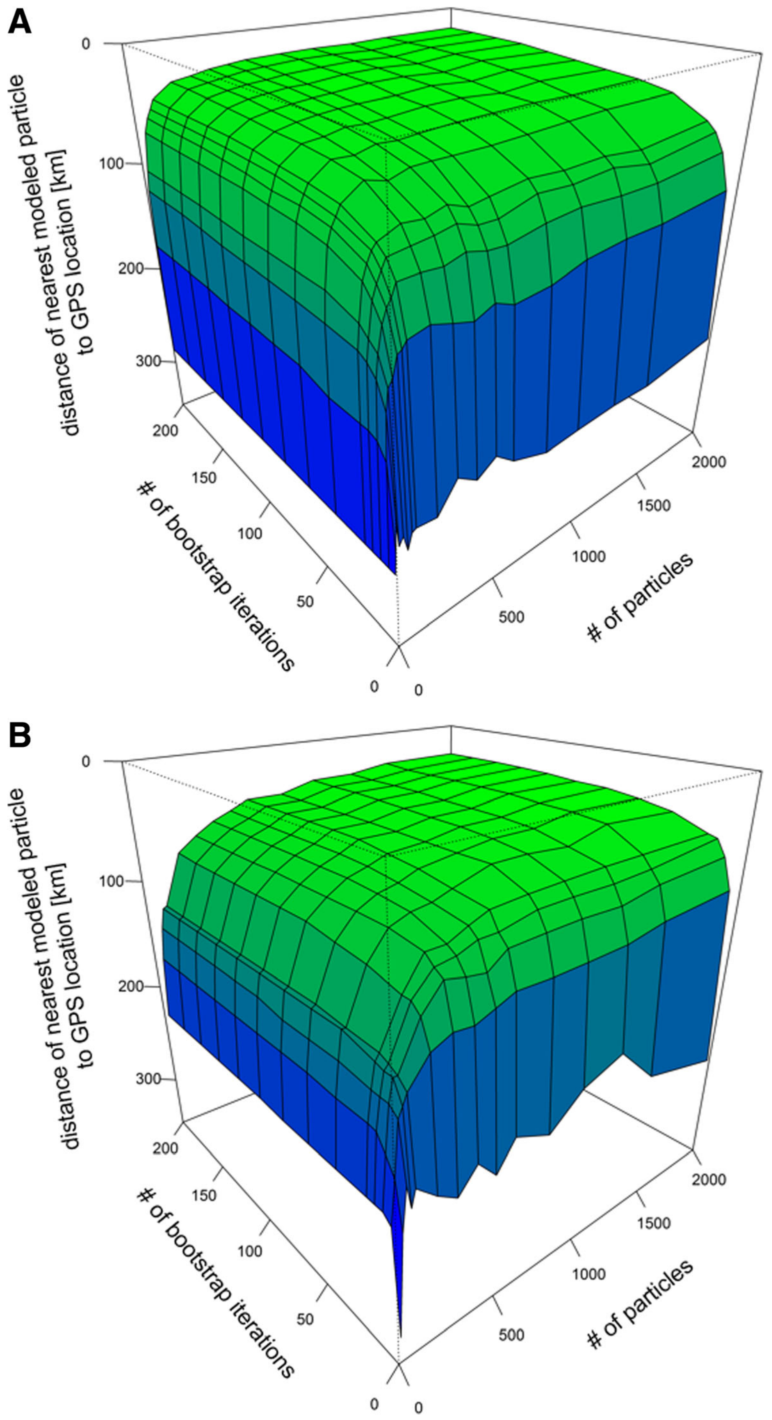

Fig. 3 Median distance between the nearest particle and its associated average GPS location in relation to number of iterations and number of particles used. **a** Black-browed albatross data during the summer solstice; **b** Wandering albatross data during the fall equinox

account for differences in shading due to behaviour and weather patterns (Table 3, Additional file 1). Based on Fig. 3, at least 800 particles are needed for stable results throughout the year. If the latitudinal uncertainty during the equinox is 180° (i.e. from pole to pole) the number of particles would need to be doubled. The minimum number of iterations needed for a consistent output was already reached at 60.

The median closest distance of each iterated location cloud to the mean GPS location of 19 and 17 km in the two time periods (Table 4) reflects the 0.25° spatial resolution of the satellite-derived SST dataset. Using a higher resolution SST dataset will likely increase the accuracy of this approach for this particular example. This illustrates that the selected weightings, as well as their resolution influence the accuracy and degree of uncertainty of a track. A high range of solar angles, a high uncertainty in twilight events and high assumed movement speed, combined with a lack of available environmental characteristics will lead to greater uncertainty and lower accuracy overall. Conversely, the accuracy of the method would increase if the range of solar angles as well as the twilight event uncertainty could be restricted based on previous knowledge (e.g. calibration periods).

We have demonstrated here that the algorithm achieves stable results with fast moving species in open landscapes (flying seabirds) and are optimistic that results would be comparable for animals inhabiting other habitats (e.g. terrestrial birds and diving organisms), especially if additional information to weight the computed particles is available. We already have preliminary indications that the algorithm performs well on diving species such as penguins. However, the suitability of the method for a wider range of species has to be confirmed in further studies.

Conclusion

We presented an intuitive and time-efficient algorithm which makes it possible to analyse geolocator data from loggers of different types and manufacturers, deployed on any animal, throughout the year, including equinox periods (if sufficient additional information is available), in a consistent way, while acknowledging the limitations and uncertainties associated with light data. We do not claim that it is the most accurate method, but rather that it can be used widely and easily, regardless of whether the data were processed using outmoded software or new methods, without requiring a subjective step in determining or filtering locations.

Additional files

Additional file 1: Twilight event uncertainty structure. (PDF 362 kb)

Additional file 2: Geographic median description. (PDF 205 kb)

Additional file 3: Recorded ground speed frequencies. (PDF 246 kb)

Additional file 4: R script for sensitivity analyses. (TXT 9 kb)

Additional file 5: Histograms of deviation of GLS computed locations to average GPS locations using two methods of light level location estimation. (PDF 257 kb)

Additional file 6: Sensitivity analysis for changing shape parameters determining the twilight event uncertainty. (PDF 308 kb)

Abbreviations

GLS: Global location sensor; GPS: Global positioning system; SSM: State space model; SST: Sea surface temperature

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Availability of data

The source code for the probGLS R package as well as an example workflow for several logger manufacturers is available on GitHub: https://github.com/benjamin-merkel/probGLS.

Authors' contributions

BMe conceived the study. BMe, RP, NY and SD developed the detailed method. BMe coded the R package. BMe wrote the first draft of the manuscript, with contributions from RP, SD, NY, BMo and HS. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

Consent for publication

Not applicable.

Ethics approval and consent to participate

All fieldwork was approved by the British Antarctic Survey Ethics Committee and carried out under permit from the Govt. of South Georgia and the South Sandwich Islands.

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Strong migratory connectivity across meta-populations of sympatric North Atlantic seabirds

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Abstract

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. To understand the potential of migrants for adjusting to perturbations, it is critical to study how different areas used during the annual cycle by different populations are connected via individual migration strategies (i.e. migratory connectivity). Using a large-scale tracking dataset of 662 individual seabirds from two sympatric auk meta-populations (common guillemots, *Uria aalge,* and Brünnich's guillemots, *Uria lomvia*) breeding in twelve colonies throughout the Northeast Atlantic, we found strong migratory connectivity, within and between species. This was apparent through a combination of seasonal space use and occupied environmental niches, grouping Brünnich's guillemot populations into two and common guillemot populations into five previously undescribed spatiotemporal clusters. Remarkably, common guillemot populations clustered in accordance with the variable population trends exhibited by the species, while Brünnich's guillemot populations are declining everywhere where known within the study area. Individuals from different breeding populations in both species were specialized in their space and environmental use, utilizing only a fraction of the potential species-wide range. Further, migratory connectivity varied among seasons, emphasising the variable constraints faced by both species during the different stages of their annual cycle. Our study highlights that considering spatiotemporal dynamics not only in space but also in occupied environmental niches, improves our understanding of migratory connectivity and thus population vulnerability in the context of global change.

Keywords: Environmental niche, inter-population mixing, large-scale spatiotemporal dynamics, light-level geolocation, murres, population spread, seasonality, *Uria aalge*, *Uria lomvia*

Introduction

Migration is a response to spatial and temporal fluctuations in resource availability during different phases of the annual cycle (Alerstam et al. 2003, Dingle and Drake 2007). It can be expressed by a multitude of strategies defined collectively as return journeys to one or several overwintering destinations after the breeding season (Newton 2008). 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 (Robinson et al. 2009, Wilcove and Wikelski 2008). Changes in the environment encountered by migrants outside their breeding season have the potential to affect population trends through, for example, an effect on individual survival (Gaston and Powell 2003, Webster et al. 2002). 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 (Webster et al. 2002).

The concept of migratory connectivity 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 area 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 areas) during the non-breeding period (Finch et al. 2017, Gilroy et al. 2016). Generally, higher population spread is associated with enhanced inter-population mixing (also termed “weak” connectivity) while lower population spread reduces inter-population mixing (i.e. “strong” connectivity). Strong migratory connectivity is necessary for differential population trends of geographically distinct breeding populations to be driven by factors away from the breeding sites (Kramer et al. 2018). Populations with smaller geographic spread have a limited variety of migratory movements and destinations and may thus be more vulnerable to perturbations than those with larger spread (Cresswell 2014, Gilroy et al. 2016).

The concept of migratory connectivity has so far focused on the geographic distribution of migrants but can be expanded to include their environmental niches. The niches used during the annual cycle can vary independently of the geographic area occupied as migrants move simultaneously in geographic space and among environmental conditions (Peters et al. 2017, Soberón 2007, Soberón and Nakamura 2009). Consequently, migrants moving in similar geographic space may potentially occupy different environmental niches and *vice versa* (Gómez et al. 2016, Peters et al. 2017). Populations utilizing many different environments are more likely to persist than those remaining within similar environments regardless of the occupied geographic area (Davies et al. 2004, Lavergne et al. 2013, Thuiller et al. 2005). Consequently, whether or not the connectivity is expressed in terms of space use, realized environmental niche or both may have different consequences for the trajectories of the species. Moreover, in addition to the spatial and environmental aspects of migratory connectivity it is also important to consider its seasonal dynamics, i.e. not only *which* sites and environments are used, but also *when* they are used. This can have manifold consequences on individual fitness (e.g. through transmission of pathogens) and therefore population dynamics (Bauer et al. 2016, Eyres et al. 2017, La Sorte et al. 2018).

Migratory connectivity is increasingly being studied in different taxa (Fayet et al. 2017, Frederiksen et al. 2016, Frederiksen et al. 2012, Godley et al. 2010, Rooker et al. 2008, Russell et al. 2013) due to the growing availability of large tracking datasets (Hussey et al. 2015, Kays et al. 2015) with a main focus on terrestrial birds (reviewed in Finch et al. 2017, Hahn et al. 2013, Kramer et al. 2018, Taylor and Stutchbury 2016), where weak migratory connectivity is most commonly reported (Finch et al. 2017). However, migratory connectivity has been addressed only within species and only in terms of space use rather than with respect to temporal variability and occupied environmental niches. Here, we assessed year round spatial and environmental migratory connectivity within and between two sympatric circumpolar seabird species, the temperate common guillemot (hereafter COGU, *Uria aalge*) and the arctic Brünnich's guillemot (hereafter BRGU, *Uria lomvia*). These two auk species share similar morphology and life history (Benowitz-Fredericks and Kitaysky 2005, Gaston and Jones 1998). Their energetic costs for flight are among the highest recorded for any vertebrate (Elliott et al. 2013) suggesting severe constraints upon large-scale movement capabilities and high sensitivity towards habitat loss (Taylor and Norris 2010). Guillemots also exhibit contrasting population trends in the Atlantic, with colonies of BRGUs generally declining within the Northeast Atlantic and those of COGUs exhibiting more variable trends (table 1, Anker-Nilssen et al. 2017, Fauchald et al. 2015, Frederiksen 2010, Frederiksen et al. 2016, Garðarsson et al. 2019, JNCC 2016). Some evidence exists that population trends as well as adult survival in *Uria* spp. are associated with environmental conditions experienced during the non-breeding period (Descamps et al. 2013, Fluhr et al. 2017, Gaston and Powell 2003, Mesquita et al. 2015) and that Atlantic-wide BRGU population trends are connected to mid-winter space use (Frederiksen et al. 2016).

Divergent population trends for these congeneric seabirds make them an ideal study system to investigate the importance of space and environmental connectivity across the migratory phase (Gilroy et al. 2016, Taylor and Norris 2010, Webster et al. 2002). To characterise migratory connectivity and the potential link to population trends in *Uria* spp., we tracked the annual movements of 327 adult COGUs and 335 adult BRGUs from twelve breeding populations, representing the entire breeding range of the Northeast Atlantic population. To evaluate migratory connectivity, in terms of inter-population mixing and population spread, within and across species we not only considered the geographic areas occupied, but also the environmental conditions experienced and their variability during different phases of the annual cycle.

Material & Methods

Study species & area

Guillemots are large (~1kg), deep diving (up to ~200m), long lived, colonial seabirds with high adult survival, high breeding philopatry, high breeding synchrony and low annual fecundity (Benowitz-Fredericks and Kitaysky 2005, Gaston and Jones 1998). Their non-breeding period can be divided into several seasons corresponding to different life history stages throughout the annual cycle. Post-breeding, successful males stay with their flightless chicks for at least a month after colony departure (Elliott et al. 2017, Harris and Wanless 1990). Further, guillemots undergo moulting of 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, Bridge 2004, Elliott and Gaston 2014, Thompson et al. 1998). Both species display periodic synchronized attendances at their breeding colonies starting up to several months prior to breeding (Gaston and Nettleship 1981) which in effect restricts them to central place foraging during this period. Hence, adult guillemots are only able to move without constraints for extended periods of time after they have renewed their flight feathers and before the pre-breeding colony attendance period starts.

Research was conducted at 16 seabird colonies spanning 56°N to 80°N and 16°W to 68°E in the Northeast Atlantic (table 1, figure 1A). For the purpose of this study we combined some colonies in close spatial proximity to each other (< 160 km) which exhibited similar space use patterns. This resulted in twelve breeding populations. BRGU and COGU breed sympatrically at four of these sites (table 1).

Tracking data

We used archival light-level loggers to estimate spatiotemporal locations of guillemot individuals throughout the non-breeding period. These devices record light intensity and time which can be used to estimate approximate latitude (i.e. day length) and longitude (i.e. time of noon) positioning twice daily (estimated accuracy: ~180 km, Merkel et al. 2016). They are attached to a leg band with cable ties (logger, band, and cable ties < 0.5% adult body mass) and need to be retrieved in subsequent years after deployment for data to be downloaded. During the summers of 2007 to 2017 we captured adult guillemots with noose poles at different sites and equipped them with geolocators which we retrieved in subsequent years (overall retrieval rate > 60%). Individuals were chosen opportunistically in most cases among birds breeding on cliff ledges on the landward edge of the colony. This resulted in 1103 annual tracks (531 BRGU, 572 COGU) of 662 individual guillemots (335 BRGU, 327 COGU, table 1). All subsequent analyses have been conducted in R 3.3.3 (R Development Core Team 2017). All loggers (Mk15: British Antarctic Survey, Cambridge, UK; Mk3006: Biotrack, Wareham, UK; F100, C250 & C330: Migrate Technology, Cambridge, UK; or L250A: Lotek, St. John's, Newfoundland, Canada) also recorded temperature and salt water immersion ("wet/dry") data which were used in combination with recorded light data to increase location accuracy. We calculated a most probable movement track for each individual and tracking year using an iterative approach utilizing probability sampling (Merkel et al. 2016 and details in SI 1). We binned the positional data into four seasons - irrespective of year tracked (assuming no inter-annual variation in the average non-breeding distributions, PAPER III) - to capture possible variability due to life history stages throughout the annual cycle. The delimitation of these seasons was based on assessment of core time periods in which little movement was observed across all individuals from all colonies and both species resulting in: autumn (10 August - 28 September), early winter (18 November - 6 January), late winter (17 January - 25 February), and spring (27 March - 25 May). We assume that autumn describes the post-breeding-moulting period; the two winter seasons capture temporal variability in movement behaviour during times without movement restrictions for most breeding populations; and spring is characterized by central place foraging restrictions due to pre-breeding attendance at most colonies.

Location estimation in both species and all breeding populations were to varying degrees affected by a lack of twilight events due to the polar night or midnight sun (table S2). Such cases concerned individuals using areas above 66°N, generally in the Barents Sea. Although sample size in some populations was potentially not sufficient to capture their entire distributional range (table 1), they nonetheless represent adequately the potential variability of exhibited migration strategies.

Environmental niche

To quantify environmental niches occupied during the non-breeding period, we used eight ecologically relevant oceanographic parameters (Fort et al. 2009, Fort et al. 2013b, McFarlane Tranquilla et al. 2015); three sea surface temperature variables, two sea surface height variables, surface air temperature, distance to the marginal sea ice zone and bathymetry (details in SI 1). The environment occupied was then assessed using the concept of environmental space (Broennimann et al. 2012) defined as the first two axes of a principal component analysis (PCA) of all environmental parameters calibrated on the available environment. To capture the variability of the available environment, we sampled 20000 points with equal spatial coverage across the entire study area (figure S2) every two weeks for the entire study period (2007-2017). The study area was defined as 18 large marine ecoregions (hereafter ecoregions, Skjoldal et al. 2013) encompassed by the annual distribution of both guillemot species in the Atlantic (Cramp 1985, Gaston and Jones 1998) (figure 1A). Ecoregions are large regions of ocean space along coasts and continental shelfs characterised by specific ecological criteria (Skjoldal et al. 2013). To accommodate the aforementioned distributions, three additional areas in the middle of the North Atlantic away from continental shelfs were defined (Labrador Sea, Mid-Atlantic, and Central North Atlantic). All individual positions were projected onto the PCA (PC1 = 44% & PC2 = 19%, figure S3). Available and occupied environmental space were then calculated using Gaussian kernel utilization distributions (UD, standard bandwidth, 200 x 200 pixel grid, `adehabitatHR` package, Calenge 2006) following Broennimann et al. (2012).

Large-scale spatiotemporal inter-population mixing

To quantify large-scale inter-population mixing and species wide spatiotemporal movement partitions we developed species-specific movement networks using network theory (Taylor and Norris 2010). All calculated bird positions were assigned to ecoregions. We then used the proportion of locations in each ecoregion in each season in seasonal cluster analysis (complete-linkage clustering) to assign each individual to a given ecoregion. To avoid pseudo-replication we used only one year of tracking, randomly selected, for each individual with repeated tracks. Optimal number of clusters was determined using overall average silhouette width (Borcard et al. 2018) for each season. For individuals affected by midnight sun conditions during the spring season we included the proportion of locations unavailable due to a lack of twilight events in the cluster analysis. Similarly, for the few instances where individuals during early winter had no locations, due to polar night influence (table S2), birds were assumed to use the ecoregion “Barents Sea”. Each breeding population present in the network was given the same weight and considered to be a node in the network (eight per species). Next, each individual in a given population got a proportional weight based on the total available tracks from that population. These scaled movements (network edges) between ecoregions and seasons (network nodes) were combined to create species-specific movement networks.

To identify possible partitioning within each species-specific network we used a Walktrap community finding algorithm (finding clusters via random walks with five steps taking into account the proportional movement between ecoregions and seasons, `igraph` package, Csardi & Nepusz 2006).

This method also returns a modularity index that ranges from 0 to 1 (the closer to 1, the more the network exhibits clustering with respect to the given node grouping). A network is considered to exhibit significant cluster structuring above a value of 0.3 (Clauset et al. 2004). Total number and proportional use of population- and species-specific most common migration strategies were identified as unique individual movement paths through each network. A high number of strategies and low proportion of individuals following the most common strategy would indicate weak migratory connectivity (the opposite would be true for strong migratory connectivity). In addition, a species-wide Mantel correlation was used as an independent method to quantify migratory connectivity (Ambrosini et al. 2009, Cohen et al. 2018), and was computed for individual ten day centroid locations throughout the non-breeding period to assess the robustness of our results (details in SI 1).

Meso-scale inter-population mixing

Individual seasonal kernel UDs in geographic space were estimated with 25 km grid resolution in polar stereographic projection and a bandwidth of 30 based on a median least square cross-validation score of all individual- and season-specific kernel UDs. In order to test whether geographic space use is population-specific or homogenous between different populations and species in each ecoregion and season, we calculated the average overlap as Bhattacharyya's affinity (Fieberg and Kochanny 2005): 1) between four random individual kernel UDs from the same population occupying the same ecoregion, and 2) between four random individual kernel UDs of the two populations compared (two individuals each). This process was repeated 1000 times for both pairs in the comparison. We used this test for all populations of either species with at least four individuals present in the same ecoregion and season. The resulting comparisons were summed to species- (within and between species, *sp*) and cluster-specific (within and across clusters, *c*) proportions of inter-population mixing within ecoregions (*P*) for each season (*t*) ranging from 0 (populations segregate) to 1 (populations mix) using:

$$P_{\mathrm{sp,c,t}} = 1 - \frac{N_{\mathrm{sig,sp,c,t}}}{N_{\mathrm{all,sp,c,t}}} \qquad \text{(Eq. 1)}$$

where, *N* is the number of considered comparisons, *sig* denotes only comparisons where within population overlap of either comparisons pairs is significantly greater than between population overlap (one tailed t-test with Bonferroni corrected significance level, p=0.05/number of correlation tests) and *all* denotes all comparisons. Ecoregion-, species- and season-specific Mantel correlations were calculated to assess the robustness of these results with an independent method (details in SI 1).

Intra- and inter-population mixing of occupied environmental niches

In order to quantify inter-population mixing of ecoregion-, species- and population-specific environmental niches occupied in each season we used the niche similarity test (Warren et al. 2008). This test compares two occupied niches and addresses whether niche 1 is more similar to the compared niche 2 than would be expected by chance. The niche as kernel UD in environmental space of one comparison pair was randomly relocated within the available environmental space while retaining the UD's shape (1000 permutations for each comparison pair). Overlap between observed niches as well as the randomly relocated and observed niches was than calculated using Schoener's D (Broennimann et al. 2012). If the observed overlap is greater than 95% of the randomly relocated niches, the compared environments are considered to be more similar than expected by chance. We tested similarity between ecoregion-, species- and population-specific environmental spaces in each season to assess migratory connectivity in environmental space as well as niche partitioning between species. These environmental similarities together with the proportional use of different ecoregion by populations are then integrated into an environmental similarity index (*S*). This index is ranging from 0 (all birds occupy distinct environments) to 1 (all birds occupy a similar environment) and is computed for each species (*sp*), population (*c*) and season (*t*) as:

$$\mathrm{S_{sp,c,t}} = \frac{\max\,(\mathrm{PR_{sp,c,t,1\&2}})^2 \; + \; \sum_{\mathrm{sig}}\,(\mathrm{PR_{sp,c,t,1}} \times \mathrm{PR_{sp,c,t,2}})}{\max\,(\mathrm{PR_{sp,c,t,1\&2}})^2 \; + \; \sum_{\mathrm{all}}\,(\mathrm{PR_{sp,c,t,1}} \times \mathrm{PR_{sp,c,t,2}})} \qquad \text{(Eq. 2)}$$

where, *PR* is the proportional use of the compared nodes (*1* & *2*), *sig* denotes only comparisons with similar environments (one way is considered sufficient, i.e. $\mathrm{niche\ 1} \cong \mathrm{niche\ 2} \mid \mathrm{niche\ 2} \cong \mathrm{niche\ 1}$) and *all* denotes all comparisons. As compared environmental spaces are population-, species- and in particular ecoregion-specific, we included a maximum term in equation 2 to account for the uneven distribution of a given population across ecoregions (figure S4). However, this term is not applicable and hence removed to compute the same index between populations and/or clusters (*c1* & *c2*) of the same species or between species (*sp1* & *sp2,* figure S4) resulting in:

$$\mathrm{S_{sp,c,t}} = \frac{\sum_{\mathrm{sig}}\,(\mathrm{PR_{sp1,c1,t}} \times \mathrm{PR_{sp2,c2,t}})}{\sum_{\mathrm{all}}\,(\mathrm{PR_{sp1,c1,t}} \times \mathrm{PR_{sp2,c2,t}})} \qquad \text{(Eq. 3)}$$

Population spread

To quantify species and population spread in space and the environment we calculated the occupied geographic and environmental space as the area covered by all relevant individual and seasonal 90% kernel UD contours in each season as well as the entire non-breeding period (all seasons combined).

Results

Large-scale spatiotemporal inter-population mixing

Both species exhibited marked spatial clustering on a large spatiotemporal scale with distinct annual migration strategies and strong migratory connectivity. Five and two distinct clusters (modularity of 0.59 and 0.36 indicating significant clustering) describing the non-breeding distribution were identified for COGU and BRGU, respectively (table 1, figure 1B/C). These clusters were also visible in each season (figure 2, SI 2) and corresponded to their population trends (i.e. COGU populations whose individuals are part of the same cluster during the non-breeding season show the same trend, table 1). For BRGU - declining all over our study area- a migratory divide was seen along the western Barents Sea edge splitting Spitsbergen BRGU populations (figure 2). Breeding populations to the west of this divide spent the autumn along eastern Greenland and move towards Iceland and western Greenland during winter while birds breeding in the rest of the Barents Sea utilized the Barents and Kara Sea during autumn and generally stayed there year round, with the exception of Bjørnøya individuals (figure S3.13). Increasing COGUs populations in the Barents Sea and decreasing populations in the Greenland and Icelandic Sea also grouped into these clusters, whereas populations in the Faroe Islands (decreasing trend), and the one along the coast of Norway (increasing trend) and eastern UK (increasing trend) displayed distinct migration strategies (table 1, figure 1 & 2). Both species exhibited little inter-population mixing between their identified clusters and COGU even less so than BRGU (table S4). An exception was visible for COGU in the Barents Sea where a varying proportion of birds from all breeding populations (except Iceland) congregated during autumn (figure 1B & 2A). Species-wide Mantel correlation was also high (> 0.5) throughout the entire non-breeding period for both species (figure S5) confirming the identified strong migratory connectivity.

Each species utilized only a small fraction of potential migration strategies (indicating strong migratory connectivity) with BRGUs (60 unique strategies = 16% of possible paths through the network given the sample size) displaying more strategies than COGUs (40 = 9%) while both species combined only displayed 91 unique strategies (11%) on this large spatiotemporal scale. At the breeding population-level, a variable, but low amount of migration strategies were displayed with birds from the North-East and North Sea clusters showing little variability (table 1). Most tracked individuals followed the most common population-specific strategy. Most variability in spatiotemporal use was visible for individuals in the Mid-West cluster, in particular for BRGUs (table 1, SI 3).

Meso-scale inter-population mixing

Individuals from a given population and species were more likely to encounter conspecifics from their own population than an individual from a different population and/or species, which occupied the same ecoregion (figure 3). During autumn, BRGUs from all populations showed population-specific space use, while COGUs mixed to some extent (figure 1B, 3). Most homogenous space use (mixing) was visible within species for individuals from the Mid-West cluster (around Greenland and Iceland). Here, principally during winter, individuals from different populations mixed within the same ecoregion occupied. Most between species-mixing was apparent during spring (figure 3), particularly for sympatrically breeding populations (figure S6). Ecoregion-specific Mantel correlation analysis corroborated these results (figure S5).

Environmental intra- and inter-population mixing and species segregation

Both species were composed of populations and clusters occupying distinct environments and hence, exhibited little inter-population mixing in occupied environmental niches. Individuals from the same population and species occupied similar environments with most variability present during winter (figure 4). BRGU populations in the Mid-West cluster - utilizing a vast area - inhabited similar environments (figure 4). In contrast, BRGU populations in the North-East cluster inhabited distinct environments throughout the non-breeding period. COGU clusters generally occupied cluster-specific environments with most variability displayed for populations in the Mid-West cluster. Differential segregation between the two sympatrically breeding species in space and sometimes environment experienced was to a variable extent displayed during all seasons, except spring (figure 4 & S6). But, the two congeneric species in the Mid-West cluster exhibited more environmental niche mixing than in the North-East cluster.

Population spread

The observed strong migratory connectivity in geographic and environmental space was also visible in species and population spread in both spaces. Compared to COGUs, BRGUs dispersed over a wider area which is characterized by more heterogeneous environments in all seasons (figure 5). For none of the breeding populations did individuals ever utilize the entire space or environment occupied by a species. However, BRGU populations generally spread out over more space and environments compared to COGU populations (figure 5). Both species exhibited more concentrated space use during autumn and spring and spread out more in the winter seasons. This pattern was also apparent at the population-level. Finally, neither species utilized its entire annual occupied range in space or the environment during any given season (figure 5).

Discussion

Our analysis of meta-population-level migratory connectivity for the genus *Uria* revealed that COGUs exhibit strong migratory connectivity - in terms of low inter-population mixing and low population spread - with population space use during the non-breeding period corresponding to their population trends. Populations of BRGUs - which are generally declining in the Northeast Atlantic (Anker-Nilssen et al. 2017, Frederiksen et al. 2016) - also show rather strong migratory connectivity and cluster into two distinct groups which have not been described previously (Frederiksen et al. 2016). Compared to COGUs, the BRGU meta-population spreads out into a wider space, characterized by more heterogeneous environments (McFarlane Tranquilla et al. 2015) and exhibits more mixing between the study populations also within ecoregions. Further, in all populations where the two species breed sympatrically, they segregate in space and often in environmental use during the non-breeding period. Generally, guillemot space use as well as environments occupied were species- and population-specific with low spatiotemporal variability. This suggests that both species are comprised of space and environmental niche specialist populations. Overall, a strong seasonal pattern in space use and environmental spread was apparent. This pattern was likely driven by life history stages of the annual cycle of the two species.

The correlation between population trends and identified migration strategy clusters in *Uria* spp. (shown for COGU in this study and for BRGU in Frederiksen et al. 2016) as well as the spatial and to some extent environmental isolation between these clusters suggests that their population trends are linked to their non-breeding distributions (Desprez et al. 2018). Alternatively, population trends might be affected by conditions during the breeding period (through a change in breeding success and propensity), although this is unlikely due to the large distance between breeding populations (Frederiksen et al. 2016). Intra- and inter-specific competition for food are predicted to play a key role in shaping population and meta-population-scale migratory strategies (Svanbäck and Bolnick 2007). Such competition may explain why the studied populations exhibited such strong connectivity and in addition seldom travelled towards the Grand Banks and the Labrador shelf during the non-breeding periods. These areas have already been identified as major seabird wintering hotspots (Fayet et al. 2017, Fort et al. 2013a, Frederiksen et al. 2012, Montevecchi et al. 2012) in particular for Canadian and West Greenland guillemot populations (Frederiksen et al. 2016, McFarlane Tranquilla et al. 2013). Guillemots breeding in the Northeast Atlantic may avoid these areas to limit the competition for food. Alternatively, the Grand Banks and Labrador shelf may be outside the migratory range for these populations. Due to extremely high flight costs (Elliott et al. 2013), *Uria* spp. have a theoretical maximum migratory range of ~3400 km from their respective breeding sites (Watanabe 2016). The Grand Banks and Labrador would thus be outside this range for all populations included in this study, with the exception of the Icelandic population. Only ten BRGU annual tracks (~2% of all BRGU tracks) and no COGU track exceeded the theoretical migration range. These ten tracks were mainly from individuals utilizing the Grand Banks and the Labrador Shelf; range: 3500 - 4600 km). This supports the hypothesis that migration distance is a limiting factor for guillemots.

The relative location of colonies to prevailing surface currents might influence breeding population-specific migration strategies, especially during autumn when both sexes are flightless and successfully breeding males accompany a flightless chick (Frederiksen et al. 2016). However, we have a poor understanding of the ontogeny of individual migration patterns and the relative roles of genetics (Liedvogel et al. 2011) and social learning therein (Jesmer et al. 2018, Keith and Bull 2017, Senner et al. 2015). Culturally acquired knowledge (Grémillet et al. 2004, Guilford et al. 2011) or the lack thereof of different historically adequate staging areas (Thorup et al. 2017, Van Moorter et al. 2016) during different seasons coupled with high flight costs (Elliott et al. 2013) and a morphologically determined maximum migration range (Watanabe 2016) as well as density-dependent competition (Alerstam and Hedenström 1998, Svanbäck and Bolnick 2007) could explain the high population-specificity and low diversity of COGU and BRGU migration strategies. In order to test this, it is essential to combine information about movement patterns of immatures and their parents, and to enhance knowledge about potential genetic differences between breeding populations. In addition, to what extent individual migration patterns are fixed or adaptive to environmental changes over an individual's life time needs to be further investigated (Senner et al. 2015) in order to test inter-annual repeatability in individual migratory behaviour (McFarlane Tranquilla et al. 2014), and in turn to better assess population level impacts of environmental change (Irons et al. 2008).

Migratory strategies evolved in order to take advantage of seasonal, energetically favourable food resources and in order to avoid unfavourable conditions (Bridge et al. 2015). Different prey species or populations might be targeted by individuals with different strategies. These in turn might be influenced by different environmental conditions and changes in these conditions (Beaugrand and Kirby 2018, Carscadden et al. 2013, Fossheim et al. 2015, Rose 2005) resulting in migration strategies linked to specific population trends, as recently documented in Atlantic puffins (*Fratercula arctica*, Fayet et al. 2017), *Vermivora* warblers (Kramer et al. 2018) and Wood thrushes (*Hylocichla mustelina*, Taylor and Stutchbury 2016). Migratory plasticity is predicted to buffer populations against perturbations at local and regional scales (Betini et al. 2015, Cresswell 2014, Gilroy et al. 2016). Here, we demonstrated strong migratory connectivity and often little variability among individual migration strategies across all study populations and both species suggesting only limited capacity to buffer against local and regional perturbations. We also demonstrated that individuals from the same breeding population and occupying different spaces tended to occupy environments with similar abiotic conditions, which may explain their general susceptibility to regional (e.g. sea level pressure, Mesquita et al. 2015, Vader et al. 1990) and large-scale climatic features (e.g. the North Atlantic subpolar gyre, Descamps et al. 2013, Fluhr et al. 2017). Variability in environmental space is implied within the population spread component of migratory connectivity, when larger spread is assumed to be associated with more diverse environments experienced by a population (Finch et al. 2017, Gilroy et al. 2016). However, we showed that variability in geographic area does not necessarily lead to variability in environmental space. Hence, an assessment of environmental variability in addition to migratory connectivity is needed to evaluate population responses to perturbations. In both species space use was most restricted during autumn and spring, with concomitantly low variability in environmental characteristics. This suggests critically low capacity to adjust to perturbations during these periods, under the constraints set by the breeding cycle (such as molt of their flight feathers and pre-breeding colony attendance, Desprez et al. 2018, Dias et al. 2011).

Conclusion

We provide evidence of strong migratory connectivity within and between two congeneric seabird species at an ocean basin scale and highlight the importance of considering not only space use, but also its seasonality and occupied environmental niches. Birds from different populations and species are specialized in both their seasonal space and environmental use, utilizing only a fraction of the potential species-wide range. Crucially, these spatiotemporal dynamics are concordant to population trends. This emphasizes the importance of migratory connectivity and the environmental conditions experienced during the non-breeding period as drivers of population dynamics in migratory species, particularly in the context of global change.

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Supplementary information

- SI 1: Additional method information, results & Mantel correlation analysis
- SI 2: Species- and breeding population-specific seasonal distributions in geographic and environmental space
- SI 3: Species- and breeding population-specific large-scale spatiotemporal movement networks

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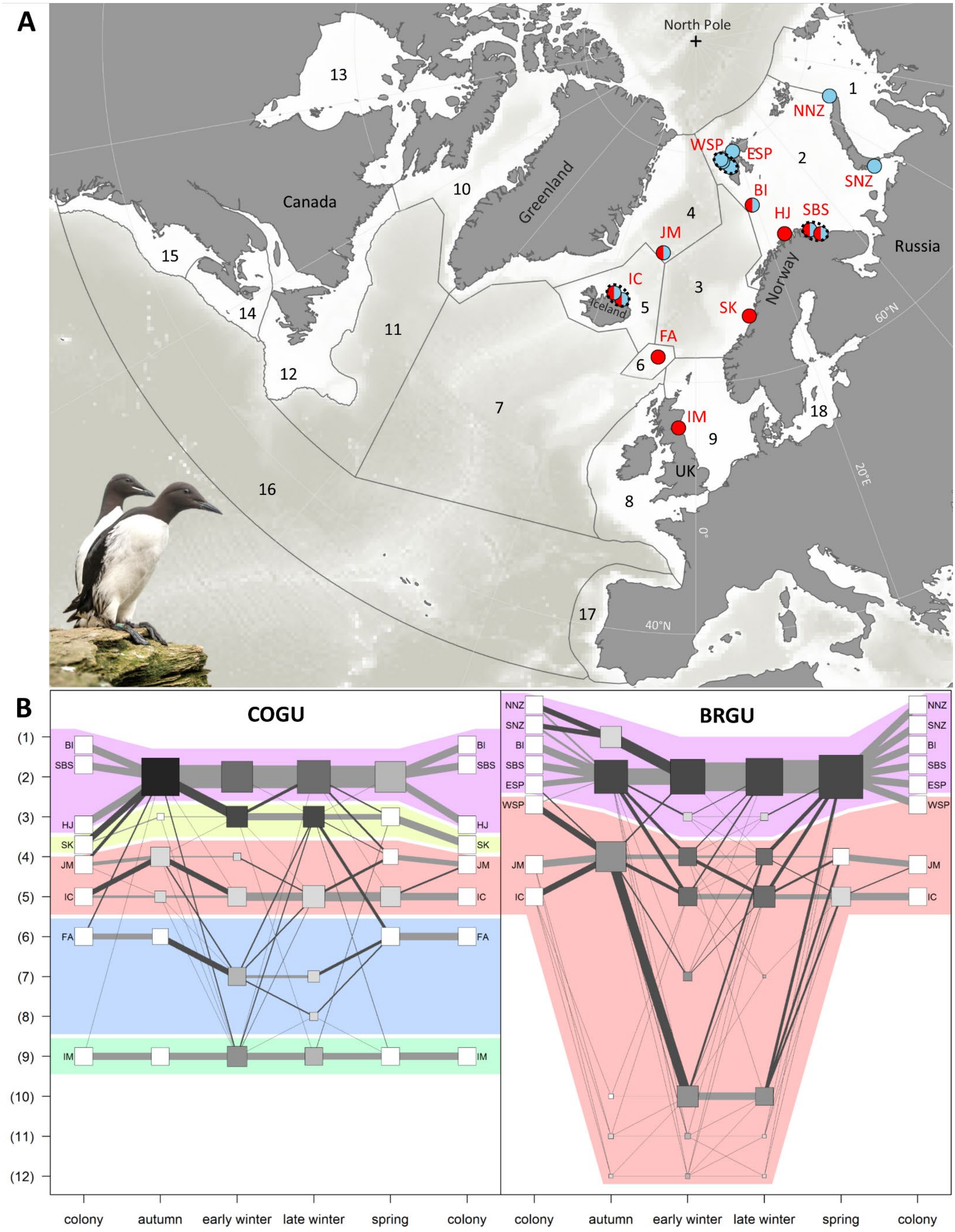
Tables and figures

Table 1. Available tracking data, published population trends, identified migration clusters, number of annual movement strategies (as unique paths through the networks in figure 1) and relative use of most common migration strategy for each breeding population and species. Some colonies (in parentheses if applicable) have been merged into populations for the purpose of this study. Tracking years denote first and last year of tracking and include gap years in many cases.

breeding population (colonies)	acronym	location	breeding population ecoregion	Common guillemot (COGU)				Brünnich's guillemot (BRGU)				cluster	# of unique strategy		% using most common strategy	
				population trend	tracking years	annual tracks	unique birds	population trend	tracking years	annual tracks	unique birds		COGU	BRGU	COGU	BRGU
Isle of May	IM	56.18°N, 2.58°W	North Sea	increasing[1,7]	2011-16	70	39	-	-	-	-	North Sea	5	-	90 %	-
Faroe Islands (Lonin)	FA	61.95°N, 6.80°W	Faroe Plateau	decreasing[2,7]	2015-16	5	5	-	-	-	-	Faroe Islands	4	-	40 %	-
Sklinna	SK	65.22°N, 10.97°E	Norwegian Sea	increasing[3,8]	2011-16	63	39	-	-	-	-	Norwegian coast	10	-	56 %	-
North-East Iceland (Grimsey, Langanes)	IC	66.44°N, 15.80°W	Iceland Shelf & Sea	decreasing[4,9]	2014-16	27	22	decreasing[4,9]	2014-16	27	24	Mid-West	6	12	78 %	46 %
Jan Mayen	JM	71.02°N, 8.52°W	Greenland Sea	decreasing[5,10]	2011-16	70	39	decreasing[5,10]	2011-16	94	54	Mid-West	15	18	24 %	29 %
Western Spitsbergen (Diabasodden, John Scottfjellet, Ossian Sarsfjellet)	WSP	78.75°N, 13.20°E	Barents Sea	-	-	-	-	decreasing[5,8]	2007-16	104	74	Mid-West	-	18	-	51 %
Hjelmsøya	HJ	71.07°N, 24.72°E	Barents Sea	increasing[5,8]	2011-16	41	27	-	-	-	-	North-East	3	-	90 %	-
Southern Barents Sea (Cape Gorodetskiy, Hornøya)	SBS	69.98°N, 32.04°E	Barents Sea	increasing[5,8]	2011-16	120	75	decreasing[6,8]	2009-16	97	64	North-East	4	15	93 %	78 %
Bjørnøya	BI	74.50°N, 18.96°E	Barents Sea	increasing[5,8]	2007-16	176	81	decreasing[5,8]	2007-16	134	59	North-East	1	13	100 %	34 %
Eastern Spitsbergen (Alkefjellet)	ESP	79.59°N, 18.46°E	Barents Sea	-	-	-	-	unknown	2015-17	14	13	North-East	-	2	-	79 %
Northern Novaya Zemlya (Oranskie islands)	NNZ	77.07°N, 67.64°E	Barents Sea	-	-	-	-	unknown	2016-17	6	6	North-East	-	2	-	74 %
Southern Novaya Zemlya (Kara Gate)	SNZ	70.59°N, 55.02°E	Barents Sea	-	-	-	-	unknown	2015-17	55	41	North-East	-	2	-	67 %

[1] (JNCC 2016), [2] (Frederiksen 2010), [3] other colonies along the Norwegian coast are decreasing as well as increasing (Fauchald *et al.* 2015; Anker-Nilssen *et al.* 2017), [4] (Frederiksen 2010; Garðarsson *et al.* in press), [5] (Fauchald *et al.* 2015; Frederiksen *et al.* 2016; Anker-Nilssen *et al.* 2017), [6] based on declining trend of Hjelmsøya BRGUs (Fauchald *et al.* 2015; Frederiksen *et al.* 2016; Anker-Nilssen *et al.* 2017), [7] 15 year trend, [8] 10 year trend, [9] 20 year trend, [10] 7 year trend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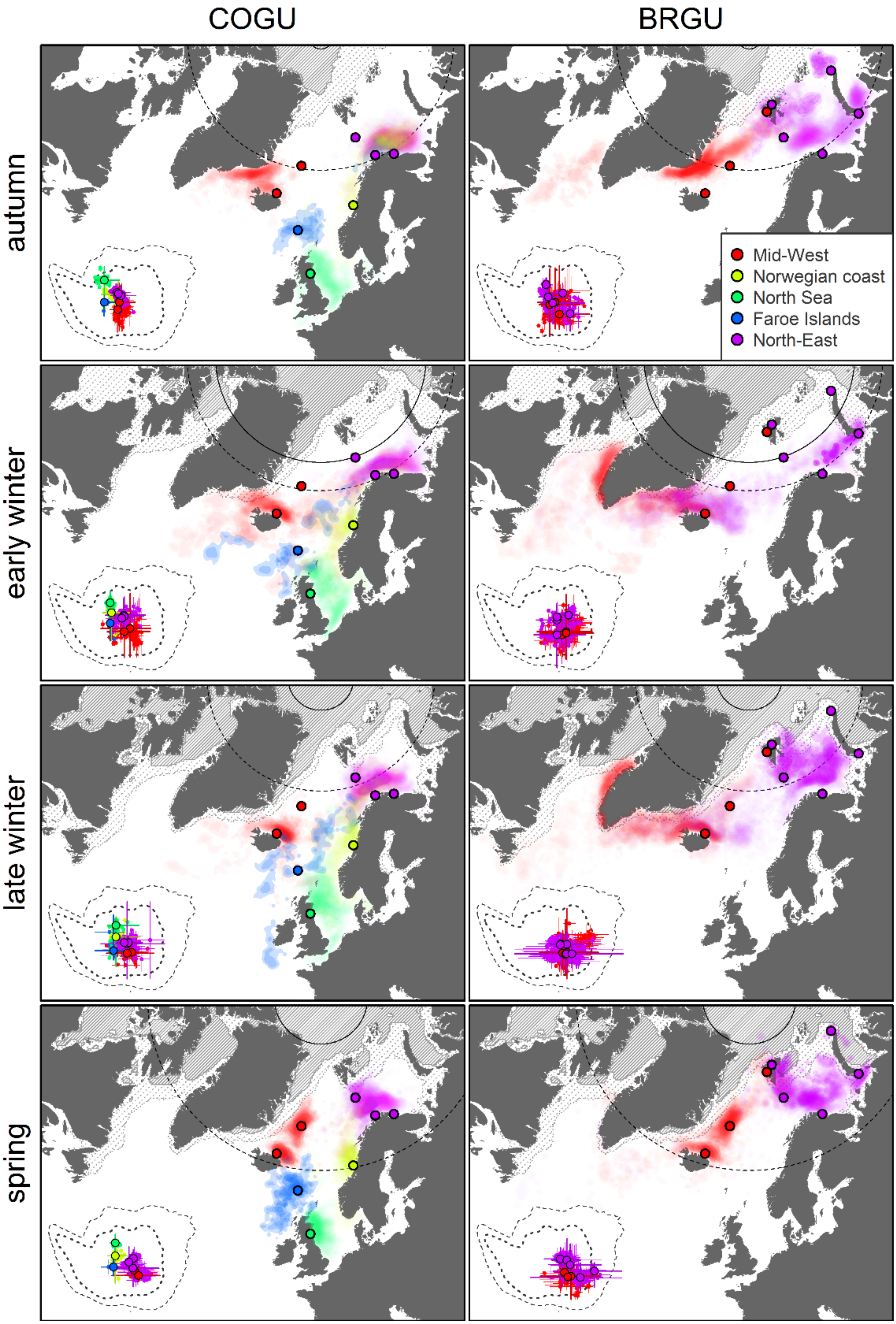
early winter
late winter
spring
colony

Figure 1. Panel A displays the **s**tudy area (in polar stereographic projection) with bathymetry (Amante & Eakins 2009; Jakobsson *et al.* 2012) and all large marine ecoregions included in the study. Circles denote study colonies with different colours indicating the presence of the two species (red = COGU, blue = BRGU, names detailed in table 1). Colonies combined for the purpose of this study are encircled with dashed ellipsoids. Panel B displays movement networks for both guillemot species by ecoregion (numbering corresponds to Panel A) and season. Each breeding population is scaled to the same size, while all nodes (squares) and edges (lines) are scaled to their proportional usage accordingly. Nodes are color-coded by number of populations present from white (only individuals from one population present) to black (8). Coloured areas in the background display identified clusters (5 for COGU, 2 for BRGU).

Ecoregions: 1 = Kara Sea, 2 = Barents Sea, 3 = Norwegian Sea, 4 = Greenland Sea, 5 = Iceland Sea & Shelf, 6 = Faroe Plateau, 7 = Central North Atlantic, 8 = Celtic-Biscay Shelf, 9 = North Sea, 10 = West Greenland & Canada East Arctic, 11 = Labrador Sea, 12 = Newfoundland & Labrador Shelf (including the Grand Banks), 13 = Hudson Bay Complex, 14 = Scotian Shelf, 15 = Northeast US Continental Shelf, 16 = Mid-Atlantic, 17 = Iberian Coastal, 18 = Baltic Sea.

Figure 2. Seasonal distributions (in polar stereographic projection) for COGU and BRGU during autumn, early winter, late winter and spring. Kernel utilization distributions (UD) show seasonal space use by breeding population as composite of individual UDs scaled to their respective population sample size. High colour intensity indicate use by several populations. Dots display colony locations. Dotted and solid circles indicate areas where location estimation was affected by or impossible due to polar night or midnight sun, respectively. Grey stippled and solid areas display 15% and 90% ten year seasonal median sea ice concentration, respectively. Insets in bottom left of each panel display seasonal environmental space occupied by each individual and breeding population (darker colours) as centre (dots) with variance (crosses). Stippled lines represent 100% and 50% kernel UD contours of available environmental space in the North Atlantic over 11 years. Colours correspond to spatiotemporal clusters identified by network analysis (figure 1).


COGU
BRGU
autumn
early winter
late winter
spring
Mid-West
Norwegian coast
North Sea
Faroe Islands
North-East

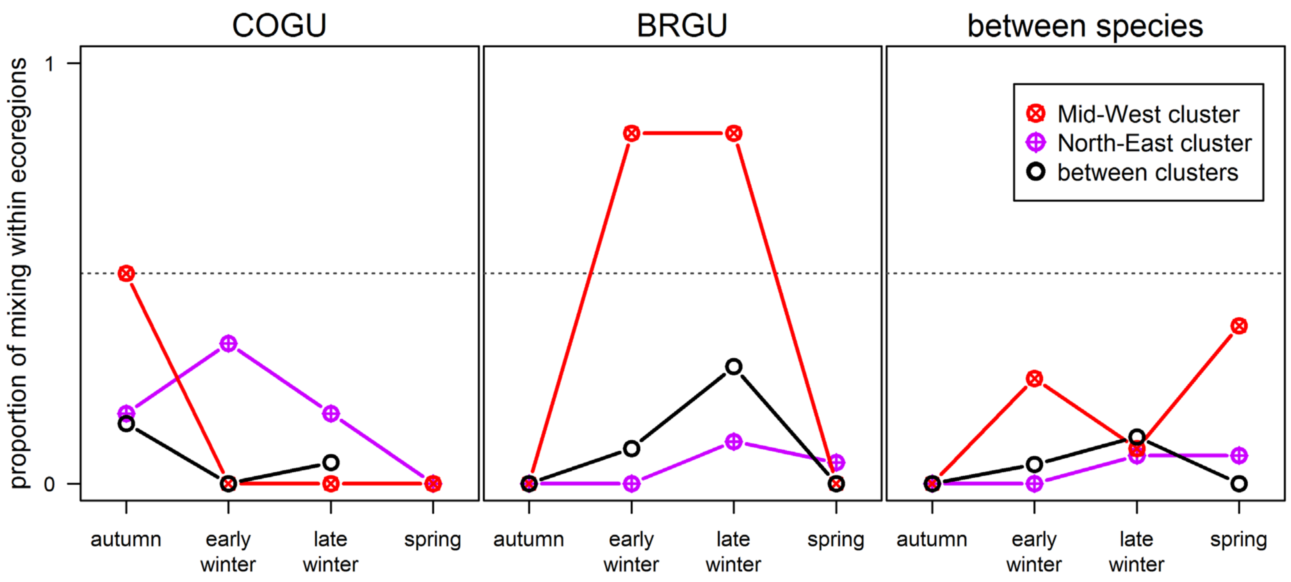


Figure 3. Overall seasonal proportion of inter-population mixing of individuals from different populations occupying the same ecoregion and belonging to the same species or different species (Equation 1). This index ranges from 0 (individuals from different populations and occupying the same ecoregion segregate) to 1 (individuals from different populations and occupying the same ecoregion mix). Colours denote comparisons within and between identified clusters. No COGU populations belonging to different clusters occupied the same ecoregion during spring (figure 1). Consequently, no proportion of mixing could be estimated. Inter-population mixing could only be calculated for the Mid-West and the North-East clusters as the other three clusters only consist of one population each.

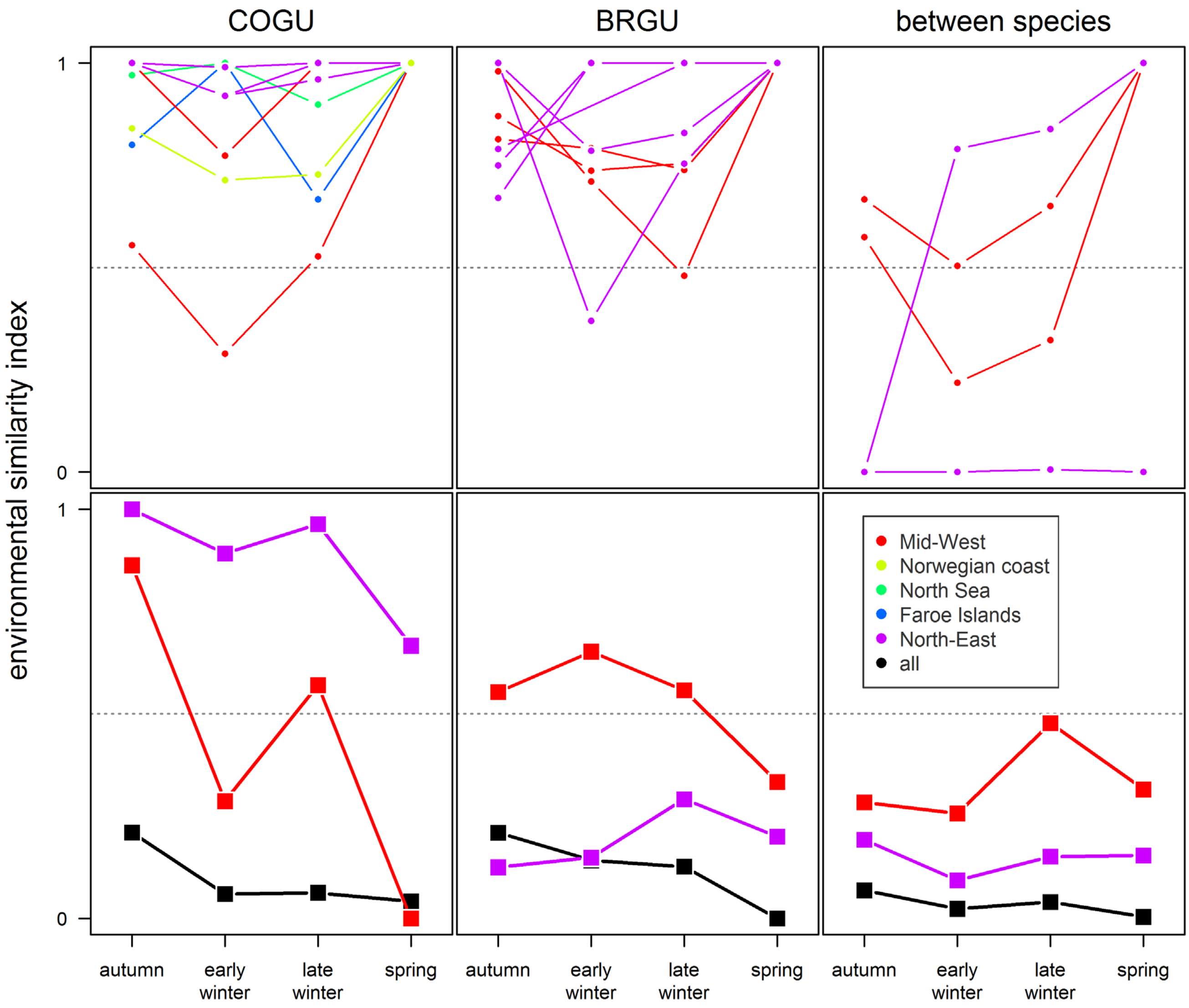


Figure 4. Environmental similarity index by season within and between species. This index is ranging from 0 (all birds occupy distinct environments) to 1 (all birds occupy a similar environment) and quantifies the seasonal inter-population mixing of ecoregion-, species- and population-specific environmental niches. Top panels (with small circles) show single population estimates, while bottom panels (with bigger squares) show comparative environmental similarities within clusters (i.e. between populations) or for all clusters combined (black).

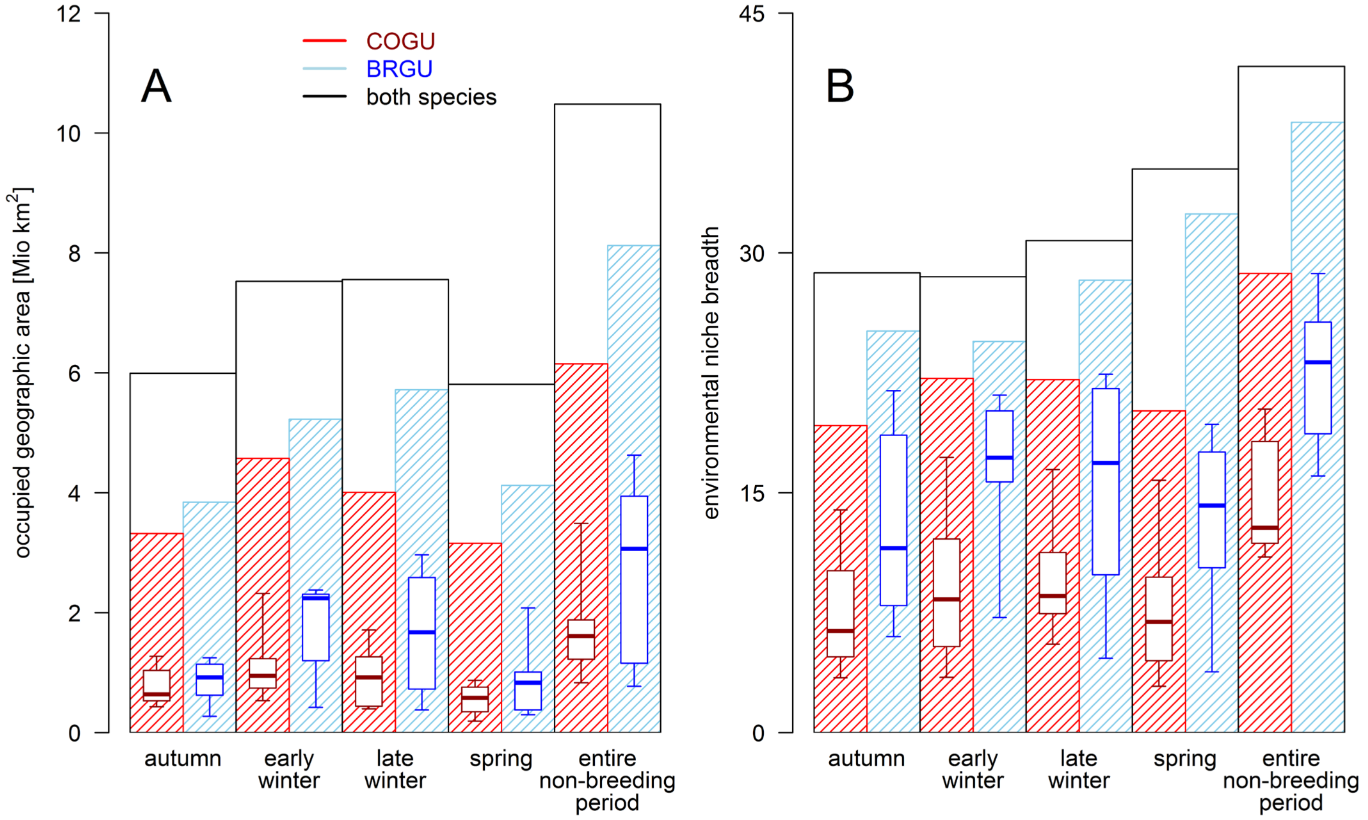


Figure 5. Size of the occupied geographic (A) and environmental space (B) in each season and both species combined as well as for COGU and BRGU. Bar plots denote the size of the entire occupied seasonal space (meta-population spread) while each boxplot displays the range of area occupied by each breeding population. Box plots illustrate 25th, 50th (median), and 75th percentiles, and error bars represent minimum and maximum values.

Supplementary information 1

Supplementary Methods

Location estimation from light-level loggers

Estimated timings of sunrise and sunset (transition times) were computed from light data using TransEdit2 (British Antarctic Survey/BAS, Cambridge, UK), and the `twilightCalc` function (`GeoLight` package; Lisovski & Hahn 2012) in R 3.3.3 (R Development Core Team 2017) for BAS, Migrate Technology and Biotrack loggers. Transition times were visually inspected for loggers retrieved during 2014-2017 by the same person. Lotek loggers did not retain raw light intensity data, but rather calculated and recorded latitudes and longitudes based on an on-board algorithm which has been shown to be biased (Frederiksen *et al.* 2016). Therefore we used these threshold method (Lisovski & Hahn 2012) derived positions to back calculate transition times using the `lotek_to_dataframe` function (`probGLS` package; Merkel *et al.* 2016). Daily experienced sea surface temperature (SST) was estimated from raw logged temperature data using the `sst_deduction` function (`probGLS` package) with a possible range of -2 to 20°C for Lotek loggers and -2 to 40°C for all other brands.

A most probable track for each individual and tracking year was calculated using an iterative method utilizing probability sampling detailed in Merkel *et al.* (2016) and implemented in the `prob_algorithm` function (`probGLS` package). Input data were logger recorded transition times, salt water immersion data as well as calculated daily recorded SST data. Daily optimal interpolated high resolution satellite derived SST, SST uncertainty estimates and sea ice concentration data for the algorithm with a 0.25° resolution were provided by NOAA (Boulder, Colorado, US; Reynolds *et al.* 2007). To improve precision we included land avoidance, an inability to enter the Baltic Sea (except for Common guillemots from the Isle of May) and an evasion of heavy pack ice (>90% sea ice concentration). Each movement path incorporated parameter values based on the ecology of the species and the oceanographic conditions in the North Atlantic (table S1). Usually, it is not possible to estimate latitude during times of equinox as day length (the proxy for latitude) is very similar everywhere on earth. However, this methodology is able to estimate locations also during times of equinox by among other things utilizing the recorded temperature data and comparing them to satellite derived sea surface temperature (SST) fields. Due to small north-south gradients in SST in certain areas of the North Atlantic (e.g. the Gulf Stream along the Norwegian coast) we limited the boundary box parameter in `prob_algorithm` for certain individuals and colonies after initial assessment of their movement track (table S1). Each computed track was afterwards visually inspected and erroneous locations particularly around polar night and midnight sun were removed (<1 % of all locations).

Environmental parameters

All chosen environmental parameters used to calculate the environmental space and their rational are listed in table S3. Fronts in sea surface temperature (SST) and sea surface height anomaly fields were calculated using a canny edge detector (package `imager`, low & high threshold at 90% & 98%, respectively). Bathymetry was log-transformed and all distance measurements were capped at 500 km as well as square root-transformed. Predictability in SST was calculated as the sum of constancy and contingency following Colwell (1974) over a ten year time period (2007-2016) with 10 equal bins using the `hydrostats` package (figure S1). All variables have been standardized (variance = 1, mean = 0).

Mantel correlation analysis

Following Cohen *et al.* (2018) we calculated species-specific Mantel correlations to validate our migratory connectivity results with an independent method. All individual annual tracks were split into 10 day bins starting 1 July. A resolution of 10 days was chosen to retain a sufficient number of locations for each bin for further analysis. Migratory connectivity for each species was quantified using Mantel correlation tests with 1000 permutations (Ambrosini *et al.* 2009). More specifically, the distance between individual breeding locations was compared to the distance between their current locations throughout the non-breeding season for each 10 day bin (as central location in each 10 day bin). For this analysis only data from the last three years of tracking was used (2014/15 - 2016/17). To avoid pseudo-replication only one year of tracking for each repeat track individual was used. Further, ecoregion- and season-specific Mantel correlation tests were computed - for ecoregions with individuals from more than one population present during the focal time period - to assess the area and season specific connectivity for each species. Results are illustrated in figure S3.

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Supplementary Tables and Figures

Table S1. `probGLS` algorithm input parameters used to compute locations. standard deviation = sd

algorithm parameter	description	value used
`particle.number`	number of particles computed for each point cloud	2000
`iteration.number`	number of track iterations	100
`loess.quartile`	remove outliers in transition times based on local polynomial regression fitting processes (Lisovski & Hahn 2012)	used with k = 10
`sunrise.sd & sunset.sd`	shape, scale and delay values describing the assumed uncertainty structure for each twilight event following a log normal distribution	2.49/ 0.94/ 0[1]
`range.solar`	range of solar angles used	-7° to -1° (except for C250 logger from SK: -4° to -2°)
`boundary.box`	the range of longitudes and latitudes likely to be used by tracked individuals	90°W to 120°E & 40°N to 81°N; except for 91% COGU tracks from IM with 40°N to 62°N; all COGU from BI and 94% COGU SK tracks with 60°N to 77°N; 6% SK tracks with 50°N to 77°N
`day.around.spring.equinox` & `days.around.fall.equinox`	number of days before and after an equinox event in which a random latitude will be assigned	spring: 21 days before & 14 days after autumn: 14 days before & 21 days after
`speed.dry`	fastest most likely speed, speed sd and maximum speed allowed when the logger is not submerged in sea water	17/ 4/ 30 m/s[2]
`speed.wet`	fastest most likely speed, speed sd and maximum speed allowed when the logger is submerged in sea water	1/ 1.3/ 5 m/s[3]
`sst.sd`	logger-derived sea surface temperature (SST) sd	0.5°C[4]
`max.sst.diff`	maximum tolerance in SST variation	3°C
`east.west.comp`	compute longitudinal movement compensation for each set of twilight events (Biotrack 2013)	used

[1] These parameters are chosen as they resemble the twilight error structure of open habitat species in Lisovski *et al.* (2012).

[2] inferred from GPS tracks (unpublished data) and (Elliott & Gaston 2005)

[3] North Atlantic current speed up to fast current speeds (i.e. East Greenland current) (Lumpkin & Johnson 2013) as the tagged animal is assumed to not actively move when the logger is immerged in seawater

[4] logger temperature accuracy

Table S2. Proportion of locations missing in each season mainly due to lack of twilight events caused by midnight sun (seasons: autumn and spring) or polar night (early and late winter) for each breeding population as well as mean and standard deviation (sd) across populations. Breeding populations: SNZ = Southern Novaya Zemlya, NNZ = Northern Novaya Zemlya, ESP = Eastern Spitsbergen, WSP = Western Spitsbergen, BI = Bjørnøya, SBS = Southern Barents Sea, HJ = Hjelmsøya, SK = Sklinna, JM = Jan Mayen, IC = Northeast Iceland, FA = Faroe Islands, IM = Isle of May

species	season	breeding populations												mean	sd
		IM	FA	SK	IC	JM	WSP	HJ	BI	SBS	ESP	SNZ	NNZ		
BRGU	autumn	-	-	-	15 %	13 %	39 %	-	29 %	15 %	58 %	11 %	47 %	29 %	17 %
	early winter	-	-	-	6 %	1 %	1 %	-	5 %	36 %	100 %	20 %	97 %	33 %	39 %
	late winter	-	-	-	0 %	2 %	1 %	-	3 %	4 %	29 %	1 %	8 %	6 %	9 %
	spring	-	-	-	30 %	45 %	73 %	-	63 %	45 %	91 %	51 %	81 %	60 %	19 %
COGU	autumn	1 %	2 %	10 %	0 %	8 %	-	12 %	14 %	4 %	-	-	-	6 %	5 %
	early winter	1 %	1 %	9 %	0 %	5 %	-	51 %	34 %	39 %	-	-	-	18 %	19 %
	late winter	1 %	0 %	1 %	1 %	3 %	-	2 %	5 %	2 %	-	-	-	2 %	2 %
	spring	4 %	12 %	14 %	31 %	46 %	-	44 %	48 %	27 %	-	-	-	28 %	16 %

Table S3. Parameter chosen to describe the environmental space.

parameter	temporal resolution	spatial resolution	rational	data source
bathymetry	static	0.25°	predictable productivity on continental shelfs	ETOPO1 & IBCAO[1]
surface air temperature	daily	0.75°	influences energy requirements[2]	ECMWF[3]
sea surface temperature (SST)	daily	0.25°	water mass indicator & physiological constraint[2]	NOAA OI SST V2[4]
SST predictability (figure S2)	static	0.25°	identifier of spatially variable SST features across seasons and years (e.g. persistent frontal systems[5])	NOAA OI SST V2[4]
minimum distance to 15%, 50% & 90% sea ice concentrations	daily	0.25°	descriptor of marginal sea ice zone	NSIDC[6]
sea surface height (SSH)	daily	0.25°	descriptor of the locations of large-scale features such as gyres and fronts	AVISO[7]
distance to SSH anomaly gradients	daily	0.25°	distance to meso-scale eddies as spatially dynamic sources of upwelling	AVISO[7]
distance to SST gradient	daily	0.25°	distance to meso- and large-scale temperature fronts[5]	NOAA OI SST V2[4]

[1] (Amante & Eakins 2009; Jakobsson *et al.* 2012), [2] (Fort *et al.* 2009), [3] (Berrisford *et al.* 2011), [4] (Reynolds *et al.* 2007), [5] (Scales *et al.* 2014), [6] (Cavalieri *et al.* 1999), [7] Aviso, with support from Cnes (http://www.aviso.altimetry.fr/)

Table S4. Large-scale movement network metrics. P-values derived by two tailed t-tests. Displayed values denote mean ± standard deviation (minimum & maximum in brackets), if not labelled otherwise. df = degree of freedom

network metric	**COGU**	**BRGU**	**p-value**	**df**
# of nodes	24	25	-	-
# of populations present at a node	2.7 (1-7)	3.5 (1-6)	0.13	46
node size	17±14% (2-56%)	16±20% (0.4-75%)	0.89	42
node size by population	**49±40% (1-100%)**	**37±38% (1-100%)**	**0.05**	**134**
total degrees (connections per node)	**6.9 (2-21)**	**10.8 (2-26)**	**0.03**	**60**
edge size	7±8% (0.2-38%)	5±8% (0.1-55%)	0.14	157
edge size by population	**36±38% (1-100%)**	**22±32% (1-100%)**	**0.001**	**202**
# of unique ecoregions used by population	3.5 (2-6)	4.8 (2-8)	0.24	12
# of unique ecoregions used by individuals	**1.5±0.7 (1-4)**	**2.3±0.9 (1-4)**	**<0.001**	**156**

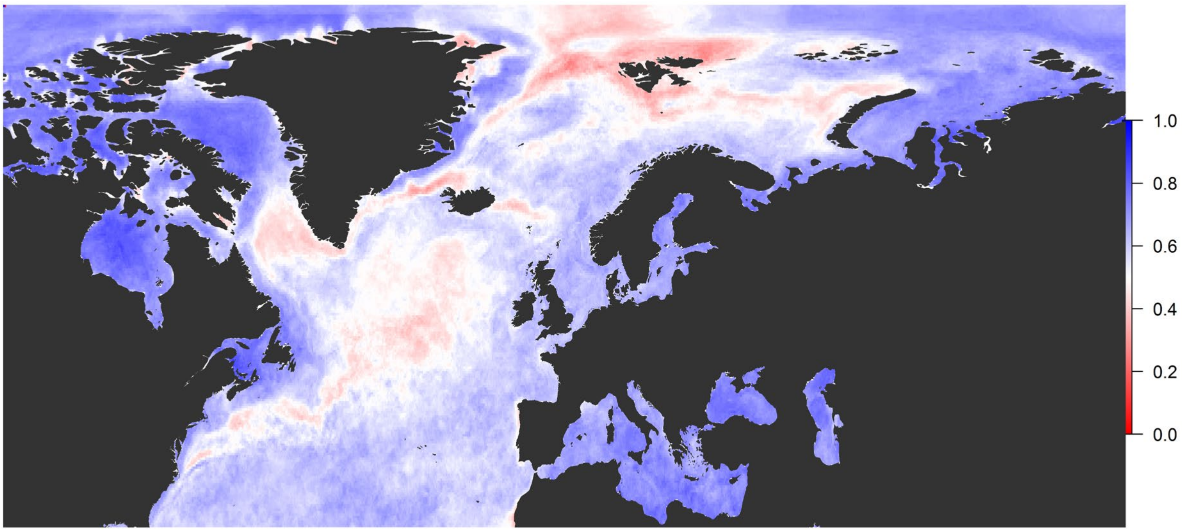


Figure S1. Distribution of SST predictability in the North Atlantic with a scale from 0 (no predictability) to 1 (very predictable).

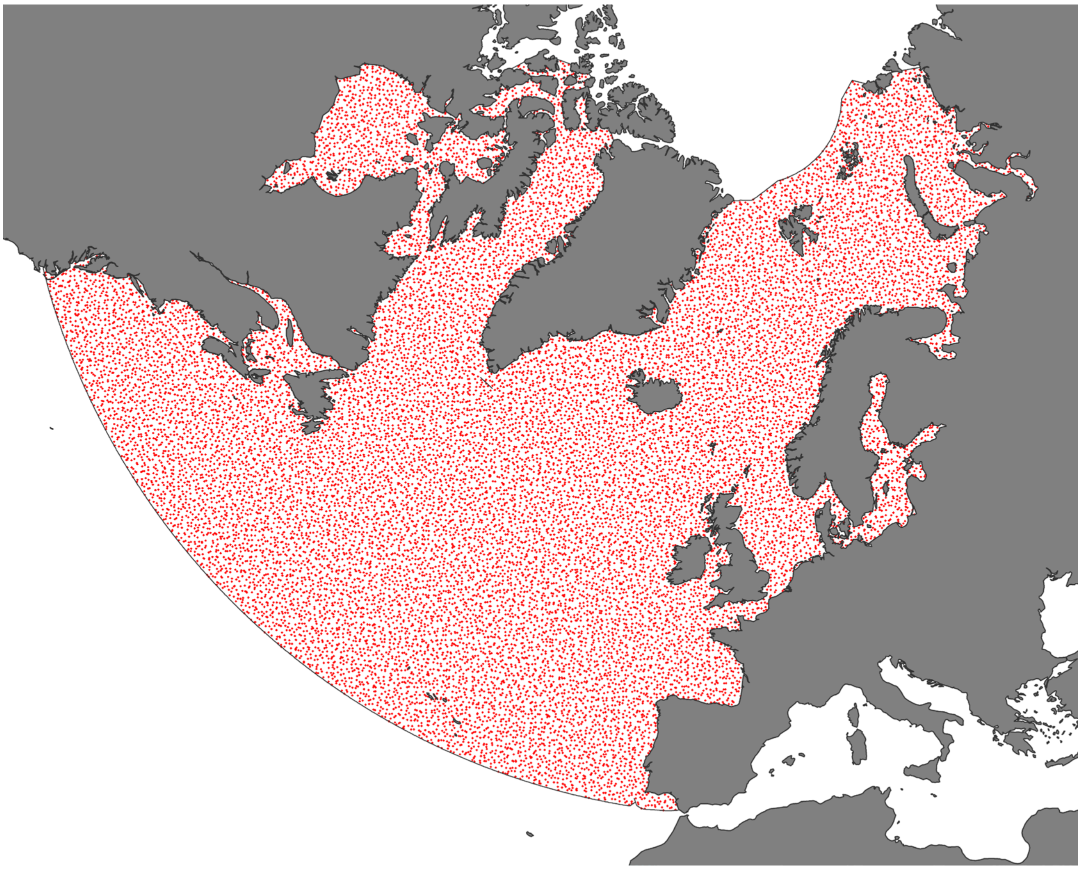


Figure S2. Map (in polar stereographic projection) displaying the study region including the 20000 stratified points (in red) used to estimate the available environmental space.

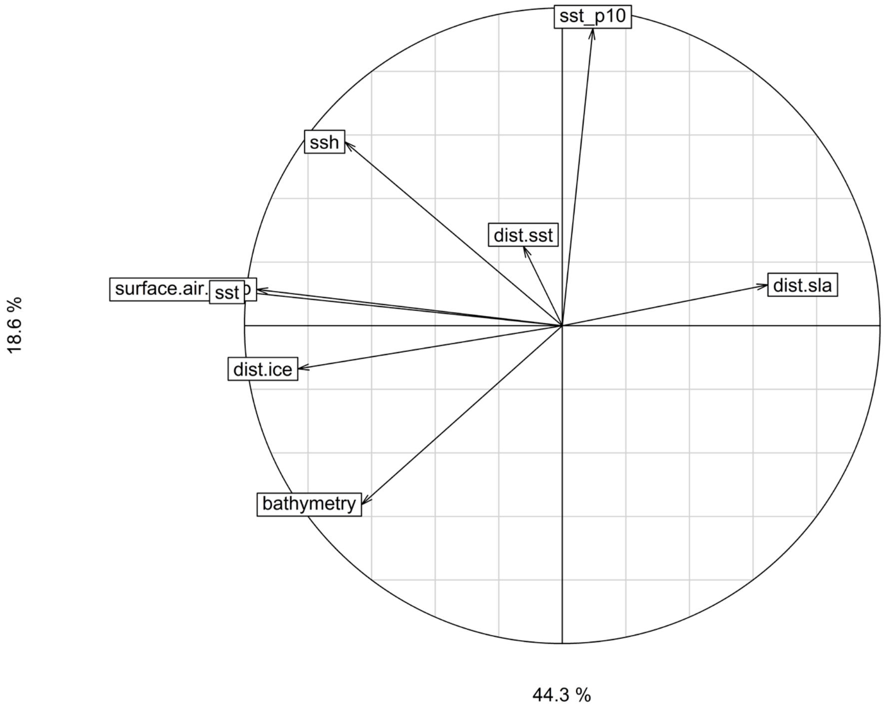


Figure S3. PCA correlation circle for the environmental space representing the North-Atlantic over the entire study period. dist.sla = distance to mesoscale eddies, dist.ice = distance to marginal sea ice zone, surface.air.temp = surface air temperature, sst = sea surface temperature, ssh = sea surface height, dist.sst = distance to temperature fronts, sst_p10 = SST predictability

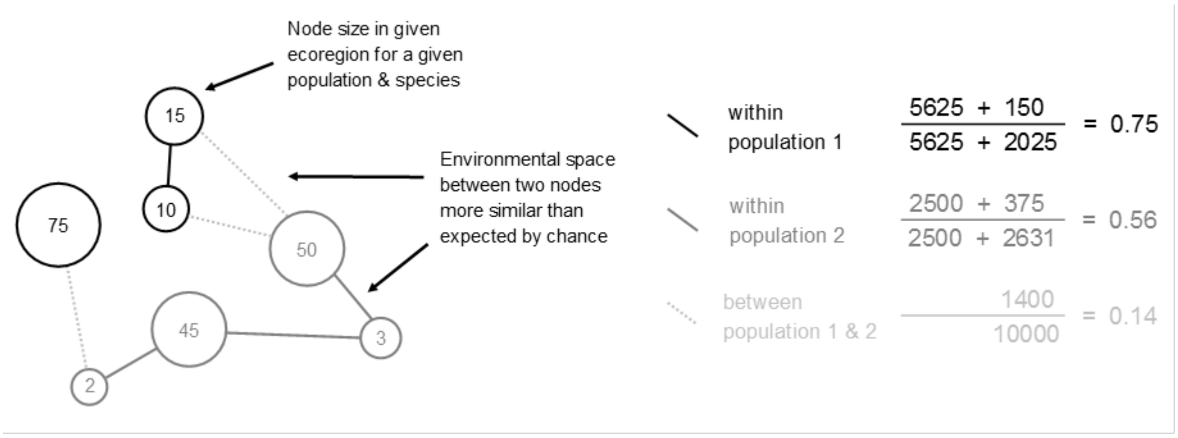


Figure S4. A schematic detailing the environmental similarity index (S) calculations in equation 1 (within example populations, solid lines) and equation 2 (between two example populations, dashed lines) using two example populations (in black and grey). The symbols denote ecoregion-, species- and breeding population-specific environmental space use. Its size corresponds to the proportional use as visualised in figure 1. Lines connect environmental spaces which are similar based on the environmental niche similarity test (one way is considered sufficient, i.e. $1 \cong 2 \mid 2 \cong 1$).

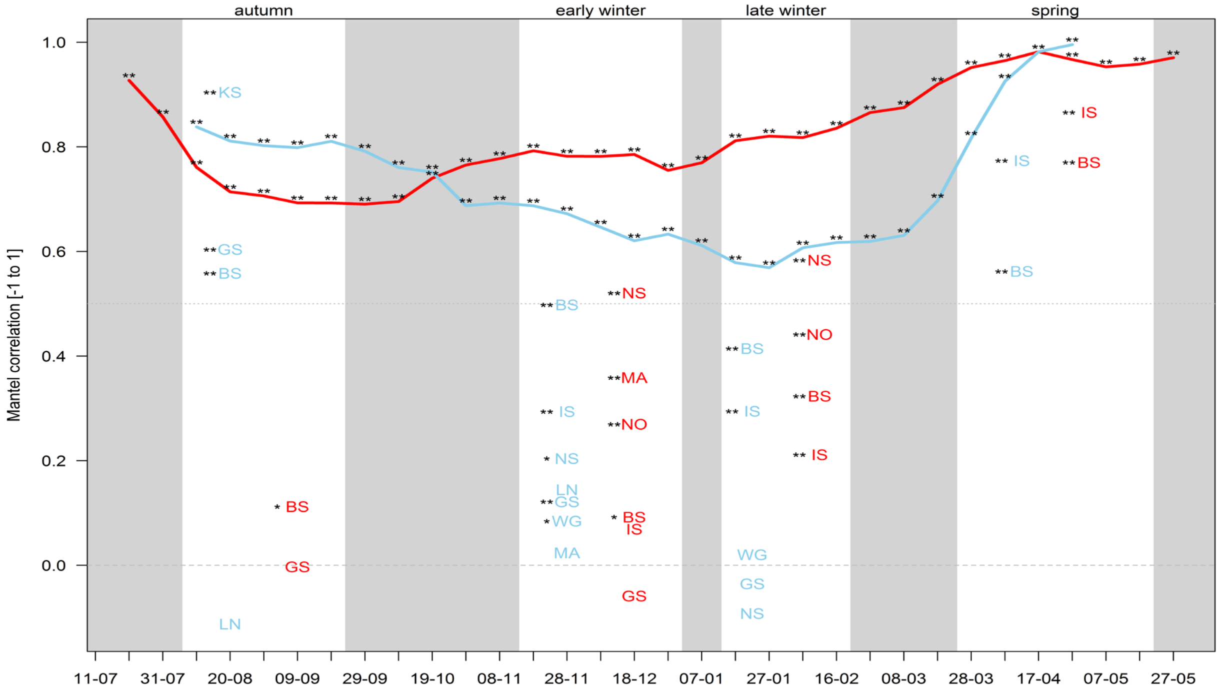


Figure S5. Species-specific mantel correlation through time (10 day bins) for all data from 2014-2017. BRGU in blue and COGU in red. Labels in each season (white boxes) denote season-specific mantel correlation values for each particular ecoregion with birds from more than one breeding population present. Significance levels based on 1 000 permutations: ** = <0.001, * = <0.05; Ecoregion abbreviations: BS = Barents Sea, KS = Kara Sea, GS = Greenland Sea, IS = Iceland Shelf & Sea, WG = West Greenland, NO = North Sea, MA = Central North Atlantic, NS = Norwegian Sea, LN = Labrador shelf & Newfoundland

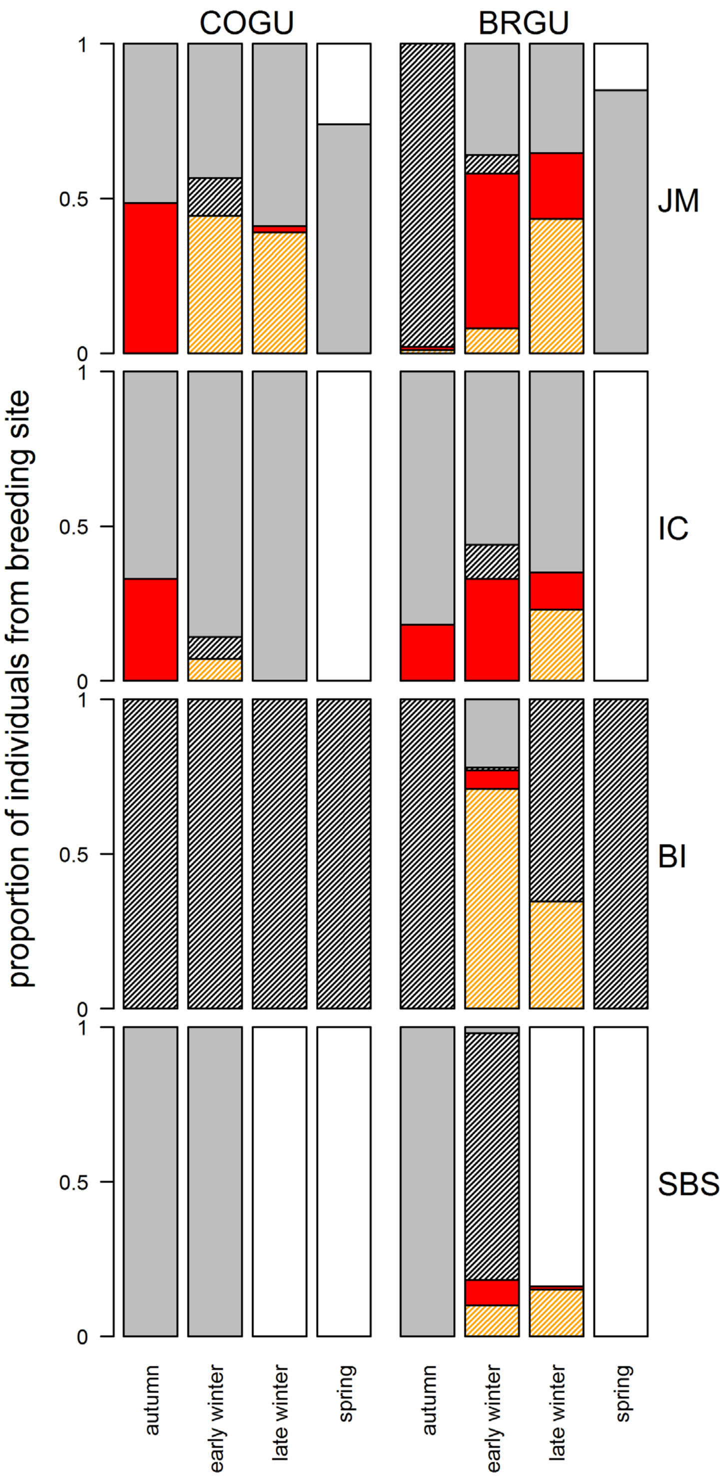


Figure S6. Seasonal proportional comparative space and environmental niche use between both species breeding sympatric at four breeding locations (JM = Jan Mayen, IC = North-East Iceland, BI = Bjørnøya & SBS = Southern Barents Sea). The proportion of the population occupying the same ecoregion with the other sympatric species breeding at the same location is indicated in white-grey-black colours while red-orange colours indicate different ecoregions used. Dark colours (grey & black) correspond to species-specific within ecoregion space use while white illustrates mixing between the species within ecoregions. Solid colours (white, grey & red) indicate similar environmental niches occupied while shaded colours denote distinct environments used (black & orange).

Supplementary information 2

Species- and breeding population-specific seasonal distributions (in polar stereographic projection) in geographic (A, C, E, G) and environmental space (B, D, F, H) during autumn (A, B), early winter (C, D), late winter (E, F) and spring (G, H). Common guillemot (COGU) breeding population distributions are displayed in figure S2.1-8 and Brünnich's guillemot (BRGU) breeding population distributions in figure S2.9-16. Colours correspond to spatiotemporal clusters identified by network analysis (figure 1).

In geographic space, kernel utilization distributions (UD) show seasonal space use as composite of individual UDs scaled to their respective population sample size. Symbols display colony locations. Dotted and solid circles indicate areas where location estimation was affected by or impossible due to polar night or midnight sun, respectively. Grey stippled and solid areas display 15% and 90% ten year seasonal median sea ice concentration, respectively.

In environmental space, each seasonal track is displayed as centre with variance. Darker crosses denote the median of all locations and the total variance displayed. Stippled lines represent 100% and 50% kernel UD contours of available environmental space in the North Atlantic over 11 years.

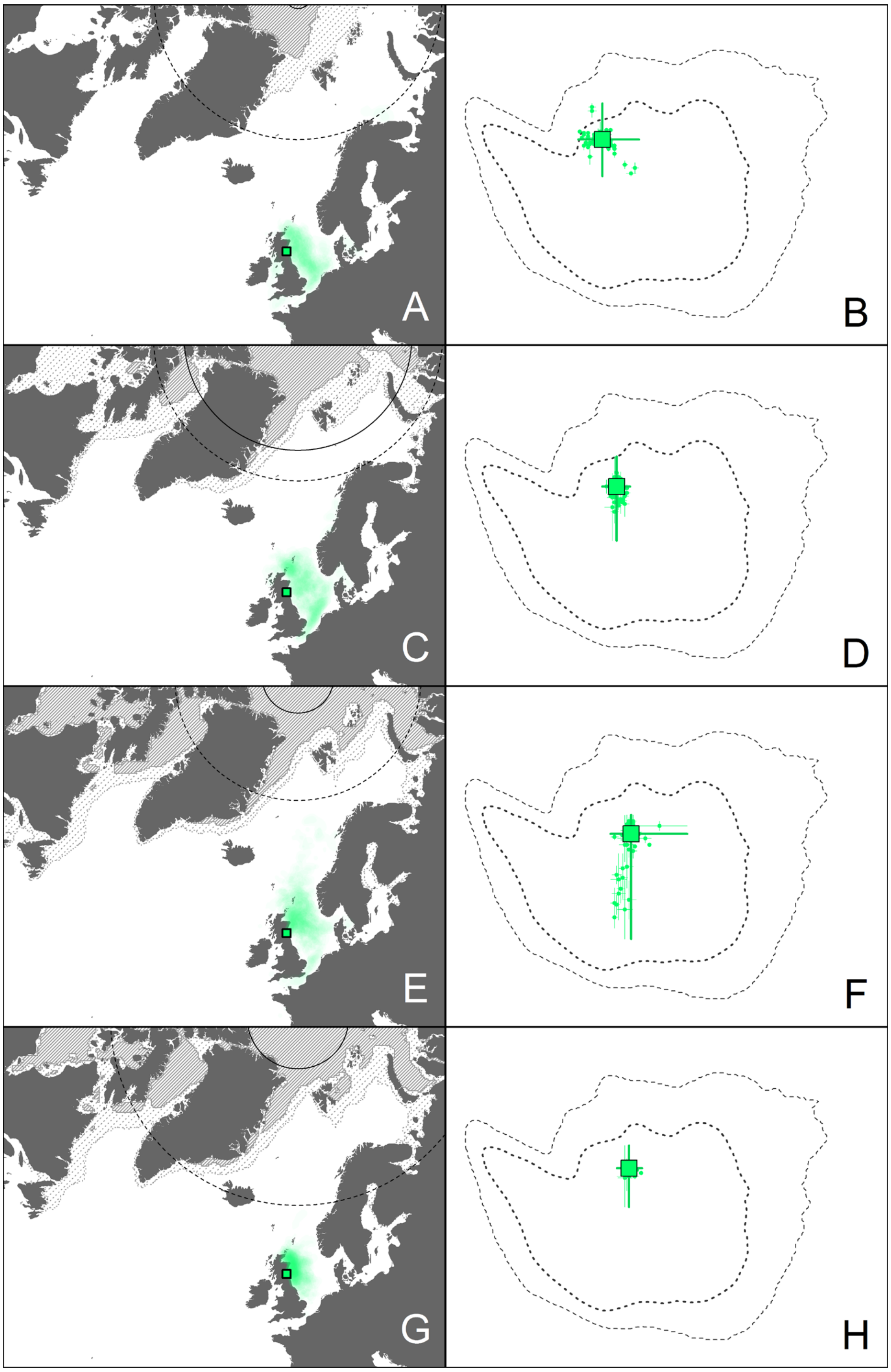


Figure S2.1. Common guillemots, Isle of May

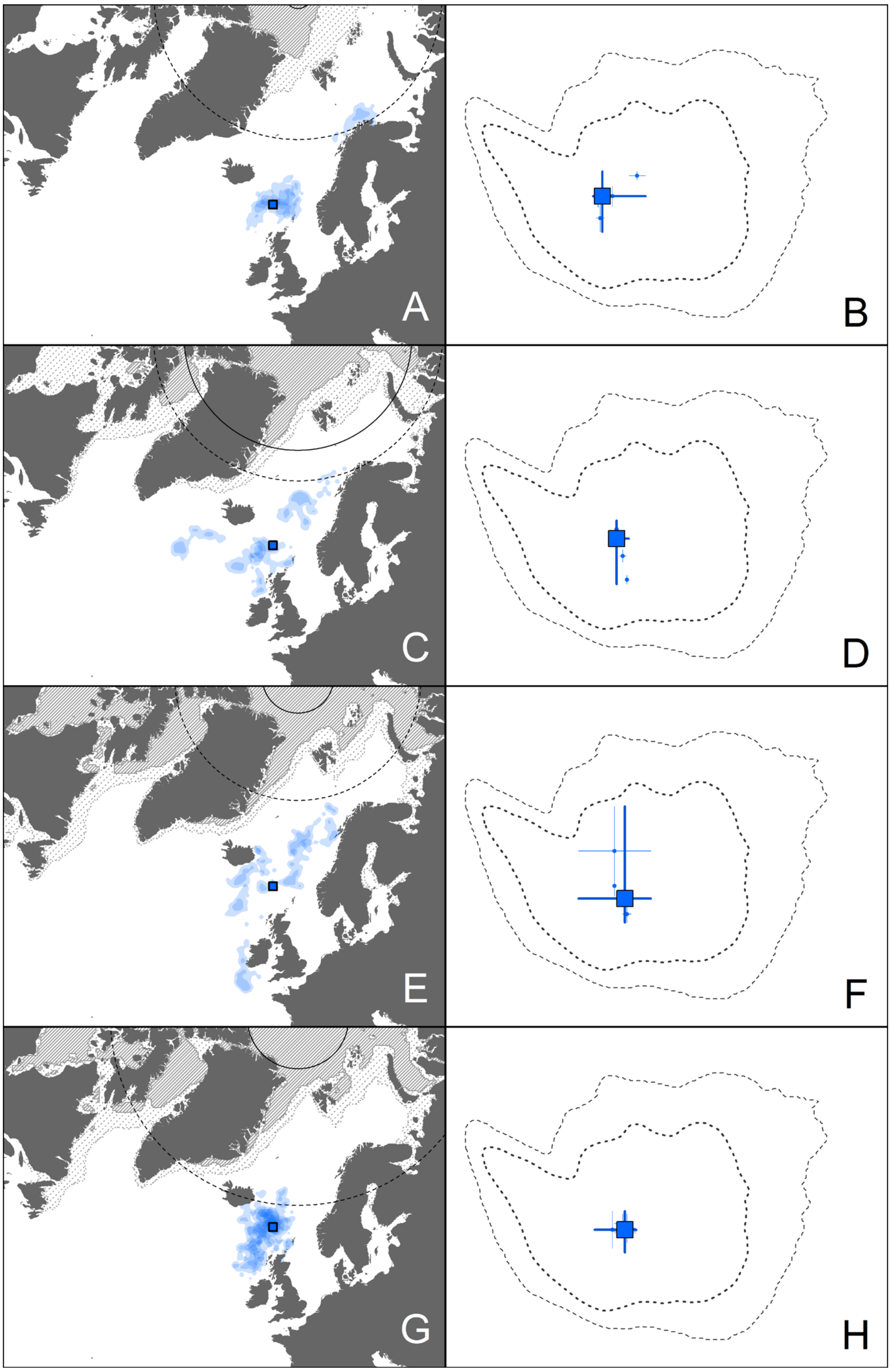


Figure S2.2. Common guillemots, Faroe Islands

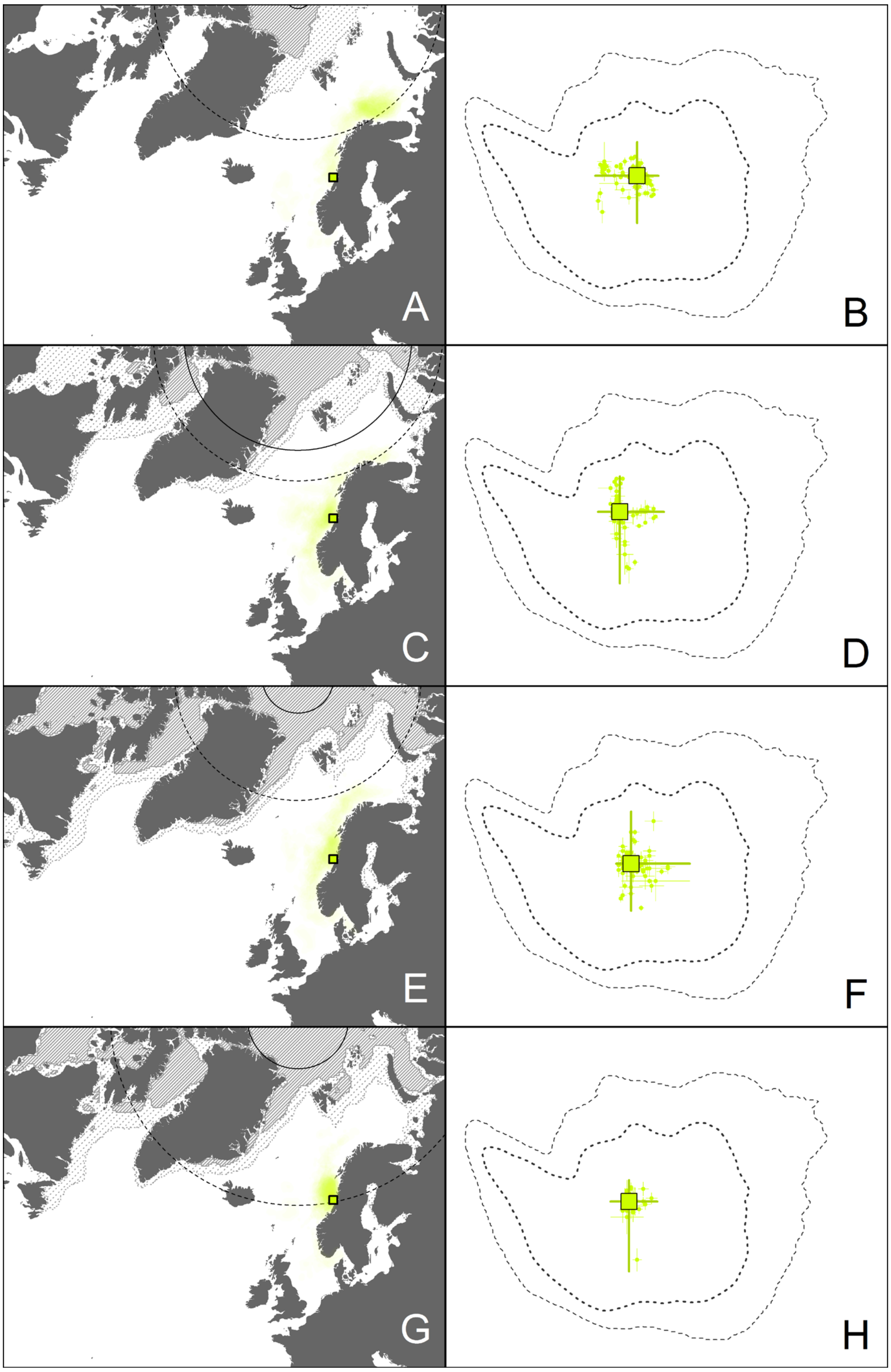


Figure S2.3. Common guillemots, Sklinna

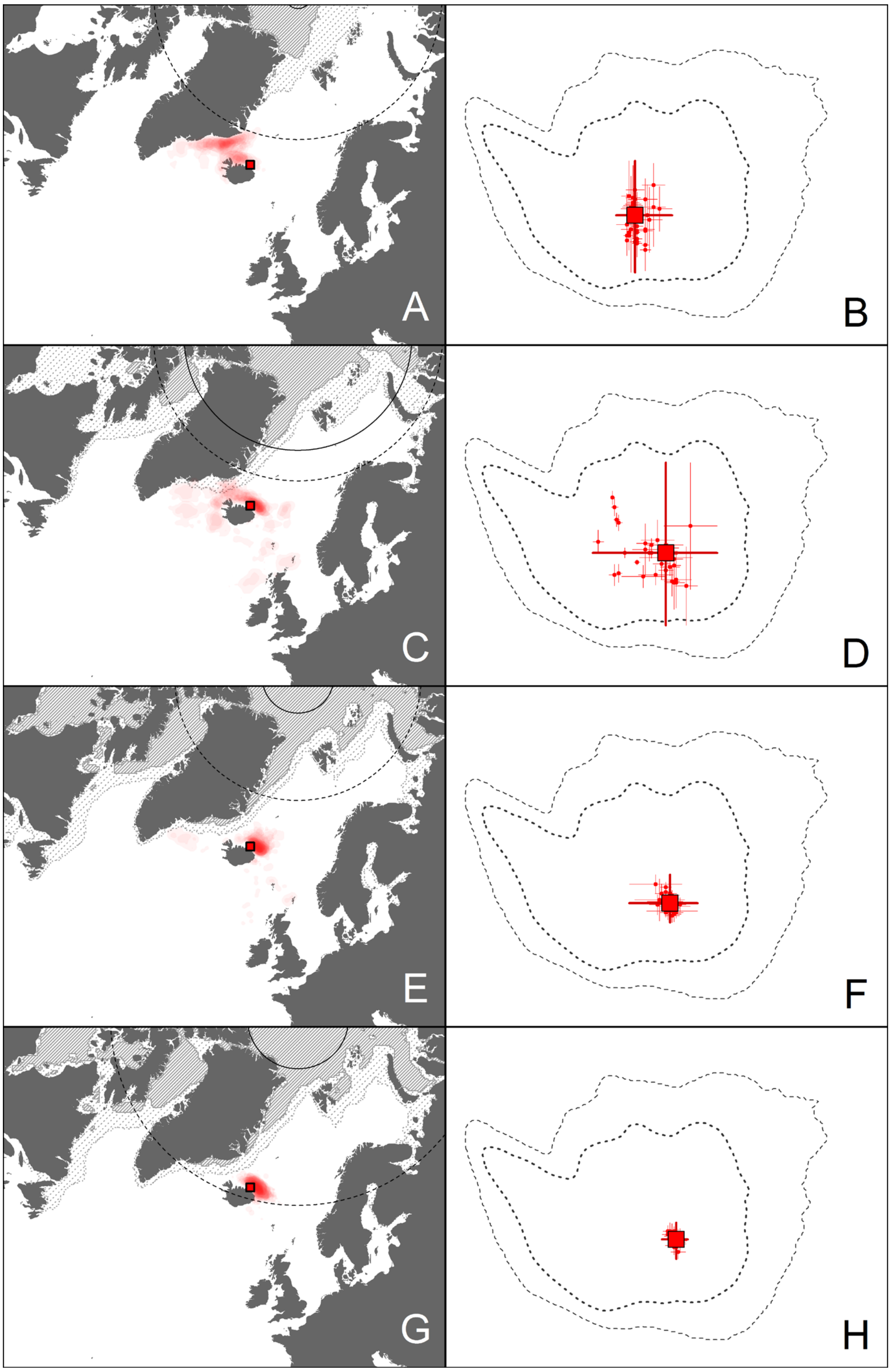


Figure S2.4. Common guillemots, North-East Iceland (Grimsey, Langanes)

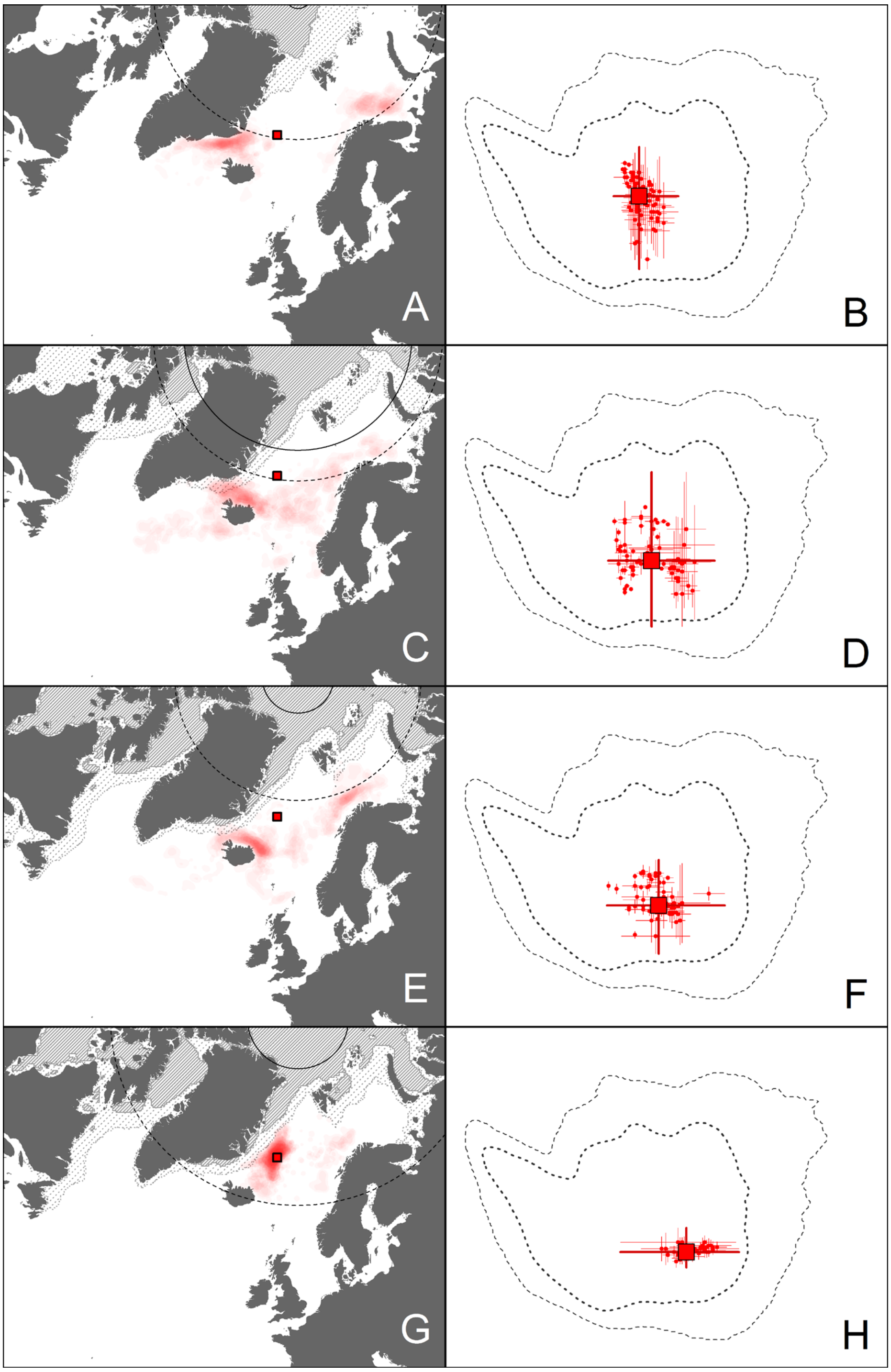


Figure S2.5. Common guillemots, Jan Mayen

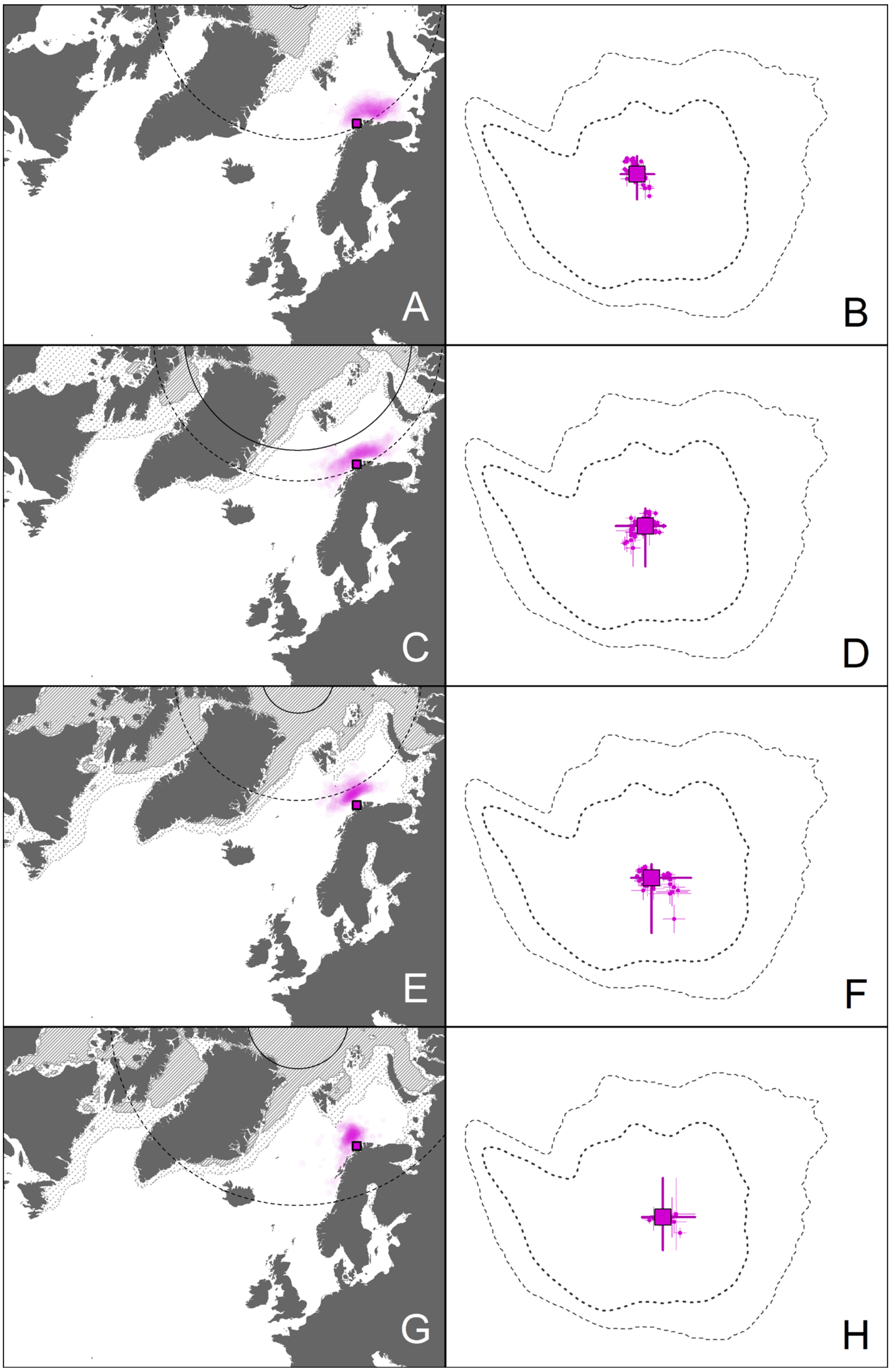


Figure S2.6. Common guillemots, Hjelmsøya

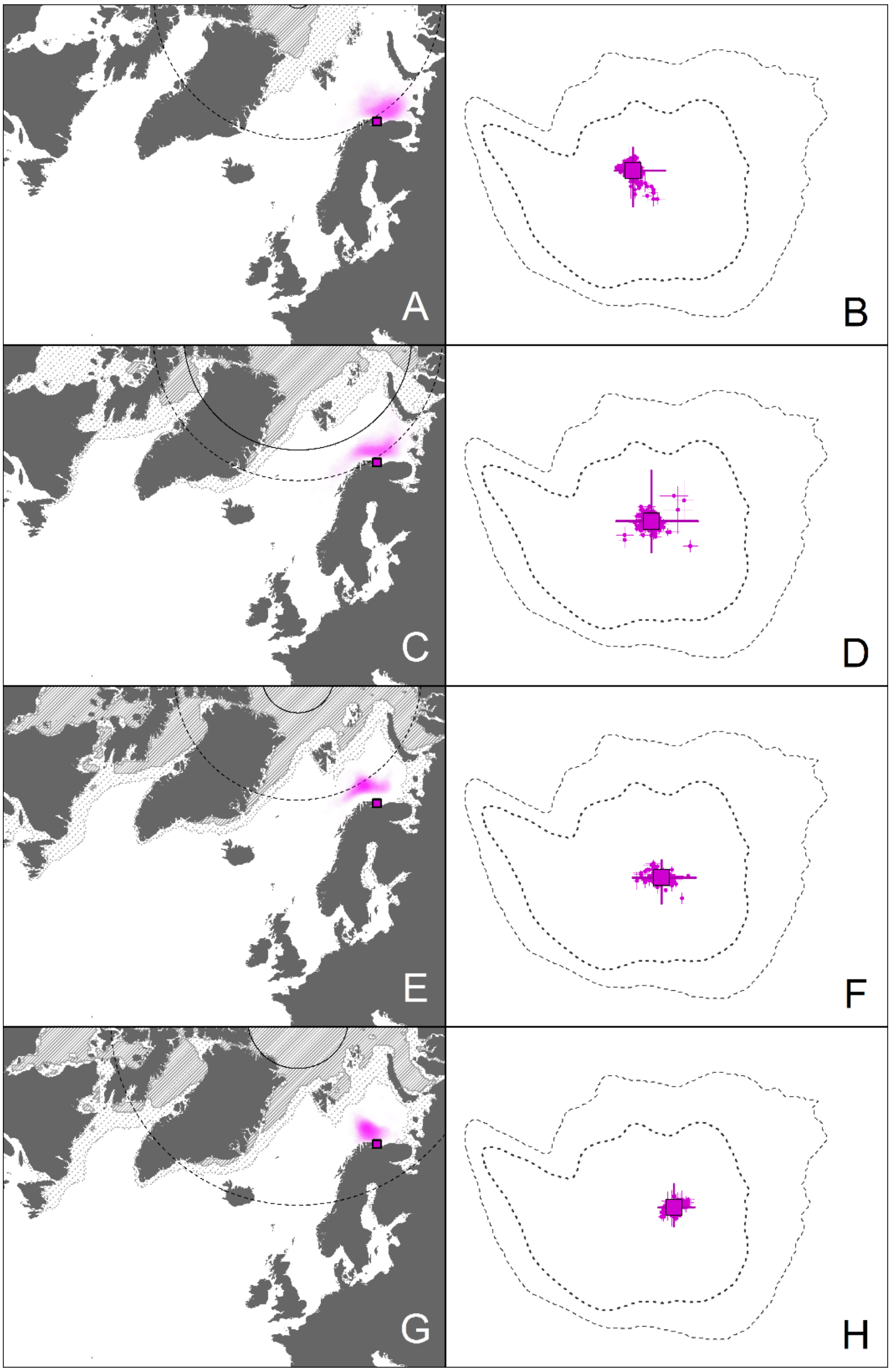


Figure S2.7. Common guillemots, Southern Barents Sea (Hornøya and Cape Gorodetskiy)

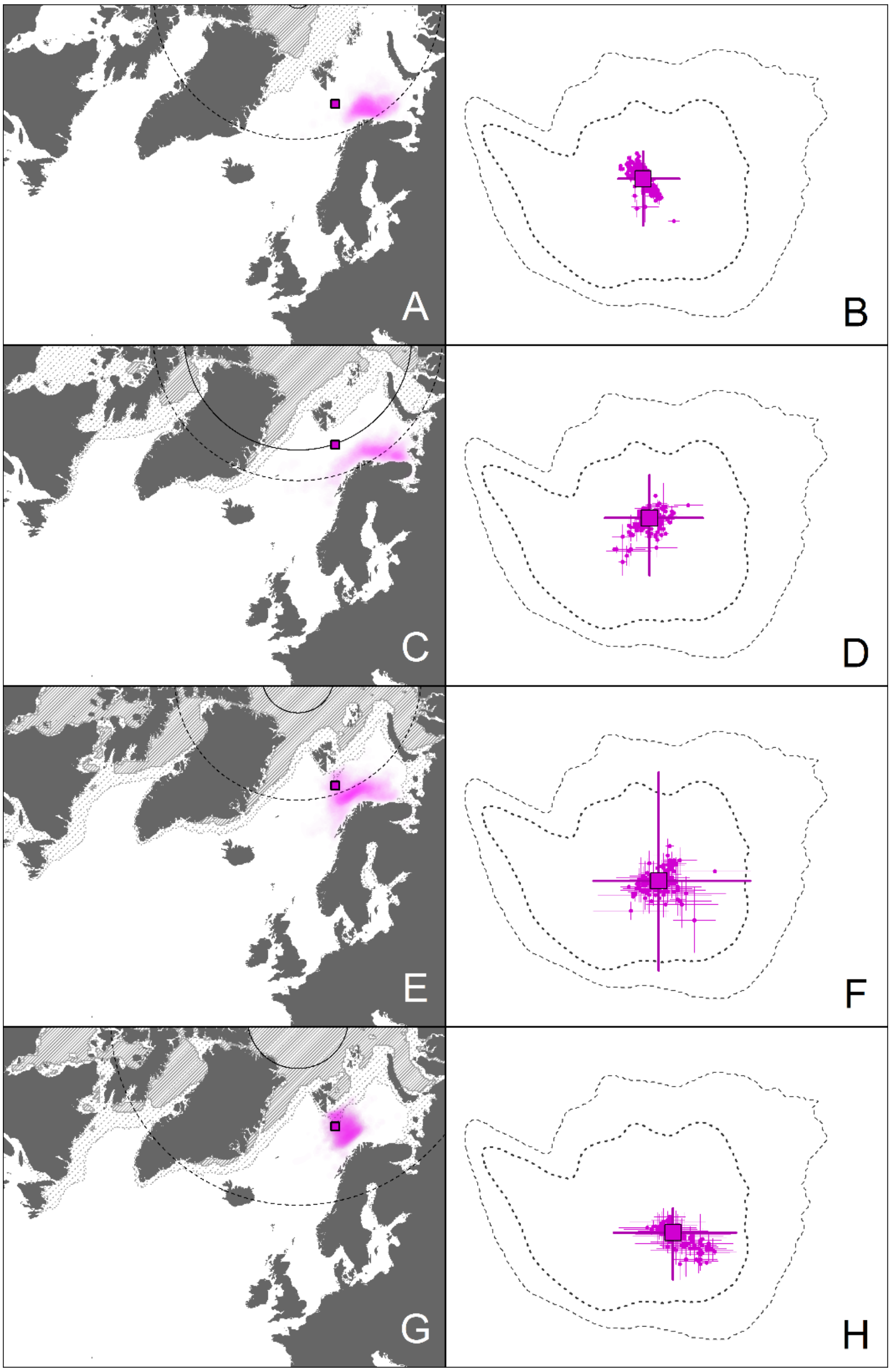


Figure S2.8. Common guillemots, Bjørnøya

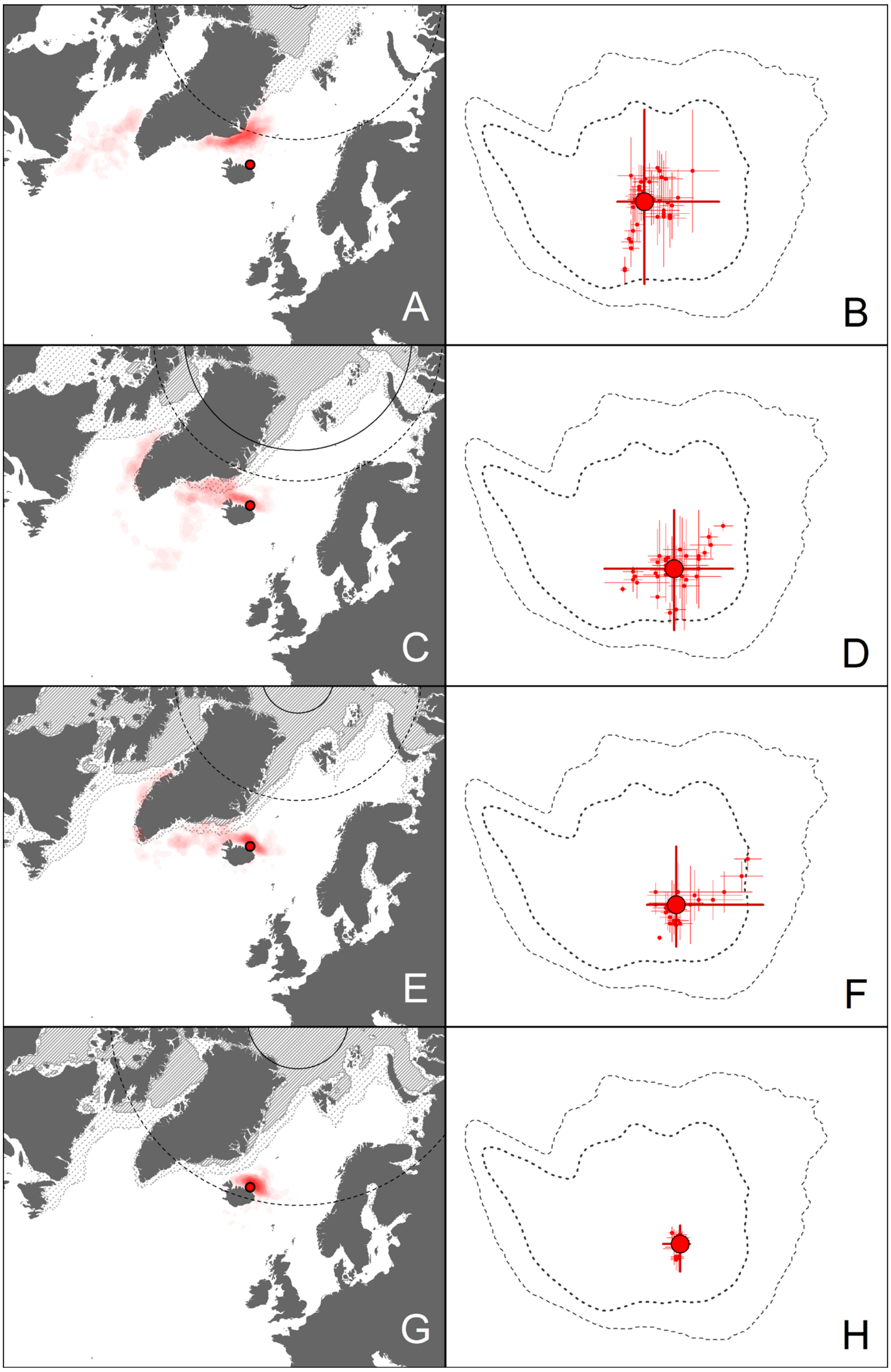


Figure S2.9. Brünnich's guillemots, North-East Iceland (Grimsey, Langanes)

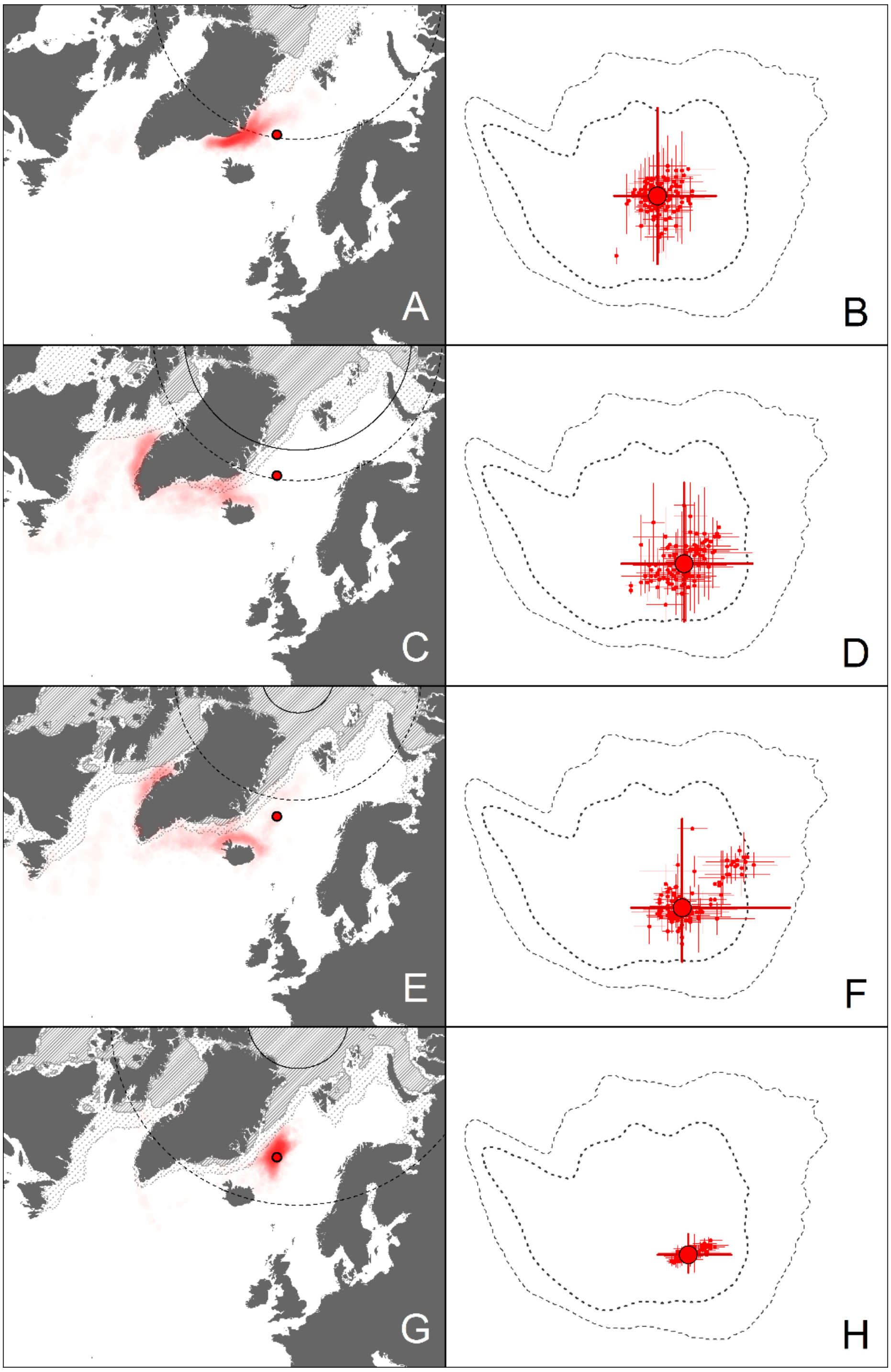


Figure S2.10. Brünnich’s guillemots, Jan Mayen

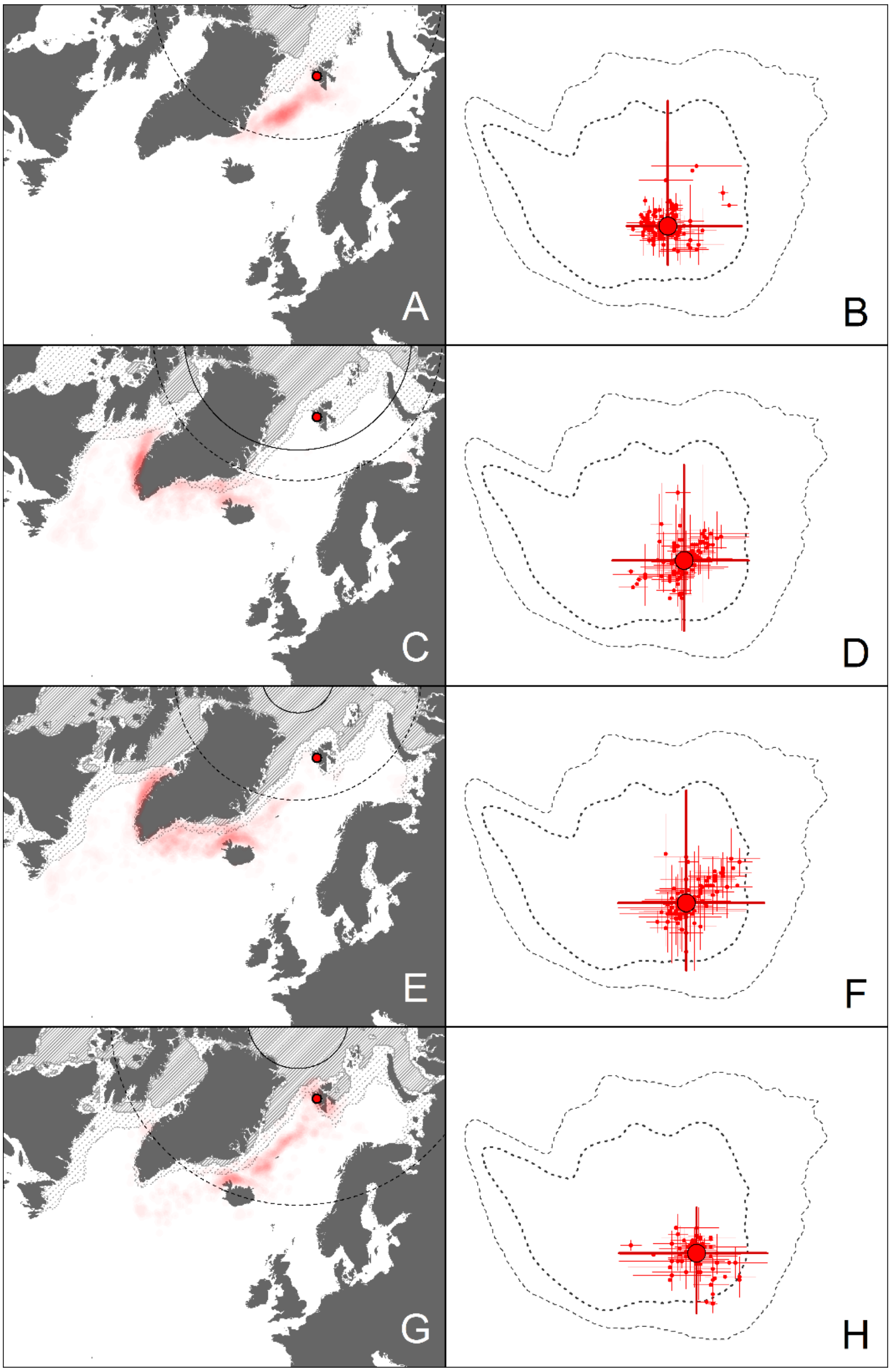


Figure S2.11. Brünnich’s guillemots, Western Spitsbergen (Diabas, Ossian Sarsfjellet and John Scottfjellet)

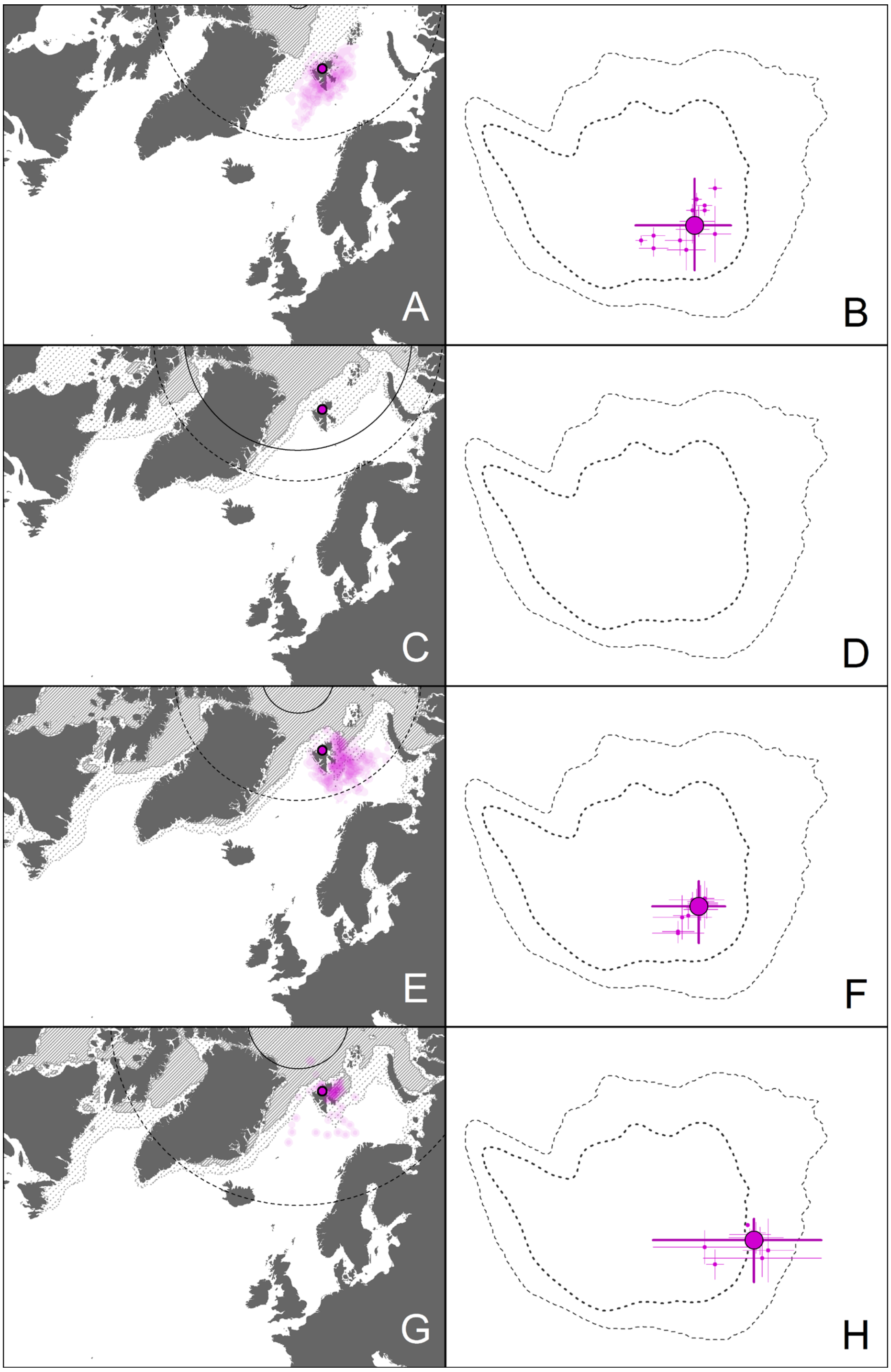


Figure S2.12. Brünnich's guillemots, Eastern Spitsbergen (Alkefjellet)

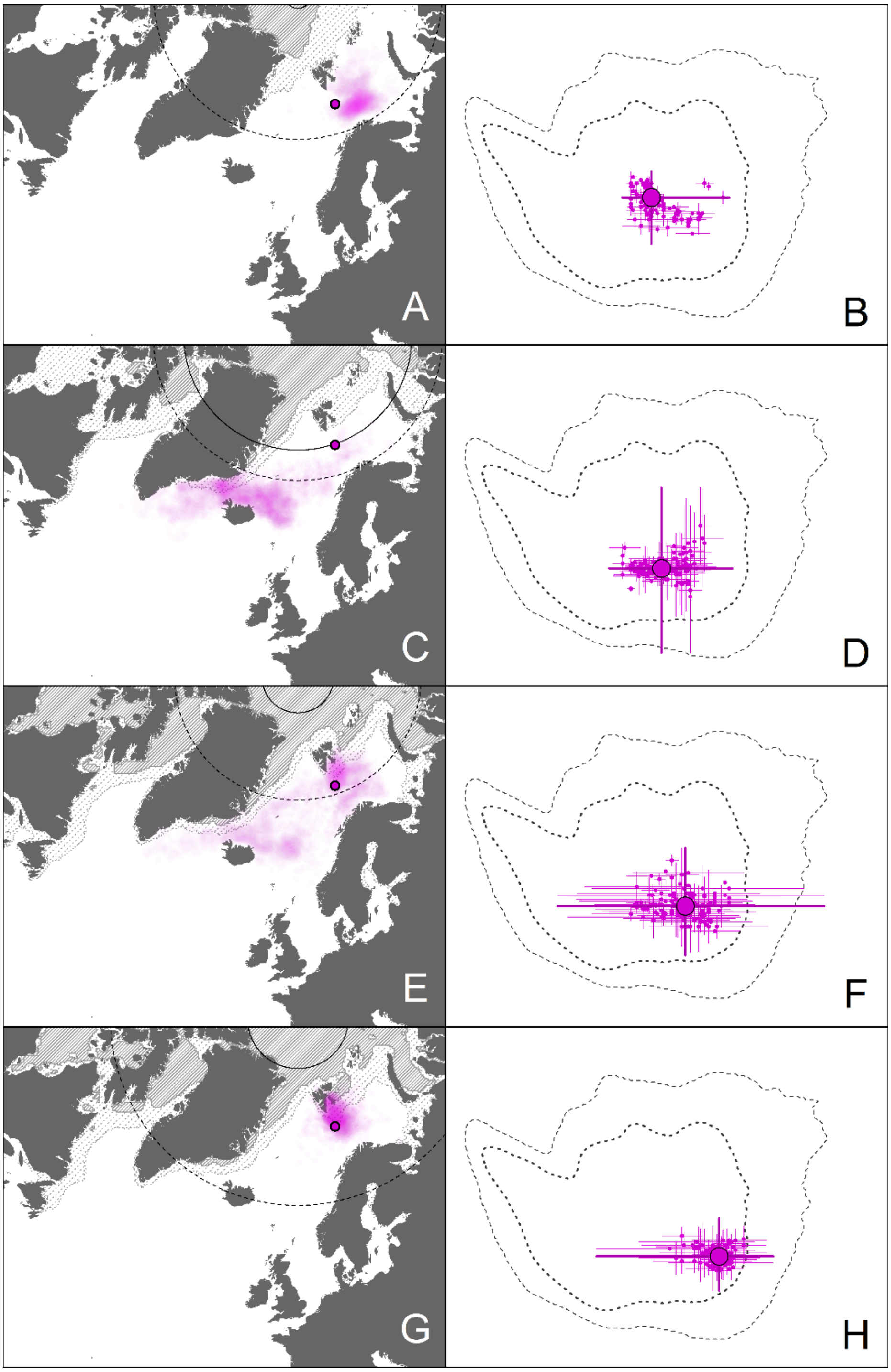


Figure S2.13. Brünnich's guillemots, Bjørnøya

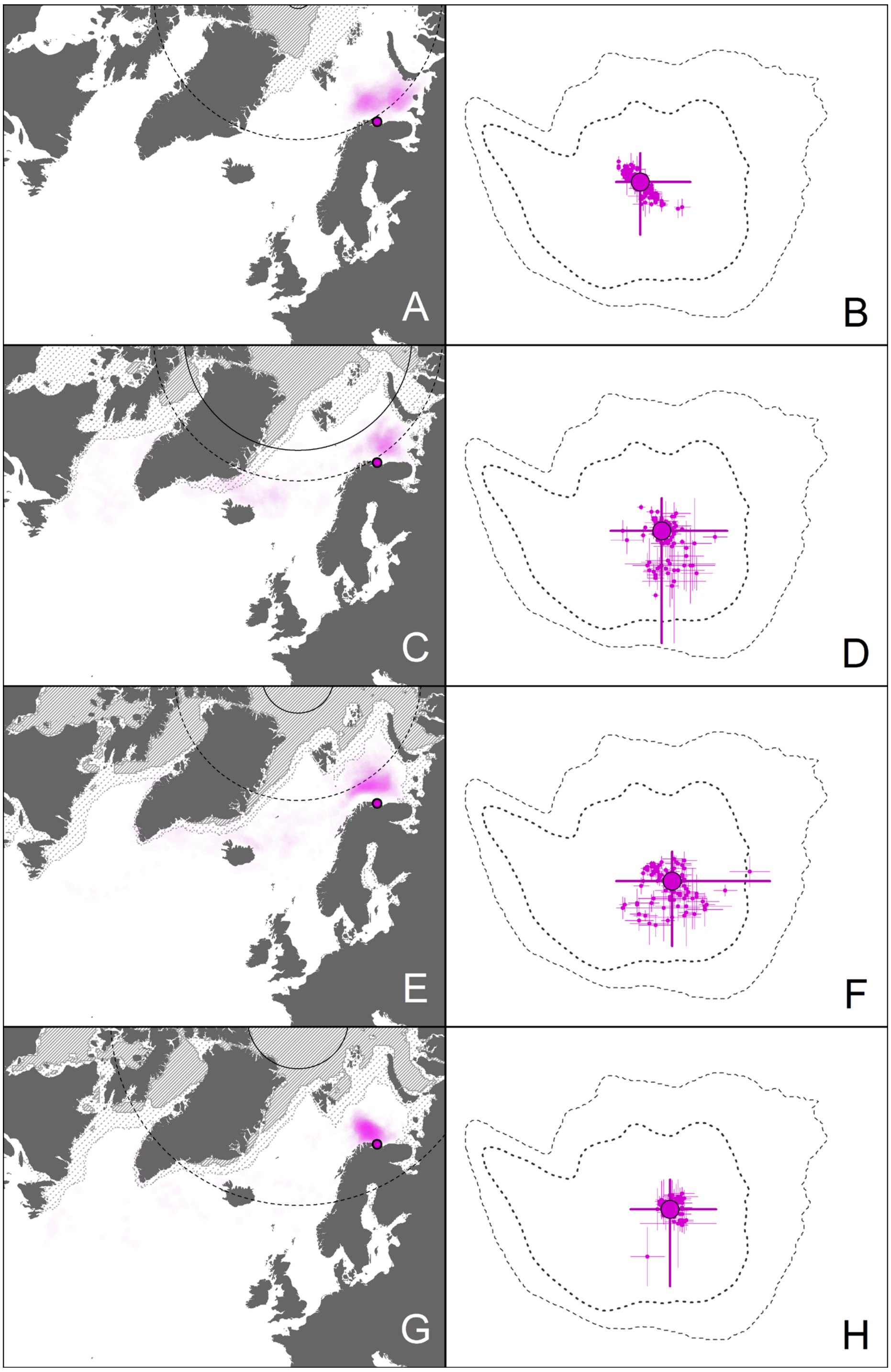


Figure S2.14. Brünnich's guillemots, Southern Barents Sea (Hornøya and Cape Gorodetskiy)

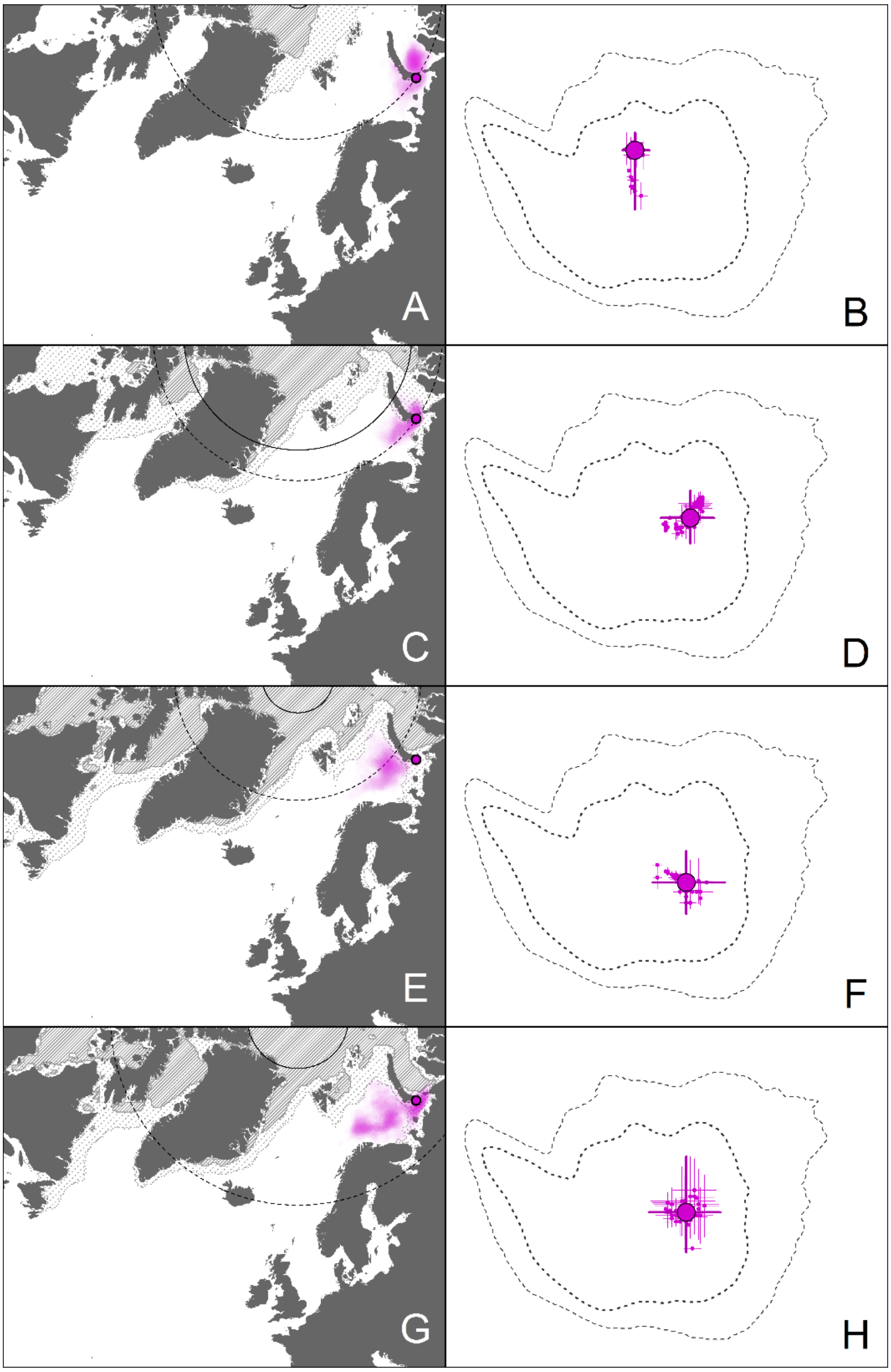


Figure S2.15. Brünnich's guillemots, Southern Novaya Zemlya (Kara Gate)

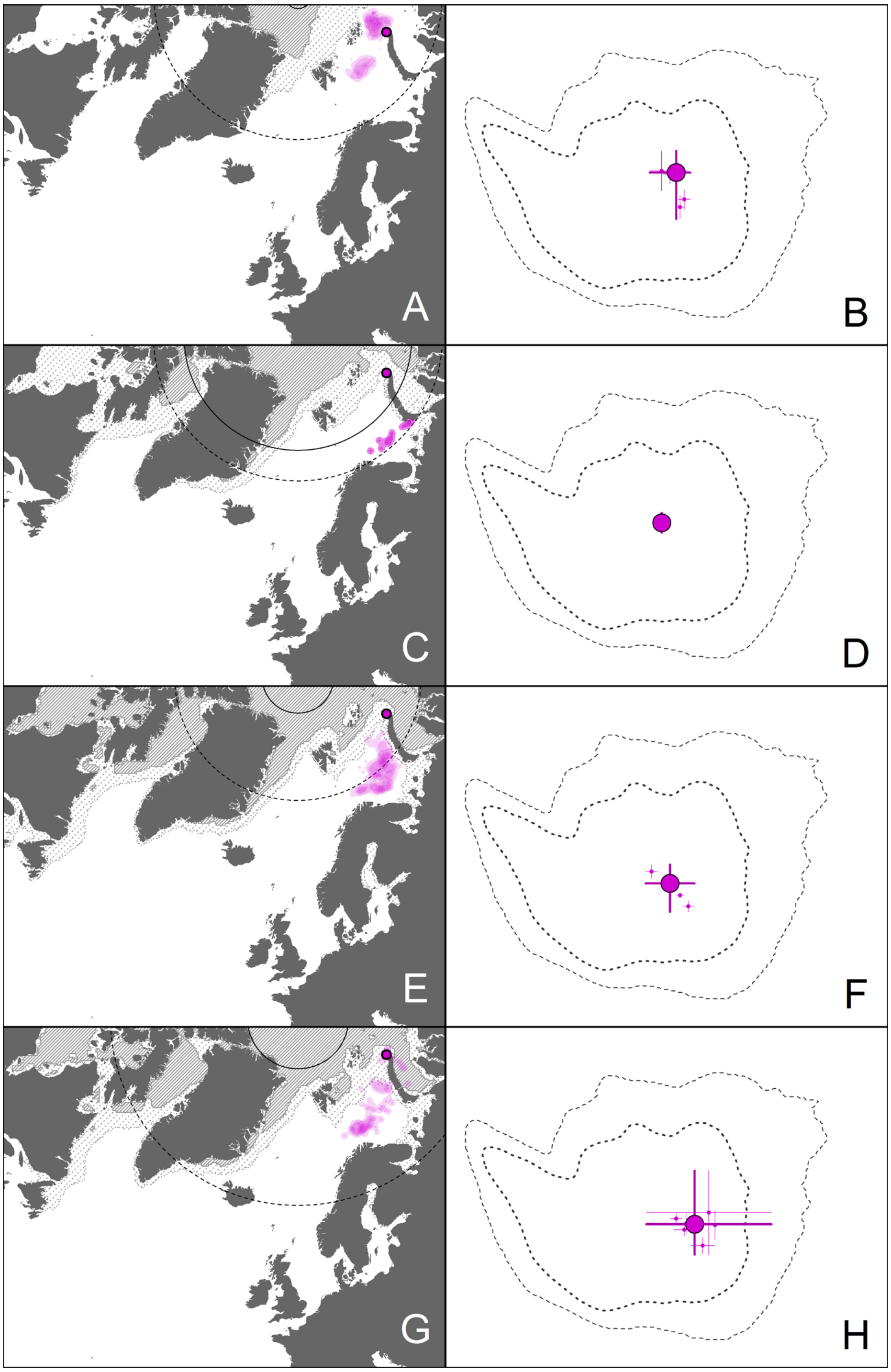


Figure S2.16. Brünnich’s guillemots, Northern Novaya Zemlya (Oranskie islands)

Supplementary information 3

Species- and population-specific movement networks by large marine ecoregion (y axis) and season (x axis). Each population is scaled to the same size and all nodes (squares) and edges (lines) are scaled to their usage accordingly. The entire species-specific movement network is plotted in grey scale in each plot and each breeding population-specific network is displayed on top. Common guillemot movement networks are displayed in figure S3.1-8 and Brünnich’s guillemot movement networks in figure S3.9-16.

Dark grey bars at the bottom of each figure denote the number of ecoregions used during each season by the entire network while dark red bars show population-specific use (scale on the left). Bars at the bottom of the figure between seasons denote the proportion of movement between (grey = entire network, black = population-specific) and within (light grey =entire network, yellow = population-specific) ecoregions with scale on the right.

Breeding population names: SNZ = Southern Novaya Zemlya, NNZ = Northern Novaya Zemlya, ESP = Eastern Spitsbergen, WSP = Western Spitsbergen, BI = Bjørnøya, SBS = Southern Barents Sea, HJ = Hjelmsøya, SK = Sklinna, JM = Jan Mayen, IC = North-East Iceland, FA = Faroe Islands, IM = Isle of May

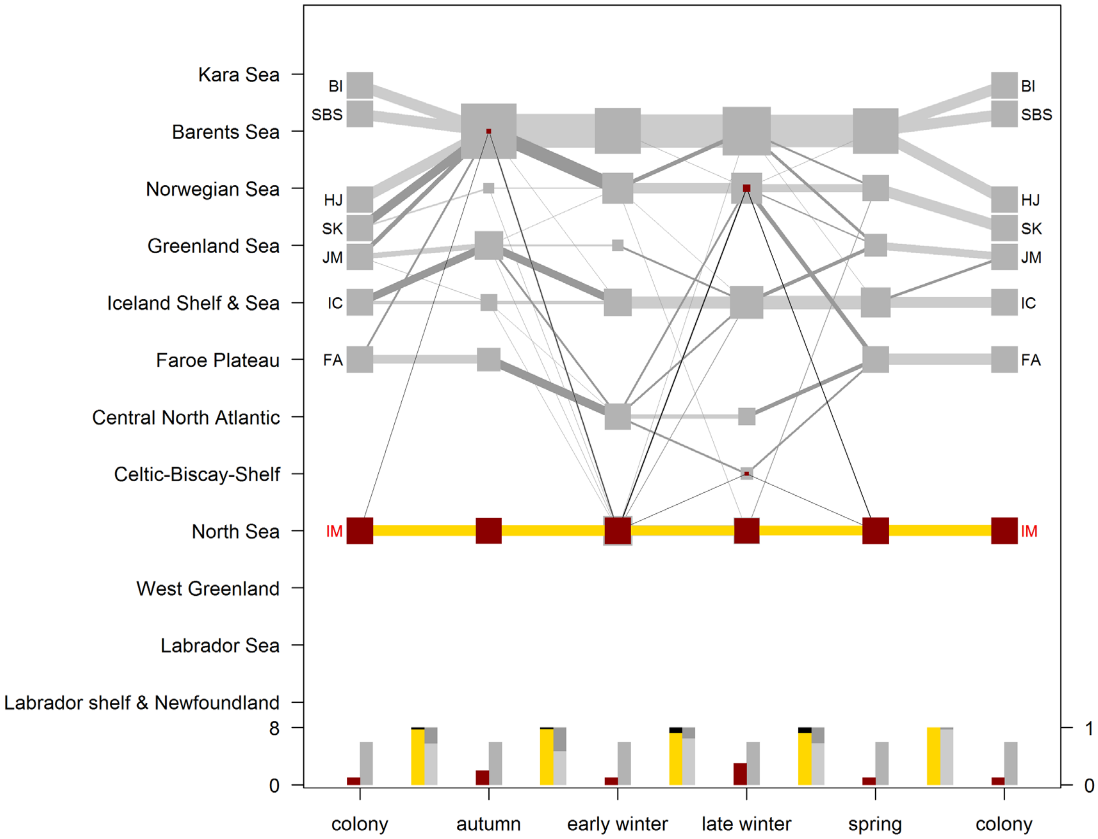


Figure S3.1. Common guillemots, Isle of May

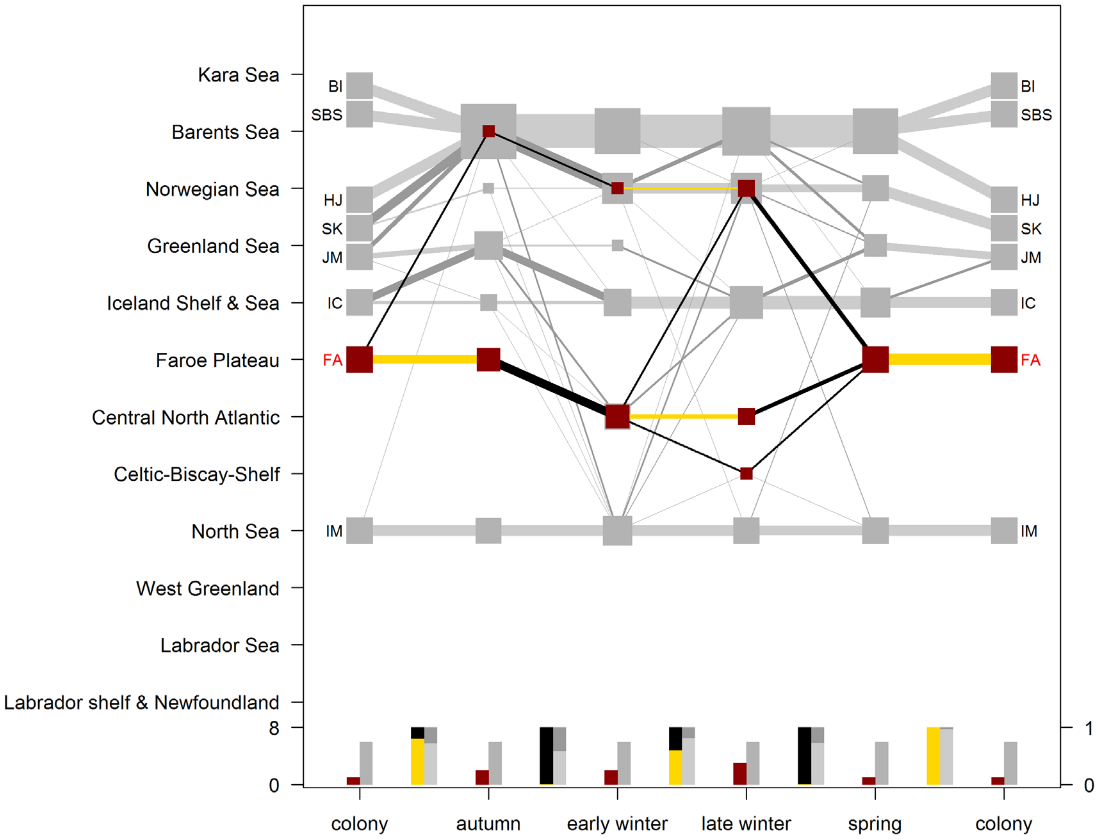


Figure S3.2. Common guillemots, Faroe Islands

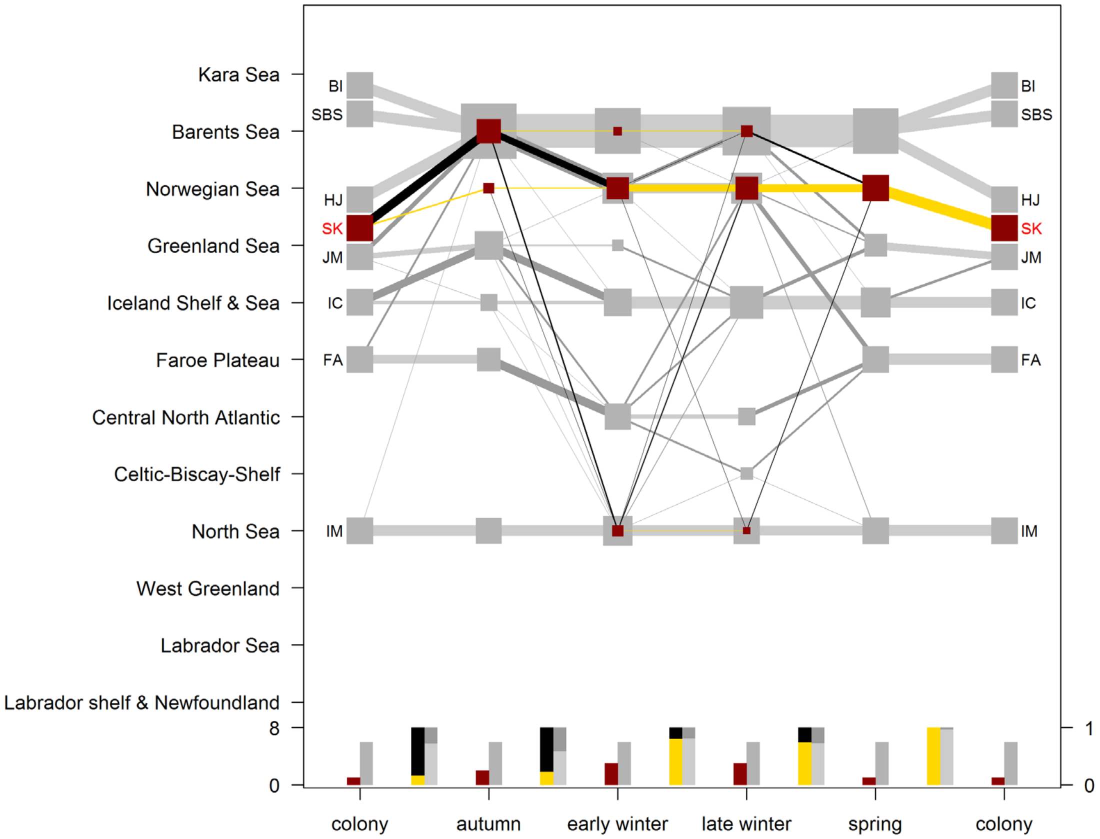


Figure S3.3. Common guillemots, Sklinna

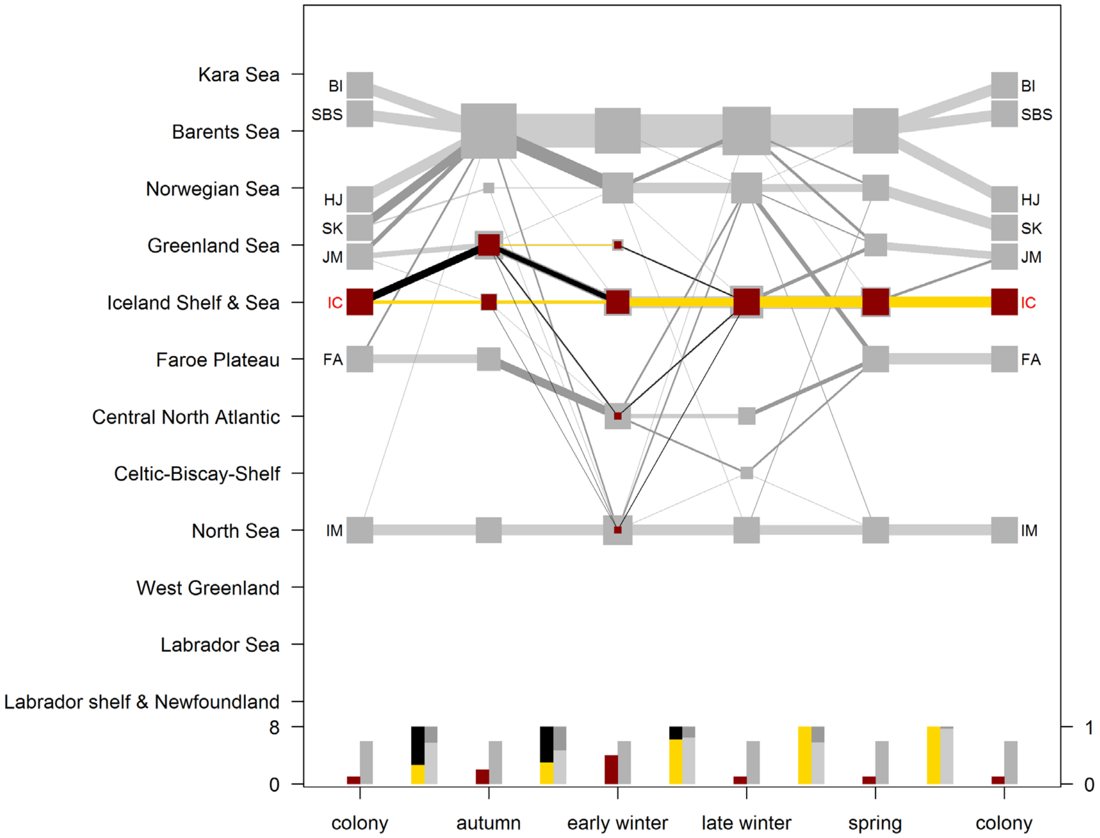


Figure S3.4. Common guillemots, North-East Iceland (Grimsey, Langanes)

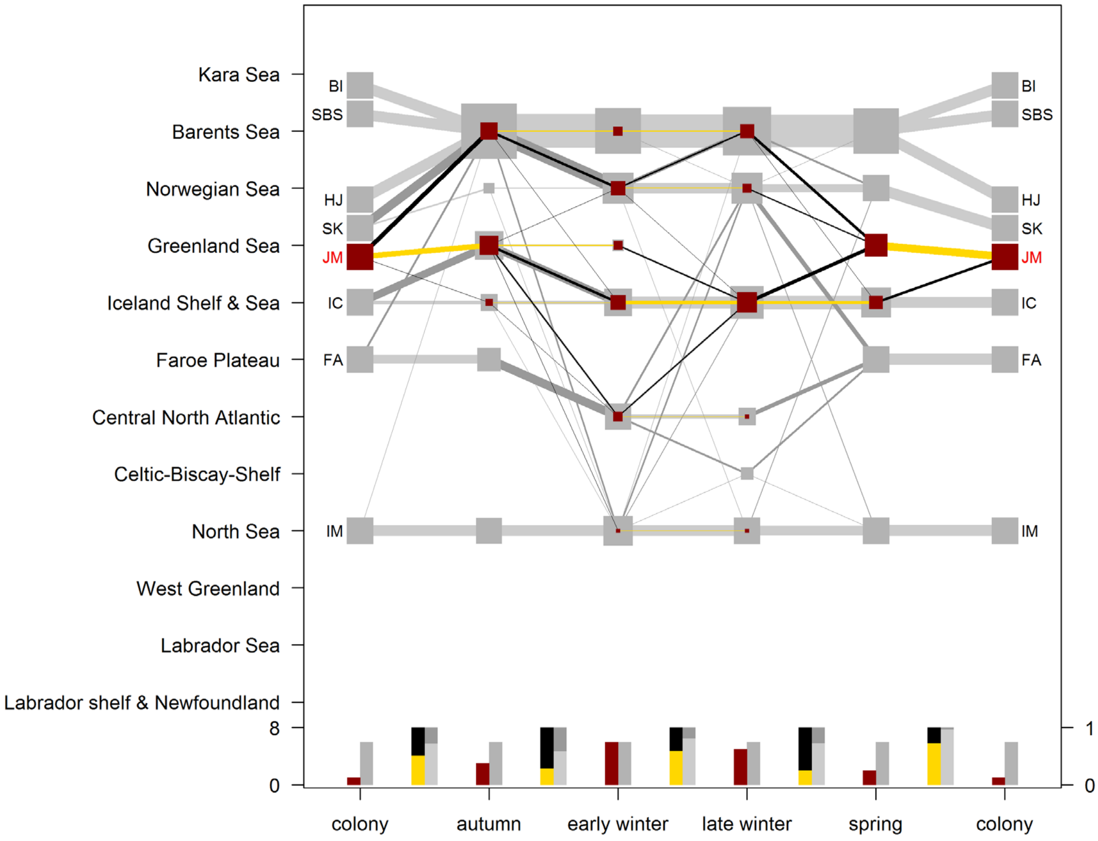


Figure S3.5. Common guillemots, Jan Mayen

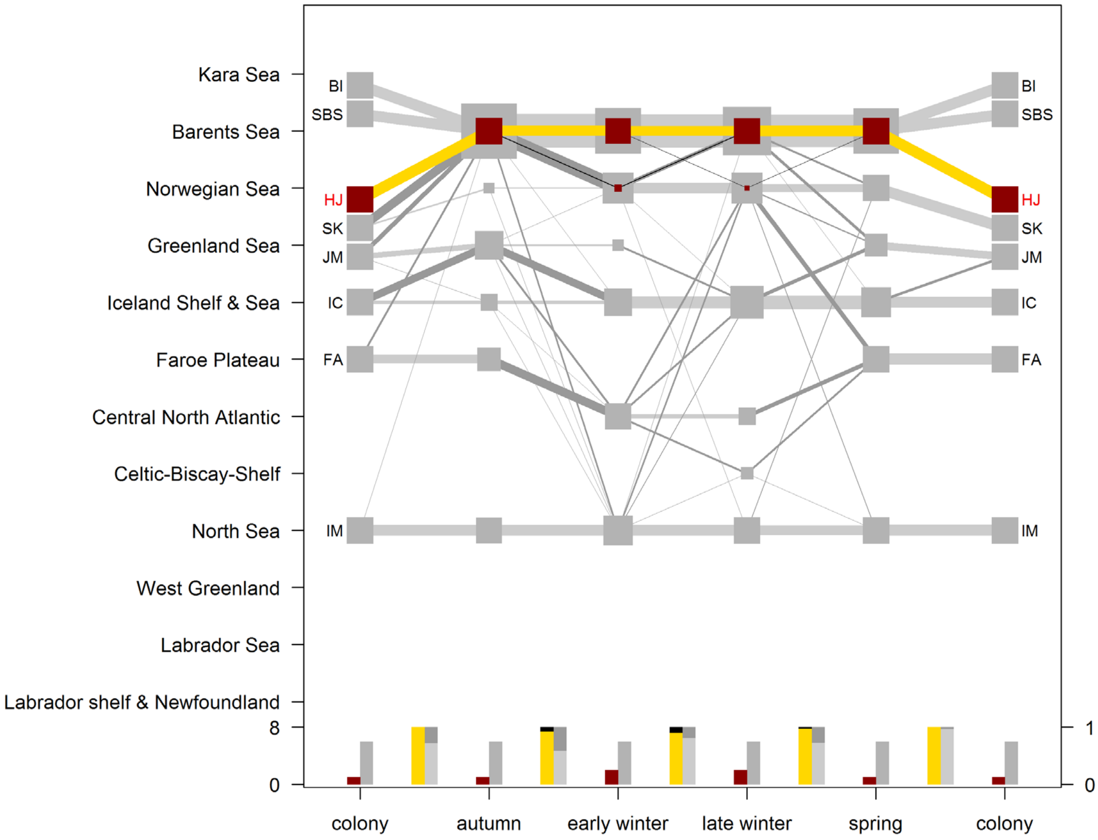


Figure S3.6. Common guillemots, Hjelmsøya

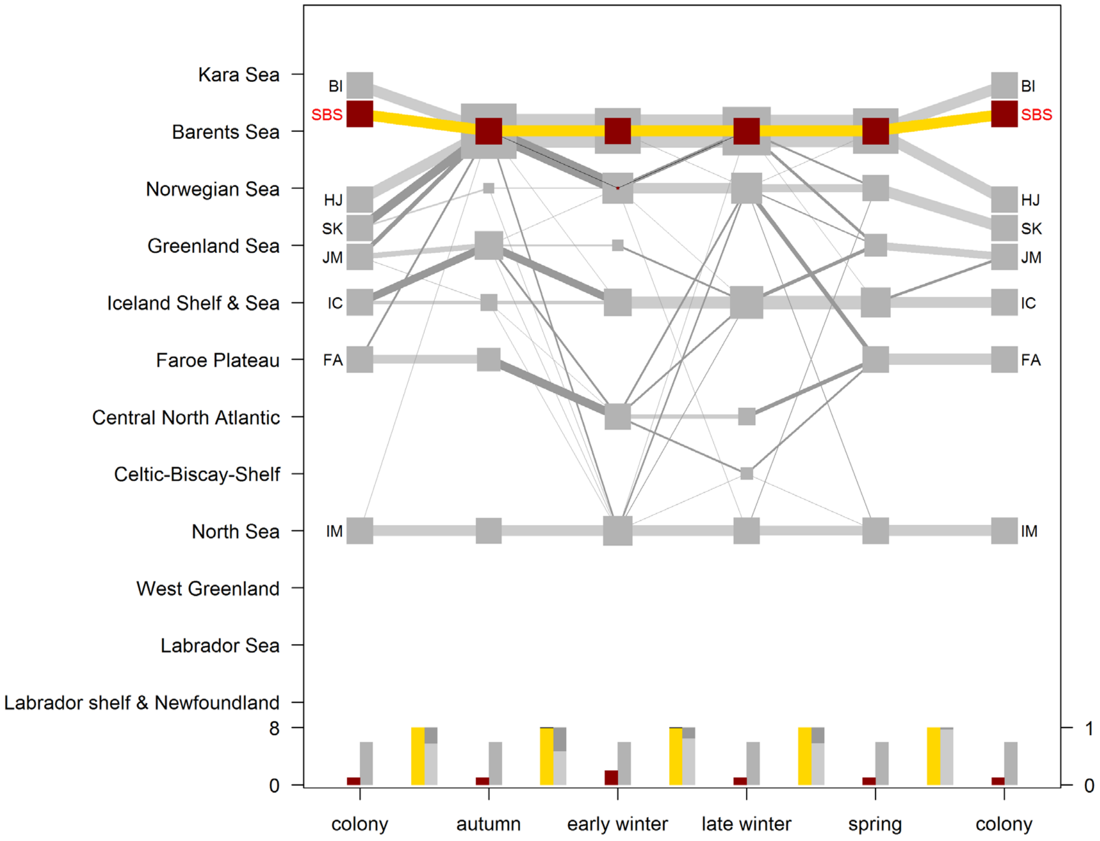


Figure S3.7. Common guillemots, Southern Barents Sea (Hornøya and Cape Gorodetskiy)

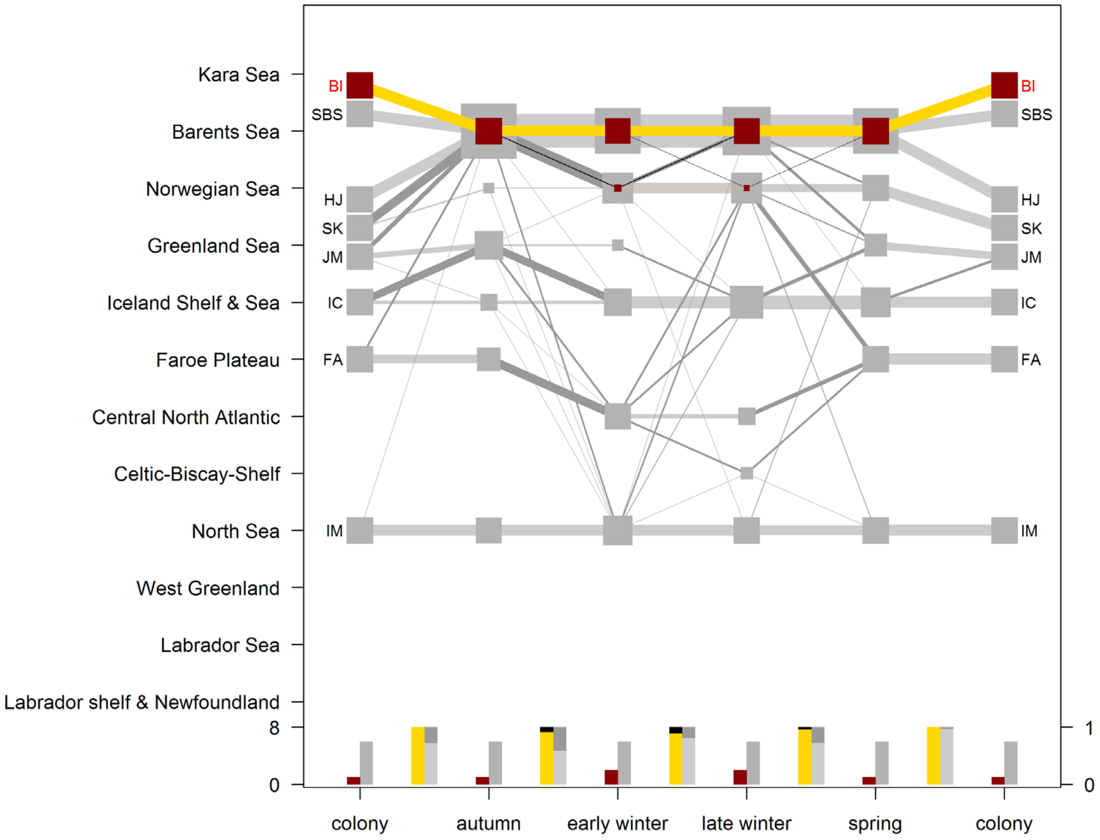


Figure S3.8. Common guillemots, Bjørnøya

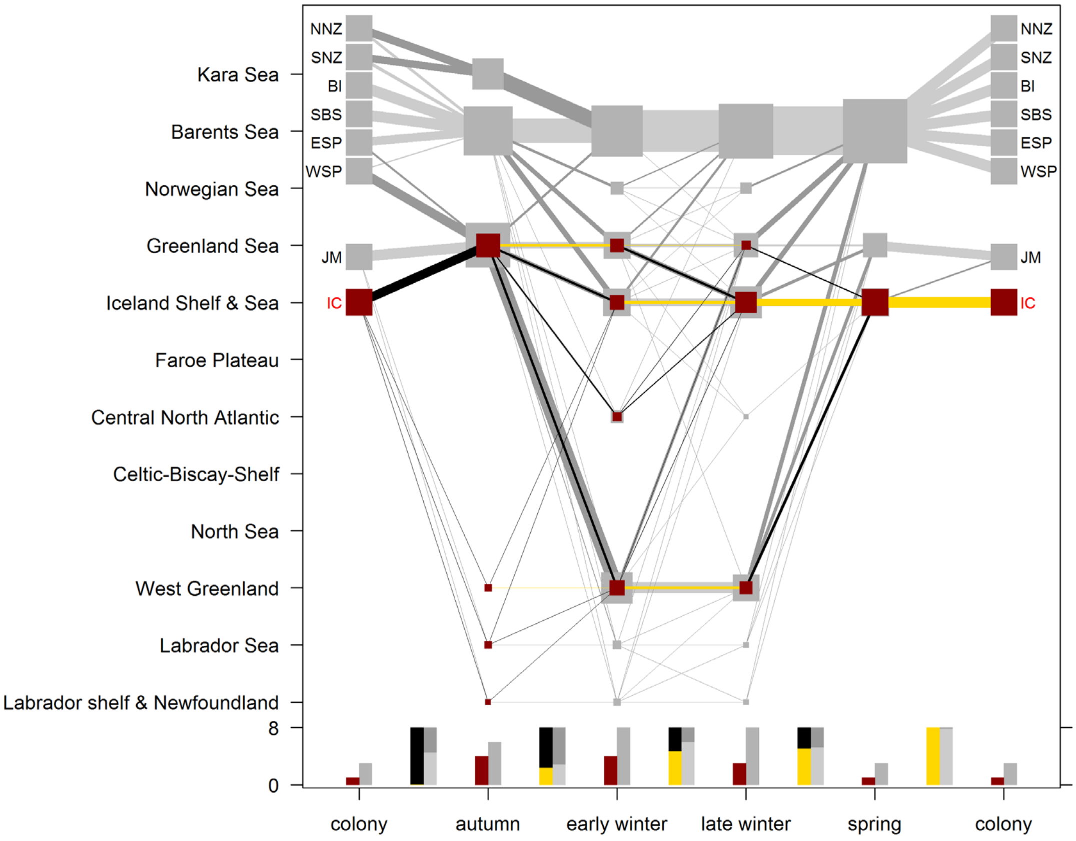


Figure S3.9. Brünnich's guillemots, North-East Iceland (Grimsey, Langanes)

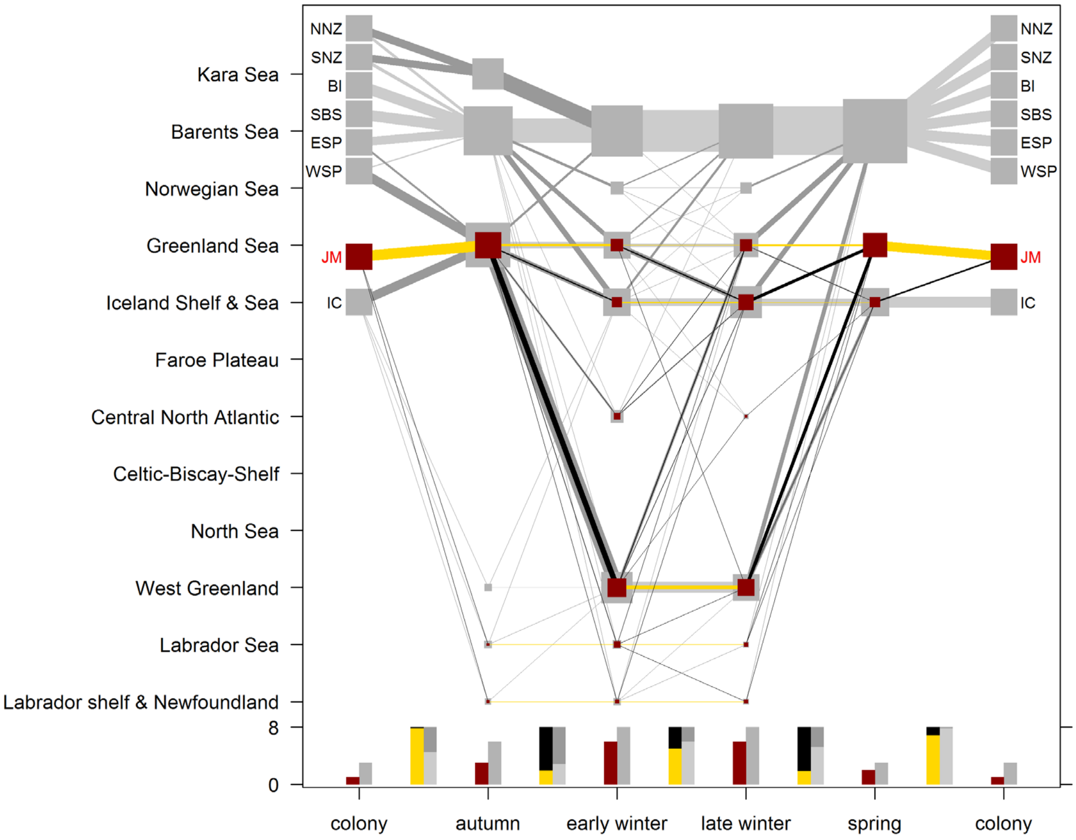
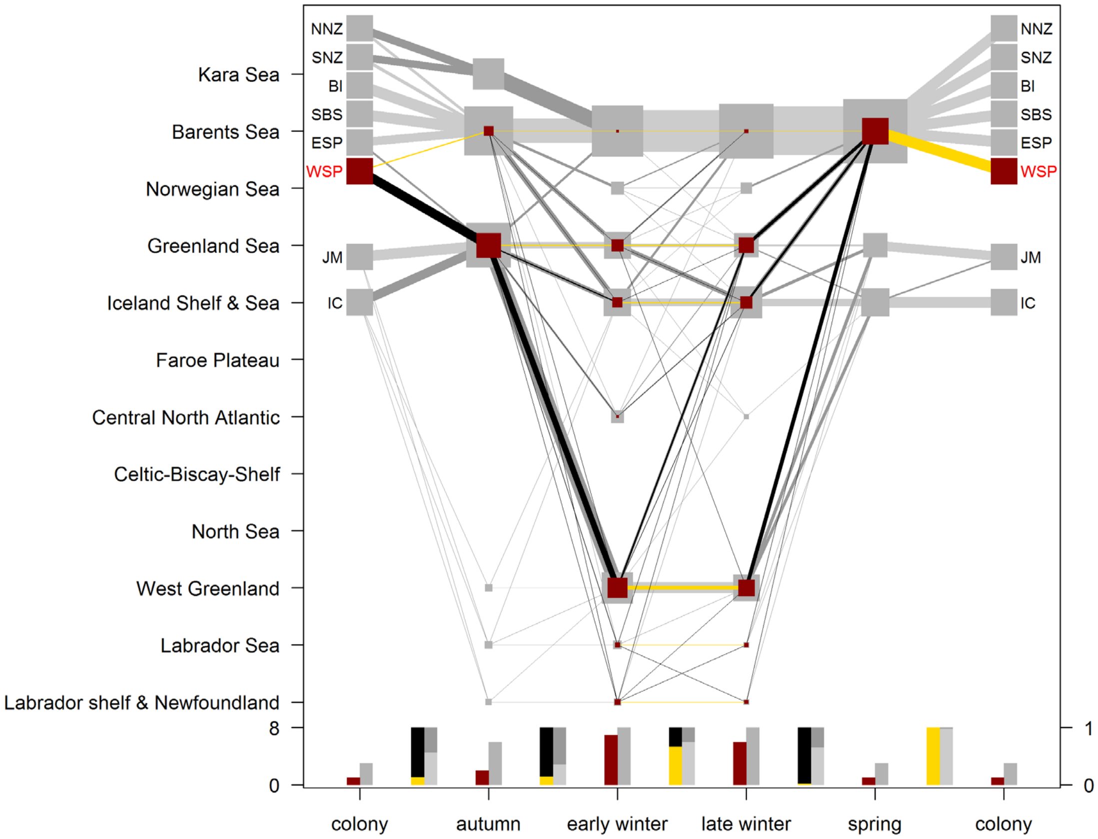


Figure S3.10. Brünnich's guillemots, Jan Mayen



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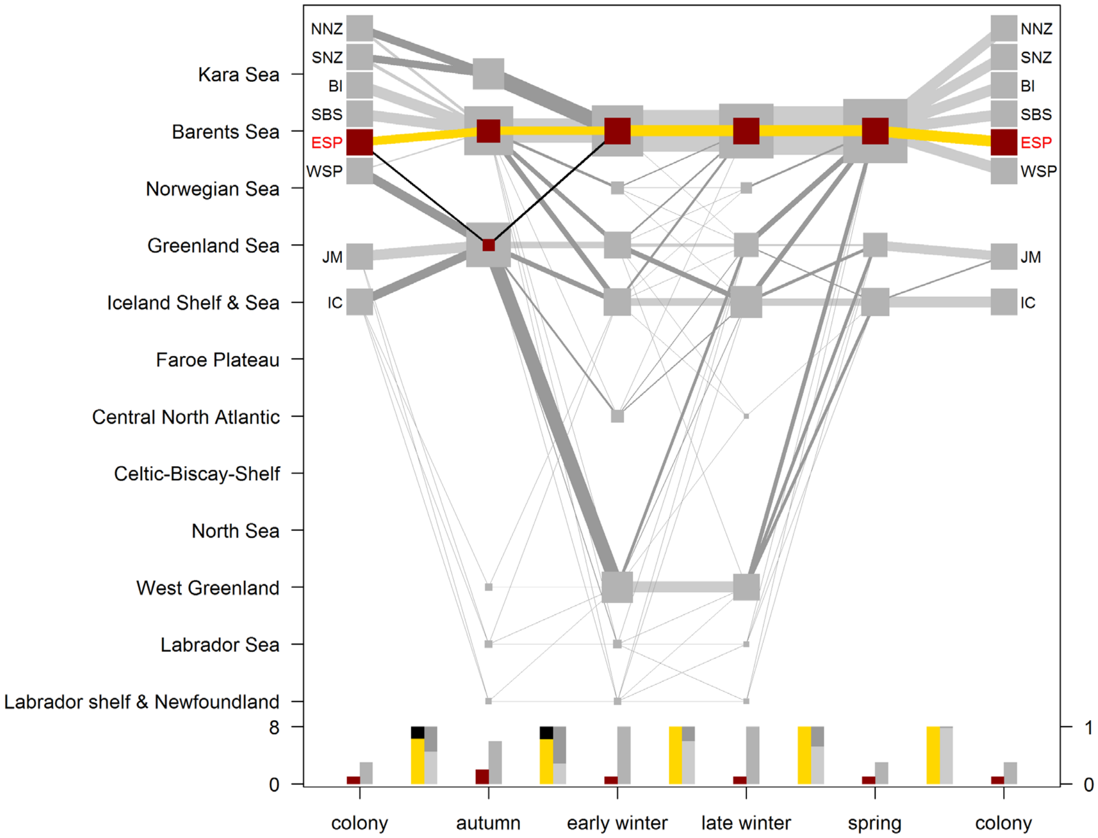

Figure S3.12. Brünnich's guillemots, Eastern Spitsbergen (Alkefjellet)

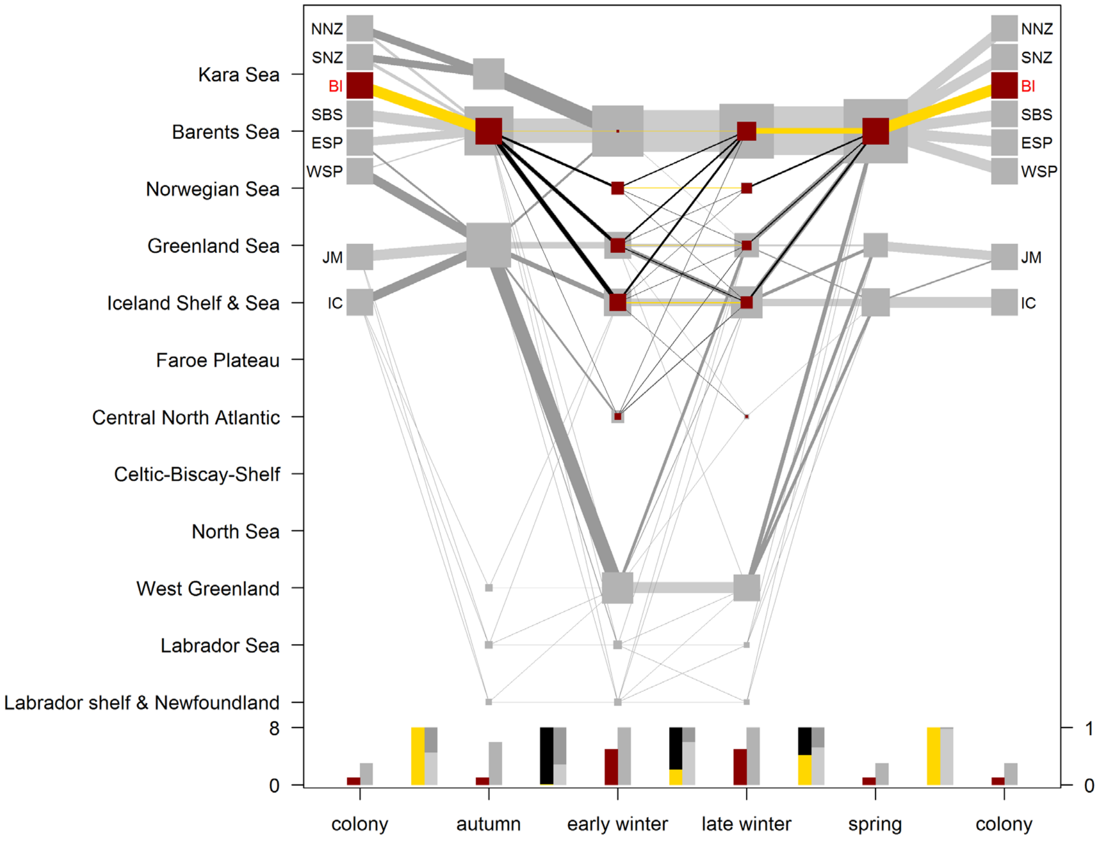

Figure S3.13. Brünnich's guillemots, Bjørnøya

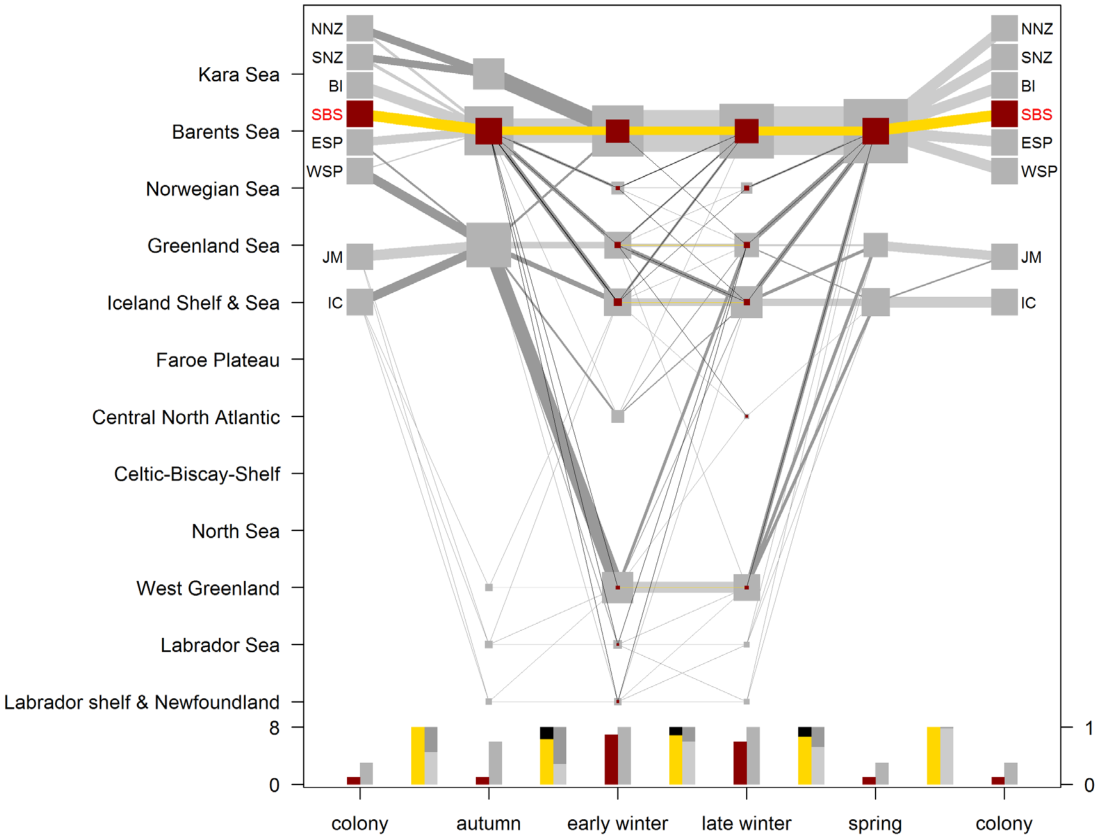

Figure S3.14. Brünnich's guillemots, Southern Barents Sea (Hornøya and Cape Gorodetskiy)

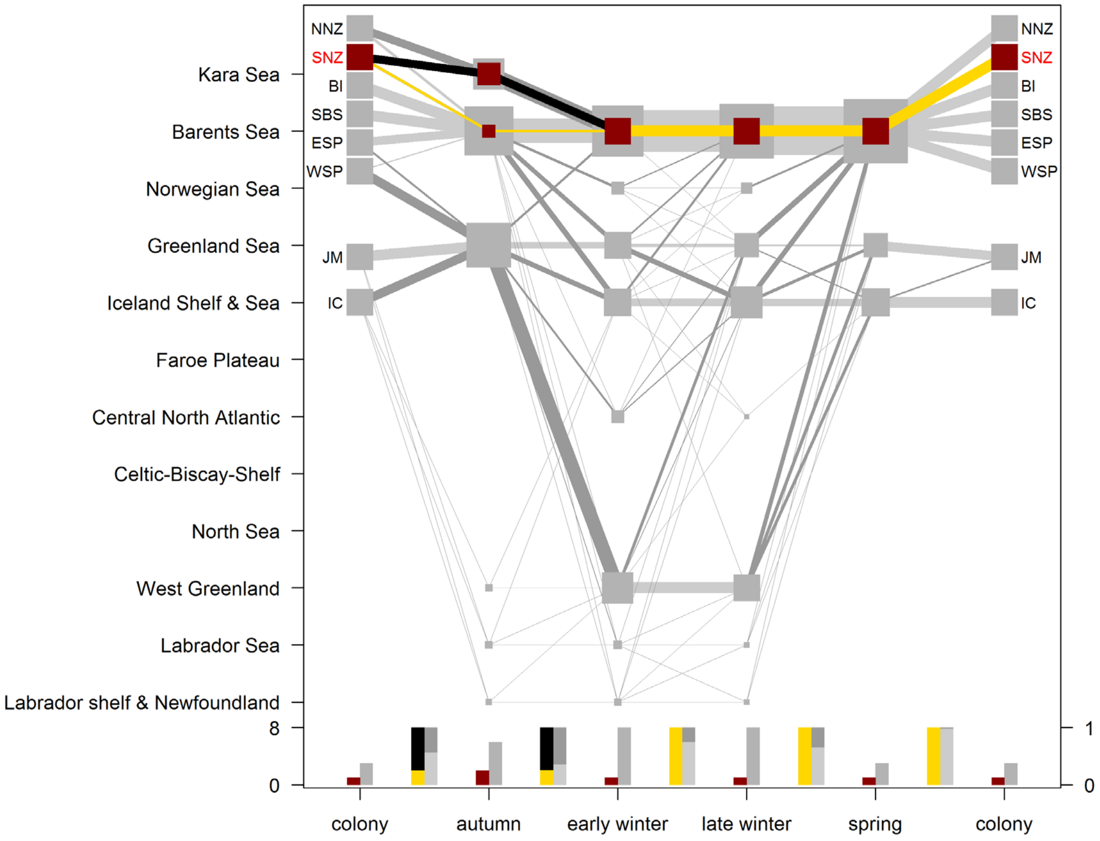

Figure S3.15. Brünnich's guillemots, Southern Novaya Zemlya (Kara Gate)

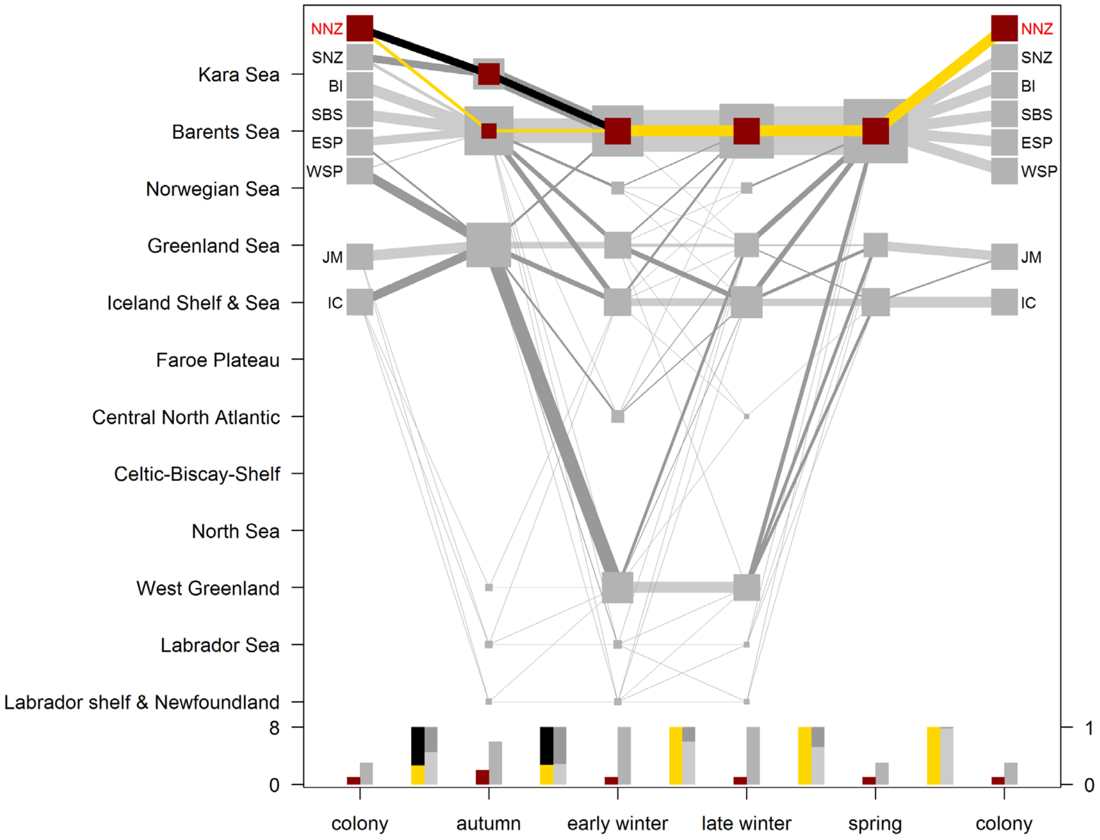

Figure S3.16. Brünnich's guillemots, Northern Novaya Zemlya (Oranskie islands)

Individual migration strategy fidelity but no habitat specialization in two congeneric seabirds

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Authorship: BM, HStr, NGY and SD designed the study; BM analysed the data with help from NGY; BM wrote the paper with contributions from SD, HStr, NGY and DG; HStr, SD, FD, KEE, AVE, MPH, MG, DG, SHL, TKR, GHS, HSte, ÞLÞ, and SW provided data; All authors commented on later drafts of the manuscript.

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Abstract

Aim: Consistent differences in individual behaviour are widespread and may affect the average population response to environmental change. In migratory species, individual migration strategy fidelity (IMSF, when individuals use fixed and individual-specific migration strategies) occurs often. It may be driven by either site familiarity (i.e. fidelity to specific sites) or habitat specialization (i.e. fidelity to specific habitats). Under climate change favourable habitats may permanently shift locations and hence IMSF may reduce individual fitness with adverse consequences for populations. Our goal was to test if individuals from the genus *Uria* have flexible or fixed individual migration strategies (i.e. IMSF), if this behaviour is consistent across large parts of the genus' range and if they were philopatric to geographical sites or a habitat feature.

Location: North Atlantic

Methods: We quantified consistent individual differences in spatial distribution and habitat occupied throughout the non-breeding period using a large geolocator tracking dataset of 376 repeatedly tracked individual adult seabirds tracked up to seven years breeding at nine different sites across the Northeast Atlantic. Additionally, we calculated relative fidelity to either geographic sites or habitats as well as persistence of spatial site fidelity over multiple years.

Results: Both, guillemot species exhibited IMSF across a large part of the genus' range which persisted over multiple years. Individuals of both species and almost all colonies did not show fidelity to specific habitats while relative fidelity to geographic sites predominated over relative fidelity to habitats. Overall, this indicates that individuals employ IMSF which is best explained by site familiarity rather than habitat specialisation.

Main conclusions: In the context of rapidly changing environments, vulnerable migratory species displaying IMSF driven by site familiarity - such as the genus *Uria* - may not be able to adjust their migration strategies sufficiently fast to sustain adult survival rates and ensure population persistence.

Keywords: guillemots, habitat specialization, individual migration strategy fidelity, light-level geolocation, murres, North Atlantic, site familiarity, *Uria aalge*, *Uria lomvia*

Introduction

Migratory animals face many challenges in a rapidly changing world (Robinson et al., 2009; Wilcove & Wikelski, 2008) as individuals need to structure their annual schedule to maximise availability of spatially and seasonally fluctuating resources (Alerstam, Hedenström, & Åkesson, 2003; Bridge, Ross, Contina, & Kelly, 2015). Many migrants, such as seabirds (Schreiber & Burger, 2001), are long-lived species. Hence, their overall population growth rate is sensitive to changes in adult survival (Lebreton & Clobert, 1991; Sæther & Bakke, 2000), which depends on their migration behaviour and ability to respond to changes during periods outside the breeding season (Abrahms et al., 2018; Alves et al., 2013; Desprez, Jenouvrier, Barbraud, Delord, & Weimerskirch, 2018). Additionally, reproductive success can also be affected by conditions experienced during the non-breeding season (Alves et al., 2013; Bogdanova et al., 2017; Catry, Dias, Phillips, & Granadeiro, 2013).

Consistent differences in individual behaviour are common in free-living populations, and these can have far-reaching implications on intraspecific competition, population persistence, community dynamics, and ultimately species diversity (Bolnick et al., 2003; Dall, Bell, Bolnick, Ratnieks, & Sih, 2012; Piper, 2011). Site fidelity - an animal's tendency to repeatedly use the same geographic area - is a common form of individual behavioural consistency (Switzer, 1993). In migrants, site fidelity during breeding has been frequently observed (Bradshaw, Hindell, Sumner, & Michael, 2004; Ceia & Ramos, 2015; Phillips, Lewis, González-Solís, & Daunt, 2017). Though, less evidence exist for 'Individual migration strategy fidelity' (IMSF) when within-individual variation in the use of space during the non-breeding period is less than that across the population as a whole (reviewed in Ceia & Ramos, 2015; Cresswell, 2014; Eggeman, Hebblewhite, Bohm, Whittington, & Merrill, 2016; Newton, 2008; Phillips et al., 2017). However, site fidelity could be the cause or a consequence of other types of specialization, such as in diet or habitat with contrasting implications in the context of climate change (Patrick & Weimerskirch, 2017; Piper, 2011; Wakefield et al., 2015; Woo, Elliott, Davidson, Gaston, & Davoren, 2008). Rapid environmental changes have the potential to favour individuals with flexible migration strategies (Abrahms et al., 2018; Switzer, 1993), while IMSF could constrain the ability of a population to track habitat changes (Keith & Bull, 2017; Wiens, 1985).

IMSF during the non-breeding period may be driven by site familiarity, defined as information accumulated about a specific area by an individual (Jesmer et al., 2018; Keith & Bull, 2017; Piper, 2011). That is, by being faithful to wintering areas, individuals reduce costs of sampling other suitable wintering areas and diminish uncertainty from successive migrations (''always stay'' strategy in Cresswell, 2014; Switzer, 1993). This is particularly important for long distance migrants as their migration routes are generally conserved from year to year (Thorup et al., 2017; Van Moorter, Rolandsen, Basille, & Gaillard, 2016). Long term site fidelity might be advantageous for long-lived species when considered over a long time period or across an entire life span even if it might not be the most favourable strategy every year (Abrahms et al., 2018; Bradshaw et al., 2004; Switzer, 1993). If a species' migration behaviour is affected by site familiarity, then site fidelity may persist across its entire range and several years as specific sites rather than habitats are selected (Switzer, 1993). Until recently, site familiarity has received little attention, yet it may play an important role in habitat selection (Cresswell, 2014; Keith & Bull, 2017; Piper, 2011).

Alternatively, exhibited IMSF could be a consequence of individual specialisation in diet and habitat choice in a patchy environment (Abrahms et al., 2018; Patrick & Weimerskirch, 2017). An individual's resource or habitat choice in heterogeneous environments such as the open ocean will be associated with spatial fidelity (Switzer, 1993). However, selection of sites and habitats are often decoupled from each other as similar habitats can co-occur at different sites (Gómez, Tenorio, Montoya, & Cadena, 2016; Peters et al., 2017). Therefore, IMSF is unlikely to be exhibited in all habitats occupied by a species across its geographic range. Additionally, resource patches can shift in space and time between years. Hence, IMSF is not expected to persist across multiple years throughout a species' range if it is a consequence of habitat specialisation (Patrick & Weimerskirch, 2017; Wakefield et al., 2015).

Here, we assessed if two migratory species, over large parts of their range, display IMSF (or alternatively generalist migratory behaviour) and if this behaviour is better explained by fidelity to specific sites or habitats. The temperate common guillemot (hereafter COGU, *Uria aalge*) and the Arctic Brünnich's guillemot (hereafter BRGU, *Uria lomvia*) are large (~1kg), numerous, deep diving, pelagic feeding, long lived, congeneric colonial seabirds (A J Gaston & Jones, 1998). They show strong breeding philopatry (Benowitz-Fredericks & Kitaysky, 2005; A J Gaston & Jones, 1998), and exhibit strong migratory connectivity throughout their non-breeding period in space as well as in environmental niches (PAPER II). Hence, different breeding populations use distinct areas and environments outside their breeding season. Their annual distribution encompasses a large range of space and environments in the North Atlantic and Arctic seas (Frederiksen et al., 2016; McFarlane Tranquilla et al., 2015). These oceans are changing rapidly under climate change (Henson et al., 2017; IPCC, 2013; Lind, Ingvaldsen, & Furevik, 2018) and species distributions (e.g. capelin, *Mallotus villosus*, Carscadden, Gjøsæter, & Vilhjálmsson, 2013) and ecosystem compositions are shifting (Beaugrand & Kirby, 2018; Fossheim et al., 2015; Perry, Low, Ellis, & Reynolds, 2005; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013; Wassmann, Duarte, AgustÍ, & Sejr, 2011). In this context, an understanding of IMSF and the relative fidelity to geographic sites and habitats as well as its persistence across a genus' range is needed to assess the species' potential resilience to ongoing climatic changes. Initial evidence indicates that individuals of both species display variable site fidelity during the winter months (McFarlane Tranquilla et al., 2014) and hence might be able to adapt quickly to their changing environment (Abrahms et al., 2018; Switzer, 1993).

Using tracking data from 372 COGUs and 357 BRGUs from nine different breeding sites across the Northeast Atlantic, where 208 COGU and 168 BRGU individuals were tracked for at least two winters (maximum of seven winters), we tested the hypothesis that individuals of both species display IMSF across large parts of their range throughout their non-breeding period. Further, we assessed if their migratory behaviour is potentially a consequence of site familiarity or habitat specialisation.

Material and Methods

Data

Fieldwork was conducted at 13 breeding colonies spanning 56°N to 79°N and 16°W to 55°E in the Northeast Atlantic (figure 1). Some colonies in close spatial proximity to each other (< 160 km) which exhibited similar space use patterns were combined resulting in nine breeding populations (table 1). BRGU and COGU breed sympatrically in four of these populations. We used archival light-level loggers (also GLS or "geolocators") to estimate the spatiotemporal locations of individuals throughout the non-breeding period. These devices record light intensity and time which can be used to estimate approximate latitude (i.e. day length) and longitude (i.e. time of noon) positioning twice daily. They are attached to a leg ring with cable ties (logger, ring, and cable ties < 0.5% adult body mass). During the summers of 2007 to 2017 we captured adult guillemots with noose poles at different sites and equipped them with light-level loggers which we retrieved in subsequent years (overall retrieval rate > 60%). Individuals were chosen opportunistically in most cases from birds breeding on cliff ledges on the landward edge of the colony. This resulted in 1332 annual tracks (641 BRGU, 691 COGU) of 729 individuals (357 BRGU, 372 COGU) of which 376 were tracked for at least two years (168 BRGU, 208 COGU, table 1). All subsequent analyses were conducted in R 3.4.3 (R Development Core Team, 2018). All loggers (models: Mk15 (British Antarctic Survey, Cambridge, UK), Mk3006 (Biotrack, Wareham, UK), F100, C250 & C330 (Migrate Technology, Cambridge, UK) or L250A (Lotek, St. John's, Newfoundland, Canada)) also recorded temperature and salt water immersion ("wet/dry") data which were used in combination with recorded light data to increase location accuracy (estimated median accuracy: 150-180 km, Merkel et al., 2016; see SI 1 for more details). In some populations, blood or feather samples were collected and used to determine the sex of individual birds (details in table 1) by DNA extraction using the DNeasy 96 Blood and Tissue Kit

(Qiagen, Hilden, Germany) and afterwards polymerase chain reaction (PCR) using Qiagen's Multiplex PCR Kit. Sex was then determined using the primers M5 (Bantock, Prys-Jones, & Lee, 2008) and P8 (Griffiths, Double, Orr, & Dawson, 1998). Gender was included in the analyses to account for the possibility of sex-specific migratory behaviour and its potential effect on our measure of site fidelity during parts of the non-breeding period.

Data Analysis

To test our hypothesis that guillemots, across a large part of their range, display IMSF throughout the non-breeding period, we used the concept of nearest neighbour distance (NND, Guilford et al., 2011). Individual annual tracks were split into ten day bins starting 1 July. A resolution of ten days was chosen to retain a sufficient number of locations for each bin for further analysis while accounting for possible seasonal differences. The centre for each individual ten day bin was estimated as the geographic median (position with minimum distance to all other locations). NND in space was calculated as Euclidian distance in polar stereographic projection between ten day centre locations for repeat tracks of the same individual in different years as well as different individuals from the same species and breeding population tracked in the same year. Next, we averaged NND of all pairwise comparisons at each time step for each individual with more than one repeat track. Following Wakefield et al. (2015), we used a randomization procedure to test for each species and population considered if intra-individual NND is smaller than population-level NND at each time step. The null hypothesis (i.e. generalist migratory behaviour) was that observed intra-individual NND is not significantly smaller than population-wide NND calculated with randomly assigned bird individuals (1000 permutations without replacement). Significance was assessed using a one-tailed t-test (significance at $p = 0.05$) at each time step. To account for the possibility of sex-specific behaviour the same procedure was also applied to each sex separately for populations where the sexes were known (table 1). To test if a lack of site fidelity could be explained by variability in timing rather than flexible space use, we calculated intra-individual as well as inter-individual NND at each time step for a very wide temporal sliding window (70 days, figure S1). Using this temporally integrated measure of fidelity we ran the same procedure as described above for both sexes combined as well as each sex separately.

To tested if individuals exhibit habitat specialisation throughout the non-breeding period we quantified the occupied habitat using eight ecologically relevant oceanographic parameters (Fort, Porter, & Grémillet, 2009; Fort et al., 2013; McFarlane Tranquilla et al., 2015); three sea surface temperature variables (absolute, distance to fronts, predictability), two sea surface height variables (absolute, distance to meso-scale eddies), surface air temperature, distance to the marginal sea ice zone and bathymetry (see SI 1 for more details). The habitat occupied was then assessed using the concept of environmental space (Broennimann et al., 2012) defined as the first two axes of a Principal Component Analysis (PCA) of all environmental parameters calibrated on the available environment. To capture the variability of the available environment, 20000 points with equal spatial coverage across the entire study area (figure S2) were sampled every two weeks for the entire study period (2007-2017). All individual positions were projected onto the PCs (PC1 = 44% and PC2 = 19%, figure S4). Occupied environmental space was then calculated using Gaussian kernel utilization distributions (UD, standard bandwidth, 200 x 200 pixel grid, adehabitatHR package, Calenge, 2006) at each ten day step following Broennimann et al. (2012). These UDs were used to calculate ten day median positions for each track. Based on these we calculated intra-individual and inter-individual NND (only for individuals from the same species, breeding at the same population and tracked during the same year) in environmental space. Using these computed NNDs and the same randomization procedure as described above for Cartesian space (Wakefield et al., 2015), we tested if individuals exhibit fidelity to specific habitat at each time step.

To discern if IMSF is better explained by site familiarity or habitat specialisation we quantified species- and population-specific relative fidelity to sites and habitats using the similarity index developed by Patrick and Weimerskirch (2017). This index is a ratio ranging from 0 (all individuals are generalists within the considered population) to 1 (all individuals are specialists). At each ten day step for each repeat individual the sum of all instances for which intra-individual NND was smaller than inter-individual NND was divided by the number of inter-individual NNDs computed (see Patrick and Weimerskirch (2017) for more details). Next, we averaged similarity for individuals with more than one repeat track. This similarity was calculated in Cartesian as well as environmental space. Relative fidelity to either space was tested by subtracting individual habitat similarity from site similarity. Using two-tailed t-tests, we determined if the estimated population-wide distribution was significantly different from 0 (significance at $p = 0.05$) and hence either site (>0) or habitat specific (<0). In addition, environmental similarity was calculated for each abiotic parameter described above and relative fidelity for sites or a given environmental parameter was tested separately to estimate the robustness of our results.

To test whether IMSF persists across years (an indication for site familiarity) or weakens linearly over time (an indication for habitat faithfulness assuming habitat is not connected to space), we modelled species- and population-specific intra-individual NND as a function of time lag (years between repeat tracks) with random slope and intercept for each individual. Next, we used likelihood ratio tests to determine whether these models explain the data better than the intercept-only models (i.e. without accounting for time lag, Wakefield et al., 2015). This procedure was run for 70 day sliding windows throughout the non-breeding period to account for potential timing effects.

Results

Do guillemots exhibit IMSF?

Overall, both species exhibited individual migration strategy fidelity (IMSF) as indicated by significantly smaller intra-individual NND compared to the Null distribution across their studied range (figure 2). However, some seasonal and population-specific variability was apparent. Generalist migratory behaviour was shown during spring (approx. February - May depending on population) and in part of the autumn (August/September) across species and populations as a consequence of little population wide variability in migration strategies. Moreover, there was some variation among populations and populations displaying little population wide NND did not generally exhibit IMSF given the accuracy of the tracking method used (median error of 150-180 km, Merkel et al., 2016). But, some populations - with little population wide NND (e.g. COGUs from Bjørnøya & Hjelmsøya) - displayed IMSF during mid-winter (December/January) when the proportion of twilight events (north of 66°N) and hence location estimates missing was high (figure S5). IMSF was also visible for each sex separately in both species and all populations tested with some populations exhibiting sex-specific differences during autumn and in part spring (figure S6 & S7).

Higher variability in intra-individual NND was apparent in some populations (e.g. BRGU Bjørnøya, particularly in late winter (February/March, figure 3). Integrating NND over a wide temporal window (70 days) demonstrated that some spatial variability could be explained by timing (i.e. similar areas have been utilised, but not necessarily at the same time), while general results remained unchanged (figure 2). Overall, IMSF persisted across multiple years (up to 9 years) in all tested populations, when accounting for the timing difference (i.e. using a 70 day sliding window), illustrating that individual site fidelity was not altered by the number of years between repeat tracks (figure 3).

Is IMSF better explained by site familiarity or habitat preference?

In all populations of both species, little individual consistency in occupied habitats was apparent (except for BRGU from Hornøya and COGU from Jan Mayen, figure S8). Further, fidelity to geographic sites rather than abiotic habitat was predominant for both species and all populations throughout the entire non-breeding period (figure 4). The same pattern could be observed for each sex (figure S9 & S10) as well as each environmental parameter (figure S11), separately. The only indication for fidelity to a specific abiotic feature rather than a specific site could be seen in both species for bathymetry during spring (figure S11).

Discussion

In this study, we identified individual migration strategy fidelity (IMSF) for the genus *Uria*, which was independent of sex, and occurred throughout the entire Northeast Atlantic during most of the non-breeding period. This was apparent as fidelity to geographic sites rather than preferences for specific habitats. Importantly, IMSF persisted across multiple years in all considered populations. Suggesting that in the Northeast Atlantic IMSF is the norm in COGUs and BRGUs - independent of occupied habitat.

IMSF in guillemots

Evidence for IMSF has been found in various taxa such as in ungulates (Jesmer et al., 2018; Sawyer, Merkle, Middleton, Dwinnell, & Monteith, 2018), fishes (Brodersen et al., 2012; Thorsteinsson, Pálsson, Tómasson, Jónsdóttir, & Pampoulie, 2012) as well as in monarch butterflies (*Danaus plexippus*, Yang, Ostrovsky, Rogers, & Welker, 2016). Further, it seems to be common in seabirds at a regional level and more ambiguous at the mesoscale (Phillips et al., 2017). In a previous study, COGU and BRGU breeding in the Northwest Atlantic were considered to exhibit flexibility in their winter space use (McFarlane Tranquilla et al., 2014). By contrast, we found strong support for the hypothesis that individuals of both species in populations in the Northeast Atlantic display IMSF at the mesoscale. However, we also observed temporal variation in space use, particularly during late winter when IMSF for some populations was not exhibited at the ten day step resolution, but only when NND was integrated over a wider 70 day temporal window. This suggests some temporal flexibility such that individuals utilize the same areas in different years, but not necessarily at the same time during the winter months as has also been shown for long tailed skuas (*Stercorarius longicaudus*, Van Bemmelen et al., 2017). However, this temporal flexibility seems to occur only within the range of known sites for a particular individual. McFarlane Tranquilla et al. (2014) also reported behavioural flexibility in the mid-winter spatial distribution (defined in their study as January), particularly BRGUs, breeding in the Northwest Atlantic, tracked over multiple winters. However, here we could illustrate that, particularly during late winter (February/March) IMSF was more variable, but could be explained by timing differences. Consequently, the reported flexibility by McFarlane Tranquilla et al. (2014) might also be explained by temporal flexibility during the winter months between individual-specific sites rather than generalist behaviour. This argument is further strengthened by the observed general persistence of IMSF when accounting for the temporal flexibility in all studied populations across multiple years.

Instances of generalist migratory behaviour

Generalist migratory behaviour, i.e. an absence of IMSF, was identified to a varying degree in all populations of COGU and BRGU. This can potentially be attributed to several season-specific circumstances originating in different life history stages during their annual cycle. First, a lack of post-breeding IMSF during autumn, could be caused by guillemots undergoing moult of their flight feathers, which renders them flightless (Birkhead & Taylor, 1977; Elliott & Gaston, 2014; Thompson, Wilson, Melvin, & Pierce, 1998). This constrains their movements and hence their capacity to demonstrate IMSF. Additionally, reproductively successful males are accompanying a flightless chick as it departs the colony, which further limits their movement (Elliott et al., 2017; Harris & Wanless, 1990). Thus, it is not surprising that some populations exhibit IMSF only for females during autumn as these are not constrained by a dependent and flightless chick and have the possibility to move large distances after breeding and prior to moulting. Second, various populations of both species displayed a lack of IMSF during spring, which corresponds to the period of pre-breeding when individuals periodically attend their colony (A. J. Gaston & Nettleship, 1981) and are thus constrained in their movement to de-facto central place foraging. However, pre-breeding commences at different times across the range of this genus and can begin as early as February on Iceland (PAPER IV) or as late as April on Spitsbergen (PAPER IV), while at least some part of the population on the Isle of May continues colony attendance after the autumn moult throughout the non-breeding period (Harris & Wanless, 2016). This variability in pre-breeding timing could explain the variability in time at which generalist migratory behaviour is observed during the end of the non-breeding period for the different populations.

Is IMSF better explained by site familiarity or habitat preference?

Persistent IMSF over multiple years was apparent in spatial consistency rather than preferences for specific habitats across the entire study region and throughout the non-breeding period. This suggests that IMSF in guillemots is better explained by site familiarity potentially through experience and the use of memory (Davoren, Montevecchi, & Anderson, 2003) rather than being a consequence of habitat specialisation. Memory has also been suggested to drive COGU foraging behaviour during breeding (Regular, Hedd, & Montevecchi, 2013). We could not identify any fidelity to habitat rather than sites for any population of either species throughout the entire non-breeding period. Further, individuals from most populations did not display any habitat fidelity at all. And, for habitat specialisation to drive site fidelity we would have expected that IMSF, if displayed at all, would not persist over multiple years across the genus' range, particularly in light of the drastic changes in the physical environment of the study region (Henson et al., 2017; IPCC, 2013; Lind et al., 2018; Sgubin, Swingedouw, Drijfhout, Mary, & Bennabi, 2017) and the shifting species distributions and ecosystem compositions (Beaugrand & Kirby, 2018; Carscadden et al., 2013; Fossheim et al., 2015; Perry et al., 2005; Pinsky et al., 2013; Wassmann et al., 2011). However, we cannot rule out the possibility that the abiotic variables selected to describe the available habitat, although ecologically relevant for the study species', might not be able to reflect guillemot foraging habitat. This is especially true for all satellite derived parameters used (such as sea surface temperature) as these only reflect surface water conditions, while guillemots are deep diving foragers.

By contrast, we identified IMSF across our studied range which persisted over multiple years for all populations with more than 2 years of data as is predicted if IMSF is caused by site familiarity (Piper, 2011; Switzer, 1993). The ontogeny of individual migration strategies and the relative roles of genetic control (Liedvogel, Åkesson, & Bensch, 2011; Newton, 2008), social learning (Jesmer et al., 2018; Keith & Bull, 2017) and individual exploration (Guilford et al., 2011) therein is poorly understood. However, subsequent migrations seem to be influenced by learning of navigational map features *en route* (potentially visual, olfactory or magnetic) which in turn lead to individual site familiarity through experience and further refinement of individual migration strategies (Guilford et al., 2011; Spiegel & Crofoot, 2016; Van Bemmelen et al., 2017). Thus, the above discussed temporal flexibility in site fidelity can also be accounted for by learning as individuals could have the potential to switch between multiple known sites if conditions at the occupied site becomes unfavourable (the "win-stay, lose-switch" rule; Switzer, 1993) and the individual is not impeded in its movement (due to moulting, chick presence or pre-breeding attendance). By being faithful to known wintering areas, individuals reduce costs of sampling other suitable wintering areas, in particular when flight costs are high such as in guillemots (Elliott et al., 2013), and thus diminish uncertainty from successive migrations (Abrahms et al., 2018; Cresswell, 2014). Site familiarity is also important as conditions at different staging sites must be considered unknown to the individual due to the large distances covered. Consequently, individual migration routes can generally be assumed to have developed in response to historically expected conditions (Thorup et al., 2017; Van Moorter et al., 2016).

Conclusion

In this study we found strong support for IMSF (individual migration strategy fidelity) for COGU and BRGU from multiple breeding populations across the Northeast Atlantic regardless of habitat utilized. Our data suggest that this was most likely driven by site familiarity (Piper, 2011; Switzer, 1993) rather than by habitat specialisation. Historically, site familiarity was most likely a sufficient strategy for these long lived species (Abrahms et al., 2018; Bradshaw et al., 2004; Switzer, 1993). In the light of a rapidly changing physical and biological environment, these species might not be able to adjust their migration strategies fast enough (Abrahms et al., 2018), particularly if migration strategies are established during the first years of life (Dall et al., 2012) as also suggested for other seabirds (Guilford et al., 2011; Van Bemmelen et al., 2017) and some ungulate species (Jesmer et al., 2018; Sawyer et al., 2018). This might also be the case for other long lived migrants, especially if they exhibit similar high costs of movement as in guillemots (Elliott et al., 2013) and consequently potential severe constraints upon large-scale movement capabilities and hence high sensitivity towards habitat loss (Taylor & Norris, 2010).

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Supplementary information

Additional method information & results

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Tables and Figures

Table 1. Available tracking data. Some colonies (in parentheses when applicable) have been merged into populations for the purpose of this study. Tracking years denote first and last year of tracking and include gap years in many cases. Number of known females (f) and males (m) are added in parentheses.

breeding population (colonies)	acronym	location	Common guillemot (COGU)					Brünnich's guillemot (BRGU)				
			tracking years	annual tracks	individuals	individuals with repeat tracks	years individuals have been tracked repeatedly	tracking years	annual tracks	individuals	individuals with repeat tracks	years individuals have been tracked repeatedly
Isle of May	IM	56.18°N 2.58°W	2011-17	91	46 (15f, 27m)	28 (12f, 15m)	2-4	-	-	-	-	-
Sklinna	SK	65.22°N 10.97°E	2011-17	83	52	25	2-3	-	-	-	-	-
Hjelmsøya	HJ	71.07°N 24.72°E	2011-17	52	34	14	2-3	-	-	-	-	-
Northeast Iceland (Grimsey, Langanes)	IC	66.44°N 15.80°W	2014-17	37	26	9	2-3	2014-17	42	28	13	2-3
Jan Mayen	JM	71.02°N 8.52°W	2011-17	86	47 (20f, 19m)	23 (14f, 9m)	2-5	2011-17	136	66 (19f, 36m)	39 (13f, 21m)	2-5
Hornøya	HO	69.98°N 32.04°E	2011-17	146	82 (16f, 24m)	53 (7f, 17m)	2-3	2009-17	140	79 (23f, 27m)	35 (12f, 16m)	2-4
Bjørnøya	BI	74.50°N 18.96°E	2007-17	196	85 (42f, 28m)	56 (27f, 21m)	2-6	2007-17	156	65 (25f, 25m)	42 (18f, 21m)	2-7
Western Spitsbergen (Amfifjellet, Ossian Sars fjellet, Diabasodden)	WSP	78.75°N 13.20°E	-	-	-	-	-	2007-17	112	78 (30f, 40m)	25 (12f, 12m)	2-3
Southern Novaya Zemlya (Cape Sakhanin)	SNZ	70.59°N 55.02°E	-	-	-	-	-	2015-17	55	41	14	2

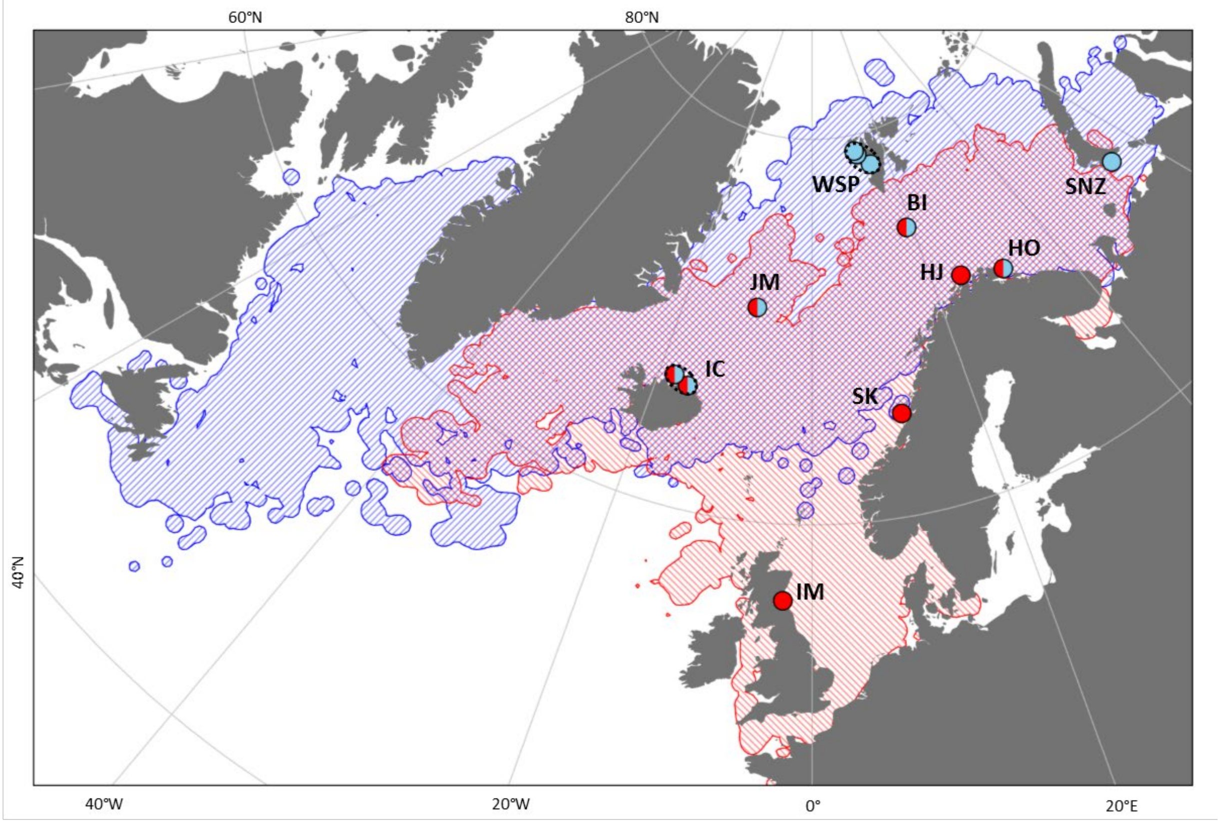


Figure 1. Map of the study extent (in polar stereographic projection). Circles denote study colonies with different colours indicating the presence of the two species (BRGU in blue & COGU in red; colony names detailed in table 1). Colonies combined for the purpose of this study are encircled with dashed ellipsoids. Shaded blue and red areas illustrate the total annual extent for each species breeding at the displayed colonies based on individuals tracked by light-level geolocation.

Figure 2. Mean species- and breeding population-specific intra-individual nearest neighbour distance (NND, black symbols) compared to the null distribution (red and blue light and dark shades indicate 95% and 50% null distribution, respectively; dark line denotes the median). Black filled symbols correspond to a mean species- and breeding population-specific intra-individual NND significantly smaller than the null distribution (i.e. IMSF). Grey stippled line in each plot represents the approximate accuracy of light-level geolocation positions. Colours correspond to species: BRGU in blue & COGU in red. Bottom row in each panel depicts individual spatial consistency over a 70 day sliding window (with black symbols corresponding to a mean intra-individual NND significantly smaller than the null).

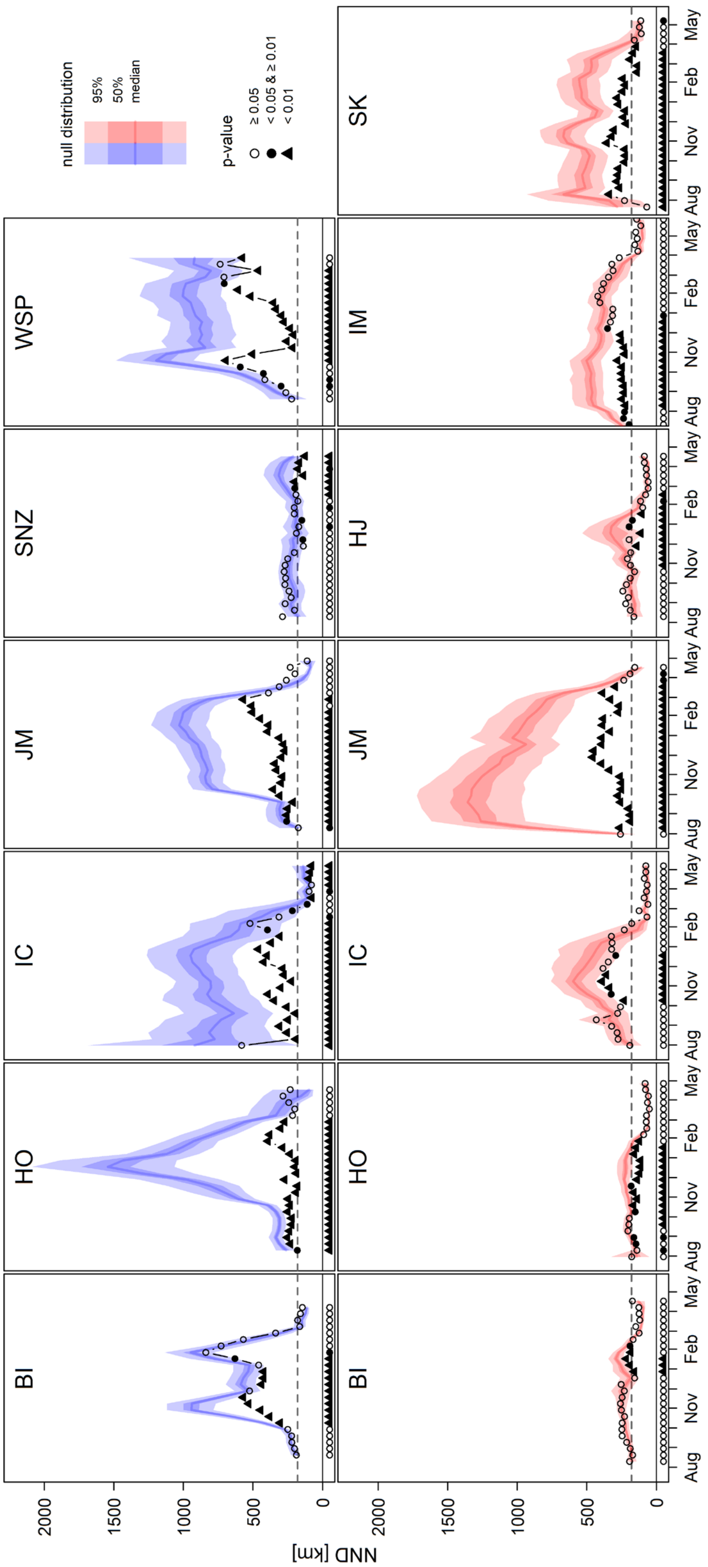
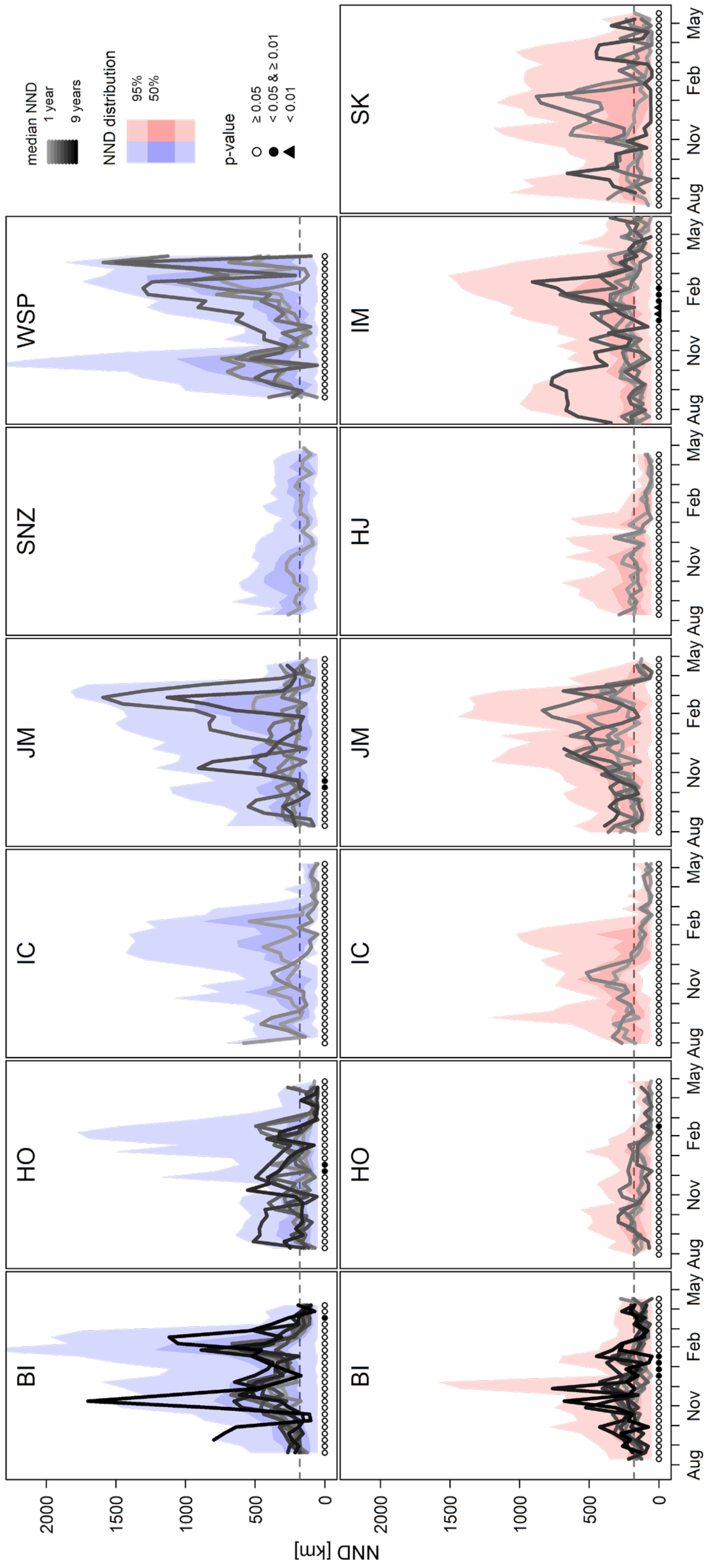


Figure 3. Species- and breeding population-specific intra-individual nearest neighbour distance (NND) with varying time lag (BRGU in blue & COGU in red). Grey shaded lines present median within-individual NND with time lag ranging from one year (grey) to nine years (black). Coloured areas in the background of each panel represent the distribution of all intra-individual NND regardless of time lag. Symbols in bottom of each panel indicate the probability that including time lag explains the data better than the null model for 70 day sliding windows. Grey stippled line in each plot represents the approximate accuracy of light-level geolocation positions.



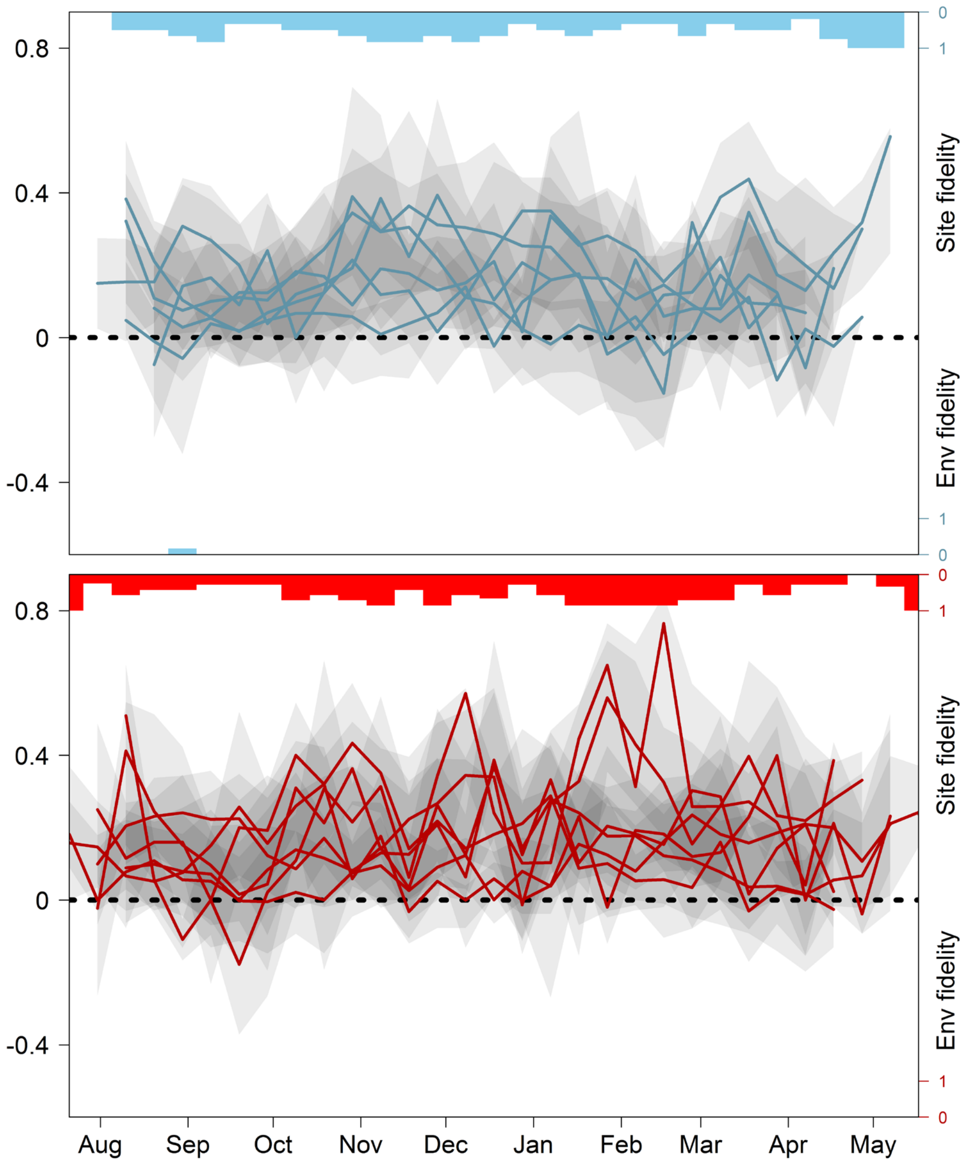


Figure 4. Species- and breeding population-specific similarity (ranging from -1 to 1) throughout the non-breeding period (BRGU in blue & COGU in red) where values above 0 indicate relative site fidelity and values below 0 indicate higher fidelity to specific habitats. Each line represents the median fidelity for a given population. Semi-transparent grey shaded areas illustrate population-wide 25% to 75% quartile range in individual fidelity values with darker colours indicating overlapping ranges between populations. Bar plots at the top and bottom of each panel illustrate the proportion of populations with significant fidelity (i.e. significantly different from 0 at p = 0.05, scale on the right) to either sites (at the top) or habitat (at the bottom) during each ten day step.

Supplementary Methods

Location estimation from geolocators

Estimated timings of sunrise and sunset (transition times) were computed from light data using TransEdit2 (British Antarctic Survey/BAS, Cambridge, UK), and the `twilightCalc` function (`GeoLight` package; Lisovski & Hahn, 2012) in R 3.4.3 (R Development Core Team, 2018) for BAS, Migrate Technology and Biotrack loggers. Transition times were visually inspected for loggers retrieved during 2014-2017 by the same person. Lotek loggers did not retain raw light intensity data, but rather calculated and recorded latitudes and longitudes based on an onboard algorithm which have been shown to be biased (Frederiksen et al., 2016). Therefore we used these threshold method derived positions to back calculate transition times using the `lotek_to_dataframe` function (`probGLS` package; Merkel et al., 2016). Daily experienced sea surface temperature (SST) was estimated from raw logged temperature data using the `sst_deduction` function (`probGLS` package) with a possible range of -2 to 20°C for Lotek loggers and -2 to 40°C for all other brands.

A most probable track for each individual and tracking year was calculated using a method detailed in (Merkel et al., 2016) and implemented in the `prob_algorithm` function (`probGLS` package). Input data were logger recorded transition times, salt water immersion data as well as calculated daily recorded SST data. Daily optimal interpolated high resolution satellite derived SST, SST uncertainty and sea ice concentration data for the algorithm with a 0.25° resolution was provided by NOAA (Boulder, Colorado, US; Reynolds et al., 2007). To improve precision we included land avoidance, an inability to enter the Baltic Sea (except for Common guillemots from the Isle of May) and an evasion of heavy pack ice (>90% sea ice concentration). Each movement path incorporated parameter values based on the ecology of the species and the oceanographic conditions in the North Atlantic (table S1). Usually, it is not possible to estimate the latitude during times of equinox as day length (the proxy for latitude) is very similar everywhere on earth. However, this methodology is able to calculate locations also during times of equinox by among other things utilizing the recorded temperature data and comparing them to satellite derived sea surface temperature (SST) fields. Due to small north-south gradients in SST in certain areas of the North Atlantic (e.g. the Gulf Stream along the Norwegian coast) we limited the boundary box parameter in `prob_algorithm` for certain individuals and colonies after initial assessment of their movement tracks (table S1).Each computed track was afterwards visually inspected and erroneous locations particularly around polar night and midnight sun periods were removed (<1 % of all locations).

Environmental parameters

All chosen environmental parameters used to calculate environmental space and their rational are listed in table S2. Fronts in sea surface temperature (SST) and sea surface height anomaly fields were calculated using a canny edge detector (package `imager`, low & high threshold at 90% & 98%, respectively). Bathymetry was log-transformed and all distance measurements were capped at 500 km as well as square root-transformed. Predictability in SST was calculated as the sum of constancy and contingency following (Colwell, 1974) over a ten year time period (2007-2016) with 10 equal bins using the `hydrostats` package (figure S3). All variables have been standardized.

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Supplementary Tables and Figures

Table S1. `probGLS` algorithm input parameters used to compute locations. standard deviation = sd

algorithm parameter	description	value used
`particle.number`	number of particles computed for each point cloud	2 000
`iteration.number`	number of track iterations	100
`loess.quartile`	remove outliers in transition times based on local polynomial regression fitting processes (Lisovski & Hahn, 2012)	used with k = 10
`sunrise.sd & sunset.sd`	shape, scale and delay values describing the assumed uncertainty structure for each twilight event following a log normal distribution	2.49/ 0.94/ 0[1]
`range.solar`	range of solar angles used	-7° to -1° (except for C250 logger from SK: -4° to -2°)
`boundary.box`	the range of longitudes and latitudes likely to be used by tracked individuals	90°W to 120°E & 40°N to 81°N; except for 91% COGU tracks from IM with 40°N to 62°N; all COGU from BI and 94% COGU SK tracks with 60°N to 77°N; 6% SK tracks with 50°N to 77°N
`day.around.spring.equinox & days.around.fall.equinox`	number of days before and after an equinox event in which a random latitude will be assigned	spring: 21 days before & 14 days after autumn: 14 days before & 21 days after
`speed.dry`	fastest most likely speed, speed sd and maximum speed allowed when the logger is not submerged in sea water	17/ 4/ 30 m/s[2]
`speed.wet`	fastest most likely speed, speed sd and maximum speed allowed when the logger is submerged in sea water	1/ 1.3/ 5 m/s[3]
`sst.sd`	logger-derived sea surface temperature (SST) sd	0.5°C[4]
`max.sst.diff`	maximum tolerance in SST variation	3°C
`east.west.comp`	compute longitudinal movement compensation for each set of twilight events (Biotrack, 2013)	used

[1] These parameters are chosen as they resemble the twilight error structure of open habitat species in Lisovski et al. (2012).

[2] inferred from GPS tracks (unpublished data) and (Elliott & Gaston, 2005)

[3] North Atlantic current speed up to fast current speeds (i.e. East Greenland current) (Lumpkin & Johnson, 2013) as the tagged animal is assumed to not actively move when the logger is immerged in seawater

[4] logger temperature accuracy

Table S2. Parameter chosen to describe the environmental space.

parameter	temporal resolution	spatial resolution	rational	data source
bathymetry	static	0.25°	predictable productivity on continental shelfs	ETOPO1 & IBCAO[1]
surface air temperature	daily	0.75°	influences energy requirements[2]	ECMWF[3]
sea surface temperature (SST)	daily	0.25°	water mass indicator & physiological constraint[2]	NOAA OI SST V2[4]
SST predictability (figure S2)	static	0.25°	identifier of spatially variable SST features across seasons and years (e.g. persistent frontal systems[5])	NOAA OI SST V2[4]
minimum distance to 15%, 50% & 90% sea ice concentrations	daily	0.25°	descriptor of marginal sea ice zone	NSIDC[6]
sea surface height (SSH)	daily	0.25°	descriptor of the locations of large scale features such as gyres and fronts	AVISO[7]
distance to SSH anomaly gradients	daily	0.25°	distance to mesoscale eddies as spatially dynamic sources of upwelling	AVISO[7]
distance to SST gradient	daily	0.25°	distance to mesoscale temperature fronts[5]	NOAA OI SST V2[4]

[1] (Amante & Eakins, 2009; Jakobsson et al., 2012), [2] (Fort, Porter, & Grémillet, 2009), [3] (Berrisford et al., 2011), [4] (Reynolds et al., 2007), [5] (Scales et al., 2014), [6] (Cavalieri, Parkinson, Gloersen, Comiso, & Zwally, 1999), [7] Aviso, with support from Cnes (http://www.aviso.altimetry.fr/)

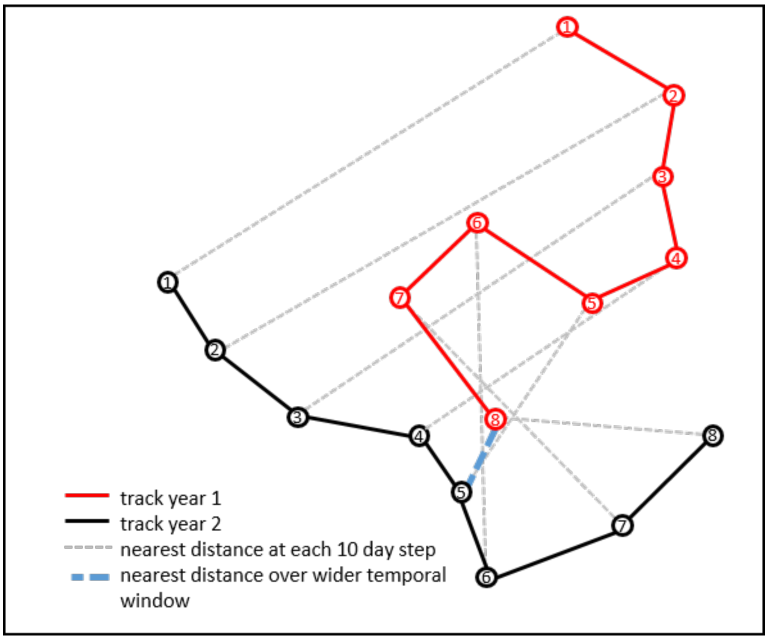


Figure S1. Schematic illustrating the calculation of NND at different time intervals

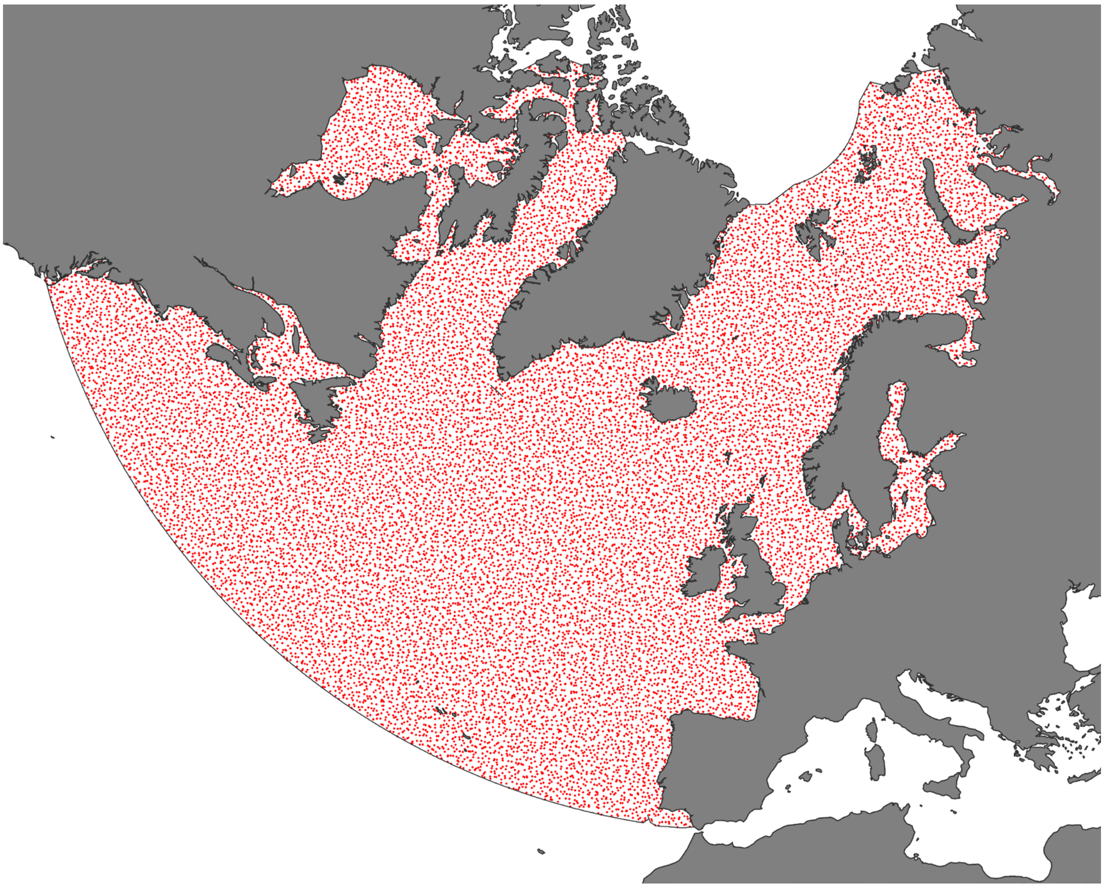


Figure S2. Map (in polar stereographic projection) displaying the study region including the 20000 points (in red) used to estimate the available environmental space.

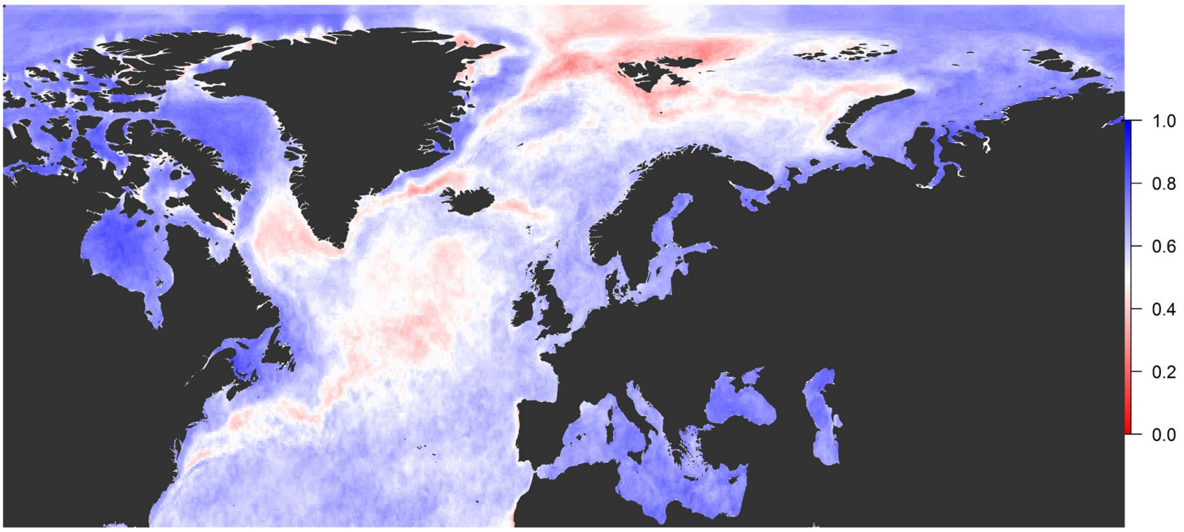


Figure S3. Distribution of SST predictability in the North Atlantic with a scale from 0 (no predictability) to 1 (very predictable).

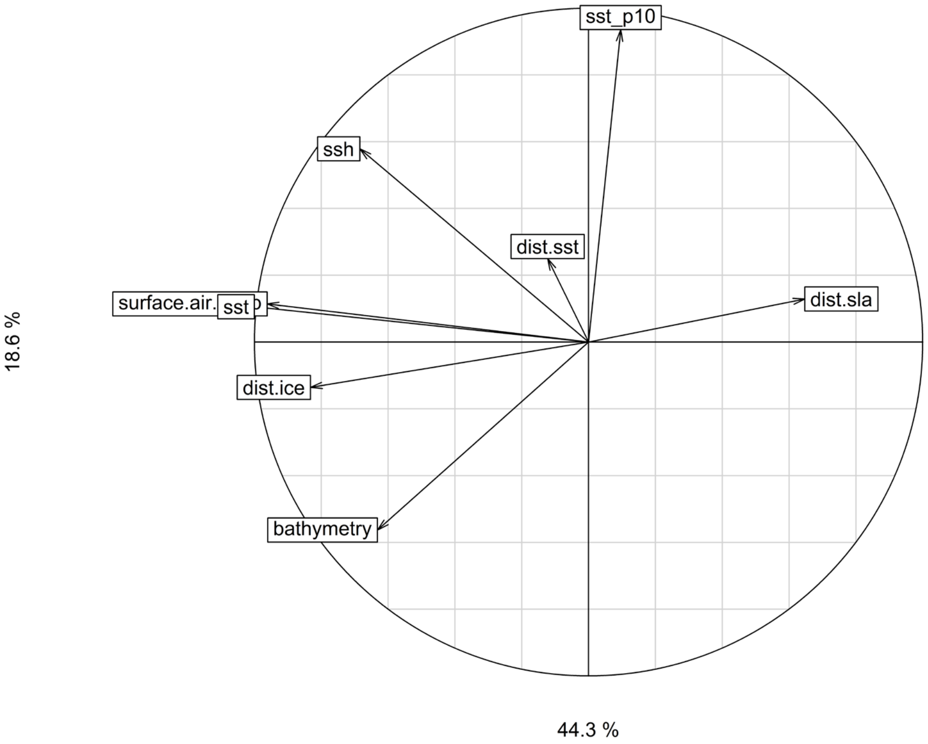


Figure S4. PCA correlation circle for the environmental space representing the North-Atlantic over the entire study period. dist.sla = distance to mesoscale eddies, dist.ice = distance to the marginal sea ice zone, surface.air.temp = surface air temperature, sst = sea surface temperature, ssh = sea surface height, dist.sst = distance to temperature fronts, sst_p10 = SST predictability

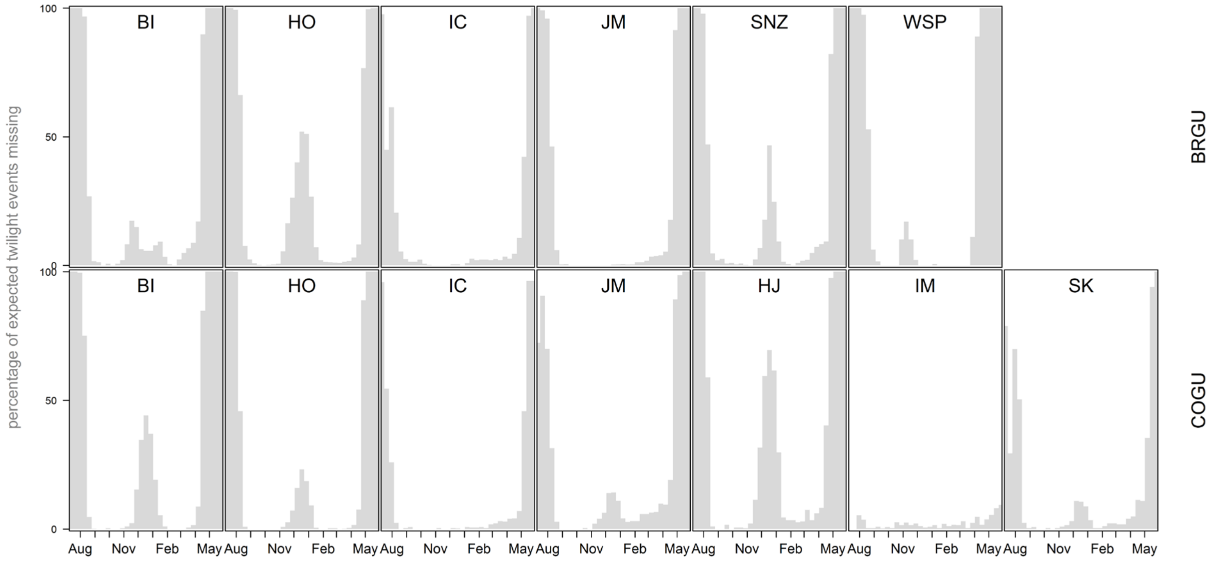


Figure S5. Species- and population-specific percentage of locations missing mainly due to lack of twilight (i.e. polar night or midnight sun).

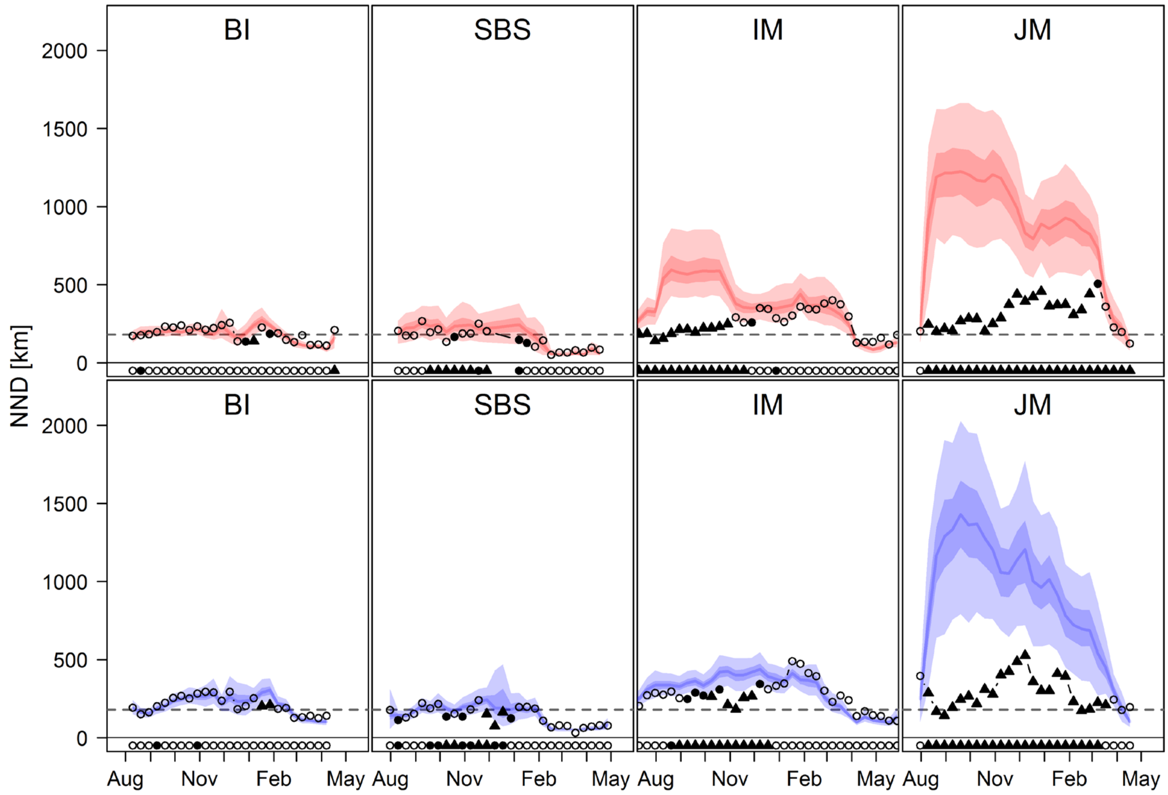


Figure S6. COGU mean sex- and breeding population-specific intra-individual nearest neighbour distance (NND, as measurement of spatial consistency) compared to the null distribution (light and dark shade indicate 95% and 50% null distribution, respectively; dark line denotes the median). Black symbols correspond to a mean intra-individual NND significantly smaller than the null (white circle = ≥0.05, black circles =<0.05 & ≥0.01, black triangle = <0.01). Colours correspond to sex (red = female, blue = male). Bottom row in each panel depicts individual spatial consistency over a 70 day sliding window (with black symbols again corresponding to a mean intra-individual NND significantly smaller than the null).

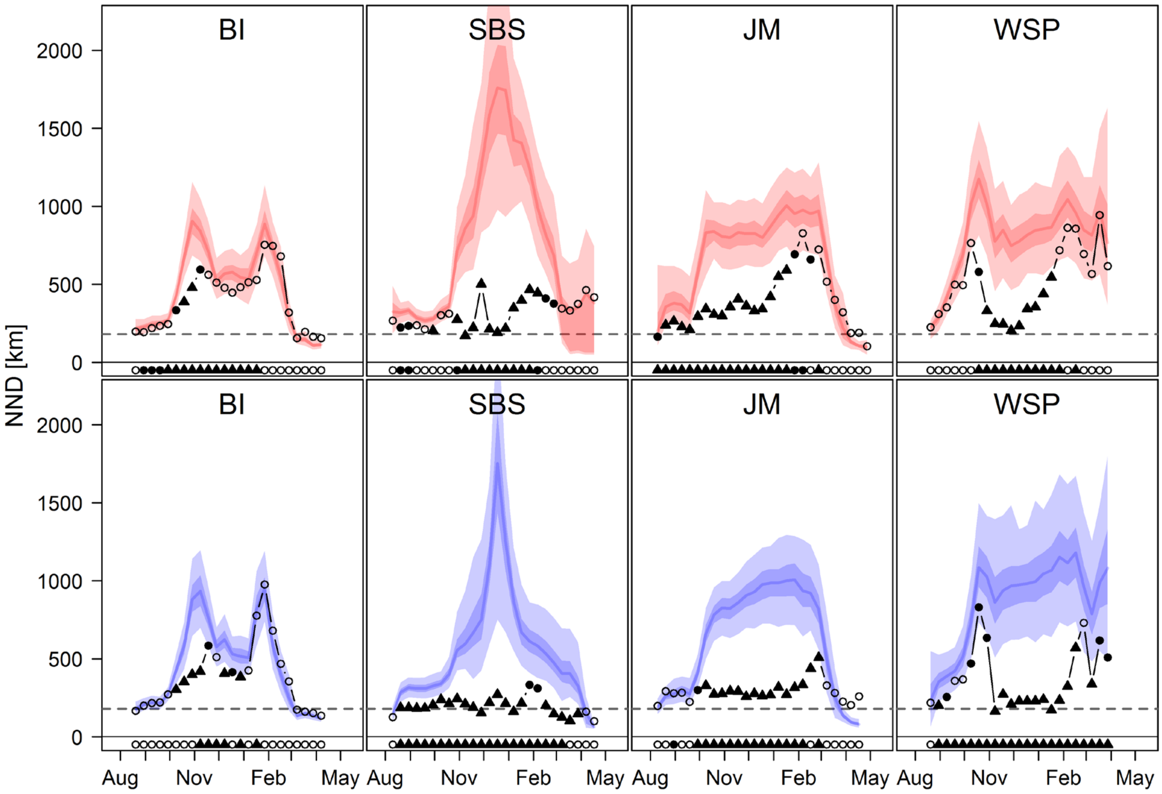
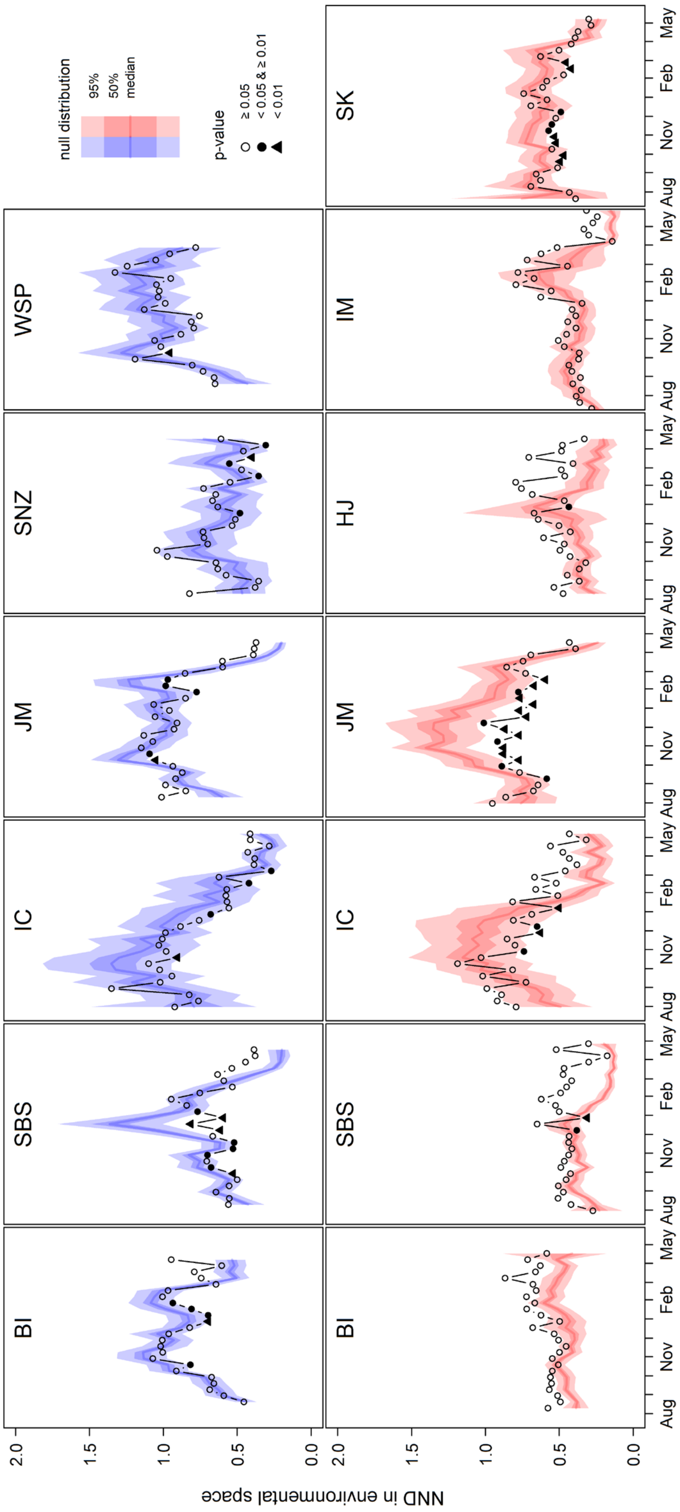


Figure S7. BRGU mean sex- and breeding population-specific intra-individual nearest neighbour distance (NND, as measurement of spatial consistency) compared to the null distribution (light and dark shade indicate 95% and 50% null distribution, respectively; dark line denotes the median). Black symbols correspond to a mean intra-individual NND significantly smaller than the null (white circle = ≥0.05, black circles =<0.05 & ≥0.01, black triangle = <0.01). Colours correspond to sex (red = female, blue = male). Bottom row in each panel depicts individual spatial consistency over a 70 day sliding window (with black symbols again corresponding to a mean intra-individual NND significantly smaller than the null).

Figure S8. Mean species- and breeding population-specific intra-individual nearest neighbour distance (NND, black symbols) in environmental space compared to the null distribution (red and blue light and dark shades indicate 95% and 50% null distribution, respectively; dark line denotes the median). Black filled symbols correspond to a mean species- and breeding population-specific intra-individual NND significantly smaller than the null distribution (i.e. IMSF). Colours correspond to species: BRGU in blue & COGU in red.



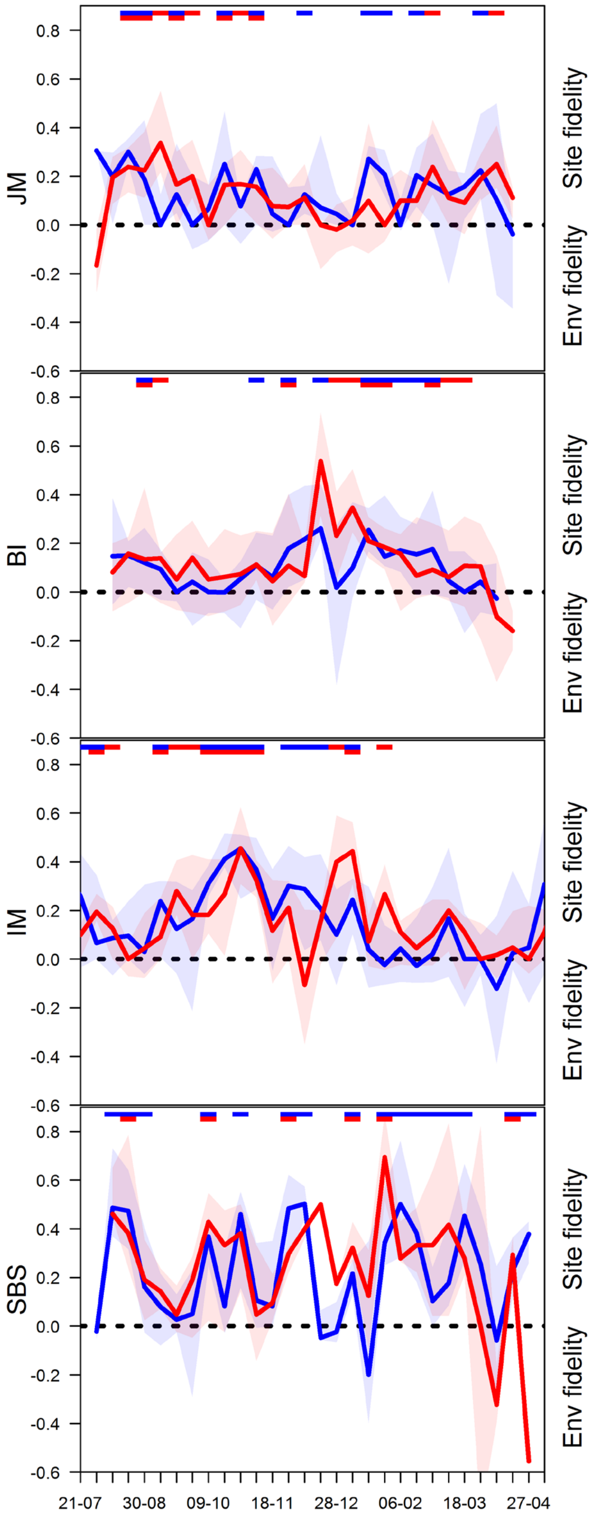


Figure S9. Sex- and population-specific similarity (ranging from -1 to 1) throughout the non-breeding period for COGUs (males in blue & females in red) where values above 0 indicate relative site fidelity and values below 0 indicate higher fidelity to specific habitats. Lines represent the median fidelity for a given sex. Shaded areas illustrate the population-wide 25% to 75% quartile range in individual fidelity values. Bars at the top and bottom of each panel illustrate significant fidelity (i.e. significantly different from 0 at p = 0.05, scale on the right) to either sites (at the top) or habitat (at the bottom) during each ten day step.

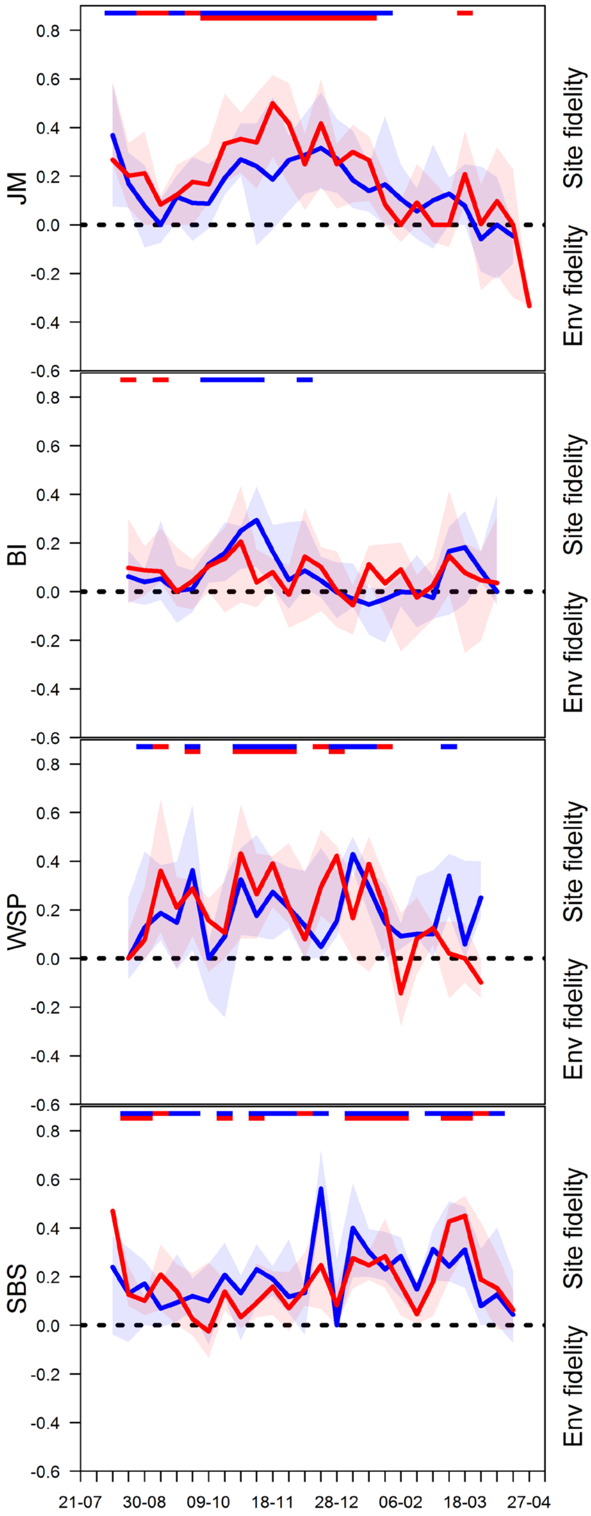
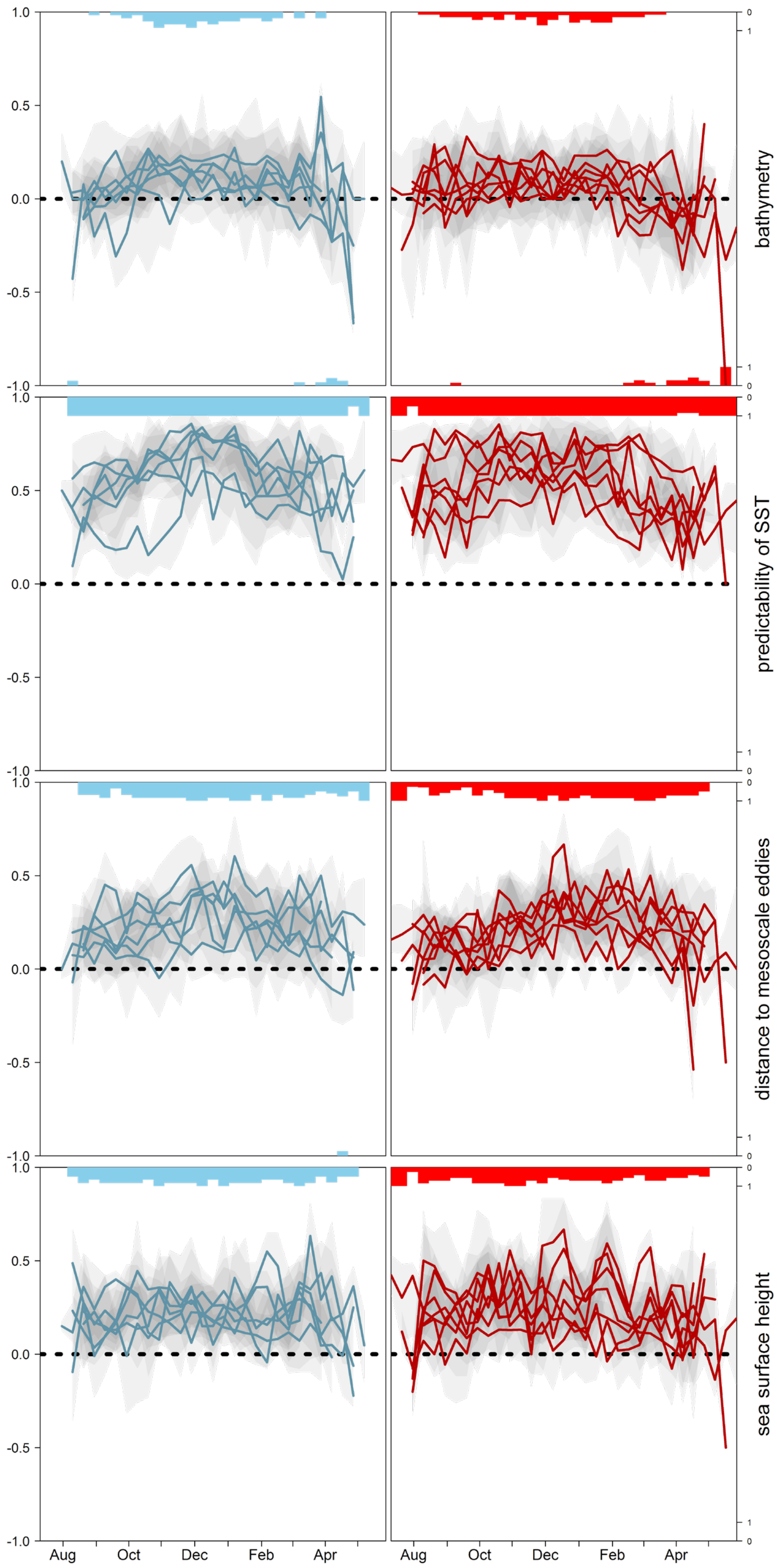


Figure S10. Sex- and population-specific similarity (ranging from -1 to 1) throughout the non-breeding period for BRGUs (males in blue & females in red) where values above 0 indicate relative site fidelity and values below 0 indicate higher fidelity to specific habitats. Lines represent the median fidelity for a given sex. Shaded areas illustrate the population-wide 25% to 75% quartile range in individual fidelity values. Bars at the top and bottom of each panel illustrate significant fidelity (i.e. significantly different from 0 at p = 0.05, scale on the right) to either sites (at the top) or habitat (at the bottom) during each ten day step.


1.0
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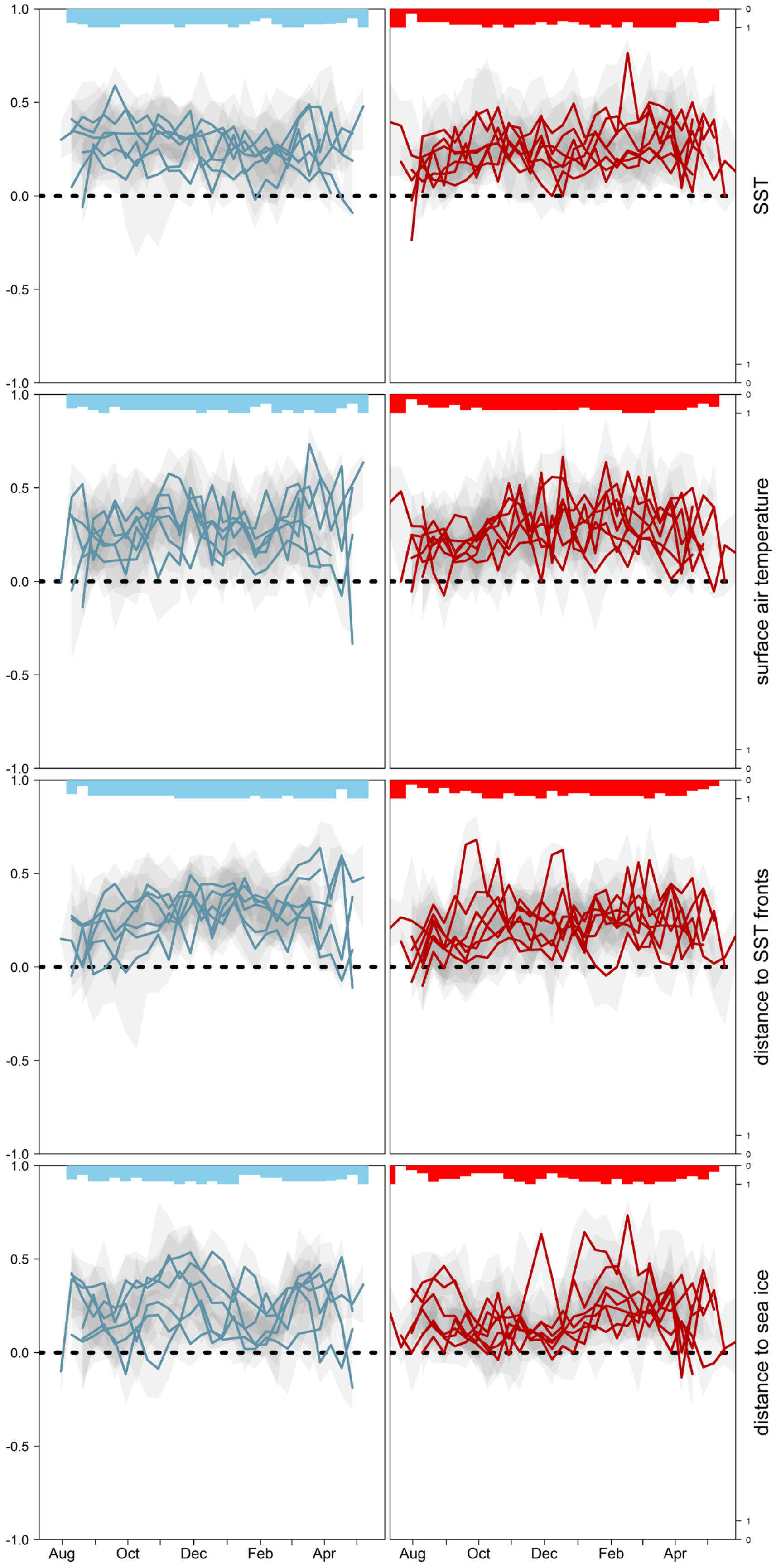
1.0
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surface air temperature
distance to SST fronts
distance to sea ice
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Dec
Feb
Apr

187

188

Figure S11. Species- and breeding population-specific similarity (ranging from -1 to 1) throughout the non-breeding period (Brünnich’s guillemots in blue & common guillemots in red) where values above 0 indicate relative site fidelity and values below 0 indicate higher fidelity to the specified environmental parameter. Each line represents the median fidelity for a given population. Grey shaded areas illustrate the population-wide 25% to 75% quartile range in individual fidelity values with darker colours indicating overlapping ranges between populations. Bar plots at the top and bottom of each panel illustrate the proportion of populations with significant fidelity (i.e. significantly different from 0 at $p = 0.05$, scale on the right) to either sites (at the top) or the specified environmental variable (at the bottom) during each ten day step. SST = sea surface temperature.

Earlier arrival despite constant breeding phenology in two congeneric seabirds

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Authorship: BM, HStr, NGY and SD designed the study; BM analysed the data with help from NGY and SD; BM wrote the paper with contributions from SD, HStr and NGY; HStr, SD, FD, JD, KEE, AVE, MPH, MG, DG, SHL, TKR, GHS, HSte, ÞLÞ, and SW provided data; All authors commented on later drafts of the manuscript.

Abstract

A global analysis recently showed that seabird breeding phenology (as timing of egg-laying and hatching) is surprisingly insensitive to changing climatic conditions and did not change over time [1]. This group, the most threatened of all birds, is therefore prone to spatiotemporal mismatches with their food resources. Yet, other aspects of the breeding phenology may also have marked incidence on breeding success, such as the arrival date of adults at the breeding site following winter migration. Here we utilized a large tracking dataset of two congeneric seabirds breeding in 15 colonies across 24° latitudes, to show that arrival date at the colony was highly variable between colonies and species (ranging 154 days) and advanced on average 1.5 days/year while timing of egg-laying remained unchanged, resulting in an increasing pre-laying duration between 2009 and 2018. Thus, we demonstrate that potentially not all components of seabird breeding phenology are insensitive to changing environmental conditions.

Keywords: pre-laying period, timing of egg-laying, *Uria aalge*, *Uria lomvia*, murres, guillemots

Introduction

Timing of life history events such as reproduction is predicted to have evolved to optimally utilize temporally favourable conditions in seasonal systems [2]. Breeding phenology is a key adaptation with direct consequences on reproductive success and population dynamics [3, 4]. Rapid climate change has led to an advancement of the annual cycle in many organisms in temperate and polar regions, while species that have not adjusted to climate change seem to be more prone to population declines [5, 6]. In seabirds, timing of egg-laying has been shown to be insensitive to changing climatic conditions globally, highlighting the vulnerability of this group to mismatches with lower-trophic-level resources [1]. Yet, spring arrival at the colony, and the pre-laying period – the time between arrival at the colony and egg-laying - are also important and rarely considered components affecting breeding success. This period allows birds to establish and defend nest sites [7], build up body condition [8, 9] and mate [10], which often starts months before egg-laying [11, 12].

Here, we took advantage of a large tracking dataset, enabling us to determine arrival dates in two seabird species, across nine years (2009 - 2018) and 15 colonies across a large latitudinal gradient (56°N - 79°N), to test if arrival date also does not exhibit any trend across years, similar to timing of egg-laying [1]. This data was available for two colonial, congeneric species, the common (hereafter COGU, *Uria aalge*) and Brünnich's guillemot (hereafter BRGU, *Uria lomvia*). These species are long-distance migrants [13-15], have similar morphology and life history [16, 17], and exhibit no trend in breeding phenology ([1] +Descamps et al. in review GCB; Keogan et al. in review GCB), but contrasting population trends [18-20]. Their arrival date is hypothesized to be driven by timing of food availability in the vicinity of the colony [21, 22], which can be roughly approximated by latitude [23], or by colony size through increasing pressure on nest site defence displayed as longer pre-laying periods in larger colonies [11, 24, 25]. We tested the hypothesis that arrival date is without trend across years, same as egg-laying date. Further, we examined if arrival date is delayed with latitude, similar to timing of egg-laying [23], or determined by colony size due to pressure on nest site defence.

Material and Methods

Data acquisition

The date of first arrival at the colony for each colony and species was estimated using salt water immersion data recorded by light-level geolocators deployed on adult breeders. Arrival date was here defined as the date when the pre-laying period commences. It was identified as the date when the majority of tracked individuals attended the colony for the first time after the non-breeding period, using the assumption that first arrival back at the colony is synchronized and independent of sex in guillemots [25-27] (details in SI). Using a colony-wide first arrival date rather than individual arrival dates resulted in more robust results due to limitations in logger data resolution and accuracy. Tracking data were available from 15 colonies (figure 1A), for one to eight years (in the period 2009 - 2018). BRGU and COGU breed sympatrically at five of these colonies. Three instances of estimated arrival dates could be validated with available time-lapse camera data at two colonies (figure S1). To estimate pre-laying duration as well as temporal changes in phenology, we gathered annual measures of breeding timing which were available as population-level mean hatching dates at twelve colonies (details in SI) for one to seven years (in the period 2009 - 2018). To assess the potential consequences of variable arrival dates on reproductive success, we used annual breeding success for which data was available from five colonies (details in SI) for four to six years (in the period 2010 - 2017).

Data analysis

Temporal trends in breeding phenology and their consequences - Colony- and species-specific inter-annual variation in arrival dates was quantified as standard deviation (SD) from mean arrival timing. To test if arrival date changes with year we applied a linear mixed effect model (LME, package `lme4`) with standardized arrival dates (SD = 1, mean = 0) as response variable (n = 80), year as fixed effects and id (as combination of colony and species) as random intercept. The same model was applied on a subset of data for which mean hatching date data were available (n = 44). Using this subset of data, we applied the same fixed and random effects to standardized pre-laying duration as well as standardized mean hatching date as response variables in order to assess if guillemot hatching timing and pre-laying duration have changed over time. Most parsimonious models were selected using Akaike information criterion [28], resulting in all instances in a removal of species and its interaction with year as predictor variables. We calculated the percentage of variance explained by the fixed effects (marginal R^2) and fixed and random effects (conditional R^2; [29]). In order to assess if a large-scale factor is driving temporal trends in arrival date, we assessed temporal synchrony as mean correlation of standardized arrival dates between colonies using the `msynch` function (package `ncf` [30]). To test if potential temporal trends in arrival date had an effect on reproductive output, we applied a LME with standardized breeding success (SD = 1, mean = 0) as response variable, standardized arrival date as fixed effect and id as random intercept (n = 37).

Effect of latitude and colony size on arrival date - To test for the effect of latitude on arrival date at the colony, we applied a linear model with mean species- and colony-specific arrival date as the response variable (n = 19) and latitude and species and their interaction as predictors. Further, if latitude drives arrival date, we would expect that colonies close to each other would exhibit similar arrival timing. Hence, we used a Mantel-correlation test with 1000 permutations (package `ade4`) to test if spatial proximity can explain mean arrival date in either species. Alternatively, to test if arrival date and consequently pre-laying duration can be instead linked to colony size, we applied a linear model with mean species- and colony-specific pre-laying duration as the response variable (n = 15) and colony size on the log-scale and species as predictors. Population counts are taken from a similar time period to account for the contrasting population trends (table S1). To account for collinearity, we also tested latitude against colony size, but found no overall latitudinal trend (linear model, $\beta_{latitude}$ = -0.10 with standard error (SE) = 0.10, adj. R^2 = <-0.01). The Isle of May (the southernmost colony in the dataset) has been excluded from the above analyses as it constituted an outlier in both models. Observational data have previously shown that most breeding birds arrive back at the colony in the autumn and in at least some years birds attend the breeding sites throughout the winter [11, 31]. Hence, an estimated arrival date in this colony is more uncertain than in all other colonies within the dataset. R (version 3.5.1, [32]) was used for all statistical analyses.

Results

Timing of colony arrival

Annual arrival dates varied between November 16 and April 18 with considerable variation across the Northeast Atlantic (figure 1B). Most of this variation is found between colonies (SD = 22.4 and 16.3 days for COGU and BRGU, respectively, figure S1) and species (SD = 14.9 days across sympatric colonies), while colony- and species-specific inter-annual variation was significantly smaller (mean SD = 7.8 and 5.4 days for COGU and BRGU, respectively).

Temporal variability in breeding phenology and its consequences

Timing of hatching in guillemots showed no trend over time (β_{year} = -0.02 with SE = 0.06, marg. R^2 = <0.01, cond. R^2 = <0.01; figure 2C). In contrast, arrival date at colony advanced on average by 1.5 days/year irrespective of species (range = 0.2 - 7.4 days/year; full dataset: β_{year} = -0.18 with SE = 0.04, marg. R^2 = 0.23, cond. R^2 = 0.23; subset with available mean hatching data: β_{year} = -0.21 with SE = 0.05, marg. R^2 = 0.33, cond. R^2 = 0.33; figure 2A). This was also visible as prolonged pre-laying duration (β_{year} = 0.17 with SE = 0.05, marg. R^2 = 0.20, cond. R^2 = 0.20; figure 2B) as arrival date and pre-laying duration were highly and negatively correlated (-0.86). Colony arrival dates did not display synchrony among each other for either species (COGU: mean correlation = 0.20 with 95% confidence interval (CI) = -0.21 - 0.74 and BRGU: 0.17 with CI = -0.43 - 0.93). And, no consequence of an advancing arrival date was detectable in exhibited breeding success for either species ($\beta_{\text{std. arrival}} = 0.06$ with SE = 0.17, marg. R^2 = <0.01, cond. R^2 = <0.01; figure 2D).

Does latitude or colony size predict arrival date?

Mean arrival date at the colony could not be explained by latitude and the two species exhibited opposite trends ($\beta_{\text{latitude BRGU}} = 1.63$ with SE = 1.24 and $\beta_{\text{latitude * COGU}} = -2.73$ with SE = 2.19, adj. R^2 = 0.23, excluding Isle of May; figure 1B). Similarly, there was weak evidence for an effect of proximity on arrival dates for COGUs (Mantel correlation = 0.19, p = 0.14), but somewhat stronger evidence in BRGUs (Mantel correlation = 0.29, p = 0.034). Contrastingly, pre-laying duration showed substantial variability between colonies (mean = 75 days, SD = 19, range = 49 - 125) and was highly correlated with colony size ($\beta_{\text{log(size)}} = 6.96$ with SE = 0.97, adj. R^2 = 0.82; figure 1C).

Discussion

The main findings of our study are that timing of first arrival at the colony of both guillemot species and all colonies was highly variable and advanced through time despite no visible trend in mean hatching date. This advancement had apparently no effect on guillemot average breeding success. Further, the duration of the pre-laying period and hence timing of arrival is not determined by latitude, but is dependent on the size of the colony, being longer in large colonies, as well as timing of egg-laying, being later at higher latitudes [1, 23].

Theoretically, the minimum pre-laying duration required in guillemots is five days, as females undertake a four day long pre-laying exodus away from the colony [33]. Yolk formation (usually 14-15 days [33]) could also occur away from the colony and fertilization occurs very soon after ovulation, which in turn occurs 24 hours before the egg is laid [10]. So, copulation right before the pre-laying exodus should be sufficient. Nonetheless, here we identified extensive pre-laying periods of more than one and up to several months with large variability between colonies and species. This may have costs and benefits associated with it. During this time period prospective breeders attend the colonies at regular intervals which restricts them to quasi central place foraging. This in turn limits their available prey options and could even lead to local depletion of food resources before spring bloom at large colonies [34], decreasing their body condition and potentially breeding probability prior to breeding. Alternatively, early return to the breeding sites might help secure nesting sites and mating partners [22], or it might be a response to unfavourable conditions experienced by these migrants during the end of their non-breeding period, resulting in an earlier return to the colony.

We showed that colony arrival date advanced in both the Brünnich's and common guillemot across the study area, while their timing of hatching did not display any trend as shown previously in seabirds globally [1] and for alcids in the Atlantic and Pacific (Descamps et al. in review GCB; Keogan et al. in review GCB). Contrary to these previous studies, concluding that breeding phenology is insensitive to climatic change, we identified a clear trend in arrival dates across both species studied. This advancement resulted in an increasing pre-laying duration as mean hatching date did not advance, suggesting that part of breeding in these seabirds is indeed sensitive to changing conditions, although we cannot derive conclusions regarding the process driving this phenomenon or if it is an adaption to a changing environment. A potential explanation could be that the cue used to time arrival across the North Atlantic is changing as has been shown in some passerine species [35], but could not be demonstrated in others [36].

Although overall timing in both species exhibits the same trend, arrival time series were not synchronized between species and colonies. This indicates that short-term fluctuations in arrival date were not parallel through time among species and/or colonies, which suggests the interaction between large-scale environmental trends acting on the entire species combined with more local features. However, environmental conditions, although exhibiting the same trend, do not change homogenously across the genus' range [37], which encompasses most of the North Atlantic for these species breeding within the study area ([13-15]+PAPER II). Hence, synchrony is not necessarily expected. As of now we could not detect any immediate consequences of advancing arrival dates on population-wide reproductive success. However, we cannot make any inference of the potential effect of advancing arrival dates on breeding propensity. Not all birds breed every year [38, 39] and the egg laying and hatching dates as well as the recorded breeding success may reflect only individuals with sufficient body condition, i.e. the ones that managed to get enough energy during the pre-laying period in order to breed [8].

Pre-laying duration and hence arrival timing at the colony could be linked with colony size [11, 24, 25] rather than latitude. This suggests that arrival date might be driven by a combination of egg-laying date and colony size, which together determine pre-laying duration, and could explain the displayed large-scale variability in arrival timings between colonies as well as the lack of synchronicity between time series. Although guillemots typically show high nest site fidelity, site changes are documented which usually increase nest site quality for the usurper and decrease it for the usurped [40] underlining the importance of nest site defence as potential driver of arrival date. But, the influence of environmental conditions on arrival timing cannot be ruled out, as unfavourable weather has already been shown to affect pre-laying colony attendance in BRGU [26].

Our large-scale approach highlights the extent and importance of the pre-laying period in contributing to the challenges faced by colonial breeders in a changing environment. The advancing trend in arrival dates elucidates that not all parts of breeding phenology in seabirds are insensitive to change across years, although we cannot make inferences if this change is adaptive or not.

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Tables and Figures

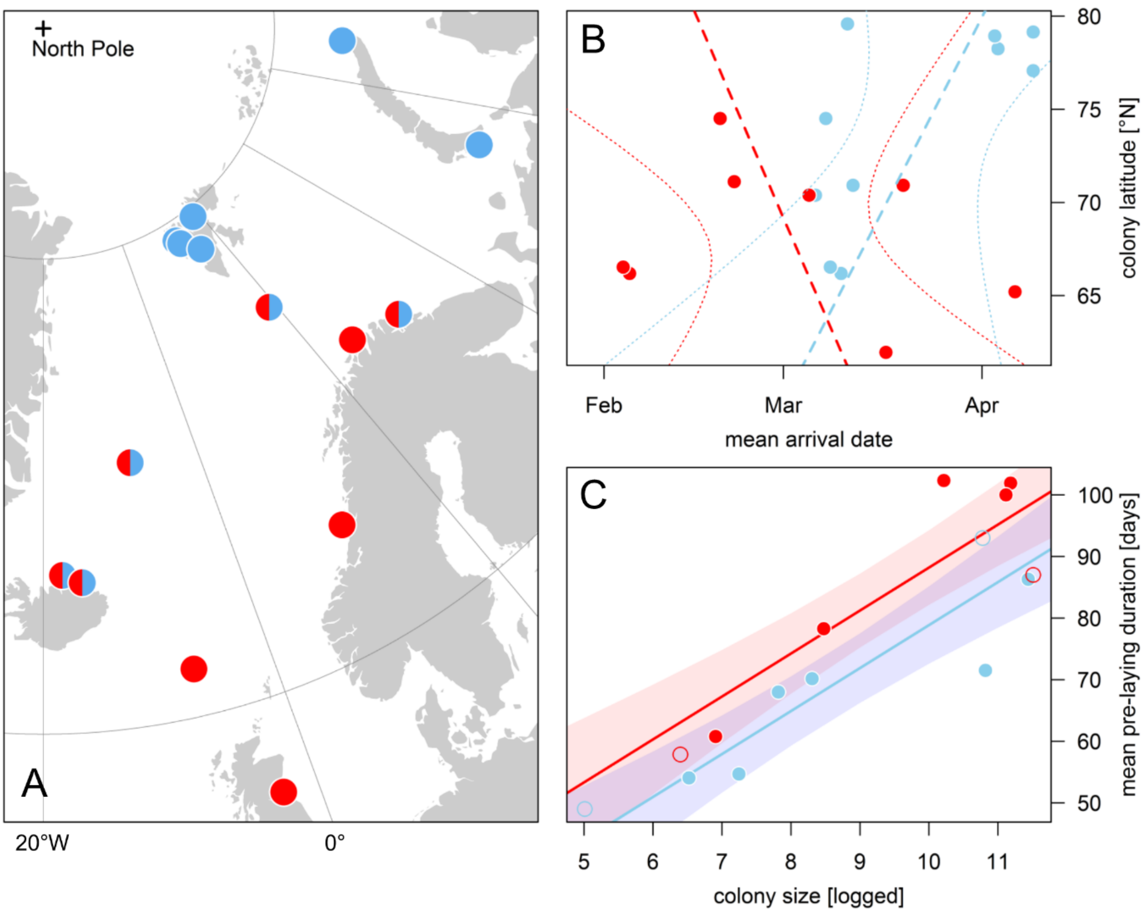

Figure 1. Panel A displays the colony locations of common (red, COGU) and Brünnich's guillemots (blue, BRGU) included in the study. Panel B illustrates the relationship between mean arrival date and latitude (excluding the Isle of May), while panel C shows the correlation of mean pre-laying duration and colony size. Colonies with less certain pre-laying duration estimates are indicated as open circles. Bands in panels B and C indicate bootstrapped 95% confidence intervals for predicted values.

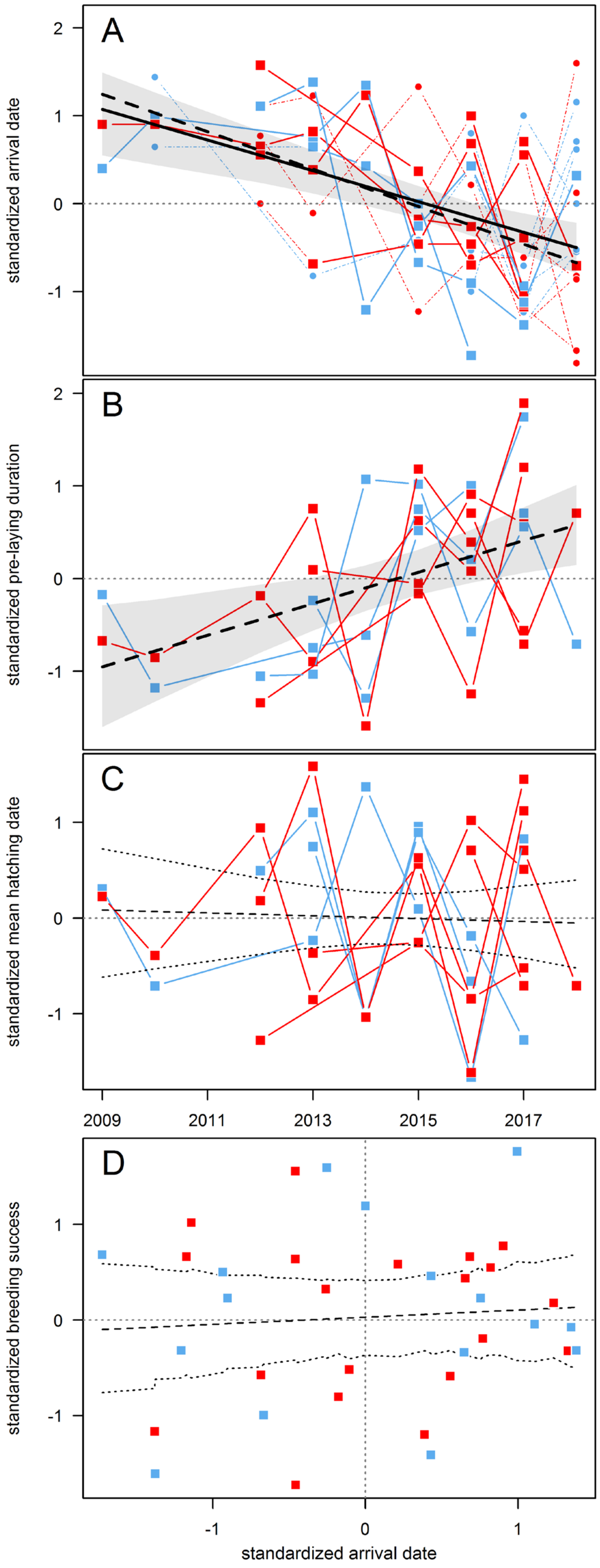

Figure 2. Temporal trends in arrival dates at the colony (Panel A), pre-laying duration (Panel B) and mean hatching date (Panel C). Dashed lines represent linear mixed effect model predictions for the subset of data for which hatching timing information was available (squares), while the solid line in panel A illustrates the same model prediction for arrival date using the entire dataset (squares and dots). Panel D shows the relationship between advancing arrival date and breeding success. Bands in all panels indicate bootstrapped 95% confidence intervals for predicted values calculated using the `bootMer` function with 1000 simulations (package `lme4`). Red and blue symbols represent common (COGU) and Brünnich's guillemots (BRGU), respectively.

Supplementary Material and Methods

Estimation of arrival dates from logger data

Annual first colony arrival dates for each colony and species were estimated using salt water immersion data recorded by light-level geolocators deployed on adult breeders (models: Mk15 (British Antarctic Survey, Cambridge, UK), Mk3006 & Mk4083 (Biotrack, Wareham, UK), F100, C65, C250 & C330 (Migrate Technology, Cambridge, UK) or L250A (Lotek, St. John's, Newfoundland, Canada)). Sampling interval for Mk15, Mk3006 & Mk4083 was every 3 seconds, F100, C65, C250 & C330 sampled the state every 30 seconds and L250A loggers sampled salt water immersion every 5 minutes. For comparability, we binned individual data into hourly bins for further analysis. Under the assumption that first arrival back at the colony is synchronized in guillemots [1, 2], we then defined annual first colony arrival dates as the first instance where the majority of the tracked breeding population attended the colony for at least two consecutive hours during daylight at the colony (defined as a solar angle above -6°, i.e. civil twilight). Meaning that two consecutive hourly bins of salt water immersion data averaged over all tracked individuals from the considered colony, species and year needed to be more at least 50% dry during daylight at the colony (example in figure S1B). We considered five individuals a sufficient minimum sample size to estimate these dates as in this case at least three individuals needed to be present during these two hours to identify an arrival date. Mean logger sample size used to derive arrival date for each colony, species and year was 16 individuals (standard deviation (SD) = 8; range = 5 – 38, table S1).

Estimation of mean hatching dates

Individual hatching dates were estimated by nest inspections at variable intervals during hatching or egg laying, while in the former case the incubation time was added (i.e. 33 days, [3]). These dates were then averaged to mean hatching dates with a mean sample size of 108 nests monitored (SD = 218; range = 10 – 760, table S1). However, three instances of estimated mean hatching dates were only rough estimates based on observed hatching events during colony visits for recapture of logger-equipped individuals (table S1). These dates have been only used to estimate mean pre-laying duration and were not considered in other analyses. Mean pre-laying duration was defined as mean hatching date averaged across years of which we subtracted a 33 day incubation period as well as mean colony arrival date.

Estimation of breeding success

To estimate breeding success, individual nests have been inspected at variable time intervals with on average 52 monitored nests (SD = 39, range = 5 – 157, table S1). Depending on colony, individual breeding success was defined differently (e.g. chick age of 20 days or medium-sized chick present) and hence all estimates have been standardized (SD = 1, mean = 0) for each colony and species to make them comparable.

Table S1. Available data for each colony and species including colony size and number of years with available data for arrival timing at the colony, mean hatching date and breeding success.

			Common guillemot (COGU)										**Brünnich's guillemot (BRGU)**									
colony	acronym	colony location	colony size (pairs* 1000)	year of count/estimate	colony trend	trend over x years	years with colony arrival date	mean # individuals tracked each year (min-max)	years with mean hatching date	mean # of nests monitored each year (min-max)	years with breeding success data	mean # of nests monitored each year (min-max)	colony size (pairs* 1000)	year of count/estimate	colony trend	trend over x years	years with colony arrival date	mean # individuals tracked each year (min-max)	years with mean hatching date	mean # of nests monitored each year (min-max)	years with breeding success data	mean # of nests monitored each year (min-max)
Isle of May	IM	56.18°N 2.58°W	16 [4]	2007	↗ [5]	15	7	17 (10-21)	4	716 (644-760)	-	-	0	-	-	-	-	-	-	-	-	-
Faroe Islands (Lonin)	FA	61.95°N 6.80°W	100 [6]	2005/06	↘ [6]	15	1	6	1[b]	-	-	-	0	-	-	-	-	-	-	-	-	-
Sklinna	SK	65.22°N 10.97°E	0.6 [7]	2006	↗ [8]	10	7	17 (7-26)	1[b]	-	-	-	0	-	-	-	-	-	-	-	-	-
Langanes	LA	66.18°N 15.99°W	27.3 [9]	2007	↘ [10]	20	3	12 (9-18)	2[d]	87 (82-91)	-	-	2.5 [9]	2007	↘ [10]	20	2	10 (5-15)	1[d]	57	-	-
Grimsey	GR	66.53°N 17.99°W	67.3 [9]	2007	↘ [10]	20	2	11 (5-16)	2[d]	15 (14-15)	-	-	4 [9]	2007	↘ [10]	20	3	11 (9-15)	2[d]	54 (53-54)	-	-
Jan Mayen	JM	71.02°N 8.52°W	1 [11]	2010	↘ [8]	7	7	13 (8-20)	6	14 (10-18)	6	17 (14-21)	50 [11]	2010	↘ [8]	7	7	19 (8-31)	6	50 (25-63)	6	73 (58-102)
Hjelmsøya	HJ	71.07°N 24.72°E	3.1 [12]	2004	↗ [8]	10	6	9 (5-14)	-	-	5	38 (5-141)	?	-	↘ [8]	-	-	-	-	-	-	-
Hornøya	HO	70.38°N 31.15°E	4.8 [13]	2006	↗ [8]	10	6	26 (21-38)	4	31 (23-41)	4	32 (29-39)	0.4 [14]	2006	↘ [8]	10	-	-	-	-	-	-
Bjørnøya	BI	74.50°N 18.96°E	72 [15]	2006	↗ [8]	10	8	22 (7-28)	7	47 (37-61)	6	102 (53-137)	93 [15]	2006	↘ [8]	10	8	17 (7-29)	7	25 (20-31)	6	52 (39-60)
Diabasodden	DO	78.25°N 15.51°E	0	-	-	-	-	-	-	-	-	-	1.4[a]	2007	↘ [8]	10	6	11 (5-16)	4	60 (10-131)	4	86 (26-157)
Ossian Sarsfjellet	OF	78.94°N 12.49°E	0	-	-	-	-	-	-	-	-	-	0.8[a]	2011	↘ [8]	10	1	7	1	41	-	-
John Scottfjellet	JS	79.15°N 11.96°E	0	-	-	-	-	-	-	-	-	-	0.1[a]	2011	?	-	1	3[e]	1[c]	-	-	-
Alkefjellet	AL	79.59°N 18.46°E	0	-	-	-	-	-	-	-	-	-	48[a]	2009	(↗)[a]	4	3	15 (12-18)	1[b]	-	-	-
Kara Gate	KG	70.59°N 55.02°E	0	-	-	-	-	-	-	-	-	-	?	-	?	-	3	20 (9-26)	-	-	-	-
Oranskie islands	OI	77.07°N 67.64°E	0	-	-	-	-	-	-	-	-	-	?	-	?	-	2	12 (7-16)	-	-	-	-

[a] S. Descamps unpublished data; [b] rough estimate based on chick sightings while visiting the colony; [c] assumed to be the same as OF as they are in close proximity to each other; [d] based on mean egg laying date; [e] only used for approximate pre-laying duration due to low sample size

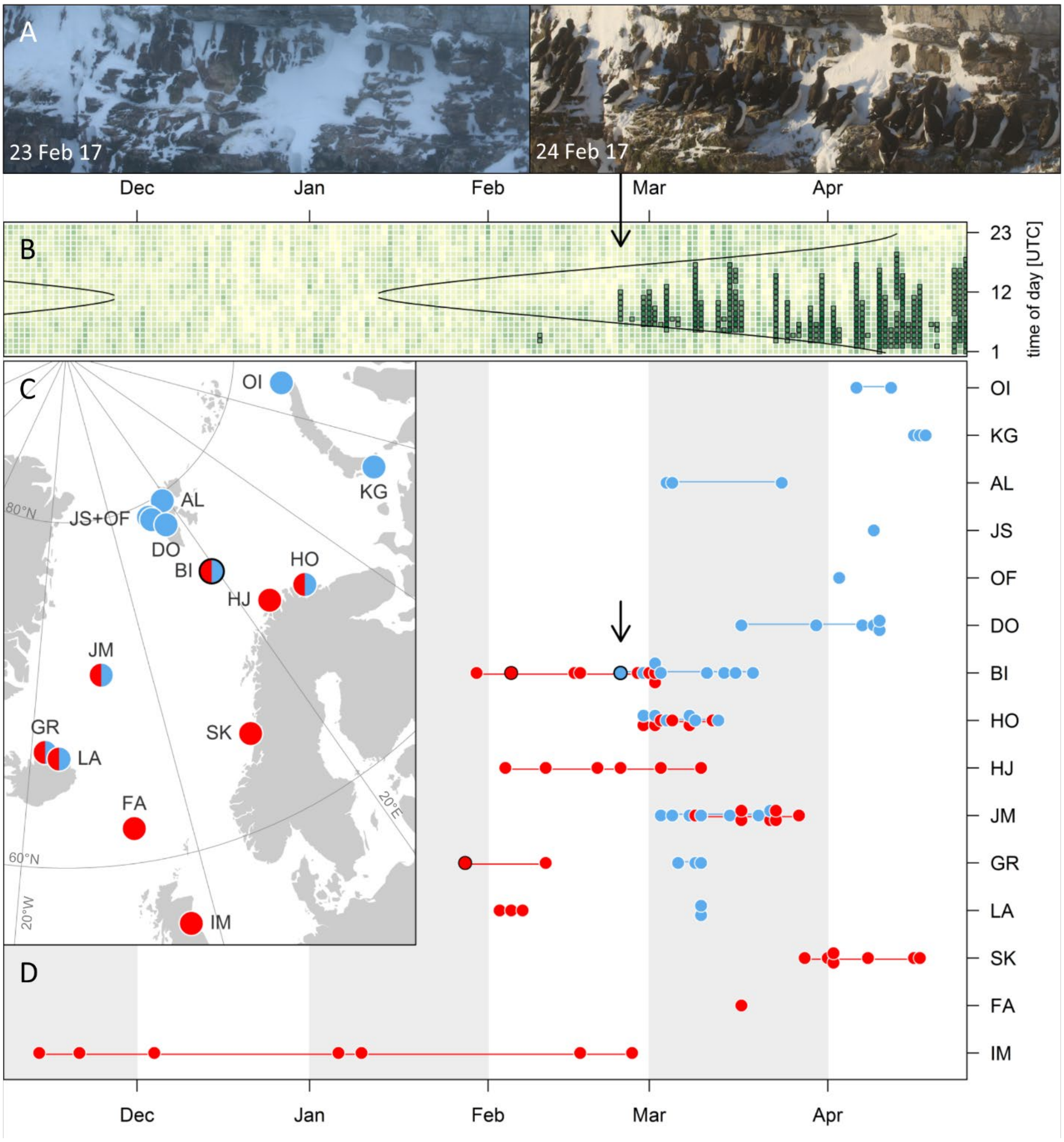

Figure S1. First annual arrival dates at the colony (panel D) for common (COGU, red) and Brünnich's guillemots (BRGUs, blue) breeding across the Northeast Atlantic (panel C). In panel D, each point represents arrival timings in a given year. Colonies in panel D are sorted from southwest to northeast similar to their depiction in panel C. Panel B illustrates an example average salt water immersion dataset in hourly bins for BRGU from Bjørnøya (BI, outlined in black in panel C) in 2016/17 (n=15) with day of the year on the x-axis and time of day (in UTC) on the y-axis. Light green indicates that all individuals were submerged in salt water. Conversely, dark green indicates all individuals being dry, while black framed bins specify the majority of tracked individuals being dry. Black lines display timings of sunrise and sunset at the colony across the year. The arrow indicates the estimated arrival timing for this example which is also indicated in panel D. Black framed points in panel D are validated with camera trap data, of which one is illustrated in panel A and corresponds to the example in panel B.

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