INTRODUCTION: REVIEW

Tracking the movements of North Atlantic seabirds: steps towards a better understanding of population dynamics and marine ecosystem conservation

Hallvard Strøm[1],*, Sébastien Descamps[1], Morten Ekker[2], Per Fauchald[3], Børge Moe[3]

[1]**Norwegian Polar Institute (NPI), Fram Centre, 9296 Tromsø, Norway**
[2]**Norwegian Environment Agency, 7485 Trondheim, Norway**
[3]**Norwegian Institute for Nature Research (NINA), Fram Centre, 9296 Tromsø, Norway**

ABSTRACT: Many seabird species undergo extensive seasonal migrations, often across large marine ecosystems or between marine areas under different national jurisdictions. With the advances of electronic tracking, especially of the application of Global Location Sensors (GLS or geolocators), it is now possible to study the seasonal movements of seabirds and link breeding populations to non-breeding habitats. To take full advantage of this development for better management and conservation, and to broaden the scope of scientific questions that can be assessed, there is a need for large-scale and multi-species programmes. The SEATRACK project with partners from 10 countries is ongoing and aims to identify the year-round distribution and movements of seabirds breeding in colonies across the northern part of the North Atlantic. By 2020, 14 534 loggers were deployed on 11 species, and data from 5440 retrieved loggers have been analyzed and compiled. This Theme Section assembles original research articles based on data collected as part of the SEATRACK project from 2014 to 2019. A series of 11 papers advances the knowledge within 4 research themes: (1) variation in migration strategies among individuals, populations and species; (2) linking migration strategies and winter distribution to seabird demography and population dynamics; (3) linking migration and winter distribution to contaminants in seabirds and (4) the use of GLS data in marine spatial planning. We review existing literature within SEATRACK's 4 themes with a focus on the temperate and arctic zones of the North Atlantic to provide a framework within which to discuss the 11 contributions and provide recommendations for future research.

KEY WORDS: Logger technology · Tracking · Marine birds · Winter distribution · Geolocator · SEATRACK · Management

1. INTRODUCTION

The global ocean contains unique biodiversity, life forms and genetic resources that provide ecosystem services of enormous value to humans (Worm et al. 2006, Sala et al. 2021). At the same time impacts of human activities on the ocean are substantial, ubiquitous and rapidly changing (Halpern et al. 2019). Large marine predators are important top consumers in marine ecosystems, and their depletion can have cascading effects on lower trophic levels (Block et al. 2011). Seabirds are one of the most threatened groups of vertebrates, with almost half of all species (47 %) experiencing population declines (Dias et al. 2019). As top predators, seabirds play key roles in marine ecosystems, making their conservation critical (Grémillet et al. 2018).

*Corresponding author: hallvard.strom@npolar.no

The North Atlantic supports some of the largest seabird populations in the world, especially in its northern part (Barrett et al. 2006, Frederiksen 2010). Many have declined dramatically over recent decades, resulting in several species now being listed in national and international lists of threatened species (Croxall et al. 2012, Dias et al. 2019). Outside the breeding season, most seabirds migrate far from their colonies and sometimes range over large areas (Harrison et al. 2018, Alerstam et al. 2019). To ensure suitable conservation actions, it is essential to have good knowledge of the population distributions in time and space and of the environmental factors that affect these populations. Until recently, it has been difficult to follow large-scale migratory movements, especially among small species, and most of our knowledge has been based on band recoveries, which may give biased results (Clark et al. 2009). The emergence and advances of light-level geolocators (also known as Global Location Sensors [GLS]; Wilson et al. 1992, Hill 1994, Wilson & Vandenabeele 2012) has, however, enabled us to study such movements in much greater detail, providing new and crucial knowledge for the management of seabirds and their marine habitats (Tremblay et al. 2009, Block et al. 2011). To be able to take full advantage of this development and to broaden the scope of scientific questions that can be answered, multi-year, multi-site and multi-species studies are necessary (Schimel & Keller 2015, Bernard et al. 2021).

The SEATRACK project (https://seapop.no/en/seatrack/) was initiated in 2014 with the main goal to assess the non-breeding distribution of seabirds breeding in colonies across the Barents, Norwegian and northern North Seas (i.e. colonies in Russia, Norway [including Svalbard and Jan Mayen], Iceland, the Faroes and the UK). Eleven species were selected as focal species, representing 5 ecological groups or foraging guilds (Fauchald et al. 2011): pelagic divers, pelagic surface feeders, coastal surface feeders, coastal diving species and coastal benthic feeders (Table 1). By doing this, the tracked species could be used as indicators of the seabird community as a whole. Thirty-nine colonies that covered most of the breeding distribution of these 11 species were selected initially. In 2019, the geographical focus was extended to cover the North Atlantic north of 48° N, and 18 additional colonies in Ireland, west Scotland, Greenland and Canada were included (Fig. 1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m676p097_supp.pdf). More than 60 scientists from 10 countries have taken part in the collaboration up to the present.

From 2014 to 2020, 14 534 GLS were deployed following a standard field protocol (available at https://seapop.no/en/seatrack). GLS are light (0.5–3.5 g) archival tags with a clock and a light-level sensor. Timing of the twilight events (sunrise and sunset) is determined from the light-level recordings to obtain positions. Latitude is estimated from daylength, longitude from time of solar midnight/noon. Average error is usually ~200 km (Lisovski et al. 2012), and due to their relatively low precision, geolocators are most appropriate for tracking large scale movements (Phillips et al. 2004). GLS also store information of when the logger is in contact with salt water, and some models record temperature when submerged. By 2020, data from 5440 retrieved loggers were ana-

Table 1. Foraging guilds, species, numbers of breeding colonies, light-level geolocators deployed, retrieved and successfully downloaded, the total number of individual birds and filtered positions, as well as the number of years tracked per individual over the period 2014–2020. PDi = pelagic divers, PSu = pelagic surface feeders, CSu = coastal surface feeders, CDi = coastal divers, CBe = coastal benthic feeders. In total, 57 colonies were studied

| Forag. guild	Species	Col.	No. of geolocators			Total N		Individuals per year-track					
			Deployed	Retrieved	Succ. downl.	Birds	Positions	1 yr	2 yr	3 yr	4 yr	5 yr	6 yr
PDi	Atlantic puffin	17	2431	805	670	453	385 104	234	115	72	23	8	1
	Brünnich's guillemot	16	1862	835	762	422	400 026	179	92	76	48	22	5
	Common guillemot	12	1848	995	868	435	502 539	153	121	71	56	26	8
	Little auk	5	875	280	244	182	96 953	120	43	17	2	0	0
PSu	Black-legged kittiwake	21	3028	1558	1401	775	846 434	349	172	134	70	33	17
	Lesser black-backed gull	8	341	55	48	37	39 706	14	14	6	3	0	0
	Northern fulmar	17	1210	547	505	293	313 451	115	78	46	29	19	6
CSu	Glaucous gull	5	542	158	150	106	66 808	49	36	12	5	4	0
	Herring gull	11	403	73	51	43	47 589	15	16	8	3	1	0
CDi	European shag	8	916	410	355	202	208 178	89	57	28	17	6	5
CBe	Common eider	9	1078	508	386	274	258 696	132	80	33	23	4	2
	Total		14 534	6224	5440	3222	3 165 484	1449	824	503	279	123	44
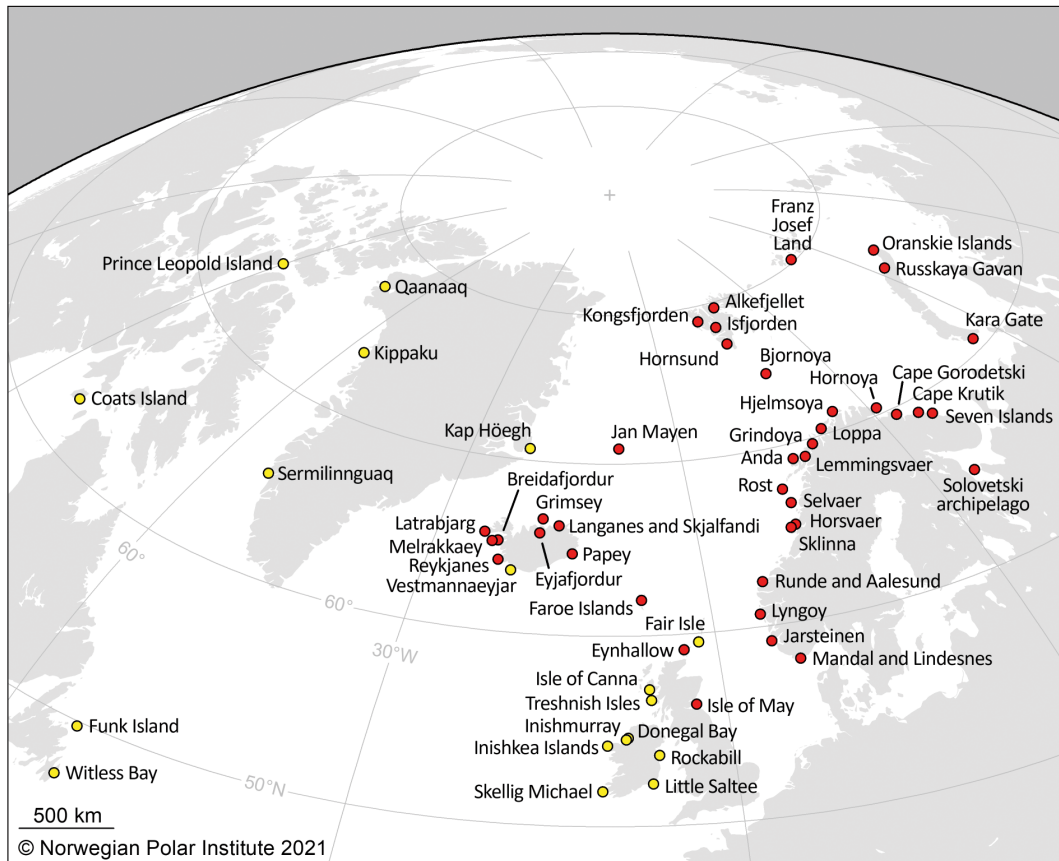
Fig. 1. Colonies included in SEATRACK where light-level geolocators have been deployed since 2014 (red dots) or since 2019 (yellow dots)

lyzed and compiled (Table 1). The protocol for obtaining positions from the raw light measurement, including filtering procedures is described in Bråthen et al. (2021). The SEATRACK website (https://seatrack.seapop.no/map/) presents seasonal distribution maps for all species and colonies.

The overreaching goal of SEATRACK is to identify the distributions of non-breeding seabirds from colonies in the North Atlantic in order to better understand how changes in environmental conditions encountered during migration or on the winter grounds affect their demography and population dynamics. Four main research themes have been defined to address these objectives: (1) the assessment of variation in migration strategies among individuals, populations and species; (2) the linkage of migration strategies and winter distribution to demography and population dynamics; (3) the linkage of non-breeding distribution to contaminants and (4) the use of tracking data in marine spatial planning.

This Theme Section assembles 11 original research articles based on data collected as part of the SEATRACK project from 2014 to 2019 cover topics

from all 4 research themes. Collectively, these contributions advance our knowledge of the non-breeding distribution and migration of North Atlantic seabirds and their impact on demographic parameters. This knowledge is essential for a sustainable management of seabird populations and marine ecosystems. In the present introductory paper, we review existing literature within SEATRACK's 4 themes with a focus on the temperate and arctic zones of the North Atlantic to provide a framework within which to discuss the 11 contributions and give recommendations for future research.

2. VARIATION IN MIGRATION STRATEGIES

2.1. Migration strategies and non-breeding movements

There is a substantial diversity in migration strategies among North Atlantic seabirds, from resident or short-distance to long-distance migrants (Daunt et al. 2006, Egevang et al. 2010, Dufour et al. 2021 in this

Theme Section). Although some species are transequatorial migrants and may experience an 'endless summer' (e.g. Arctic tern *Sterna paradisaea*, Egevang et al. 2010; Sabine's gull *Xema sabini*, Stenhouse et al. 2012; long-tailed skua *Stercorarius longicaudus*, Gilg et al. 2013; Cory's shearwater *Calonectris borealis*, Dias et al. 2012; Manx shearwater *Puffinus puffinus* Guilford et al. 2009; Leach's storm petrel *Oceanodroma leucorhoa*, Pollet et al. 2019; Bulwer's petrel *Bulweria bulwerii*, Dias et al. 2015), most species migrate to lower latitudes and remain in the North Atlantic throughout the year (e.g. Anker-Nilssen et al. 2000, Fort et al. 2013, McFarlane Tranquilla et al. 2013, White et al. 2013, Amélineau et al. 2021 in this Theme Section). By doing so, the seabirds benefit from longer periods of daylight for feeding, but they may also migrate to lower latitudes for other reasons, such as more favourable food availability, weather and sea-ice conditions (Gilg et. al. 2010, Fort et al. 2013). Some populations or individuals may, however, stay at high latitudes during winter and thus experience the polar night (Table 2). These seabirds are generally diurnal and visual predators such that finding food when there is no or very little light may prove challenging. European shags *Phalacrocorax aristotelis*, for example, survive such conditions in northern Norway by concentrating their foraging during the available twilight (Moe et al. 2021 in this Theme Section). Twilight foraging has also been observed in great cormorants *Phalacrocorax carbo* and Steller's eiders *Polysticta stelleri* in northern Norway, where they adjust their foraging times towards midday as winter progresses (Johansen et al. 2001, Systad & Bustnes 2001). Great cormorants in western Greenland, however, forage extensively in darkness (Grémillet et al. 2005), suggesting that diving birds may have the capacity to use non-visual cues to target fish. Some seabirds may also be exposed to artificial light from boats, installations and harbours. Dupuis et al. (2021 in this Theme Section) showed that foraging activity by the northern fulmar *Fulmarus glacialis* may be associated with artificial light from fishing vessels, but whether (or to what degree) the artificial light may help the fulmar locate the fishing vessels rather than target the offal and unwanted catch as they are discarded is not known.

Table 2. Examples of populations that remain at high latitudes in winter and experience the polar night, along with the approximate proportion (based on subjective assessments of the publications) of individuals using this strategy

Group (family)/species	Breeding population	Proportion of individuals	References
Sea ducks (Anatidae)			
Common eider (*Somateria mollissima*)	Spitsbergen	Small	Hanssen et al. (2016)
	Barents Sea region, northern Norway	High	Anker-Nilssen et al. (2000)[a]
King eider (*S. spectabilis*)	Northern Russia	High	Bustnes et al. (2010)
Steller's eider (*Polysticta stelleri*)	Northern Russia	High	Systad & Bustnes (2001)
Alcids (Alcidae)			
Black guillemot (*Cepphus grylle*)	Barents Sea region, northern Norway	High	Anker-Nilssen et al. (2000)[a]
Common guillemot (*Uria algae*)	Bjørnøya, northern Norway and Russia	High	Amélineau et al. (2021)
Brünnich's guillemot (*U. lomvia*)	Novaya Zemlya, Kola Peninsula, Spitsbergen	High	Amélineau et al. (2021)
Atlantic puffin (*Fratercula arctica*)	Finnmark/northern Norway	High	Amélineau et al. (2021)
Little auk (*Alle alle*)	Franz Josef Land	High	Amélineau et al. (2021)
Gulls (Laridae)			
Black-legged kittiwakes (*Rissa tridactyla*)	Novaya Zemlya	Moderate	Ezhov et al. (2021)
	North Atlantic	Very small	Frederiksen et al. (2012)
Glaucous gulls (*Larus hyperboreus*)	Barents Sea region	Moderate/high	Anker-Nilssen et al. (2000)[a]
Herring gulls (*L. argentatus*)	Barents Sea region, northern Norway	Moderate/high	Anker-Nilssen et al. (2000)[a]
Great black-backed gull (*L. marinus*)	Barents Sea region, northern Norway	Moderate/high	Anker-Nilssen et al. (2000)[a]
Fulmars (Procellariidae)			
Northern fulmar (*Fulmarus glacialis*)	Spitsbergen, Bjørnøya	High	Amélineau et al. (2021)
	North Atlantic	Very small	Amélineau et al. (2021)
Cormorants and shags (Phalacrocoracidae)			
European shag (*Phalacrocorax aristotelis*)	Northern Norway	Moderate/high	Moe et al. (2021)
Great cormorant (*P. carbo*)	Western Greenland	Small	White et al. (2013)
	Northern Norway	Moderate/high	Johansen et al. (2001)[a]

[a]Results from Anker-Nilssen et al. (2000) and Johansen et al. (2001) are not based on tracking data and specific breeding populations, or proportions are not well known

Seabirds generally migrate along the coast or off-shore (Dias et al. 2011, Klaassen et al. 2012, Dias et al. 2015), but some populations or individuals may migrate over land (Bustnes et al. 2013, Wynn et al. 2014, Wikelski et al. 2015, van Bemmelen 2019). While many terrestrial birds or shorebirds fly non-stop over long distances (the most extreme example is the bar-tailed godwit *Limosa lapponica baueri* that may fly non-stop for ~10 000 km across the Pacific Ocean; Gill et al. 2009), seabirds can to a varying degree forage in the ocean during their journey. They may, however, be challenged by areas where ocean productivity and food availability are low or wind conditions less favorable. The decision to fly over these areas or to slow down to forage and rest, based on experience of previous or current conditions, depends probably on the ratio of energy accumulated while feeding to energy spent on travel (Strandberg & Alerstam 2007). Accordingly, there seems to be a range of strategies from continuous fly-and-forage movements to distinct segments of directional and fast movements between staging/foraging areas (McKnight et al. 2013, Amélineau et al. 2021). Furthermore, seabirds do not necessarily remain in a single final non-breeding destination but may continue to move over relatively large ocean areas throughout the non-breeding season. Seabirds generally use preferred routes to reach specific wintering areas instead of dispersing in an arbitrary direction from the colony (Amélineau et al. 2021). Segments of movements have previously been identified throughout the entire non-breeding season among long-tailed skuas (van Bemmelen et al. 2017). Based on the SEATRACK dataset, Amélineau et al. (2021) have found that 6 pelagic species (fulmars, black-legged kittiwakes *Rissa tridactyca* [hereafter kittiwake], common guillemots *Uria aalge*, Brünnich's guillemots *Uria lomvia*, little auks *Alle alle*, Atlantic puffin *Fratercula arctica* [hereafter puffin]) had on average 3 to 4 migration phases and 2 to 3 distinct stationary phases when they occupied different areas during the non-breeding season. Differences in conductivity data (indicating wet/dry locations of tracked birds) and daily activity patterns were small between migratory and stationary phases, suggesting that the tracked birds continued to forage during the migration phases. Different methods exist to separate migratory and stationary phases, e.g. based on speed (Gilg et al. 2013) or net square displacement (Amélineau et al. 2021). We refer to migration as the movement during such migratory phases. Since staging and final non-breeding areas are destinations of migration, and time spent in these areas determines time between migration bouts, we also consider the staging and non-breeding areas as part of the migration strategy.

2.2. Migratory connectivity

Tracking studies, especially multi-colony, allow us to identify the different areas used by different populations during the non-breeding season (Frederiksen et al. 2012). Migratory connectivity describes the link between the different breeding populations and these non-breeding areas (Webster et al. 2002, Finch et al. 2017). Migratory connectivity is strong when breeding populations migrate to unique non-breeding areas and the mixing of breeding populations during the non-breeding period is low. Conversely, migratory connectivity is weak when breeding populations share non-breeding areas and the mixing of breeding populations is high (Webster et al. 2002). Potential negative effects of perturbations or threats in the non-breeding area should thus be stronger within a population with strong migratory connectivity, while the effects on populations with weak migratory connectivity should be more diffuse, since only some of the individuals would be exposed to the threat. Population spread is an important aspect of migratory connectivity, and depends on the size of the occupied non-breeding area. Populations wintering within a smaller area (i.e. low spread) may be more vulnerable to perturbations and threats than those in a large area, where there may be more opportunities for finding unaffected patches.

An increasing number of studies has demonstrated a large variation in migration strategies, routes and destinations between and within populations of the same North Atlantic seabird species (Frederiksen et al. 2012, 2016, Dean et al. 2015, Fayet et al. 2017a, van Bemmelen et al. 2017, Merkel et al. 2021a, 2021b in this Theme Section, Moe et al. 2021). For example, in 2 sympatric meta-populations of common and Brünnich's guillemots in the Northeast Atlantic, Merkel et al. (2021b) showed that different breeding populations had specific non-breeding habitats implying a strong migratory connectivity. This was apparent through a combination of seasonal space use and occupied environmental niches. Frederiksen et al. (2012) found a high degree of mixing among 19 kittiwake populations in a core wintering area in the Northwest Atlantic. Since this wintering area is very large, a local threat such as a spatially restricted oil spill would only affect a relatively small part of the area occupied by kittiwakes. By contrast, a large-scale ecosystem change occurring in this area due to

e.g. climate change could effectively impact the entire population of kittiwakes in the North Atlantic. In other words, the effect of connectivity and spread on the vulnerability of populations is a matter of scale.

Individual arctic skuas *Stercorarius parasiticus* from northern Norway spread out and target different winter locations in the North Atlantic (Gulf of Mexico, Caribbean Sea, the Mediterranean Sea and Canary Current), South Atlantic (Falkland Current, Benguela Current) and Indian Ocean. In the North Atlantic wintering areas, they mix with arctic skuas from other colonies (van Bemmelen et al. 2019). As a result, this species represents an extreme end of the continuum for population spread and inter-population mixing. Kittiwakes breeding in Novaya Zemlya in northern Russia are another particular example of population spread (Ezhov et al. 2021 in this Theme Section). Within this population, a remarkable migratory divide is apparent, with some individuals migrating across the Arctic Ocean to winter in the Pacific, while the rest winter in the North Atlantic. Ezhov et al. (2021) suggest that the migratory divide reflects the genetic origin and early migration strategies of the Pacific and Atlantic black-legged kittiwakes that colonized Novaya Zemlya. Such trans-polar migration might also become more frequent as a phenotypic response to global warming and reduced sea ice in the Arctic Ocean (Clairbaux et al. 2019).

2.3. Individual consistency

Individual consistency is another aspect of the migration strategies important for the vulnerability of seabirds to environmental changes, perturbations and threats (Phillips et al. 2017). Paradoxically, the life history and mobility of seabirds may lead to contrasting expectations. On one hand, seabirds are highly mobile and could be expected to be flexible and respond to environmental changes. On the other hand, seabirds are long-lived animals that can be highly consistent in their migration strategies due to tightly scheduled migration itineraries and fixed dependency on specific sites (Phillips et al. 2017). Individuals with fixed migration strategies could thus be more vulnerable to environmental changes along flyways and in their non-breeding areas (Phillips et al. 2017). Common and Brünnich's guillemots show consistent strategies indicating fidelity to specific sites rather than to specific habitats (Merkel et al. 2021a). If the locations of favourable habitats change, such species may not be able to adjust their migration strategies and non-breeding distributions sufficiently.

Individuals with fixed and consistent migration strategies may also be repeatedly exposed to the same environmental conditions or threats (such as pollution) over successive non-breeding seasons.

There seems to be a continuum from consistent to flexible migration strategies among North Atlantic seabird populations and species. Some individual Cory's shearwaters are very flexible and shift non-breeding destinations between hemispheres in the Atlantic Ocean (Dias et al. 2011), whereas individual Arctic skuas are very consistent in their non-breeding areas (van Bemmelen 2019). Most seabird studies show rather high fidelity and consistency of individuals to the same region in the non-breeding season (Merkel et al. 2021a, Phillips et al. 2017), whereas routes, staging areas or timing of migration are somewhat more flexible (Dias et al. 2011, McFarlane Tranquilla et al. 2014, Müller et al. 2014, but see Phillips et al. 2017). From 10 yr of geolocation tracking data, Léandri-Breton et al. (2021 in this Theme Section) showed that kittiwakes were rather consistent in targeting wintering sites across years but more flexible in time, i.e. duration on the winter grounds and timing of departure and arrival. The degree of consistency may also depend on the size of the wintering area considered. For example, individuals may show high fidelity to a large wintering area but at the same time move considerably within this area (Guilford et al. 2011, van Bemmelen et al. 2017, Léandri-Breton et al. 2021). Furthermore, individuals from the same population may also exhibit different levels of consistency, with some visiting more non-breeding areas, as shown for long-tailed skuas and kittiwakes (van Bemmelen et al. 2017, Léandri-Breton et al. 2021).

Among puffins, individuals from some colonies show a dispersive migration and spread in virtually all directions away from the colonies (Guilford et al. 2011, Fayet et al. 2017a, Amelineau et al. 2021). However, adults nevertheless show high consistency in their migration strategies and target the same wintering areas every year. From this pattern, Guilford et al. (2011) proposed the explorative-refinement hypothesis for the development of migration routes in seabirds as an alternative to 2 earlier hypotheses concerning genetic control or social learning (Fayet 2020). Guilford et al. (2011) proposed that young seabirds that fledge from their colonies without being escorted by their parents have a phase of dispersion. The immature birds subsequently acquire more experience and gradually refine their migration strategies to become more consistent as adults. This hypothesis has received support from tracking of 4 to 9 yr

old immature Cory's shearwaters (Campioni et al. 2020). However, more studies on post-fledging movements are clearly needed to test this hypothesis. With few exceptions (e.g. Ramos et al. 2019), post-fledging movements and migration strategies have so far been studied using satellite transmitters on larger species like albatrosses and shearwaters (e.g. Weimerskirch et al. 2006, Yoda et al. 2017, Orben et al. 2018). While geolocators can be deployed on juveniles and immature individuals of smaller seabird species, recapture is challenging, because mortality rates of juveniles tend to be high, and birds that do not return to the same subcolony are difficult to relocate. Due to the difficulties in tracking the period from fledging to recruitment, this period has been termed the 'lost years'. Obtaining data for those years will be particularly important in future research.

3. CONSEQUENCES OF MIGRATION STRATEGIES FOR SEABIRD DEMOGRAPHY AND POPULATION DYNAMICS

Seabirds, by definition, spend most of their life at sea, especially during the non-breeding season when they are no longer central-place foragers. Differences in wintering areas or migration routes can result in different energetic costs (i.e. flight expenditure) or benefits (i.e. food availability), with potential fitness consequences (e.g. Alves et al. 2013, Schultner et al. 2014a, but see Pelletier et al. 2020). Understanding the drivers of such differences in wintering strategies as well as their potential carry-over effects on subsequent survival or reproduction is of primary importance to understand population trajectories. The importance of the non-breeding season in the regulation of seabird populations was highlighted more than 50 yr ago (Lack 1966) and confirmed by subsequent empirical studies (e.g. Gaston 2003, Gilchrist & Mallory 2005, Sæther et al. 2016 and see Sections 3.1, 3.2 and 3.3 below). However, understanding the relationships between seabird demography and the environmental conditions experienced during the non-breeding period (Fig. 2) has proved extremely challenging. We review evidence for North Atlantic

seabirds (in the temperate and polar zones only) showing how the environment experienced during migration or on the wintering grounds may affect vital rates and dynamics.

3.1. Linking non-breeding distribution and population dynamics

Most seabirds are long-distance migrants. Travelling long distances may be energetically costly especially for species with high flight costs like the auks (Elliott et al. 2013) and migrating birds often cross unproductive areas to reach their non-breeding grounds (e.g. Sahara Desert crossing, Strandberg et al. 2010; transit across unproductive tropical waters for trans-equatorial migrants, Egevang et al. 2010, Gilg et al. 2010). The non-breeding season may also be characterized by harsh environmental conditions (e.g. Frederiksen et al. 2008, Guéry et al. 2019, Reiertsen et al. 2021 in this Theme Section). Consequently, environmental conditions experienced during the non-breeding season are expected to have a strong influence on seabird populations. However, few studies have addressed the link between envi-
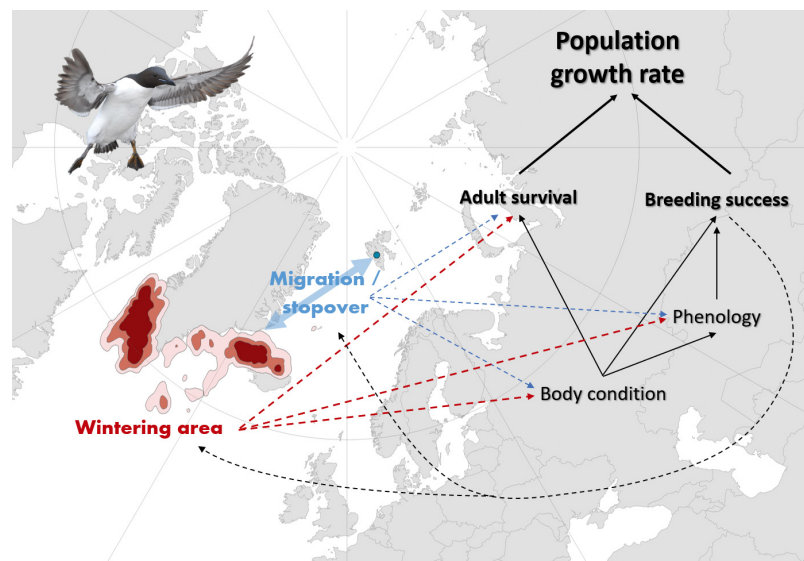

Fig. 2. Conceptual links between seasonal habitats (i.e. during migration and winter periods) and population growth of migratory seabirds. The background map shows the winter distribution of Brünnich's guillemots from Isfjorden in west Spitsbergen, Svalbard (25, 50 and 75% probability contours [with increasing colour intensity] of kernel distributions of geolocator tracking data for the period 2012–2019 from https://seapop.no/en/seatrack/). Thick black arrows: relationships between population growth rate and adult vital rates; thin black arrows: relationships between individual body condition, (breeding) phenology and vital rates; dashed blue and red arrows: effects of the environmental conditions experienced during migration or on the winter grounds, respectively, on individual condition, breeding phenology or survival

ronmental conditions during the non-breeding months and seabird population dynamics in the North Atlantic. Traditionally, such relationships have been identified through the use of large-scale climatic indices, notably the North Atlantic Oscillation (Thompson & Ollason 2001, Drinkwater et al. 2003). Such studies (e.g. Sandvik et al. 2005), however, have been rather vague when it comes to identifying or interpreting the mechanisms behind these relationships, as they were not able to identify which specific environmental parameters in a particular wintering area were driving the observed relationships. Very few studies have ventured beyond such approaches, but a handful have identified seabird winter distribution using tracking (geolocator) data and infered the environmental drivers of population trajectories. For example, in the North Atlantic, a multi-colony tracking of Brünnich's guillemots revealed a striking link between non-breeding distribution and population trends (Frederiksen et al. 2016). Virtually all populations that remained in the west Atlantic during the winter were stable, while those wintering in the eastern part of the Atlantic (East Greenland and around Iceland) were declining. This decline may be linked to changes in the strength of the subpolar gyre that affects the oceanographic conditions (and ultimately prey availability) in this region (Descamps et al. 2013). Merkel et al. (2021) also found that the distributions of different common guillemot populations in the Northeast Atlantic relate to the variable population trends. These results exemplify the usefulness of combining tracking studies with long-term monitoring data at a large spatial scale to better understand changes in seabird populations. More studies linking winter conditions to population trajectories in the North Atlantic are required. Very little has yet been done to extract key environmental parameters from the core areas used by nonbreeding seabirds and to link these to the trends or inter-annual fluctuations in population sizes.

3.2. Linking non-breeding distribution and adult survival

Whereas very few studies in the North Atlantic have linked winter environmental conditions and population growth rates, more have tested relationships with specific demographic parameters such as adult survival (Table 3). These studies concern 9 seabird species, and the vast majority is recent (9 out of 11 were published in or after 2012; Table 3). They all used capture-mark-recapture (CMR) modelling to es-

timate survival rates (including 2 that also considered recruitment probabilities, based on multi-state or multi-event modelling), and most were based on geolocator data to identify seabird migration routes or winter distribution (2 were based on band recoveries only; Table 3). All identified significant relationships between environmental conditions experienced during the non-breeding season and annual survival. Because adult survival rates have a strong influence on seabird population dynamics (Sæther & Bakke 2000), these results support the key role played by environmental conditions during the non-breeding season in regulating seabird populations. Such a regulating role is apparent in Reiertsen et al. (2021) and Reynolds et al. (2011), who suggest that being exposed to the same environmental conditions during the non-breeding season partly synchronizes inter-annual fluctuations in puffin or common guillemot survival.

These results do not mean that winter environmental conditions are always the main and only driver of seabird survival, and other phases of the non-breeding season (e.g. autumn or spring migration) may also play an important role. Descamps et al. (2021 in this Theme Section) found that wintering in the same area was not enough to synchronize adult survival among different little auk populations. This suggests that survival was also affected by conditions encountered during the rest of the year. This may sound like a trivial conclusion, but it does stress the need to not only consider the winter period when investigating the main drivers of seabird survival, but also the inward/outward migration periods (Newton 2007) and the breeding season (e.g. Hovinen et al. 2014). Identifying the habitat used by seabirds during these different periods of their life cycle and assessing the relative importance of the periods in driving seabird demography is critical but has rarely been done. Tools and data now exist, and such research should be given priority in order to understand how bird populations are regulated and to identify the key periods and habitats.

Other studies also linked winter distribution to survival but without specifically considering environmental conditions. These studies compared the survival rates among several groups of birds or populations that had different migration strategies (Harris et al. 2013, Deakin et al. 2019, Pelletier et al. 2020). None provided clear evidence that winter distribution of a specific group of individuals (e.g. specific colony or specific sex from a given colony) was clearly associated with their average survival (Table 3). Such lack of clear relationships is not surprising considering how sensitive individual fitness is to changes in adult

survival in long-lived organisms like seabirds (Sæther & Bakke 2000). Indeed, if a specific migration strategy was associated with lower adult survival, one would expect that it would rapidly disappear from the population (assuming that migration strategy has some genetic or social determinant, which seems often to be the case; Pulido & Berthold 2003). The co-existence of different migration strategies within the same population may thus indicate that these strategies have a similar energy balance (see Garthe et al. 2012 and Pelletier et al. 2020 for examples on the northern gannet *Morus bassanus*) and then similar fitness costs and benefits.

3.3. Linking non-breeding distribution and reproduction

The environmental conditions experienced by seabirds in one season have the potential to affect their life-history later in the annual cycle through carry-over effects (Norris 2005, Norris & Taylor 2006). Weather conditions and/or prey availability during the non-breeding season may indeed impact the body condition of individuals and their phenology (e.g. arrival on the breeding grounds, migration departure; e.g. Saino et al. 2004) which can subsequently affect their reproduction (e.g. Norris et al. 2004). Our review of North Atlantic seabirds (Table 3) identified 9 studies (on 7 species) that investigated the carry-over effects of non-breeding distribution, movements or activity on reproductive parameters. Most of these studies were recent, 8 being published in or after 2016. They confirmed that such carry-over effects are not rare in seabirds and individual activity (e.g. distance travelled) or distribution may affect future breeding phenology or success (Table 3). Interestingly, Dufour et al. (2021) found 2 very distinct migration strategies in the little auk breeding on Svalbard: some birds spent the winter around the southern tip of Greenland, while others halved the migration distance by wintering north of Iceland. Flight costs are expected to be very high for a diving species like the little auk (Elliott et al. 2013), but, nevertheless, the large difference in migration distance (1500 vs. 3100 km on average) between these 2 strategies had no detectable carry-over effect on their reproduction (timing or success). This clearly suggests that the extra energetic costs in birds migrating longer distances can be offset by benefits through e.g. better feeding conditions along or at the end of the longer route (see Aharon-Rotman et al. 2016 for similar results in a shorebird).

The number of studies identified in our literature review is too low to make general conclusions about the general role and importance of the non-breeding season in driving subsequent reproduction. However, the studies indicate that, even though such carry-over effects are not rare, migrating further or wintering in different locations does not necessarily entail any fitness cost. Such costs may indeed vary depending on the life-history trait considered, on the species and on the year studied. Indeed, the cost of a given migration strategy may be context-dependent, although all strategies may result in the same long-term average fitness, enabling the co-existence of several strategies in the same population.

References listed in Table 3 concern the potential carry-over effects of the non-breeding distribution or behaviour on survival and reproduction. However, previous studies also found that carry-over effects may work the other way round, and the migration and non-breeding distribution may depend on the previous reproductive outcome (Phillips et al. 2017). Such effects have been observed in kittiwakes (Bogdanova et al. 2011, 2017, Schultner et al. 2014b) and Cory's shearwaters (Catry et al. 2013, Fayet et al. 2016b). Carry-over effects of reproductive outcome on subsequent migratory behavior can differ among males and females (Bogdanova et al. 2011, Catry et al. 2013, Schultner et al. 2014b) and may likely also vary among colonies or years. Accordingly, raising a chick successfully may thus not always affect the subsequent migration and non-breeding distribution (Bogdanova et al. 2017).

4. CONSEQUENCES OF MIGRATION STRATEGIES FOR CONTAMINANT BURDENS

Exposure to and impacts of contaminants has been recognized as a health concern for wildlife for several decades (e.g. Letcher et al. 2010, AMAP 2018, Dietz et al. 2019). Seabirds are near the apex of most marine food chains and may accumulate high concentrations of contaminants through biomagnification (Bustnes et al. 2003, Leat et al. 2011). Such high levels of contaminants may affect breeding and survival of individuals and ultimately the dynamics of the population in some species (e.g. Erikstad et al. 2013). Seabirds are mainly exposed to contaminants through their food, and contaminant levels are thus varying according to diet and location (e.g. Leat et al. 2019).

Concentrations of contaminants can be highly variable within or between populations, and a large sample size of tracked birds may be required to detect differences among seabirds wintering in different

areas. Although not specifically designed for contaminant studies, SEATRACK offers a suitable platform with which to study the origin of contaminants in collaboration with other programmes, e.g. ARCTOX (https://arctox.cnrs.fr/en/home/) that addresses mercury (Hg) contamination in Arctic marine food webs using seabirds as bio-indicators. The contribution from Albert et al. (2021b in this Theme Section) stems from this collaboration. Hg is a highly toxic pollutant for humans and wildlife, causing severe health impairments, even at low concentrations (e.g. Dietz et al. 2019). Although naturally occurring in the environment, anthropogenic activities have increased Hg concentrations since the industrial revolution (UNEP 2019). Among marine apex predators, seabirds show some of the highest Hg concentrations (Atwell et al. 1998), with reported deleterious effects on behaviour, physiology and reproduction (e.g. Tartu et al. 2015). Understanding the relationship between seabird distribution and Hg contamination is therefore important for the conservation of these species.

By analyzing Hg concentrations in blood and feathers and combining these results with data on bird movement and wintering areas, Fort et al. (2014) found that little auks breeding in Greenland were ~3.5 times more contaminated in the non-breeding

Table 3. Importance of the non-breeding season in driving North Atlantic seabird demography, based on studies focusing specifically on seabird non-breeding distribution (for detailed study results see Table S2 in the Supplement). NAO: North Atlantic Oscillation, GLS: Global Location Sensor, PTT: Platform Transmitter Terminal, SST: sea surface temperature, SOI: Southern Oscillation Index, ENSO: El Niño Southern Oscillation, CORT: corticosterone. Parameter effects are indicated in brackets: (+) significantly positive, (−) significantly negative, (ns) non-significant. (s): compared groups differed significantly. Several signs together represent the effects observed in different populations or on different life-history traits

Species	Country	Life-history trait
Link between survival and winter environmental conditions		
Atlantic puffin	Norway, UK	Survival
Black-legged kittiwake	Norway	Survival
Brünnich's guillemot	Norway	Survival
Common eider	Canada, Norway	Survival
Common guillemot	UK	Survival
	UK	Survival, recruitment
Common tern	Germany	Survival, recruitment
Cory's shearwater	Spain	Survival
	Portugal	Survival
European storm petrel	Spain, France	Survival
Sabine's gull	Canada	Survival
Variation in survival as a function of the migration strategy		
Atlantic puffin	UK	Survival
	Norway, UK	Survival
Common guillemot	UK	Survival
Little auk	Norway	Survival
Northern gannet	Canada	Survival
	UK	Survival
Variation in breeding parameters as a function of winter strategy		
Atlantic puffin	UK	Breeding phenology, breeding success
	Iceland, UK, Norway	Breeding success[d]
	UK	Breeding phenology, breeding success
Black-legged kittiwake	UK, Iceland, Norway	Breeding success
Cory's shearwater	Portugal	Breeding success
Great cormorant	Denmark	Timing of arrival, fledging production, lifetime reproductive success
Little auk	Norway	Breeding phenology, breeding success
Manx shearwater	UK	Breeding phenology, breeding success, egg/chick size
Northern gannet	Canada	Breeding phenology[e], breeding success

[a]Based on geolocator data from another study; [b]Comparison among years (changes in winter distribution associated with changes in mean survival); [c]Test of the prediction that similar winter distribution should lead to synchronous survival interannual fluctuations; [d]Average productivity at the colony level; [e]Timing of arrival at the colony (not breeding phenology per se)

period than in the breeding period, and that Hg accumulated during the winter period was negatively related to egg size the following breeding season. This is one of few studies investigating effects of contamination on breeding parameters in relation to non-breeding distribution. The pattern with winter Hg concentrations remaining consistently higher than in summer has been confirmed by other studies and for other migrating alcid species (Fort et al. 2016, Renedo et al. 2020, Albert et al. 2021a).

Fort et al. (2016) examined inter-annual changes in mercury (Hg) contamination in little auks and their zooplankton prey in East Greenland and found an increasing trend in summer contamination (3.4 % per year over the 8 yr period, 2006–2014), whereas the winter exposure to Hg decreased over the same period. Renedo et al. (2020) investigated Hg concentrations in little auks from 5 Atlantic Arctic breeding colonies and found a consistent latitudinal pattern with birds from northern Arctic regions (northern Barents Sea) exposed to lower Hg concentrations compared to those from more southern regions (Labrador Sea).

In a study based on 5 species of seabirds from 17 breeding colonies distributed from Iceland to Russia, Albert et al. (2021b) found that individuals with high fidelity to a wintering ground had more similar Hg concentrations between years than individuals with low fidelity, suggesting an effect of their migratory strategy on Hg contamination. These results confirm the spatial differences in Hg concentration throughout the North Atlantic Arctic with an east to west increase in Hg concentrations (Provencher et al. 2014, AMAP 2018, Albert et al. 2019).

Table 3 (continued)

Parameters tested	Method to assess non-breeding distribution or activity	Reference
Extratropical cyclones (+/−), NAO (−)	GLS	Reiertsen et al. (2021)
Prey availability (+)	GLS and PTT	Reiertsen et al. (2014)
Subpolar gyre (+), NAO (+), SST (ns)	GLS[a]	Fluhr et al. (2017)
Extratropical cyclones (−)	GLS, PTT	Guéry et al. (2019)
NAO (−), SST (ns)	Band recoveries	Votier et al. (2005)
SST (−)	Band recoveries	Votier et al. (2008)
Primary productivity (+), NAO (ns), SOI (ns), fish abundance (ns)	GLS[a] and band recoveries	Szostek & Becker (2015)
SOI (−), NAO (ns), hurricanes (ns)	GLS[a]	Genovart et al. (2013)
SOI (−), SST (−)	GLS	Ramos et al. (2012)
Western Mediterranean Oscillation Index (−/ns), St. Helena index (−/ns), ENSO (−/ns), SOI (ns), Multivariate Enso Index (ns), NAO (ns)	Band recoveries and resightings	Matović et al. (2017)
Tropical-Northern hemisphere pattern (−), NAO (ns), SOI (ns)	GLS	Fife et al. (2018)
Winter distribution[b] (ns)	GLS	Harris et al. (2013)
Synchrony[c] (s)		Reiertsen et al. (2021)
Synchrony[c] (s)		Reynolds et al. (2011)
Synchrony[c] (ns)	GLS	Descamps et al. (2021)
Activity as a function of migration strategy (ns)	GLS	Pelletier et al. (2020)
Sex effect (on winter distribution and survival) (s)	GLS	Deakin et al. (2019)
Winter distribution (s/ns)	GLS	Fayet et al. (2016a)
Migration distance (−), wintering latitude (−)	GLS	Fayet et al. (2017a)
Similarity in partner migration route (−/+), winter foraging effort (−)	GLS	Fayet et al. (2017b)
Non-breeding distribution (ns)	GLS	Bogdanova et al. (2017)
CORT (in winter feathers) (+)	GLS	Pérez et al. (2016)
Migration distance (−/ns)	Band resightings	Bregnballe et al. (2006)
Migration distance (ns)	GLS	Dufour et al. (2021)
Winter activity / migration timing (s)	GLS	Fayet et al. (2016b)
Activity (as a function of migration strategy) (ns)	GLS	Pelletier et al. (2020)

5. SEABIRD NON-BREEDING DISTRIBUTION AND MARINE SPATIAL PLANNING

5.1. Seabirds in marine spatial planning

Seabird populations are impacted by a multitude of anthropogenic stressors operating in various environments and at different scales (Dias et al. 2019). Predation by invasive and alien species and anthropogenic activities like hunting and trapping are widespread threats that mainly operate in the breeding colonies. Other important threats operate at sea, including extreme weather events (e.g. Reiertsen et al. 2021), by-catch in fisheries (Anderson et al. 2011, Žydelis et al. 2013, Bærum et al. 2019), direct competition with fisheries (Grémillet et al. 2018), chronic and accidental oil pollution (Dunnet 1982, Votier et al. 2005, Camphuysen 2010), habitat loss due to expanding marine industries and collision risk with offshore wind farms (Furness et al. 2013). Improving the conservation status of seabirds would therefore require several targeted management measures, operating at different scales and involving different economic sectors and different levels of governance (Dias et al. 2019).

For example, while the ultimate causes of food shortages related to climate change and overfishing need to be solved by institutions at the national or international level, spatially explicit marine stressors are often addressed by ecosystem-based marine spatial planning (MSP). MSP is a public process in which human activities are balanced and planned to achieve environmental, social and economic sustainability (Douvere 2008). Because MSP provides a framework for explicitly managing multiple human activities (White et al. 2012), it has been instrumental for implementing ecosystem-based management. Importantly, by balancing human activities and the need for protection of ecologically and biologically sensitive areas, MSP can foster improved ocean health and reduce the risk of unsustainable cumulative anthropogenic impacts on the marine environment (Douvere 2008, Collie et al. 2013).

Seabirds are sensitive to a range of spatially restricted marine human activities and, combined with poor conservation status, are thus highly relevant ecosystem components to consider in the MSP process. Moreover, as highly mobile and migratory marine top-predators, seabirds often congregate in areas of high biological productivity and diversity (e.g. Bost et al. 2009, Fauchald 2009), suggesting that their distribution could reflect important ecosystem properties (Sydeman et al. 2007). It has therefore been argued that seabirds and other marine top predators can serve as proxies for identifying areas of ecological significance (Block et al. 2011, Reisinger et al. 2018, Hindell et al. 2020), as well as priority sites for marine conservation (Lascelles et al. 2012).

5.2. Using tracking data to identify important biodiversity areas

Prioritizing marine areas for seabird conservation requires knowledge of at-sea distribution, habitat use and provenance (Dunnet 1982). Tracking data using GPS, PTT (Platform Transmitter Terminal) and light-level geolocators deployed on individual birds may resolve these issues and have accordingly become increasingly important sources of information in conservation and marine spatial planning (Lascelles et al. 2012, Harrison et al. 2018, Hays et al. 2019). Recently, seabird tracking data have been used in several studies to identify important bird and biodiversity areas (IBAs; Delord et al. 2014, Lascelles et al. 2016, Dias et al. 2017, Augé et al. 2018, Heerah et al. 2019, Requena et al. 2020, Davies et al. 2021). One marine IBA criterion, as defined by Birdlife International, is an area holding more than 1% of the global population of a congregatory seabird species (Lascelles et al. 2016). This straightforward definition is especially useful when identifying important at-sea areas for pelagic species breeding at a restricted number of breeding sites. To identify IBAs under this criterion from tracking data, Lascelles et al. (2016) suggested a method based on estimation of kernel densities. In short, kernel utility distribution (UD) is estimated for each individual track, and the 50% UD area is defined as the individual's 'core area'. The frequency of use is simply calculated by counting the number of overlapping core areas. Finally, to account for population size, the frequency of use is multiplied by the size of the breeding population. Lascelles et al. (2016) suggested a simple test to address the representativeness of the sample for a wider population, and a standardized approach to choose the smoothing parameter for the kernel estimation.

Marine IBAs are, among other factors, used as input to identify ecologically or biologically significant marine areas (EBSAs). An EBSA is defined by 7 scientific criteria adopted by the Convention on Biological Diversity (CBD). While designation as an EBSA does not result in any formal legislative power that can be applied within the area, they are used by governmental bodies to inform MSP and to prioritize candidate areas for marine protected areas (MPAs;

Dunn et al. 2014). Since the concept of EBSAs was embraced by the CBD in 2010, EBSAs have been established around the world according to a formalized process (Johnson et al. 2018). Marine birds are mentioned in 63 % of the EBSA descriptions (Johnson et al. 2018), and more than 600 marine IBAs, mostly identified using tracking data, are included in EBSAs (Hays et al. 2019).

5.3. Estimating seabird habitats with species distribution models

While the use of kernel densities is useful in the quantification of the distribution of seabirds from a given breeding site, species distribution models (SDMs) represent a more general framework for estimating habitat use (Guisan & Thuiller 2005, Elith & Leathwick 2009). SDMs are empirical models that relate occurrence data (e.g. tracking data) to environmental predictors (Guisan & Zimmermann 2000). The relationship between the occurrences and the environment is estimated by various statistical methods, reflecting the species' environmental niche. If the niche is constant across space, the estimated relationship can be used to predict the spatial distribution of the species in areas where the environmental variables are known (Guisan & Thuiller 2005, Elith & Leathwick 2009). Accordingly, SDMs could be used to predict the distribution of seabirds from colonies not covered by tracking data, and could therefore be used to predict the regional distribution of the species (Wakefield et al. 2017, Hindell et al. 2020, Fauchald et al. 2021 in this Theme Section).

There are, however, several methodological and partly unresolved issues related to SDMs of tracking data (Aarts et al. 2008, Wakefield et al. 2017, Fauchald et al. 2021). First, to apply SDMs to presence-only data, the presences need to be modeled against the habitat 'available'. This can be approached in several ways. Wakefield et al. (2011) generated a null-model, in which the probability of locations being used (i.e. available habitat) declines with distance from the breeding colony (see also Aarts et al. 2008). Alternatively, Raymond et al. (2015), Reisinger et al. (2018), Péron et al. (2018) and Hindell et al. (2020) simulated random walks from the tagging location (e.g. the colony) to generate null models. Clearly, these methods could be useful in periods when the birds are strongly constrained by the location of the breeding colony. However, during the non-breeding period, when the birds are free to roam over larger areas (see Amélineau et al. 2021, Merkel et al. 2021b), the

available habitat needs to be defined less strictly (Fauchald et al. 2021). Accordingly, Fauchald et al. (2021) defined the available habitat as an area that included all recorded occurrences of the species in the dataset and included distance to colony as a covariate in the SDMs. The non-breeding habitat utilized by pelagic seabirds in the North Atlantic is highly complex and colony-specific (Amélineau et al. 2021, Fauchald et al. 2021, Merkel et al. 2021b). In line with this, Torres et al. (2015) found that colony-specific SDMs of the grey petrel *Procellaria cinerea* in the Southern Ocean performed well for each population but had poor transferability to an out-of-sample colony, suggesting that the populations had contrasting habitat preferences. Thus, the transferability of SDMs for pelagic seabirds seems to be low, and any model predicting the distribution of birds from colonies not covered by tracking data should assess the transferability of the model, or how well the model predicts the distribution of birds from other colonies (Torres et al. 2015, Péron et al. 2018, Fauchald et al. 2021). A multi-colony design with respect to tracking data is therefore needed.

A second problem related to SDMs based on tracking data are the spatial dependencies or serial autocorrelation, among positions of the same individual (Aarts et al. 2008). Spatial dependencies will increase the tendency of model overfitting and the detection of spurious relationships with environmental variables. Aarts et al. (2008) suggested an alleviation of this problem by including random terms that allow individual variability in response to environmental covariates (i.e. generalized additive mixed models, or GAMMs; Wood 2017). However, these models are computationally demanding and often have convergence problems in complex settings (Raymond et al. 2015, Fauchald et al. 2021). To reduce the effect of overfitting, Fauchald et al. (2021) suggested restricting the non-linear complexity of the models. It is, however, more important to test the predictive performance of the model using valid out-of-sample cross-validation and adequate performance indicators (Fauchald et al. 2021). Moreover, robust methods, such as cluster bootstraps (Fauchald et al. 2021), should be used to estimate the uncertainty of the predicted distribution.

Although a number of statistical modelling tools exists, spatial modelling of seabird habitat use is challenging and, as exemplified by Fauchald et al. (2021), there are several methodological issues that are vital to address in order to maximize the potential of tracking technology in marine spatial planning. Moreover, the complex and population-specific migra-

tion strategies possessed by North Atlantic seabirds highlight the importance of spatially explicit multi-colony studies such as the SEATRACK project when assessing important seabird areas during the non-breeding season.

6. CONCLUSIONS AND PERSPECTIVES

Over the last 20 yr, animal tracking has been revolutionized, providing a wealth of new information about seabird migration strategies and non-breeding distribution in the North Atlantic. This can mainly be ascribed to the development of light-level geolocators that now weigh only 0.5–3.5 g with a battery life of 0.5–5 yr and are widely used on small to large seabirds. Extraordinary variation among individuals, populations and species has been revealed in core aspects of migration strategies such as distance travelled, movement patterns, destinations, spread, mixing and consistency. Such variation in the migration and non-breeding distribution among individuals and populations can lead to variation in vital rates, population dynamics and contamination by pollutants.

The North Atlantic, and marine ecosystems in general, are under pressure from anthropogenic activities and global climate change, and seabird migration strategies and distributions are expected to change accordingly. It is therefore important to map and understand existing migration strategies to be able to reveal changes and understand the potential consequences. For this, large-scale tracking, with coordinated deployments in multiple colonies is essential. Wide collaboration across countries is probably the most crucial element and prerequisite to be able to move from a single colony/species approach to a more holistic approach to understand the non-breeding distribution of seabirds and support their conservation (Bernard et al. 2021).

The SEATRACK project has contributed to a substantial increase in our knowledge of seabird distribution outside the breeding season in temperate and arctic zones of the North Atlantic. At the same time, long-term population monitoring data exist from many colonies, species and countries. Linking this information to infer what drives seabird populations should now be given priority. The increasing availability of long-term demographic data represents an invaluable and necessary tool to improve our understanding of how the non-breeding environment affects individuals and populations, but important gaps clearly remain. In particular, very little is known about the at-sea distribution of immature birds from fledging to colony recruitment and about their survival and breeding probabilities. Studying their distribution at sea is extremely challenging, but previous studies in the North Atlantic, some using geolocator tags, have shown that it is possible (e.g. Ramos et al. 2019, Campioni et al. 2020). Further research should ideally focus on young age classes to understand how seabird populations are regulated. Assessing the potential individual variation in the environment–demography relationship is also a priority. Such individual variation may depend on many factors (e.g. sex, age) and may strongly affect the dynamics of a population in a changing environment (Vindenes & Langangen 2015). However, whether environmental effects on individual survival or reproduction are mediated by individual variation in their at-sea distribution remains virtually unknown. Data and methods now exist to answer these questions, and such studies should become a priority. Likewise, determining the mechanisms (energetics, physiology) linking distribution and habitat use to body condition, breeding probability, breeding success and survival of individuals should be given priority, given its importance for understanding population dynamics (Crossin et al. 2014).

According to the Ocean Panel (Stuchtey et al. 2020, p. v) the 'ocean health is more at risk than we thought, because different pressures add up and contribute to rapid and unpredictable changes in ocean ecosystems. […] We need a comprehensive approach to sustainably manage 100 percent of the ocean'. Sustainable management of the oceans is necessary to solve our main, global challenges related to biodiversity, climate change and human food security (Sala et al. 2021). Marine protection (e.g. through MPAs) is regarded as an effective tool for restoring marine biodiversity and ecosystem services (Worm et al. 2006, Sala & Giakoumi 2018, Sala et al. 2021). At present less than 3% of the oceans are highly protected (based on data from the Marine Conservation Institute: http://mpatlas.org). Traditionally, site protection is a slow and demanding process, also with respect to necessary identification, documentation and delineation. In a rapidly and unpredictably changing environment where the valued ecosystem components are relocating fast, the need for effective indicators is critical. By informing the necessary processes of sustainable marine planning and utilization, approaches like SEATRACK are important tools not only to safeguard healthy seabird communities, but also improve (global) ocean health.

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