Ocean-wide drivers of migration strategies and their influence on population breeding performance in a declining seabird

Annette L. Fayet1*,1, Robin Freeman2, Tycho Anker-Nilssen3, Antony Diamond4, Kjell E. Erikstad5,6, Dave Fifield1, Michelle G. Fitzsimmons6, Erpur S. Hansen7, Mike P. Harris10, Mark Jessopp11, Amy-Lee Kouwenberg7, Steve Kress12, Stephen Mowar2, Chris M. Perrins1, Aivar Petersen13, Ib K. Petersen14, Tone K. Reiertsen6, Gregory J. Robertson7, Paula Shannon12, Ingvar A. Sigurdsson9, Akiko Shoji15, Sarah Wanless10 & Tim Guilford1

1 Department of Zoology, University of Oxford, Radcliffe Observatory Quarter, Woodstock Road, Oxford, OX2 6GG, UK
2 Institute of Zoology, Zoological Society of London, Regent’s Park, London NW1 4RY, UK
3 Norwegian Institute for Nature Research, P.O. Box 5685 Torgard, NO-7485 Trondheim, Norway
4 Atlantic Laboratory for Avian Research, University of New Brunswick, PO Box 4400, Fredericton, NB E3B 5A3, Canada
5 Norwegian Institute for Nature Research, Fram Centre, P.O. Box 6606 Langnes, NO-9296 Tromsø, Norway
6 Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, NO-7491, Trondheim, Norway
7 Environment and Climate Change Canada, 6 Bruce Street, Mount Pearl, NL A1N 4T3, Canada
8 Memorial University of Newfoundland, St John’s, NL A1B 3X7, Canada
9 South Iceland Nature Research Centre, Strandvegur 50, IS-900 Vestmannaeyjar, Iceland
10 Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK
11 MaREI Centre, Environmental Research Institute, University College Cork, Haulbowline Rd, Ringaskiddy, Co. Cork P43 C573, Ireland
12 National Audubon Society Seabird Restoration Program, 12 Audubon Road, Bremen, ME 04551, US
13 Brautarland 2, 108 Reykjavik, Iceland
14 Department of Bioscience, Aarhus University, Grenaavej 14, DK-8410 Roende, Denmark
15 Department of Fisheries Sciences, Hokkaido University, 3-1-1, Minato-cho, Hakodate, Hokkaido 041-8611, Japan

*Corresponding author: Annette L. Fayet, annette.fayet@gmail.com
Lead contact: Annette L. Fayet

Keywords: Atlantic puffin, competition, density-dependence, migratory connectivity, migration, seabirds, seasonal interactions

This is a pre-copyedited, author-produced PDF of an article accepted for publication in the journal Seabird following peer review. The version of record can be found here:


Summary

Which factors shape animals’ migration movements across large geographical scales, how different migratory strategies emerge between populations, and how these may affect population dynamics, are central questions in the field of animal migration [1], which only large-scale studies of migration patterns across a species’ range can answer [2]. To address these questions we track the migration of 270 Atlantic puffins *Fratercula arctica*, a red-listed, declining seabird, across their entire breeding range. We investigate the role of demographic, geographical, and environmental variables in driving spatial and behavioural differences on an ocean-basin scale, by measuring puffins’ among-colony differences in migratory routes and day-to-day behaviour (estimated with individual daily activity budgets and energy expenditure). We show that competition and local winter resource availability are important drivers of migratory movements, with birds from larger colonies or with poorer local winter conditions migrating further and visiting less productive waters; this in turn led to differences in flight activity and energy expenditure. Other behavioural differences emerge with latitude, with foraging effort and energy expenditure increasing when birds winter further north in colder waters. Importantly, these ocean-wide migration patterns can ultimately be linked with breeding performance: colony productivity is negatively associated with wintering latitude, population size and migration distance, which demonstrates the cost of competition and migration on future breeding, and the link between non-breeding and breeding periods. Our results help understand the drivers of animal migration and have important implications for population dynamics and the conservation of migratory species.
The drivers of animal migration across large geographical scales are poorly understood. Tracking studies have started to reveal the diversity of long-distance migration strategies, and the need to broaden the usual definition - a long return journey to a specific overwintering destination following the breeding season [3] - to encompass a larger range of migration patterns, including journeys to a single [4] or multiple [5,6] areas, sometimes using various routes to get there [7]. Studies examining species’ migration patterns across multiple populations have increased, but few are sufficiently large-scale to reveal the migration landscape of entire species, and those which are remain largely descriptive [2,8]. Therefore our understanding of which factors shape species’ migration movements, how different migration strategies emerge between populations, and whether these affect population dynamics, remains poor [1]. Potential drivers of migration include competition, leading to density-dependent migratory distance (animals from large populations migrating further [9]) or quality-dependent migratory distance (sub-dominant, low quality individuals migrating further [10]), as well as winter resource availability close to the breeding grounds (animals in low quality habitat are more likely to migrate [11]). Differences could have a genetic basis, resulting in closely-related colonies following similar migration patterns [12]. Whether such mechanisms drive intraspecific differential migratory strategies across large scales, and whether these may affect populations’ fitness, is unknown. These questions are particularly important for species with high migratory connectivity, where different populations migrate to distinct areas [13], as they could help understand how different populations may be under different selective pressures due to migratory differences, as shown in invertebrates [14], fish [15] and birds [16]. This could also have important implications for conservation by making specific species or populations more vulnerable to changes in their winter habitat [17,18]. Breeding and migration are linked throughout annual cycles [19], and fitness differences between populations or individuals migrating to different destinations have been found in multiple species [20-22]. Determining how differences in migration strategies can shape fitness landscapes across multiple populations and perhaps even across an entire species’ range is therefore paramount to understanding migratory species’ population dynamics.

We address these questions in an unprecedented large-scale and in-depth study of the migration strategies of a long-distance migrant, the Atlantic puffin *Fratercula arctica*, across its entire range. Puffins around the
British Isles show considerable variation in migration strategy [23-25], and there is evidence from a single-colony study that breeding success varies among migratory routes [26]. Whether this diversity of migration strategies exists across the species’ range, and whether it has fitness consequences, are particularly important questions to answer, because some puffin populations (but not all) have dramatically declined in the last few decades [27-29], and the species is now endangered in Europe [30]. This apparent variability in migratory strategies and population trends among populations makes puffins an ideal species to investigate species-wide drivers of migration and the potential fitness consequences of different migration strategies. We track the migration of 270 adult puffins from 13 populations covering all major breeding grounds across the North Atlantic, including novel data from 12 populations in Canada, Iceland, Ireland, Norway, UK and USA. We combine spatial, behavioural, and environmental data to: (i) determine puffins’ full non-breeding distribution, their migratory connectivity between colonies, and assess spatial and behavioural differences between colonies; (ii) investigate ocean-wide migration strategies and the role of geographical, environmental and demographic variables on shaping these spatial and behavioural patterns; (iii) test the potential consequences of different migration strategies on colony productivity.

Distributions differed substantially between colonies (Figure 1, Figure S1). No colony was totally spatially segregated; all 90% occupancy kernels overlapped with 2-4 other colonies (Table S2), but overlap decreased with distance between colonies (LM, \( n=28, F_{1,26}=11.45, P=0.002 \)). Wintering hotspots were found around and south of Ireland, south west of Iceland, at the entrance of the Labrador Sea and near the Charlie-Gibbs Fracture Zone in the mid-North Atlantic (Figure 1c). Segregation was high between core utilisation areas (50% kernels), most colonies overlapping by <3% (Table S2). Most birds wintered in multiple locations and so distributions varied throughout the winter (Figure S1). Colonies differed in the total distance covered overwinter, with birds from some colonies covering thousands of km more than others (LMM, \( n=215, \chi^2=80.5, P<0.001 \); Table 1; Table S3), and in the birds’ average distance from the colony, ranging from <250km to >1,700km (\( n=215, \chi^2=261.8, P<0.001 \); Table 1; Table S4). These spatial differences led birds from different colonies to experience different environmental conditions overwinter (Table 1), both in terms of temperature and water productivity (\( n=190, \text{SST}: \chi^2=301.3, P<0.001 \); chlorophyll-a: \( \chi^2=118.6, P<0.001 \)).

The SST experienced by puffins was bimodal, with peaks around 6 °C and 11 °C (Figure S2).
Colonies also differed behaviourally (Table 1), with different flight and foraging effort \( (n=162, \text{flight: } \chi^2=72.8, P<0.001; \text{foraging: } \chi^2=49.7, P<0.001) \). Exposure to different day lengths at different latitudes (Table 1, \( n=190, \chi^2=70.2, P<0.001 \)) presumably affected the opportunity to engage in flight and foraging (puffins do not dive at night [31]) and their intensity. To account for this we compared the proportion of daylight hours spent flying and foraging between colonies (“intensity”). Flight and foraging intensity differed between colonies \( (n=190, \text{sustained flight: } \chi^2=95.5, P<0.001; \text{foraging: } \chi^2=69.0, P<0.001) \). Sustained flight was the least frequent behaviour (0.6-4.9% of daylight hours) but varied greatly between colonies, with birds spending 17-102h in flight (5-29min/day). Puffins spent 15-35% of daylight hours foraging, or 385-753h in total (1.8-3.5h/day). Therefore all birds spent the majority of daylight hours sitting on the water. Daily and total energy expenditure varied significantly among colonies (DEE: \( n=190, \chi^2=367.4, P<0.001 \); total EE: \( n=168, \chi^2=252.5, P<0.001 \)).

We tested whether geographical (latitude), environmental (SST and chlorophyll-a) and demographic (population size) variables drive migratory behaviour. We found ocean-wide migration patterns, mainly driven by colony size and wintering latitude, and mediated by environmental factors (Figure 2a). A first key finding is that puffins from larger colonies, and where local winter conditions were poorer, migrated further (LM, \( n=12, R^2=0.63 \), colony size: p.e.=0.15±0.08, \( F_{1,9}=14.7, P=0.004 \); chlorophyll-a: p.e.=0.53±0.22, \( F_{1,9}=6.1, P=0.036 \), Figure S3), which supports competition as a driver of migration. These birds spent more time in flight (p.e.=0.03±0.01, \( F_{1,9}=6.7, R^2=0.36, P=0.029 \)) and consequently increased their DEE (p.e.=1.0±0.4, \( F_{1,9}=5.8, R^2=0.33, P=0.038 \)); interestingly they also visited waters with lower chlorophyll-a (p.e.=5.9e^{-4}±9.9e^{-5}, \( F_{1,10}=34.5, R^2=0.75, P<0.001 \), Figure 2b). Latitude, strongly linked with temperature, also drove ocean-wide migration patterns. Puffins wintering at higher latitudes spent more time foraging (p.e.=0.25±0.09, \( F_{1,9}=7.4, R^2=0.39, P=0.024 \)), experienced colder waters (p.e.=0.03±0.009, \( F_{1,10}=13.7, R^2=0.53, P=0.004 \)), and had higher DEE than birds wintering further south (p.e.=-32.9±6.9, \( F_{1,9}=22.9, R^2=0.69, P<0.001 \), Figure 2c). How far from the colony birds migrated was unrelated to latitude (p.e.=0.03±0.03, \( F_{1,10}=2.2, R^2=0.09, P=0.171 \)), so these two patterns occurred in parallel.

A second key finding is that these ocean-wide patterns were related to colony productivity. More specifically, colony productivity was best predicted by a combination of winter latitude, colony size, average
distance from the colony, and winter chlorophyll-a levels (overall additive model compared to the null model: LM, \( n=11 \), \( F_{4,6}=13.6 \), \( R^2=0.84 \), \( P=0.004 \), \( \Delta AIC=-17.4 \), Figure 3). In this model, all explanatory variables were negatively correlated with colony productivity but with only marginal significance for chlorophyll-a (latitude: residual p.e.=-1.8e^2±4.8e^{-3}, \( t_9=-3.7, P=0.009 \); colony size: residual p.e.=-5.8e^2±1.6e^{-7}, \( t_9=-3.6, P=0.011 \); distance from colony: residual p.e.=-2.8e^4±1.1e^{-4}, \( t_9=-2.6, P=0.039 \); chlorophyll-a: residual p.e.=-0.3±0.1, \( t_9=-2.3, P=0.061 \) – where residual p.e. represents the effect of a single predictor on the residual variation in productivity after taking into account the other three predictors). These relationships occurred together and not separately, therefore latitude, colony size and migration distance all explained a significant amount of variation in colony productivity not explained by the other three (see STAR Methods for details). In other words, high winter latitude, large colony size and long migration distance (and to a marginal extent, low ocean productivity at the wintering grounds) were all associated with low colony productivity.

**Discussion**

We investigated the role of environmental, geographical and demographic factors as large-scale drivers of migration strategies across a species’ range. We found that colony size, local winter resource availability, and latitude drive large-scale spatial and behavioural migratory patterns, and that these patterns are ultimately linked with colony breeding productivity.

The overall winter distribution, likely representative of the puffin world population, covers most of the winter range known from ringing recoveries [32], across the North Atlantic from the 30° parallel to north of the Arctic Circle. During breeding, puffins forage close to their colony [32] and our study populations should be completely segregated. This segregation stops during non-breeding, with some limited migratory connectivity evident, as distributions of all colonies overlap with one to three others. Some of the areas visited by multiple colonies are known hotspots for other marine species [7,33-36], most likely because of highly productive waters [37].

Migration routes varied strikingly between colonies, some birds migrating >1700 km away while others stayed within <250km from their colony. These complex patterns do not fit the well-known “leap-frog” or
“chain” migration patterns often observed in species breeding across a wide latitudinal range [3,38], and are unusual. Species often share one wintering site (European rollers *Coracias garrulus* [8]) or a few (black-legged kittiwakes *Rissa tridactyla* [2], Monarch butterflies *Danaus plexippus* [5], bobolinks *Dolichonyx oryzivorus* [39], with the exception of a few (mostly marine) species such as Atlantic cod *Gadus morhua* [40] and leatherback turtles *Dermochelys coriacea* [6]. The drivers of such complex migratory patterns are unclear. In cod, there is evidence for the role of quality-dependent competition, with only large, strong individuals going on long migrations; however industrial fishing seems to have changed the selection pressures on migratory distance [41]. There is evidence in puffins from the Celtic Sea that individuals taking the longest migration route to the Mediterranean Sea breed more successfully [26]. This however remains to be shown for other colonies.

Distance from the colony was unrelated to colony latitude, suggesting that all birds did not search for the same environmental conditions. In fact, puffins from different colonies experienced different day length, temperature and water productivity, which led to different behavioural patterns and energy expenditures. This may result different populations being under different selective pressures, as occurs in thrushes [16] or salmon [15]. We identified multiple ocean-wide patterns in migratory strategies, driven by three main variables. One was colony size, a good predictor of migration distance. Density-dependent competition is therefore likely to be an important driver of migration. Larger populations may deplete resources near colonies and lead birds to exploit more distant areas and spread more [42]. This is an adaptation of Ashmole’s hypothesis for migratory behaviour [9,43]. Supporting theoretical predictions, local winter resource availability also plays a role. Models of partial migration predict increasing migrants to residents ratios when the relative difference in habitat quality between breeding and wintering site increases [11,44]. Support for this hypothesis has been found in multiple taxa, including birds [45], mammals [46], and amphibians [47]. While most puffin populations seem to be fully migratory, our finding that individuals from colonies with poorer local winter water productivity migrate further implies a similar process. In other words, birds migrate further from the colony both when local habitat quality is poor and intra-specific competition (mediated by colony size) is high.
Birds migrating further spent more time in flight, leading to higher DEE (flight is costly in auks [48]). Puffins migrating to higher latitudes visited colder waters and, despite experiencing shorter days, spent more time foraging, which also resulted in higher DEE. Higher foraging effort at high latitudes may not reflect lower resource availability (we found no correlation between chlorophyll-a and SST) but increased calorific requirements, due to the larger mass of birds further north and lower temperatures requiring additional thermoregulation [49]. Therefore, we show that geographical and environmental parameters and demographics shape the wintering behaviour and energy expenditure of a migratory species at a population level across its entire range. A key result is that these ocean-wide patterns are linked with population productivity across the species’ range. Although qualitative, the first link between wintering area and breeding success at a similar scale was found in thick-billed murres *Uria lomvia*, with stable populations mostly wintering near Canada and declining populations mostly wintering east of Greenland [33]. Here we found three predictors of colony productivity: colony size, wintering latitude and migratory distance (and, to a lesser extent, water productivity at the wintering grounds). Larger colonies where birds migrated further, to higher latitudes and poorer waters, had lower productivity, which demonstrates a cost of migration at a species’ range level. These birds spent more time engaged in energy-demanding activities such as flight and foraging, experienced colder temperatures, and consequently had higher winter energy expenditure. Whilst only experimental studies can definitively identify causal processes, one consistent mechanism could be that because of increased energy expenditure overwinter birds may return to the colony in poorer condition, which is known to delay breeding and reduce breeding success in many species. Winter habitat quality affects arrival time at the breeding grounds, body condition, and subsequent breeding performance in many migratory terrestrial species [50]. In marine species, SST can affect subsequent breeding success in a colony [51,52]. We show that this is true across a much larger scale. Spring or summer environmental conditions have been linked to breeding performance in several seabirds, probably by affecting prey availability during chick-provisioning [27,53,54]. Reproductive performance is therefore likely to be affected by a combination of prey availability during breeding (itself affected by colony size through density-dependent competition), and adult body condition related to previous winter conditions. The negative relationship between colony size and productivity raises questions about the origin and maintenance of large colonies. The answer presumably relates to food availability near the colony during breeding [27]. While we cannot investigate changes in migratory paths, environmental conditions and breeding productivity over time with our current
dataset, our findings suggest that large puffin colonies may not be sustainable anymore, perhaps because of long-term changes in environmental conditions near the breeding [55] or wintering grounds [56], affecting both the birds’ ability to refuel in winter and feed their offspring in summer. This is also likely to be the case for other species which have undergone similar declines in large northern colonies [57].

Our study provides unprecedented insight into the spatial and behavioural migration patterns of an avian species. It reveals how competition, geographical and environmental parameters drive a species’ migratory strategies across its range, and how migration patterns are reflected in population-level breeding performance. This study starts to uncover these important relationships and warrants further research into the species-wide drivers and fitness consequences of migration, with important points such as the effect of migration strategies on survival and the consistency of these patterns over time waiting to be explored. Our findings highlight the need for, and benefits of, large-scale collaborative studies to help understand the mechanisms behind the development of animals’ migratory routes and determine which factors most influence breeding performance and population dynamics. Such knowledge is also invaluable to understand and tackle widespread population declines in migratory species, with marine species especially under threat by fisheries, pollution and climate change.

**Author Contributions**

ALF and TG conceived the study, all authors collected data, ALF, RF and GJR analysed the data. All authors critically discussed the results. ALF wrote the manuscript with the help of all authors.

**Acknowledgements**

We thank the many people who helped with fieldwork on all the different colonies, with special gratitude to Dave Boyle (Skomer), Francis Daunt (Isle of May), Jeremy Tornos and Tanguy Deville (Hornøya) and Stefanie Collar (Machias Seal Island). ALF is funded by a Browne Junior Research Fellowship at The Queen’s College (Oxford). AS is supported by a JSPS Fellowship for Young Scientists. This work was supported by Microsoft Research Cambridge, the Department of Zoology of Oxford University, the Mary
Griffiths Fund, the RSPB, the Wilson Ornithological Society, the Welsh Ornithological Society (Skomer), by

The Natural Environment Research Council and Scottish Natural Heritage (Isle of May), the Norwegian
Research Council (project 216547 to KEE) and the SEAPOP programme (Hornøya and Røst, Norway),
Science Foundation Ireland and the Zoological Society of London Good Gifts Programme (Ireland),
Canadian Wildlife Service, Environment and Climate Change Canada, New Brunswick Wildlife Trust Fund,
with logistic support by Canadian Wildlife Service and Canadian Coastguard (Machias Seal Island).

References


11


Figure 1. Winter distribution of Atlantic puffins across their range. (A) Density distribution of puffins from all study colonies across the non-breeding season, obtained by weighting occupancy kernels by colony size (colony or archipelago sizes are indicated with circles of different size). Italic names after each colony’s name represent the name used to describe the colony in the main text. The unit of the grey parallels and meridians is 5°. The blue parallels indicate the approximate latitudinal breeding range of puffins. (B) Occupancy kernels for each colony across the non-breeding season, with each colony in a different colour (the kernel for the Irish colony is contoured in green for clarity). (C) Overlap between the 90% occupancy kernels of 2 to 4 different colonies. On the lower panels, colonies are indicated with black squares. The light blue shade represents the approximate ice edge at its mid-winter level. See also Figure S1 and Table S2. (photo: A. Fayet).

Figure 2. Ocean-wide patterns of puffins’ migratory strategies. (A) Summary of the ocean-wide patterns of migratory strategies driven by colony size, winter latitude and environmental variables at the whole population level. Arrows indicate significant relationships between variables (see main text for statistics). (B-C) Graphical representations of some of the relationships from the summary figure (A), more specifically the association between (B) winter chlorophyll-a and distance from the colony and between (C) winter DEE and winter SST. Regression lines, 95% confidence intervals (grey areas), $R^2$ and $P$ values are obtained from linear models. See also Figure S3.

Figure 3. Relationship between ocean-wide patterns and colony productivity. Effect size plots for the model of colony productivity as a function of winter latitude, colony size, distance from colony and chlorophyll-a, obtained from the best model of colony productivity. Each plot represents the effect of a single predictor on the residual variation in colony productivity after the variation explained by the other three variables was taken into account. The slope of the relationship is represented by a black line, with the 95% confidence intervals in grey. All values are obtained from the LM of colony productivity. See also Figure S4.
Table 1. Spatial, behavioural and environmental characteristics of puffin migratory routes from different colonies. The “intensity” values of time represent the percentage of daylight hours spent engaged in a particular behaviour, while total time represents the number of hours spent in this behaviour over the whole non-breeding season (mean±SE). See also Figure S2, Table S3 and S4.
STAR Methods

Contact for Reagent and Resource Sharing

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Annette Fayet (annette.fayet@gmail.com).

Experimental Model and Subject Details

Between 2007 and 2015, adult Atlantic puffins Fratercula arctica were caught on 13 colonies across their breeding range (Table S1). Birds were caught at the nest (all colonies) or in a mist net (Røst only) during the chick-rearing period in June-July, between 2007 and 2015. Birds were ringed using a metal ring, and a geolocator was attached either to the metal ring or an additional plastic ring (models Mk13, Mk14, Mk18 - British Antarctic Survey, Mk4083, Mk4093 or Mk3005 – Biotrack, C65 – Migrate Technology, or LAT2900 - Lotek). Birds were recaptured in subsequent years using the same technique to remove or replace the device. All work was conducted after ethical approval from the appropriate organisation from each respective country. To avoid disturbance, handling was kept to a minimum. Recapture rate was high (>70% on average) and when it was possible to compare survival of manipulated and control birds no detectable difference was found [23,26].

Method Details

Study sites

Puffins breed across the North Atlantic, approximately between 42° and 80° latitudes and -70° and 65° longitudes. Our study colonies include all major breeding areas across this range (Figure 1a), except Svalbard (< 10,000 pairs, often inaccessible) and the Faroe Islands (~400,000 pairs). While colonies vary in size from a few hundred to several hundred thousand pairs, most are part of archipelagos and we used the total population of the archipelago as a measure of population size. Because the definition of archipelago can vary among archipelagos and sometime includes extremely distant islands, we only included population estimates from islands located within 100km of each study colony, well over the distance where puffins from
distinct colonies would be expected to overlap during breeding, as they are thought to forage within ~30km of the colony during breeding. A list of the archipelagos used is available in Table S1.

**Spatial data**

In total 270 migration tracks (including 240 complete ones) were collected, representing 270 different individuals (Table S1). Light data were decompressed and processed using the BASTrack software suite (British Antarctic Survey) and MatLab R2010b (MathWorks Inc.). Data were filtered using speed and equinox filters identical to those used in [26], and data corresponding to the breeding season were removed (15 March – 15 August – a wide window chosen to encompass breeding across all colonies). We calculated 2-day median positions for all tracks and filtered out those with high standard error (SE$_{\text{longitude}} > 150$ km, SE$_{\text{latitude}} > 150$ km) or unrealistic locations (longitude $> 65^\circ$ or $<-73^\circ$, latitude $<30^\circ$ or $>80^\circ$). After filtering the average latitudinal range used by birds was $3007\pm247$ km, and the average longitudinal range was $3108\pm435$ km (Table S1). The range was not simply proportional to the number of birds tracked from each colony (LMs, latitudinal range: p.e. = $0.2 \pm 0.2$, $t_6 = 1.4$, $P = 0.215$; longitudinal range: p.e. = $0.5 \pm 0.9$, $t_6 = 0.6$, $P = 0.576$); for example the latitudinal range of birds from the North Sea (55 birds) was ~2.5 smaller than the one of birds from the Icelandic colony of Stórhöfði (8 birds). Average winter latitude reflected colony latitude (LM, p.e.=$0.9\pm0.1$, $F_{1,6}=47.6$, $P < 0.001$). Spatial occupancy kernels were calculated with ArcGIS 10.0 (ESRI) and Geospatial Modelling Environment 0.7.2 (Spatial Ecology LLC) (parameters: bandwidth ~275km, resolution ~20km) and the overlap between colonies was calculated with the \{adehabitat\} package in R. We estimated distance from the colony as the great-circle distance between the colony and each position. To account for the flight around the Iberian Peninsula for birds visiting the Mediterranean Sea (puffins do not fly far over land), distance from the colony was calculated as the distance between the actual position and the Strait of Gibraltar, and added to the shortest distance between the Strait and the colony. A similar correction was applied to birds flying from the North Sea around the north of Scotland into the Atlantic. Daily average distance and total distance covered were calculated for each track by averaging or summing the great-circle distances between each 10-day median from 15 August to 15 March.

**Activity budgets and energy expenditure**
We estimated at-sea activity budgets using the same method as in [26], using salt-water immersion data collected by geolocators. Briefly, each 10-minute interval during daylight (defined as with light levels >15% of the maximum light level recorded by the geolocator) between mid-August and mid-March was allocated one of three categories: mostly (≥ 98%) dry, mostly (≥ 98%) wet and intermediate (> 2% dry and > 2% wet). These have been shown to represent 3 main classes of behaviour (sustained flight, sitting on the water, and foraging-related activity, respectively) by other studies using additional GPS, dive loggers and automated classification methods (e.g. Hidden Markov Models) in a shearwater species [58]. The 98% threshold-based classification leads to very similar results to automated classification [59]. For each behaviour two daily variables were calculated: the proportion of time spent in the behaviour per total amount of daylight available (flight or foraging “intensity”); and the total amount of time spent in this behaviour (flight or foraging “effort”). These daily measures were then averaged (proportions of time) or added (total amount of time) over the entire non-breeding period. On some occasions saltwater-immersion loggers stopped before birds returned to the colony, and so only tracks for which saltwater-immersion data were available for at least 70% of the non-breeding season were included in this analysis, and only complete or nearly-complete tracks (> 75% complete, adjusted to the total non-breeding duration) were used to calculate cumulative variables over the whole winter (by “winter” we mean the entire non-breeding season, as there was no obvious migration-wintering-migration pattern but rather multiple bouts of movements alternated with bouts of “stopover” throughout the whole non-breeding period). We estimated daily energy expenditure (DEE) with the same method as in [26]. Briefly, we used day-time and night-time activity budgets (night-time behaviour was classified into sitting on the water and sleep, with sleep periods identified by long dry bouts when birds tuck one leg under their wing) and DEE and allometric equations from physiological studies of free-living auks [48,60]. The birds’ mass used in the allometric equation was the average mass measured at each colony during breeding, using a sample of > 10 birds (Table S1). More details on the activity budget classification and the estimation of DEE can be found in [26]. As the 3 classes of behaviour are complementary (the 3 proportions adding to 1), we only included time in flight and foraging activity in our analysis to avoid using variables constrained by each other. We considered flight and foraging to be the most relevant variables on account of being more energy consuming, more directly related to energy intake, and potentially more likely to be related to overall body condition.
Environmental data

Sea-surface temperature (SST, °C) and chlorophyll-a concentrations (mg/m³, a proxy for ocean productivity) were extracted from the NASA OceanColor website using data from the MODIS Terra and Aqua satellites, using a spatial resolution of 50 km (~ the maximum resolution of geolocation data) and a temporal resolution of 8 days (to limit gaps in the data due to cloud cover), and were smoothed over a 350 km-grid (~ twice the average resolution of geolocation data). Each location from the dataset was assigned an SST and chlorophyll-a value. To test whether environmental conditions were potential drivers of at-sea behaviour and explain inter-colony differences in spatial and behavioural migratory strategies, each track was assigned an SST and chlorophyll-a value averaged over the whole track, and average values were calculated for each colony. To estimate local winter habitat quality near the colony, chlorophyll-a was extracted at regular 0.1° longitude and latitude intervals within a 250km radius around each colony (points on land were excluded) from September to February, on the year corresponding to the tracking period, and averaged for each colony.

Colony productivity

It was not possible to collect individual breeding success data of tracked birds at all colonies (birds were not always caught at their nest), and so colony productivity was used instead to allow consistency of measurements across colonies. Productivity was measured at all but one colony (only qualitative data were available for Ireland and so were not included, Table S1). Note that the productivity at Hornøya may have been affected by mink predation, which occurred concurrently with the tracking study. The methods were comparable across all colonies (see [26,53,61] for examples of published protocols) and are briefly described here. Each year a set number of burrows were observed at regular intervals during the breeding season to determine occupancy. Occupied burrows were checked later in the season to determine the proportion which hatched chicks, and later on the proportion of nests whose chick (i) had fledged or (ii) survived long enough to be very likely to fledge successfully (chick mortality is high in the first week but chicks which survive their first 2-3 weeks are very likely to fledge successfully). The observation methods varied slightly between colonies, and were done either by direct observation of the nest (by hand or with an infrared endoscope) or by repeated observations of puffin activity at the nest (e.g. regular 24h watches looking for parents bringing fish to the burrow, an unmistakable sign of chick provisioning). Colony productivity was calculated as the
average number of chicks fledged per occupied burrow at each colony (maximum one chick per nest per
year). In this study we averaged the productivity of each colony over the tracking period or as close to the
tracking period as possible, to reflect the productivity of the colony at the time the birds were tracked.

Quantification and Statistical Analysis

Some colonies were pooled for the spatial analyses because of small sample sizes, their proximity to others,
and the lack of major differences between tracks. The 4 Icelandic colonies (~ 300 km apart) were pooled as
one “Iceland” group, the two colonies from Maine and the colony from the Bay of Fundy (< 150 km apart)
were pooled as one “Gulf of Maine” group, resulting in 8 principal colonies. For readability, all colonies or
groups of colonies in the main text are called by the name of the body of water they represent (or, when not
possible, their country). The 8 principal colonies are therefore hereafter referred to as Barents Sea, Celtic
Sea, Gulf of Maine, Iceland, Ireland, Newfoundland, North Sea and Norwegian Sea (Figure 1a). When
investigating potential relationships between behaviour, latitude and environmental conditions, all colonies
were counted separately (n=12, with the two very close Maine colonies remaining pooled together) but
sample sizes vary depending on the variables included in the model (colony productivity is only available for
11 colonies, and immersion data for 10).

Linear Mixed-Effects Models (LMMs) including year as a random effect (\{lme4\} package in R) were used to
test for among-colony differences in spatial characteristics (total distance covered, average distance from the
colony), activity budgets (proportion of time and total amount of time spent in different behavioural states),
energy expenditure, and environmental conditions. For analyses including population size, the population
size of the entire archipelago was taken for colonies within an archipelago (Table S1). Although study year
varied between colonies, we did not include it in the models for lack of degrees of freedom and because
evidence suggests puffins are repeatable in their migration route [26] and large scale environmental changes
usually take place over longer periods, hence our metrics are unlikely to vary significantly over the duration
of our study. Posthoc pairwise comparisons between colonies were realised with \{lsmeans\} in R (with
adjustment for multiple comparisons). Relationships between at-sea behaviour and environmental factors
were tested with LMMs with year and colony as random effects. Linear models (LM) were used in R to test
for relationships between behaviour, latitude and environmental conditions across colonies. To determine
whether ocean-wide patterns could help predict colony productivity, we used Akaike Information Criteria and $R^2$ to select the best model predicting colony productivity (using additive models without interaction between variables given our limited degrees of freedom). Data were log-, arcsin- or sqrt-transformed to meet parametric assumptions when necessary (residuals were checked for normality). Means expressed in the text are ±SE unless stated otherwise. Significance was defined at the 5% level. All statistical details for each test (e.g. sample size, parameter estimates, degrees of freedom, test statistics, P-value) can be found in the Results section. Note that in the first part of the Results the sample size $n$ refers to the number of birds (or migration tracks), while in the second part, when we investigate ocean-wide patterns, it refers to the number of populations.

Model of colony productivity

Colony productivity was best predicted by four variables, and covariance analyses were run on these variables. Out of the four predictors of colony productivity (winter latitude, colony size, distance from colony and chlorophyll-a), chlorophyll-a decreased with distance from the colony ($p.e.=-5.9e^{-4}±9.9e^{-5}$, $F_{1,10}=34.5$, $R^2=0.75$, $P<0.001$) which itself increased with colony size ($p.e.=0.26±0.08$, $F_{1,10}=9.8$, $R^2=0.44$, $P=0.011$). All other predictors were not correlated with each other. Chlorophyll-a was not correlated with winter latitude ($p.e.=-0.02±0.02$, $F_{1,10}=2.4$, $R^2=0.11$, $P=0.150$) or with colony size ($p.e.=-7.3e^{-7}±5.5e^{-7}$, $F_{1,10}=1.7$, $R^2=0.06$, $P=0.216$). Colony size was not correlated with winter latitude ($p.e.=4295±10128$, $F_{1,1}=0.2$, $R^2=0.08$, $P=0.681$), and distance from the colony was not correlated with winter latitude ($p.e.=0.03±0.03$, $F_{1,10}=2.2$, $R^2=0.09$, $P=0.171$). Despite the covariance between chlorophyll-a and migration distance, and migration distance and colony size, the relationships between these variables and colony productivity still held after the variation explained by their covariates was taken into account (as illustrated on Figure 3). In other words, the effect of each of the four predictors on colony productivity remains significant (or marginally significant, for chlorophyll-a), even after the variation explained by the other three variables has been taken into account. Therefore, these relationships are not artefacts of the covariance between explanatory variables. For example, this means that migration distance explains a significant amount of variation in colony productivity once the variation caused by colony size has been removed. Therefore at least some variation in productivity must be controlled by migration distance independently of a direct effect of colony size. Our findings suggest that long migration movements arise from both higher density-
dependent competition (driven by larger colony size) and from poor local conditions. These long movements, which we show result in higher energy expenditure, combined with the relatively lower resource availability at the wintering grounds, may lead birds to return to the colony in reduced body condition, which may affect their chance to breed early or rear a chick successfully. These processes do not exclude additional effects on productivity related to colony size during breeding.