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Diversity and Distributions

Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale

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ABSTRACT

Aim An understanding of the non-breeding distribution and ecology of migratory species is necessary for successful conservation. Many seabirds spend the non-breeding season far from land, and information on their distribution during this time is very limited. The black-legged kittiwake, *Rissa tridactyla*, is a widespread and numerous seabird in the North Atlantic and Pacific, but breeding populations throughout the Atlantic range have declined recently. To help understand the reasons for the declines, we tracked adults from colonies throughout the Atlantic range over the non-breeding season using light-based geolocation.

Location North Atlantic.

Methods Geolocation data loggers were deployed on breeding kittiwakes from 19 colonies in 2008 and 2009 and retrieved in 2009 and 2010. Data from 236 loggers were processed and plotted using GIS. Size and composition of wintering populations were estimated using information on breeding population size.

Results Most tracked birds spent the winter in the West Atlantic, between Newfoundland and the Mid-Atlantic Ridge, including in offshore, deep-water areas. Some birds (mainly local breeders) wintered in the North Sea and west of the British Isles. There was a large overlap in winter distributions of birds from different colonies, and colonies closer to each other showed larger overlap. We estimated that 80% of the 4.5 million adult kittiwakes in the Atlantic wintered west of the Mid-Atlantic Ridge, with only birds from Ireland and western Britain staying mainly on the European side.

Main conclusions The high degree of mixing in winter of kittiwakes breeding in various parts of the Atlantic range implies that the overall population could be sensitive to potentially deteriorating environmental conditions in the West Atlantic, e.g. owing to lack of food or pollution. Our approach to estimating the size and composition of wintering populations should contribute to improved management of birds faced with such challenges.

Keywords
Black-legged kittiwake, geolocation, migration, non-breeding ecology, North Atlantic, *Rissa tridactyla*.

INTRODUCTION

Understanding the non-breeding ecology of migratory species is important since individuals often move long distances to avoid seasonal deterioration in weather and food availability around breeding sites and may face energetically challenging conditions during the non-breeding period (Newton, 2008). As a consequence, peak mortality often occurs in winter (e.g. Harris & Wanless, 1996), with important implications for population dynamics (Sillett *et al.*, 2000). There have been few coordinated studies of the non-breeding distribution of different populations across a species' breeding range despite the important role that variability among populations might play in determining local demographic processes (Reynolds *et al.*, 2011). Conditions experienced during the non-breeding period may have long-term (carry-over) effects on breeding performance (Harrison *et al.*, 2011), and this may affect population growth rate. Consequently, there are important management implications: where individuals from different breeding areas share wintering grounds, vulnerability to local anthropogenic impacts may increase (Esler, 2000). In response, conservation efforts can be targeted at areas where the majority of the population, or particularly vulnerable segments, congregate. It is thus important to know whether populations share non-breeding areas and to what extent population dynamics are linked to conditions in these areas.

Many species of seabirds spend most of the year away from their breeding sites, often far from land. Distances moved vary widely, with some species performing some of the longest known annual migrations of any animal (Shaffer *et al.*, 2006; Egevang *et al.*, 2010). Consequently, the distribution and ecology of non-breeding seabirds are poorly known, creating important gaps in our understanding of their biology. For example, most mortality of adult seabirds probably occurs outside the breeding season and away from the colonies (e.g. Harris *et al.*, 2007), making environmental conditions during the non-breeding season important drivers of demographic variation and population dynamics (e.g. Barbraud & Weimerskirch, 2003; Bertram & Harfenist, 2005; Grosbois & Thompson, 2005). However, to identify specific environmental drivers, more information on non-breeding ecology is needed, particularly for threatened or declining species.

In the past, information about non-breeding distributions of seabirds has come from two sources: recoveries of ringed birds and at-sea surveys. While recoveries have provided much useful information, they suffer from pronounced biases owing to spatial variation in how likely birds are to die and be recovered (Wernham & Siriwardena, 2002). At-sea surveys are useful for mapping non-breeding distributions on the continental shelf (Certain *et al.*, 2007; Zipkin *et al.*, 2010), but generally do not provide information on the breeding origin and demographic status of the birds observed. For more oceanic areas with low bird densities, it is logistically difficult and expensive to collect sufficient survey data for robust mapping of distributions.

Recent technological advances have allowed researchers to follow individuals throughout the year. Satellite [platform terminal transmitter (PTT)] tags have provided much information on offshore distribution of seabirds, but size and cost have limited their application to relatively large species (e.g. albatrosses, BirdLife International, 2004), and deployment periods have been relatively short. Light-based geolocation provides a lighter, cheaper, but lower-precision alternative and has recently become a widely used technology for mapping large-scale distributions and migration patterns of marine vertebrates, including seabirds (Wilson *et al.*, 1992; Weimerskirch & Wilson, 2000; Saunders *et al.*, 2011). Many studies have used geolocation to follow individuals from one or a few study sites (e.g. Daunt *et al.*, 2006), but the wide geographical distribution of some species calls for large-scale, spatially integrated surveys to better assess the variability and extent of the non-breeding distribution of whole (meta)populations. The geolocation method is now sufficiently low cost to allow the deployment of a large number of devices at a range-wide scale.

Here, we use geolocator data from 18 colonies of the black-legged kittiwake (hereafter kittiwake), *Rissa tridactyla*, throughout the species' North Atlantic range to map the distribution during the non-breeding season and investigate the extent to which individuals from multiple breeding populations share wintering areas. The kittiwake is a relatively small (350–400 g) colonial gull, which outside the breeding season occurs primarily offshore (Hatch *et al.*, 2009). The Atlantic breeding population is large (estimated 2.5–3 million pairs, Heubeck, 2004), but in many areas the species has experienced food shortages, poor breeding seasons and widespread population declines in recent decades, and it is red-listed in several countries including Norway, the Faroes and Greenland (Frederiksen, 2010). The underlying reasons for these declines are only partially understood, but at least in some areas, there appears to be a link to increasing sea temperatures (Frederiksen *et al.*, 2004). The widespread nature of the declines may indicate common causation linked to shared wintering areas, or alternatively widespread low food availability linked to large-scale climate patterns in summer or winter. Ringing recoveries suggest some sharing of wintering areas, as the majority of kittiwakes ringed at colonies in the UK, Denmark and Norway have been recovered during winter in essentially the same two regions: around the British Isles (including the North Sea and Bay of Biscay) and around the Labrador Sea, particularly in SW Greenland and Newfoundland (Coulson, 2002; Bakken *et al.*, 2003; Bønløkke *et al.*, 2006). Recent information from regional studies using geolocation supports this picture (Bogdanova *et al.*, 2011; González-Solís *et al.*, 2011). Birds ringed in the Faroes, Iceland, Greenland and Canada have also been recovered in the Labrador Sea area in winter, but only rarely in Europe (Petersen, 1998; Lyngs, 2003; Gaston *et al.*, 2008; S. Hammer, pers. comm.). However, the at-sea distribution of birds from these areas and the overlap between populations are essentially unknown. The North Atlantic is affected by many, regionally variable threats to

seabirds (e.g. longline, trawl and gillnet fisheries, shipping, hydrocarbon extraction). To improve conservation efforts for kittiwakes, we need to understand better where they spend the non-breeding season and hence their vulnerability to regional anthropogenic impacts. Our main aims are as follows: (1) to document the non-breeding distribution of adult kittiwakes breeding in the Atlantic, (2) to quantify the overlap in wintering areas between birds of different breeding origin and (3) to estimate the composition (in terms of breeding origin) of wintering populations in various parts of their range.

METHODS

Study species and field methods

In the North Atlantic, kittiwakes breed from the high Arctic (c. 80° N) to mid-temperate latitudes (c. 40–45° N) on both sides of the ocean, often in large colonies. Outside the breeding season, they occur throughout the Atlantic south to Morocco, the Azores and Florida (Coulson, 2002 and references therein; Hatch et al., 2009).

Since the kittiwake is studied at many sites in the Atlantic (Frederiksen et al., 2005), it was possible to design a large-scale study involving colonies well dispersed throughout the breeding range (Figs 1a & 2a, Table 1). The main study involved geolocators deployed in 2009 and retrieved in 2010, but at some colonies, loggers were also deployed in 2008 and retrieved in 2009 and 2010 (Table 1). At all sites, breeding adult kittiwakes were captured on the nest using noose poles and equipped with British Antarctic Survey (BAS) Mk14 (2008) and Mk13 (2009) geolocators (20 × 9 × 6.5 mm, 1.8 g; British Antarctic Survey, Cambridge, UK) mounted on a plastic leg ring. At one study colony (Prince Leopold Island), Lotek LAT2500 loggers (35 × 8 × 8 mm, 3.6 g; Lotek Wireless, Newmarket, ON, Canada) were deployed in 2008 and retrieved in 2009. Numbers of loggers deployed and retrieved at each colony are listed in Table 1. A previous study found no negative effect of geolocators on kittiwake breeding success or the probability of returning to the colony in the following year (Bogdanova et al., 2011).

Analytical methods

All data from BAS loggers were processed by one person (B.M.). Data processing involved evaluating the reliability of each recorded transition (sunset or sunrise) and converting these to noon and midnight geographical positions using the BASTRAK software package (Fox, 2010). Logger sensitivity was calibrated by examining positions of a subset of 15 individuals from five colonies south of the Arctic Circle for the post-breeding period (see Appendix S1 in Supporting Information). The smallest bias in latitude was obtained with a threshold light intensity of 10 and sun angle of −3°, and these settings were used for all loggers. Subsequently, data were filtered, removing unreliable positions from the breeding

season (with many shading events) and equinox periods, when the weak latitudinal trend in day length precludes reliable determination of latitude. Because the logger detects the sun below the horizon, the time of apparent equinox (as experienced by the logger) is shifted towards the winter solstice (Hill & Braun, 2001); for an angle of −3°, this shift is c. 8 days. Latitudes were unreliable for c. 3 weeks each side of apparent equinox, and we thus removed data for 8 September–20 October and 20 February–3 April. Positions were also unobtainable for periods when birds (mainly high-Arctic breeders) were in regions of constant daylight or occasionally constant darkness. Data from Lotek loggers were processed in LAT Viewer Studio (Lotek Wireless) using the template fit option (Ekstrom, 2004) and a filtering process as above, with equinox data removed for 18 September–4 October and 1 March–24 March. Lotek loggers only provide one (noon) geographical position per day.

Positions derived from geolocation have an average error of c. 185 km (Phillips et al., 2004), and to reduce the influence of outliers when calculating distances and allocating positions to areas of interest, we smoothed positions using a three-position moving average based on spherical trigonometry. Distances between successive smoothed positions, and distances from each position to the home colony, were calculated as great circle distances assuming a spherical Earth. Mapping was performed in ArcMap 10 (ESRI, Redlands, CA, USA). We mainly concentrated on identifying important areas in December, when birds were less mobile (mean distance between successive smoothed positions = 81 km vs. 99–125 km for other non-breeding months). Kernel densities and 50% kernel contours (representing core areas used) were estimated for each colony using raw noon positions and the Animal Movement extension (Hooge & Eichenlaub, 1997) to ArcView 3.1 (ESRI), with the appropriate degree of smoothing determined by least-squares cross validation. Areas of pairwise overlap zones between 50% colony kernel contours were calculated in ArcMap using an equal-area projection and scaled to proportions as $(2a_{overlap})/a_1 + a_2$, where a_1 and a_2 are the areas of the two respective kernel contours and $a_{overlap}$ is the area of overlap. Pairwise great circle intercolony at-sea distances were estimated in ENCARTA Interactive World Atlas 2000 (Microsoft Corporation, Redmond, WA, USA). The significance of the correlation between intercolony distances and pairwise kernel overlaps was tested using a Mantel test with 100,000 permutations (Legendre & Legendre, 1998).

To estimate the size and composition of the wintering populations of adult kittiwakes in various parts of the range in the 2009/10 winter, we first allocated all smoothed positions from December 2009 (December 2008 for Prince Leopold Island) to 'areas of interest' defined as follows. For coastal and shelf regions, we used large marine ecosystems (LMEs) (Sherman, 2006). Positions on land (< 5%) were considered erroneous and allocated to the nearest LME. For offshore regions of the North Atlantic with substantial numbers of positions, we defined latitude–longitude blocks
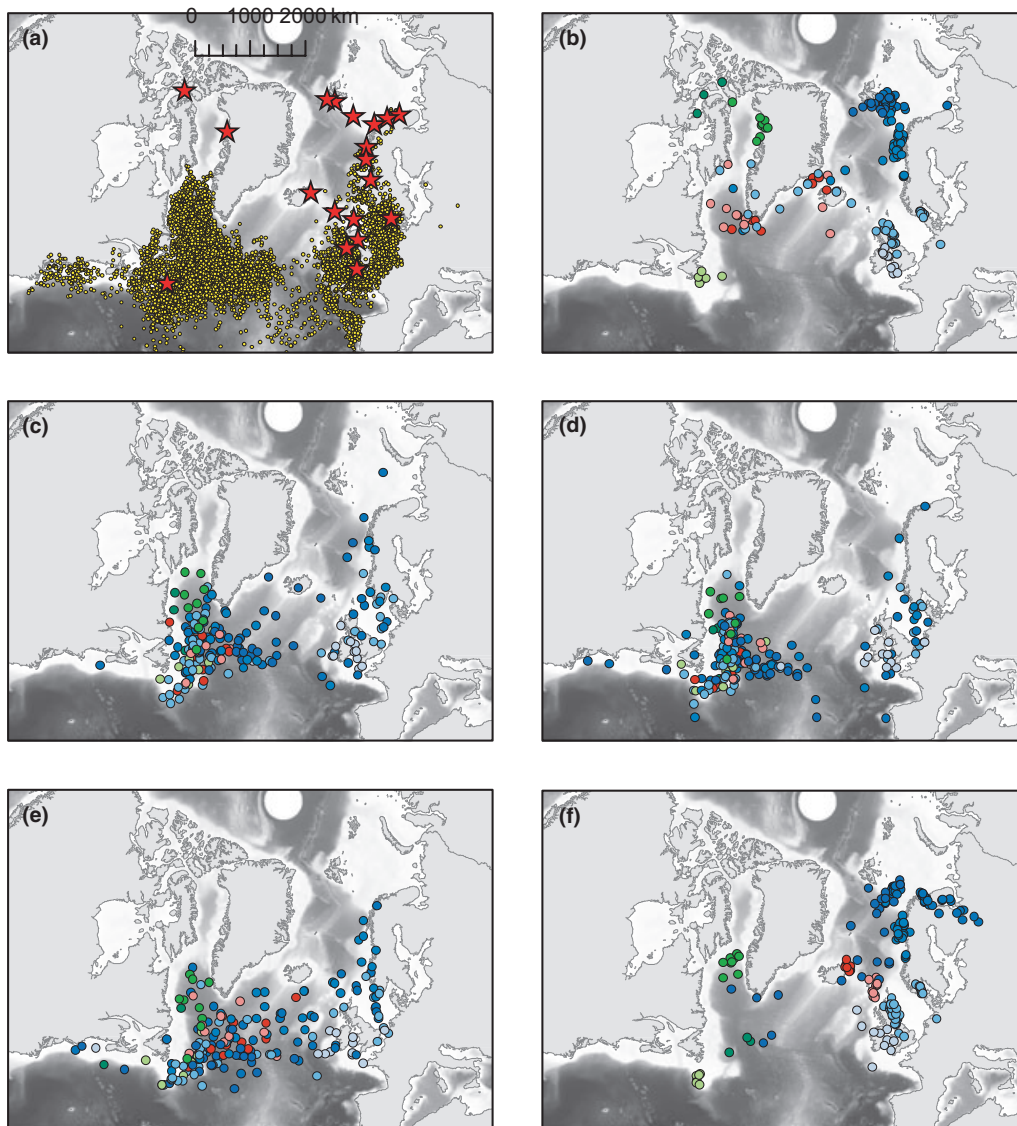
Figure 1 Distribution of instrumented kittiwakes in the North Atlantic in the non-breeding season 2009/10: (a) shows all smoothed positions from December 2009, and the location of the study colonies; (b)–(f) show the median position of each bird in (b) August, (c) November, (d) December, (e) January and (f) April, including birds from Prince Leopold Island in 2008/09. Medians were calculated in ArcMap 10 on projected data (i.e. not using spherical trigonometry), and are shown here only for display purposes. Median positions are colour-coded using the scheme in Fig. 2b, with blue shades representing large marine ecosystems (LMEs) on the European shelf, red LMEs in the Mid-Atlantic (Iceland and Faroes), and green LMEs on the North American shelf. Darker shades represent more northerly LMEs. Map projection: equidistant conic. Bathymetry according to ETOPO1 (Amante & Eakins, 2009).

of approximately equal area (Fig. 2b). We then averaged the proportions of positions occurring in each area of interest across colonies within each LME, assuming that our study birds and sites were representative of larger regions. Estimates of breeding population size in each LME were taken from the most up-to-date published information, supplemented by more recent unpublished data (Table 2). Winter populations of adults were assumed to comprise two individuals for each breeding pair. Winter populations from each LME were then distributed among areas of interest proportional to the average proportion of positions in that area. Finally, total populations of adults wintering in each area were summed across LMEs of origin:

$$Pw_j = \sum^i 2Pb_i * \overline{\left(\dfrac{pos_j}{\sum\limits^j pos_j}\right)},$$

where Pw_j is the wintering population in area of interest j, Pb_i is the breeding population in LME i and the average proportion of positions in each area of interest is taken across colonies within each LME.

Table 1. Overview of study colonies (listed by LME), including numbers of data loggers deployed, retrieved and included in the study. All loggers were deployed on breeding adults. A few loggers malfunctioned, and one was excluded owing to consistently biased data. At Prince Leopold Island, 10 of 13 loggers deployed and two of the three retrieved were Lotek LAT2500 rather than BAS Mk13/14. The high-Arctic colonies were not included in LMEs as defined by UNEP (see Fig. 2b), so we defined two additional LMEs in west Spitsbergen and Arctic Canada and extended the West Greenland Shelf LME to include the entire west Greenland coast

| LME/Colony	Latitude	Longitude	2008/09			2009/10		
			Deployed	Retrieved	Included	Deployed	Retrieved	Included
West Spitsbergen								
Kongsfjorden	78° 54′ N	12° 13′ E	10	8	7	13	12	11
Grumant	78° 10′ N	15° 09′ E	0	0	0	20	16	15
Barents Sea								
Bear Island	74° 23′ N	19° 08′ E	0	0	0	20	15	15
Cape Krutik	69° 09′ N	35° 57′ E	0	0	0	20	12	12
Hornøya	70° 23′ N	31° 09′ E	10	9	6	20	15	14
Hjelmsøya	71° 09′ N	24° 44′ E	0	0	0	19	0	0
Norwegian Sea								
Anda	69° 04′ N	15° 10′ E	0	0	0	20	12	12
Røst	67° 30′ N	12° 05′ E	19	15	14	35	22	19
Halten	64° 11′ N	09° 25′ E	0	0	0	20	3	3
North Sea								
Fair Isle	59° 32′ N	01° 38′ W	0	0	0	18	15	15
Bulbjerg	57° 09′ N	09° 01′ E	0	0	0	20	13	13
Isle of May	56° 11′ N	02° 33′ W	0	0	0	25	16	16
Celtic-Biscay Shelf								
Skomer	51° 44′ N	05° 18′ W	0	0	0	14	8	7
Rathlin	55° 29′ N	06° 19′ W	0	0	0	18	5	5
Faroe Plateau								
Stóra Dímun	61° 41′ N	06° 45′ W	0	0	0	20	10	10
Iceland Shelf								
Hafnarhólmi	65° 32′ N	13° 45′ W	0	0	0	20	12	12
West Greenland Shelf								
Kippaku	73° 42′ N	56° 40′ W	20	11	11	26	10	9
Arctic Canada								
Prince Leopold Island	74° 02′ N	90° 00′ W	13	3	3	0	0	0
Newfoundland–Labrador Shelf								
Gull Island	47° 14′ N	52° 46′ W	0	0	0	19	7	7
Total			72	46	41	367	203	195

LME, large marine ecosystem.

RESULTS

Usable data were extracted from 41 loggers for the 2008/09 season and 195 loggers for the 2009/10 season, although a minority of loggers did not contain data for the full year. Following filtering and smoothing, 12,738 and 71,668 positions were available for 2008/09 and 2009/10, respectively. We present mainly data for the 2009/10 season, except for Prince Leopold Island where only 2008/09 data were available. Where data exist for both 2008/09 and 2009/10, distribution patterns were generally similar (see Appendices S2–S4).

Birds were distributed throughout the North Atlantic outside the breeding season, with a major concentration in central and western parts (Fig. 1a, see Appendix S2). Shelf areas (< 200 m depth) and shelf edges on both sides of the Atlantic were extensively used, as well as much deeper (up to > 4000 m) offshore areas in the Labrador Sea and east of the Newfoundland shelf, extending to the Mid-Atlantic Ridge. The southernmost areas used were off north Portugal in the East Atlantic (c. 40° N) and off Cape Hatteras in the West Atlantic (c. 35° N). The offshore East-Central Atlantic, from the Porcupine Bank west of Ireland to the Mid-Atlantic Ridge, was used almost exclusively by birds in transit. While many birds remained near the colonies throughout August (Fig. 1b), others moved to specific post-breeding areas in the Barents Sea southeast of Spitsbergen, the Denmark Strait between Iceland and Greenland, and the Labrador Sea. In November (Fig. 1c), most birds had reached wintering areas generally south of 62° N, but some birds remained in the Norwegian Sea. In December, the majority of birds were concentrated in the western Atlantic, with substantial numbers also in the North Sea and west of the British Isles (Fig. 1d). By January, some
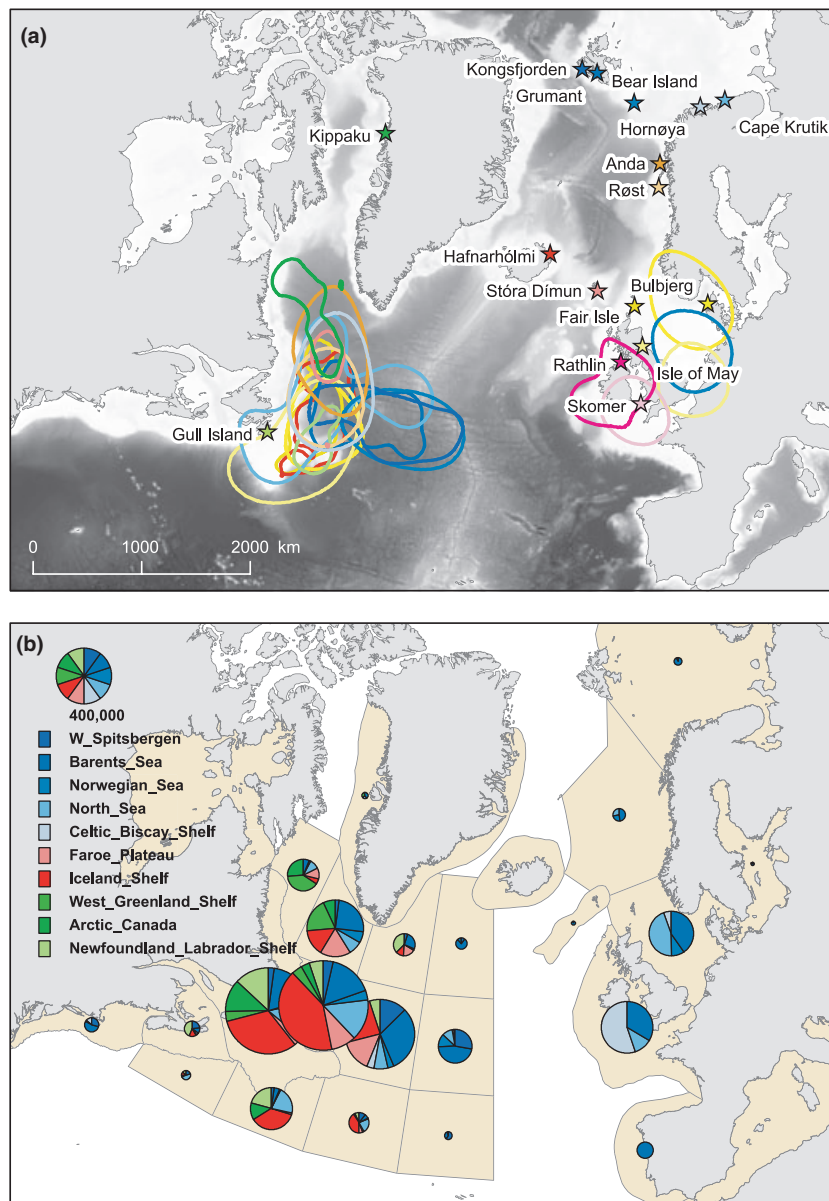
Figure 2 Areas used by wintering adult kittiwakes in the North Atlantic. (a) shows 50% kernel contours for each colony in December 2009. Study colonies are also shown, with the same colour scheme used for kernel contours and colonies. Kernels were not calculated for colonies represented by < 5 birds (Halten, Prince Leopold Island). (b) shows the estimated number of adult kittiwakes wintering in each large marine ecosystem (LME) and offshore block, indicated by symbol size, and their distribution by breeding origin (LME), indicated by colour shading as shown. Map projection: equidistant conic. Bathymetry according to ETOPO1 (Amante & Eakins, 2009). LMEs shown as defined by UNEP and downloaded from http://www.lme.noaa.gov/.

birds were moving back towards the colonies, particularly in Norway (where breeding started very early in 2010; T. Anker-Nilssen and T. Boulinier unpublished data), while others had shifted more towards the Central Atlantic (Fig. 1e). After the equinox period in April, most birds were back in the vicinity of their colonies, but high-Arctic breeders remained in offshore parts of the Barents Sea and Davis Strait, with a few birds still off Newfoundland (Fig. 1f).

The timing of the migration cycle varied greatly among colonies (Fig. 3, see Appendix S3). At some colonies such as

Stóra Dímun in the Faroes, birds started migration very early, and median distance from the colony was relatively constant at > 2000 km from August to February. In most colonies, the start of migration was much more gradual, with median distance from the colony increasing from August to November–December. The timing of return migration also differed among colonies; although most birds remained far from the colonies throughout February, others started moving much earlier, e.g. Røst in the Norwegian Sea where median distance from the colony declined from > 3000 km to < 1500 km in

Table 2 Estimated kittiwake breeding population sizes in the North Atlantic LMEs. The unit generally used is AON (apparently occupied nests), here assumed to correspond to two breeding adults. Small numbers of kittiwakes (< 10,000 AON in total) also breed in the East Greenland Shelf, Scotian Shelf and Iberian Coastal LMEs

| LME	Estimate (AON)	% of Atlantic population	Source
West Spitsbergen	117,000	5.2	H. Strøm (unpublished data)
Barents Sea	539,900	24.2	H. Strøm (unpublished data), Barrett *et al.* (2006) and Heubeck (2004)
Norwegian Sea	80,000	3.6	Barrett *et al.* (2006)
North Sea	311,290	13.9	Barrett *et al.* (2006), Frederiksen (2010) and Heubeck (2004)
Celtic-Biscay Shelf	122,347	5.5	Heubeck (2004)
Faroe Plateau	160,000	7.2	Frederiksen (2010)
Iceland Shelf	530,000	23.7	A. Garðarsson (unpublished data)
West Greenland Shelf	103,348	4.6	Labansen *et al.* (2010)
Arctic Canada	121,000	5.4	A.J. Gaston & M.L. Mallory (unpublished data)
Newfoundland–Labrador Shelf	150,000	6.7	Hatch *et al.* (2009)

LME, large marine ecosystem.
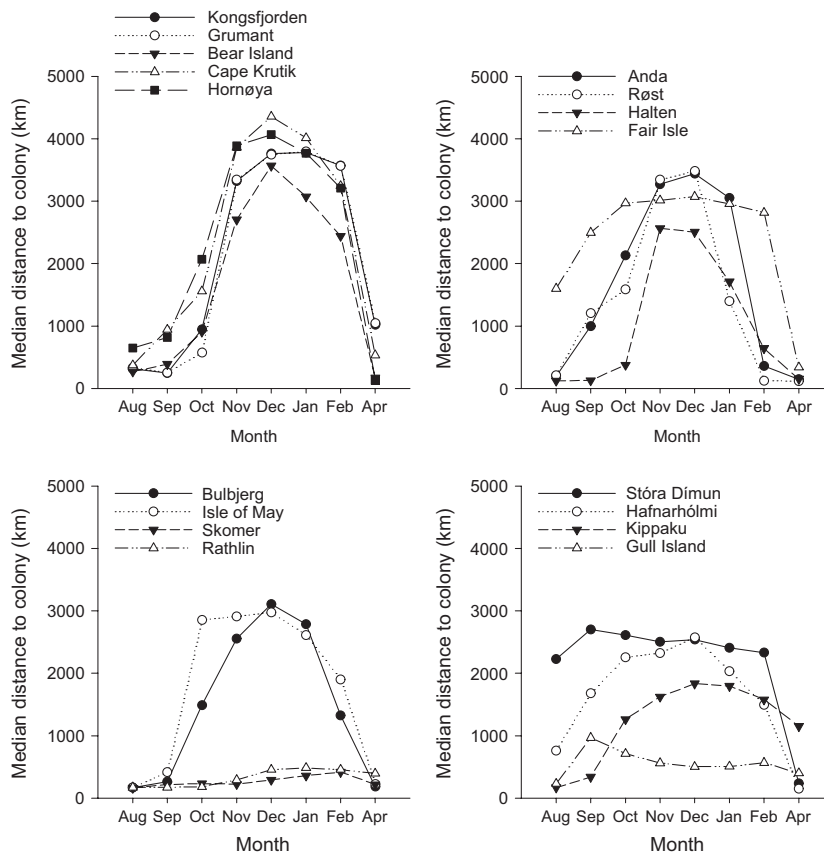
Figure 3 Monthly median distance to the colony for birds from all study colonies in 2009/10. The median distance across birds and days was based on smoothed positions.

January 2010, and to < 2500 km in January 2009 (Fig. 3, see Appendix S3).

In December 2009, birds from most colonies were concentrated in the West Atlantic, as illustrated by 50% kernel contours (Fig. 2a, see Appendix S4). The exceptions were Rathlin and Skomer, where nearly all birds remained near the colonies

throughout the year, and Bulbjerg, Isle of May and Bear Island, where 50% kernels were split between the North Sea and the Central and West Atlantic (Fig. 2a). Overlaps between 50% December kernels were generally highest for colonies within the same or adjacent LMEs (see Appendix S5), the main exception being the high overlap between Hafnarhólmi in Iceland and
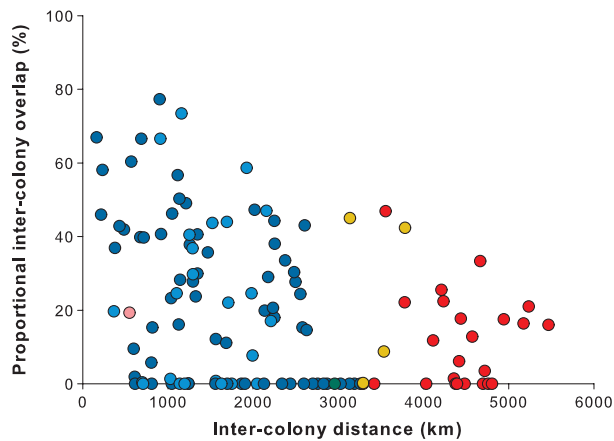
Figure 4 Proportional intercolony overlap between 50% kernels for December 2009 (cf. Fig. 2a), plotted against intercolony great circle at-sea distances. Colours indicate the location of the respective colonies [east, central (Iceland and Faroes) or West Atlantic]: east–east (dark blue), east–central (light blue), east–west (red), central–central (pink), central–west (orange), west–west (green).

several of the Norwegian colonies. In particular, the Svalbard colonies (Grumant, Kongsfjorden and Bear Island) showed very similar winter distributions, with a concentration of birds in the West-Central Atlantic (Fig. 2a, cf. Fig. 3). Similarly, birds from the colonies along the coast of northern Norway and Russia (Røst, Anda, Hornøya and Cape Krutik) were concentrated east of Newfoundland with large intercolony overlaps. Intercolony overlaps were negatively correlated with intercolony distances (Fig. 4; $r = -0.357$, $n = 16$ colonies, 120 distances), and this correlation was statistically significant (Mantel test, $P = 0.018$), indicating a tendency for closer colonies to show more similar December distributions.

We estimated the total winter population of adult kittiwakes in the Atlantic at 4.5 million birds (see Appendix S6), with the largest populations breeding in Iceland and the Barents Sea. Of these, 15% were estimated to be present in December in LMEs on the European side, 23% in LMEs on the North American side, 61% in offshore areas shown in Fig. 2b and 2% elsewhere. The highest numbers were found in the Newfoundland–Labrador Shelf LME (950,000) and in the offshore block immediately northeast of there (1,030,000). Kittiwakes from all LMEs wintered in these areas, with particularly large numbers from Iceland, the Barents Sea and the North Sea, in addition to local breeders (Fig. 2b). Areas further east in the Central Atlantic were dominated by birds from the Barents Sea and western Spitsbergen (Fig. 2a,b). In the main European LMEs, the North Sea and the Celtic-Biscay Shelf, most wintering birds were either of local origin or from the Barents Sea. With the exception of breeders in the Celtic-Biscay Shelf, the majority (> 70%) of birds from all LMEs wintered in the Central and West Atlantic, and no birds from western and central LMEs (green and red shades in Fig. 2b) wintered in the East Atlantic. In total, 1.6 million adult kittiwakes from LMEs on the

European shelf were estimated to cross the Atlantic, in addition to the 1.4 million from Iceland and the Faroes.

DISCUSSION

Distribution patterns

For the first time, we have mapped the non-breeding distribution of a widespread and numerous but declining seabird, using overwinter tracking of individuals from breeding populations representative of a large part of the species' breeding range. Our results confirm that shelf areas in Western Europe and around the Labrador Sea are important for wintering adult kittiwakes, but at the same time reveal that a very large part of the Atlantic population winters in offshore areas west of the Mid-Atlantic Ridge; a wintering area that, although suspected, was not previously confirmed because of the limitations of ring recoveries. We also show that the majority of adults from all parts of the European breeding range (except the western British Isles) migrate across the Atlantic. There is thus extensive sharing of wintering areas among most Atlantic populations, and this has profound implications for their demography, population dynamics and conservation status. In particular, the observed correlation between intercolony distance and overlap in winter distribution (Fig. 4) implies that regional breeding populations may be threatened by the lack of food or increased mortality in specific wintering areas. Shared wintering areas appear to be common in seabirds (González-Solís *et al.*, 2007; Polito *et al.*, 2011) and probably other migratory animals.

Determinants of winter distribution

Outside the breeding season, when seabirds no longer act as central-place foragers, they are expected to select areas where they can maximize net energy gain while minimizing mortality risk. Predation risk at sea is presumably very low, and the key factors determining kittiwake winter distribution are therefore likely to be food availability, thermoregulatory costs and possibly day length (Fort *et al.*, 2009). Breeding season studies show that kittiwake flight costs are relatively high (Jodice *et al.*, 2003), but given that direct migration across the Atlantic can be accomplished in 4–5 days (data not shown), migration costs are unlikely to be an important determinant of choice of wintering area within the North Atlantic. Unfortunately, very little is known about the winter diet of kittiwakes, making it hard to identify factors determining their distribution. They are regarded as mainly surface feeders, but can also plunge-dive to *c.* 1 m (Hatch *et al.*, 2009). A study from the Barents Sea in March (Erikstad, 1990) found that kittiwakes took mainly fish [polar cod (*Boreogadus saida*) as well as juvenile Atlantic cod (*Gadus morhua*) and redfish (*Sebastes* spp.)]. However, none of the sampled birds had eaten recently, so only indigestible prey remains were found in the stomachs, probably biasing results. It is likely that kittiwakes in winter also feed on a variety of large zooplankton, including amphipods and euphausiids

(Mehlum & Gabrielsen, 1993; Lewis *et al.*, 2001). In any case, kittiwake prey is likely to be largely dependent on the dominant mesozooplankton in the North Atlantic: calanoid copepods. Most copepods with life cycles > 1 year overwinter at depth and are thus unavailable to near-surface predators, but in the West Atlantic (including the Labrador Sea), the most important species *Calanus finmarchicus* is relatively abundant in near-surface waters even in winter (Planque *et al.*, 1997). This concentration of an important secondary producer might explain the importance of this area to many wintering seabirds, including kittiwakes (Brown, 1986). Recent simultaneous tracking of various top predators in the North Pacific has demonstrated important multispecies hot spots and pointed to environmental drivers of these patterns (Block *et al.*, 2011).

Reliability and generality of results

We found that an estimated 80% of Atlantic kittiwakes wintered in the Central and West Atlantic, including the Labrador Sea, the shelf edges off Newfoundland and offshore areas extending to the Mid-Atlantic Ridge. Most of the remaining birds (15%) spent the winter in the North Sea and west and south of the British Isles. However, this pattern represents one non-breeding season only (2009/10), and although the sample size was relatively large, some breeding areas were less well represented than others. For example, the large Icelandic population was only represented by 12 birds from one colony, in contrast to 41 birds from three colonies in the equally large Barents Sea population, and no colonies in the Gulf of St. Lawrence were included. We have attempted to compensate for this imbalance in our calculations, but a possibility remains that birds from large, unrepresented colonies behave differently from those included in the study. Distribution patterns may also vary between years to an unknown extent, perhaps linked to interannual variation in prevailing weather patterns or distribution of important prey. A comparison with patterns from the 2008/09 season for the four colonies where data were available showed that the overall patterns were similar (see Appendices S2–S4), but that a few birds spent time in late winter around the Azores and in the Canary Current off north-western Africa – an area where no instrumented birds were found in 2009/10, despite much larger sample size. Ringing studies have previously shown that kittiwakes occasionally use this area in winter (Coulson, 2002; Bakken *et al.*, 2003). A previous study in 2007/08 of Isle of May kittiwakes also showed a very similar pattern to that observed in 2009/10 (Bogdanova *et al.*, 2011).

In addition to environmental conditions, the movements of wide-ranging, opportunistic feeders such as kittiwakes are influenced by their own state or condition. For example, Bogdanova *et al.* (2011) found that unsuccessful breeders from the Isle of May were more likely to migrate across the Atlantic than successful breeders. This could perhaps explain the pronounced differences in departure time and migration distance observed among colonies in this data set (Figs 2a and 3). For example, all study birds from Fair Isle and Stóra

Dímun, where breeding success had been close to zero for several years including 2009 (D. Shaw & B. Olsen, unpublished data), left the colony early and crossed the Atlantic. Males and females may also differ in migratory behaviour (Bogdanova *et al.*, 2011).

Our approach underestimates the number of birds wintering north of about 69° N, primarily in the Barents Sea. In this area, polar night precludes geolocation even though the logger detects the sun 3° below the horizon, and many positions are lost. One bird from Hornøya spent the entire winter in the Barents Sea (Fig. 1c–e), but in December, only 15 smoothed positions were obtained of a possible 62 (two per day). The estimated number of birds wintering in the Barents Sea could thus be four times as high as shown in Appendix S6, although even if this were the case, only a small minority of birds would winter in this area. Collectively, we believe that our results give a robust indication of where Atlantic kittiwakes spend the winter, although absolute numbers given in Appendix S6 and Fig. 2b should only be taken as indicative.

Importantly, we have only mapped the distribution of adults. While ring recoveries indicate that pre-breeders show a broadly similar winter distribution (e.g. Coulson, 2002; Bakken *et al.*, 2003), the specific areas used and timing of movements may well differ considerably among age groups (Barrett & Bakken, 1997; Reynolds *et al.*, 2011). Future studies should address this issue, although technical challenges are considerable.

Conservation implications

Our results show that kittiwakes from different parts of the breeding range mix extensively in winter and that a large proportion of the total wintering population is concentrated in a particular sector of the West Atlantic. This has important implications for the conservation and management of Atlantic kittiwake breeding populations, many of which are declining and have recently been regionally red-listed. The importance of the Newfoundland–Labrador Sea area for wintering kittiwakes is confirmed by at-sea surveys that regularly encounter high densities both on the shelf and particularly along the shelf edge northeast of Newfoundland (Fifield *et al.*, 2009), although these surveys do not cover offshore areas during winter. Chronic oil pollution has been identified as a serious threat to wintering auks in the same area (Wiese *et al.*, 2004), but no assessment has been made of the potential impact on kittiwakes. Any major changes in food availability in this part of the West Atlantic (e.g. projected changes in distribution of *C. finmarchicus*; Reygondeau & Beaugrand, 2011) would be likely to affect the entire Atlantic population, and future demographic studies should investigate the relationship between adult survival and environmental conditions in this area, preferably linked with better information on winter diet.

Impacts of deterioration in environmental conditions in the non-breeding range are particularly strong and widespread when widely separated breeding populations share wintering areas. Examples include migrant songbirds affected by drought and habitat degradation in their tropical wintering areas

(Winstanley *et al.*, 1974; Szep, 1995), as well as albatross populations severely affected by bycatch mortality in longline fisheries far from their breeding colonies (Small & Taylor, 2006; Rolland *et al.*, 2008). In general, synchronization of mortality among population subsets (e.g. age classes or local populations) decreases population growth rate and increases the likelihood of extinction (Fieberg & Ellner, 2001).

The strong spatial mixing in winter is consistent with the relatively weak population genetic structure observed for kittiwakes in the Atlantic (McCoy *et al.*, 2005) and for other pelagic seabirds (e.g. Riffaut *et al.*, 2005), implying that gene flow exists among the various populations. The occurrence of large concentrations of birds of widely mixed geographical origin could also be important in the context of directly transmitted infectious agents such as Avian Influenza viruses (Toennessen *et al.*, 2011), although little is known about the potential transmission risk of such agents among pelagic birds while at sea.

Overall, there is a clear tendency for kittiwakes to overwinter in the regions of the North Atlantic that are most influenced by human activities (cf. Halpern *et al.*, 2008). Combined with a high degree of interpopulation mixing in winter, this implies that successful conservation of this declining species is likely to require coordinated action from management agencies responsible for regulating these activities on national and trans-national scales. Future initiatives towards ecosystem-based resource management should take account of the habitat and food requirements of overwintering seabirds, including kittiwakes. More generally, conservation of migratory species in a rapidly changing world is dependent on understanding the degree of population mixing in non-breeding areas. Without this knowledge, well-intended initiatives targeting regional breeding populations may have little effect and lead to waste of limited financial resources. Our approach to estimating the size and composition of regional wintering populations could be extended to other taxa and ecosystems if and when data become available and thus contribute to successful management of migratory species. Further miniaturization of data loggers will allow this approach to be applied with smaller species, e.g. songbirds (Tøttrup *et al.*, 2011).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Estimation of the optimal sun angle.

Appendix S2 Locations of instrumented kittiwakes 2008/09.

Appendix S3 Monthly mean distance to colonies 2008/09.

Appendix S4 Areas used by kittiwakes December 2008.

Appendix S5 Overlap matrix of 50% kernels December 2009.

Appendix S6 Estimated numbers of kittiwakes in areas of interest December 2009.

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BIOSKETCHES

Morten Frederiksen is a senior researcher at Aarhus University. His main research interest is in documenting how environmental change affects the population size and distribution of vertebrates, with seabirds as the favourite study organisms. Increasingly, he works on large spatial scales, mainly in the Arctic and North Atlantic.

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