BTO Research Report No. 671

Dispersal and Movements of Lesser Black-backed Gull in Europe

Authors

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EXECUTIVE SUMMARY

1 Lesser Black-backed Gull numbers have fluctuated across this species' breeding range in recent decades, with a sharp rise in the latter half of the Twentieth Century followed by declines in some areas, including in the UK. The Lesser Black-backed Gull is a polytypic species with three subspecies, one of which (*Larus fuscus graellsii*) commonly breeds in the UK. This project aimed to investigate the drivers behind these fluctuating population trends by studying this species' population across its range.

2 Ringing data from 62,752 individual Lesser Black-backed Gulls ringed across Europe between 1910 and 2013 were analysed to investigate the movements and distribution of this species. These data confirmed much of what is already understood about the distribution of the three subspecies, and showed a contraction in breeding and wintering range with age, as has been demonstrated with smaller ringing datasets at specific breeding colonies and wintering sites.

3 There was evidence of changes in these birds' behaviour over the decades. The distance that birds of breeding age, recovered dead during the breeding season, were found to have moved from their ringing sites has changed significantly, becoming smaller since the mid-Twentieth Century. This could indicate that birds are recruiting closer to their natal colonies than in earlier decades, or are travelling less far to find food. However, this could also be an artefact of changes in ringing practices and study effort at breeding colonies.

4 There was some indication of birds that hatched in Britain recruiting to breed in Belgium and the Netherlands (the breeding range of the *Larus fuscus intermedius* subspecies) in recent years, such that these areas could form, or is beginning to form, a metapopulation, but the number of birds involved is small. More birds had apparently moved from the UK to the Netherlands/Belgium than birds had moved in the opposite direction.

5 Further work is needed to investigate the drivers of Lesser Black-backed Gull population changes in the UK and elsewhere in Europe.

1. INTRODUCTION

The population status and therefore optimal management of the Lesser Black-backed Gull *Larus fuscus* in the UK and other European countries is somewhat unclear (Ross-Smith *et al*. 2014a). This species, which breeds across northern and western Europe (Cramp & Simmons 1983) increased sharply in numbers during the Twentieth Century (Mitchell *et al*. 2004, Wetlands International 2014), but this trend has apparently levelled off or reversed in recent years in some areas, including in the UK (Wetlands International 2014). However, it is not known whether these population trends take account of all areas where this species breeds, particularly urban colonies which are not systematically counted throughout much of this species' range (Rock 2005; Ross-Smith *et al*. 2014a). Many of these urban colonies have grown in recent decades, bringing the Lesser Black-backed Gull into conflict with humans who may consider it as a pest and a public health risk. This urban population growth has coincided with a decline at "traditional" coastal colonies, suggesting the possibility that the national scale Lesser Black-backed Gull decreases recorded could actually be a redistribution of breeding birds from rural to urban areas (Ross-Smith *et al*. 2014a). Furthermore, at the species level, declines in one country could be buffered or offset by increases in others (Ross-Smith *et al*. 2014a).

Lesser Black-backed Gulls have been ringed across their range for more than a century, and ringing data can illustrate population and demographic changes (Baillie *et al*. 2009). Recent examination of data from Lesser Black-backed Gulls ringed in England showed evidence for metapopulations, suggesting non-uniform population trends and pressures on this species throughout the country (Ross-Smith *et al*. 2014b). This project extends this analysis of Lesser Black-backed Gull movements to a European scale to improve understanding of the population status and conservation needs of this species across its breeding range. The primary objective is to understand more about Lesser Black-backed Gull populations and metapopulations, and whether Lesser Black-backed Gulls breeding in England make up part of a metapopulation that extends into different countries. The report also examines how much interchange there is between breeding populations and whether the biological scales at which metapopulations might exist can be defined.

The specific aims of this project are as follows:

1. To seek evidence for breeding population shifts, especially between English designated sites and overseas sites; and
2. To characterise the degree of interchange between 'sites' (irrespective of any breeding population shifts) to provide any evidence relating to metapopulation partitioning – i.e. understanding the sub-population scale.
3. To make recommendations on likely population and metapopulation scales, identifying any evidence gaps that prevent firm conclusions.

1.1 Classification and Distribution

The Lesser Black-backed Gull is a polytypic species split into three subspecies - *graellsii*, *intermedius* and *fuscus* (Olsen & Larsson 2004, Collinson *et al*. 2008). As well as clinal variation in appearance (notably, the darkness of the mantle), these subspecies differ in their migratory strategies and how long individuals take to acquire full adult plumage (Olsen & Larsson 2004).

L. f. fuscus is the smallest and darkest of the Lesser Black-backed Gull subspecies. It achieves full adult plumage three years after hatching, and has a more slender bill, longer wings and shorter legs compared to the other subspecies (Olsen & Larsson 2004). As its alternative name, the Baltic Gull,

suggests, *L. f. fuscus* largely breeds on the Baltic coasts of Finland, Sweden and Estonia, with small populations on the northwest Russian coast and parts of northern Norway (Olsen & Larsson 2004, Hario & Nuutinen 2011), and migrates to sub-Saharan Africa in winter (Kylin *et al*. 2010, 2011, Bustnes *et al*. 2013).

L. f. intermedius and *L. f. graellsii* are morphologically and behaviourally more similar to one another than they are to *fuscus*. There is evidence of genetic mixing between *intermedius*, which normally breeds from Belgium and the Netherlands eastwards into western Scandinavia, and *graellsii*, which breeds in the United Kingdom, Ireland, France, northwest Spain, Portugal, Iceland and Greenland (Snow & Perrins 1998, Piotrowski 2003, Boertmann 2008, Collinson *et al*. 2008, BirdLife International 2014). *Intermedius* tends to have a darker mantle than *graellsii*, but there is considerable overlap between the subspecies (Olsen & Larsson 2004). Both take four years to attain adult plumage (Olsen & Larsson 2004), and largely winter in southwest Europe and northwest Africa (Marques *et al*. 2010, Hallgrimsson *et al*. 2012, Klaasen *et al*. 2012), although some Icelandic birds migrate to the eastern USA (Olsen & Larsson 2004), and increasingly birds remain in northern Europe throughout the year (Burton *et al*. 2013).

1.2 International Population Trends

In common with other large white-headed gull species, the global Lesser Black-backed Gull population grew rapidly in the Twentieth Century (Wetlands International 2014), in a trend thought to be driven largely by this species' ability to take advantage of the predictable and plentiful food provided by humans in the form of refuse and fishing discards (Camphuysen 2013; Ross-Smith *et al*. 2014a). In more recent years, population declines have been reported in parts of its range (Wetlands International 2014). Nevertheless, the Lesser Black-backed Gull is categorised as "Least Concern" by the International Union for the Conservation of Nature (BirdLife International 2014).

Of all the Lesser Black-backed Gull subspecies, *L. f. fuscus* currently has the smallest population (around 18,000–19,000 breeding pairs, or 56,000 individuals, Wetlands International 2014) and has experienced a strong decrease in numbers in recent years to the extent that it is now considered by some to be globally threatened (Olsen & Larsson 2004). This reduction might be partly linked to pesticide use at its wintering grounds (Hario *et al*. 2004, Hario & Nuutinen 2011). There is evidence that the chemicals involved are passed on to embryos in the egg and cause liver failure in young chicks, leading to widespread breeding failure (Hario *et al*. 2004), although the level of contamination may now be reducing (Hario & Nuutinen 2011). Other factors, such as high levels of chick predation by Herring Gulls, have also influenced *fuscus* population trends at some colonies (Hario 1994).

Populations of both *L. f. intermedius* and *L. f. graellsii* experienced substantial growth through the mid- and late-Twentieth Century, bringing today's numbers to approximately 325,000-440,000 breeding pairs for *intermedius* and 530,000-570,000 pairs for *graellsii*. However, both subspecies have experienced population fluctuations in parts of their range in more recent years (e.g. Camphuysen *et al*. 2010, Sellers & Shackleton 2011), which amount to widespread declines in England and the rest of the UK (JNCC 2014).

1.3 Lesser Black-backed Gull Ringing

Lesser Black-backed Gulls have been fitted with uniquely numbered leg rings since the turn of the Twentieth Century. Reports of these rings (recoveries) can be used to investigate the movements of Lesser Black-backed Gulls from different breeding areas across Europe. Many Lesser Black-backed Gulls also carry colour rings to enable them to be re-identified without being recaptured, known as a

resighting. Ringing, resighting and reporting depend heavily on volunteer effort, and on birds being found in places that humans live or visit. There are fewer biases in the reporting of dead birds than in the resighting of living individuals, because while the geographical distribution of ringers and of resighters is concentrated at certain localities, reports of dead birds tend to have a more even distribution as they are usually the result of chance encounters, rather than targeted effort (Wernham *et al.* 2002; Korner-Nievergelt *et al*. 2010). Despite these biases, analysis of ringing data can reveal important information about population trends and their drivers (Baillie *et al*. 2009).

2 METHODS

Recoveries of Lesser Black-backed Gulls were obtained from the EURING databank (EDB, du Feu 2010), which holds recoveries generated by ringers in all the member schemes across Europe. Data submitted to the EDB by February 2015 (230,031 records) were extracted.

2.1 Data Selection

As we were concerned with temporal changes in location, we eliminated reports with inaccurate date of finding, which would potentially bias the geographical distribution of recoveries at any particular time of year. We selected recoveries for which the accuracy of the finding date was at least within two weeks of the date coded (i.e. EURING accuracy of date codes 0 to 4 inclusive only were considered in the report)[1]. This gave 227,390 records spanning the years 1910 to 2014. As we were looking at differences between breeding populations, we selected individuals of known breeding origin. This included birds that were ringed as pulli (EURING age code 1) and older birds ringed in the breeding season (defined here as April to July, after Ross-Smith *et al*. 2014b), that were presumed to be largely breeding adults, or subadults captured for ringing while they were prospecting at or close to colonies. This selection gave records of 62,752 individual birds, which were ringed between 1910 and 2013 (Table 1).

[1] Not all reports of dead birds are dated. For example, sometimes a letter is sent that does not give the date of finding, in which case the postmark is used. Therefore, the "finding date" is not always very accurate.

Country of ringing	Subspecies	Number of birds ringed
Britain	*Graellsii*	18,412
Channel Islands	*Graellsii*	1,436
Faroe Islands	*Graellsii*	250
France	*Graellsii*	5
Ireland	*Graellsii*	114
Iceland	*Graellsii*	242
Spain	*Graellsii*	21
	Total graellsii	*20,480*
Belgium	*Intermedius*	2,347
Denmark	*Intermedius*	1,175
Germany	*Intermedius*	238
Netherlands	*Intermedius*	29,099
	Total intermedius	*32,859*
Finland	*Fuscus*	8,322
Sweden	*Fuscus*	1,091
	Total fuscus	*9,413*

Table 1 Country of ringing and presumed subspecies of Lesser Black-backed Gulls of known breeding origin (i.e. birds ringed as pulli, and birds ringed as adults or subadults during the breeding season – April-July).

Birds found dead, or critically injured, such that they would not be released back to the wild (EURING condition codes 1, 2, 3, 5 and 6) were analysed separately from those recaptured and resighted (EURING condition codes 7 and 8) because of the differences in the biases associated with the reporting rate of dead and living birds (Wernham *et al*. 2002). The different countries that contribute to the EDB have different protocols for reporting recoveries of living birds (see http://www.euring.org/data_and_codes/obtaining_data/recovery_definitions.htm). For example, in Britain and Ireland, Lesser Black-backed Gulls recaptured or resighted by ringers within 40 km of the site of ringing have not historically been added to the database (although all reports of dead birds and resightings by members of the public have been added), while in other countries, such as the Netherlands and Finland, all reports of ringed birds were included. This increases potential bias in the numbers reported, but will have less effect on the spread of finding locations. Many birds found dead did not die of natural causes – many were culled or otherwise deliberately killed. These birds (EURING circumstance codes 10-26) were also considered separately from those that died naturally.

Subspecies identity was rarely assigned at ringing, so we used individuals' presumed countries of origin to derive this variable. Individuals ringed (as chicks or breeding adults) in Iceland, the Faroe Islands, Great Britain, Ireland, the Channel Islands, France and Spain were classed as *graellsii*. Those from Belgium, the Netherlands, Germany and Denmark were deemed to be *intermedius*, while birds ringed in Finland, Sweden and Norway were classified as *fuscus* (after Olsen & Larsson 2004). Kernel density plots were generated in the R package 'maprec' (Robinson 2015) to examine the overall biogeographic ranges of the three subspecies[2]. As this report is primarily concerned with the wider movements and distribution of Lesser Black-backed Gull breeding populations that are associated with England, and *fuscus* do not breed in England, some of the more detailed kernel maps for this subspecies can be found in Appendix 1 (Figures A1-A4).

[2] The colour scheme of all figures in the report mirrors the mantle colour of the subspecies, i.e. palest (kernel or line colour) for *graellsii* and darkest for *fuscus*.

Data were further examined by age class. This was done for birds ringed as pulli only as these were of known age. Very few birds were assigned an age when they were recovered, so age on finding was determined using the elapsed time between when each bird was ringed (as a pullus) and when it was recovered. Three age classes were selected – "first-year birds", "subadults" and "adults". First-year birds were records of birds in the year they were ringed and up until the end of the breeding season (end of July) in the year following ringing. Subadults were birds reported from August in the year following ringing up until the start of the breeding season (the end of March) four calendar years after hatching and adult birds were those reported at any time subsequently (i.e. birds in their fourth summer and older). For dead recoveries, a further age category was defined – "pulli". This was defined as birds found 10 km or less from their site of ringing in the same year they were ringed as pulli. This age bracket was chosen to separately classify birds that almost certainly died at or close to their natal colony as a result of mortality shortly before, or not long after, fledging. Kernel density plots were produced to contrast the distributions of these birds in the breeding season (April-July) and the winter (October-February, after Ross-Smith *et al*. 2014b).

In order to examine the level of movements between breeding populations of each country, birds ringed as pulli but found as adults during the breeding season in a different country four or more calendar years later (i.e. once they were of breeding age) were extracted from the database.

Data were manipulated and analysed in R (R Core Team 2015) using the additional package 'lubridate' (Grolemund & Wickham 2011) along with 'maprec' (Robinson 2015). The base maps used in all plots are based on data from Natural Earth (naturalearth.org).

2.2 Data Analysis

The distance between sites of ringing and recovery was modelled to investigate changes over time (per decade[3]), and how this varied with age class, subspecies and country of origin. This was done for dead Lesser Black-backed Gulls that were not deliberately killed only. Analysis was undertaken using general linear models (GLM), which were simplified using stepwise deletion.

[3] Note that the decade classed as the "2010s" in all tables and figures is not yet complete, so the sample sizes etc are not equivalent.

3 RESULTS

3.1 Recoveries

3.1.1 Recoveries of birds found dead

There were 14,344 records of individual birds ringed as pulli or as subadults and adults during the breeding season that were subsequently found dead between the years 1910 and 2014 (Table 2).

Decade ringed	Number of birds	Decade recovered	Number of birds
1910s	90	1910s	85
1920s	91	1920s	79
1930s	339	1930s	316
1940s	147	1940s	136
1950s	591	1950s	511
1960s	3,352	1960s	1,715
1970s	1,814	1970s	2,469
1980s	2,939	1980s	2,839
1990s	2,793	1990s	2,525
2000s	1,977	2000s	3,016
2010s	265	2010s	707

Table 2 Number of Lesser Black-backed Gulls ringed as pulli or as subadults and adults during the breeding season found dead per decade.

Of these, 8,401 were *graellsii*, 2,970 were *intermedius* and 2,973 were *fuscus*, based on country of ringing. Table 3 shows the countries where these birds were ringed and recovered. Approximately 25% (3,530 individuals) of birds reported dead were killed deliberately, for instance as a result of culling or hunting. 2,437 of these birds were *graellsii*, 267 were *intermedius* and 826 were *fuscus*. Figures 1-3 show the distribution of recovery sites for each subspecies, comparing all birds found dead with those deliberately taken and those that died of other causes. Dead recoveries (for birds ringed as pulli) were grouped together in the rest of the report apart from the analysis of movements over time (section 3.1.2.3) for which birds that were deliberately killed were excluded.

Country	Birds ringed	Birds found dead	Country	Birds ringed	Birds found dead	Country	Birds ringed	Birds found dead
Algeria	0	14	Finland	2,346	1,668	Namibia	0	3
Angola	0	1	France	0	397	Netherlands	1,652	1,585
Armenia	0	1	Gambia	0	2	Nigeria	0	4
Austria	0	3	Georgia	0	7	Norway	0	27
Belarus	0	12	Germany	90	142	Poland	0	46
Belgium	467	329	Ghana	0	4	Portugal	0	643
Benin	0	3	Gibraltar	0	4	Romania	0	4
Britain	7,846	6,297	Greece	0	3	Russia	0	107
Bulgaria	0	3	Greenland	0	1	Saudi Arabia	0	3
Cameroon	0	3	Guinea Bissau	0	1	Senegal	0	9
Central African Rep	0	3	Hungary	0	1	Sierra Leone	0	1
Chad	0	3	Iceland	224	198	Slovenia	0	1
Channel Islands	113	77	Ireland	53	124	South Africa	0	3
Congo	0	5	Italy	0	59	Spain	0	516
Croatia	0	3	Jordan	0	1	Sudan	0	1
Cyprus	0	2	Kazakhstan	0	2	Sweden	627	556
Czech Republic	0	2	Kenya	0	5	Switzerland	0	4
DR Congo	0	20	Latvia	0	29	Tanzania	0	8
Denmark	799	681	Lebanon	0	12	Tunisia	0	21
Djibouti	0	1	Libya	0	18	Turkey	0	39
Egypt	0	34	Lithuania	0	14	Uganda	0	7
Eritrea	0	4	Mali	0	2	Ukraine	0	59
Estonia	0	37	Malta	0	4	Western Sahara	0	15
Ethiopia	0	13	Mauritania	0	12	Yemen	0	1
Faroe Islands	177	113	Moldova	0	2	Zambia	0	1
Finland	2,346	1668	Morocco	0	257	Other (e.g. at sea)	0	65

Table 3 Number of dead Lesser Black-backed Gulls ringed as pulli or as subadults and adults during the breeding season, by country of ringing and country of recovery.

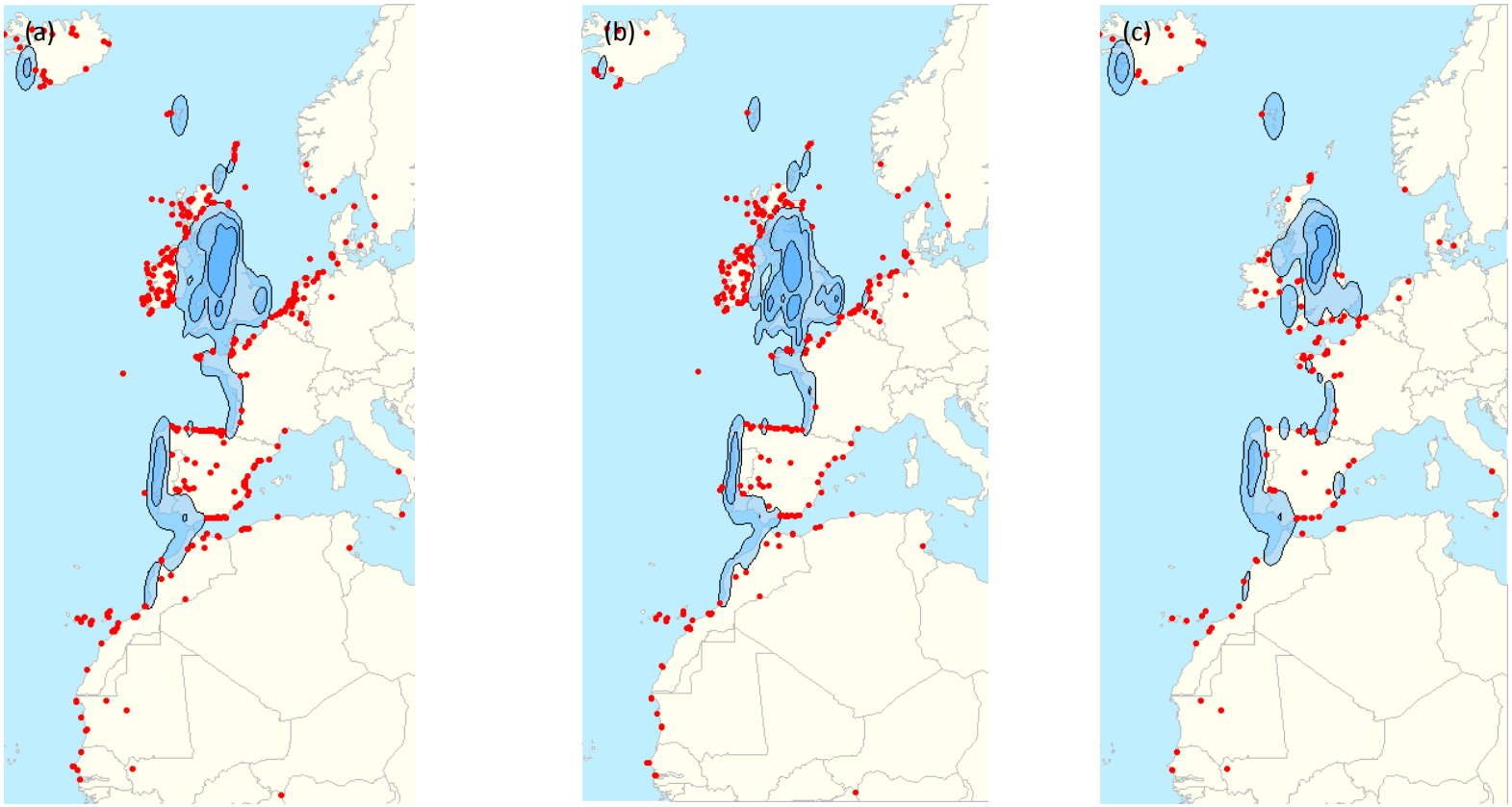

Figure 1 Kernel maps of (a) all 8,401 dead recoveries (b) a subset of 5,964 birds that were not intentionally killed and (c) a subset of 2,437 birds deliberately killed for the Lesser Black-backed Gull subspecies *Larus fuscus graellsii*. Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries, only those outside the 90% kernel are shown.

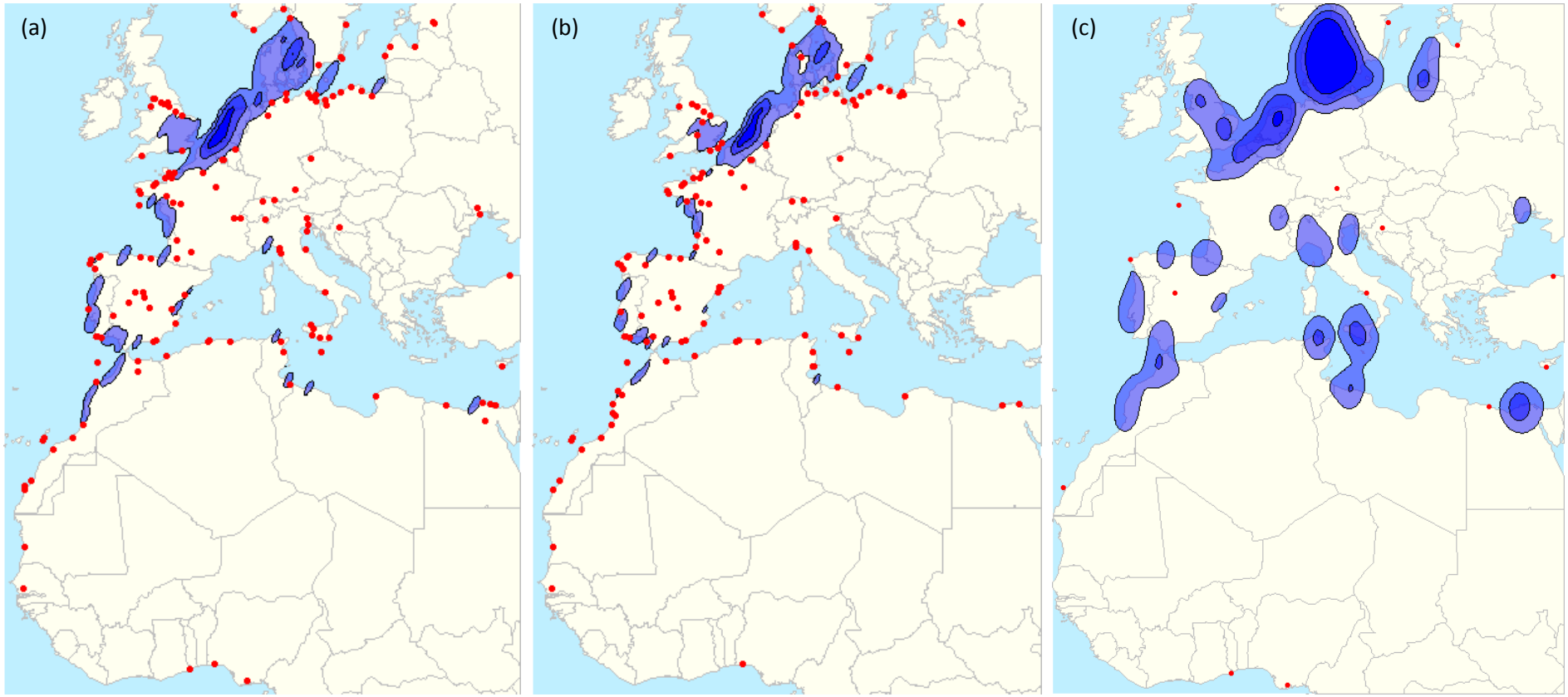

Figure 2 Kernel maps of (a) all 2,970 dead recoveries (b) a subset of 2,703 birds that were not intentionally killed and (c) a subset of 267 birds deliberately killed for the Lesser Black-backed Gull subspecies *Larus fuscus intermedius*. Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries, only those outside the 90% kernel are shown.

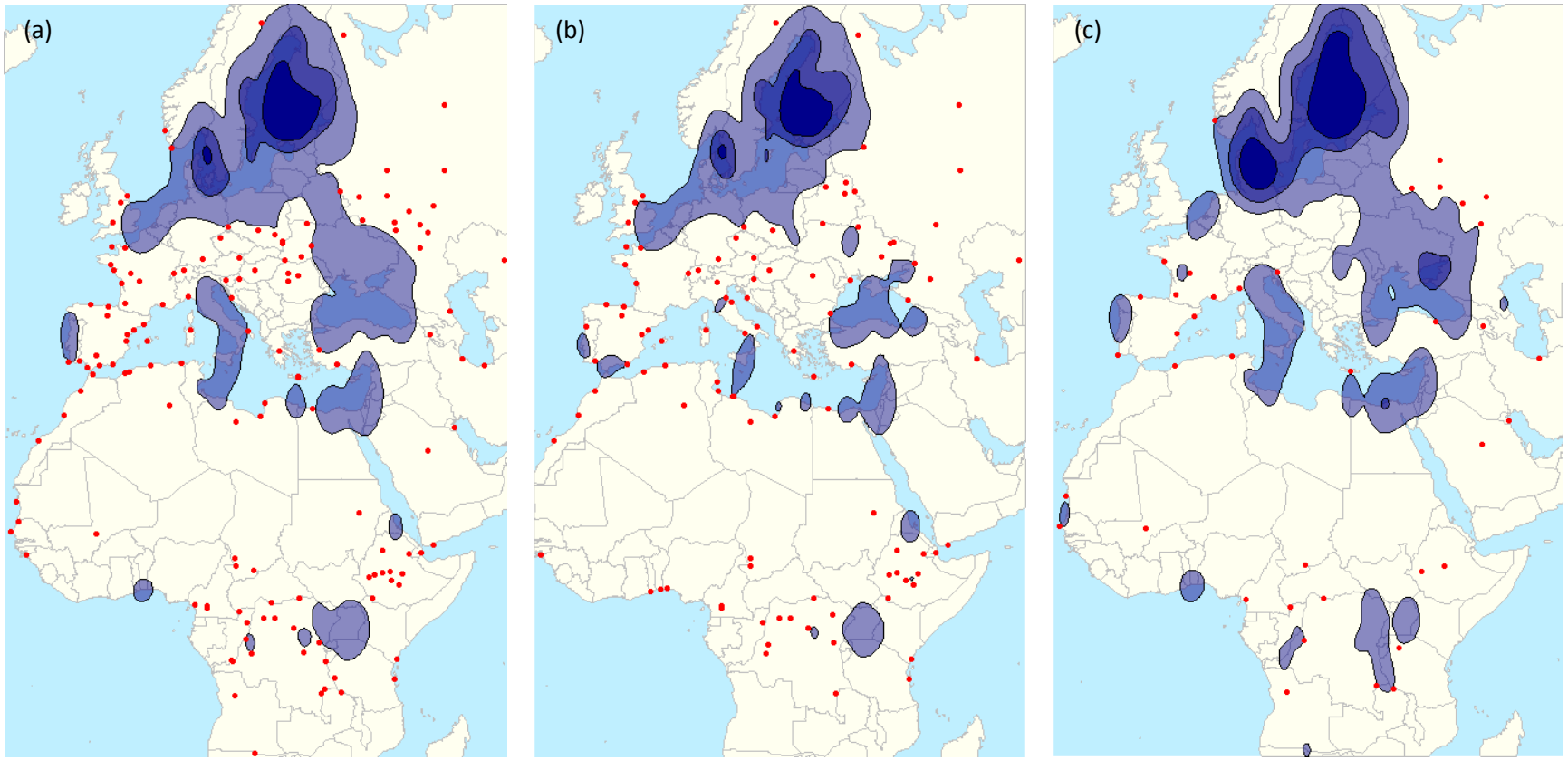

Figure 3 Kernel maps of (a) all 2,973 dead recoveries (b) a subset of 2,147 birds that were not intentionally killed and (c) a subset of 826 birds deliberately killed for the Lesser Black-backed Gull subspecies *Larus fuscus fuscus*. Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries, only those outside the 90% kernel are shown.

Although these maps do not distinguish between different age classes or time of year, they clearly show the different biogeographical ranges of each subspecies. *Fuscus* has the broadest range of the three, spanning the most distant countries across the year, from Scandinavia to Sub-Saharan Africa. *Intermedius* and *graellsii* are much more similar to each other than they are to *fuscus*, with a lot of overlap, especially in Britain, France, Iberia and North Africa. However, the range of *graellsii* extends further north and west than that of *intermedius*.

Certain "hotspots" stand out on the maps of the birds that were deliberately killed, for example parts of the southern Mediterranean for *fuscus* and *intermedius* where birds are commonly hunted. There are also notable concentrations of birds that have been deliberately killed around breeding colonies, which reflect the extensive Lesser Black-backed Gull culling programmes that have taken place over the years. For example, there is a culling "hotspot" in North-West England for *graellsii* and *intermedius*, which corresponds to periods when birds were culled at Bowland Fells (O'Connor 1995).

3.1.2 Dead recoveries of birds ringed as pulli

The EDB contained 12,921 records of Lesser Black-backed Gulls ringed as pulli that were later found dead due to all causes, including deliberate killing (Table 4). Of these, 6,077 birds were found during the breeding season (April-July) and 2,437 during winter (October-February). Figures 4-6 show the distribution of finding sites for each subspecies.

Subspecies	Number of dead recoveries (all year)	Number of dead recoveries (breeding season)	Number of dead recoveries (winter)
Graellsii	7,486	3,906	1,414
Intermedius	2,591	990	499
Fuscus	2,844	1,181	524

Table 4 Birds ringed as pulli that were later found dead, split by subspecies and season of recovery.

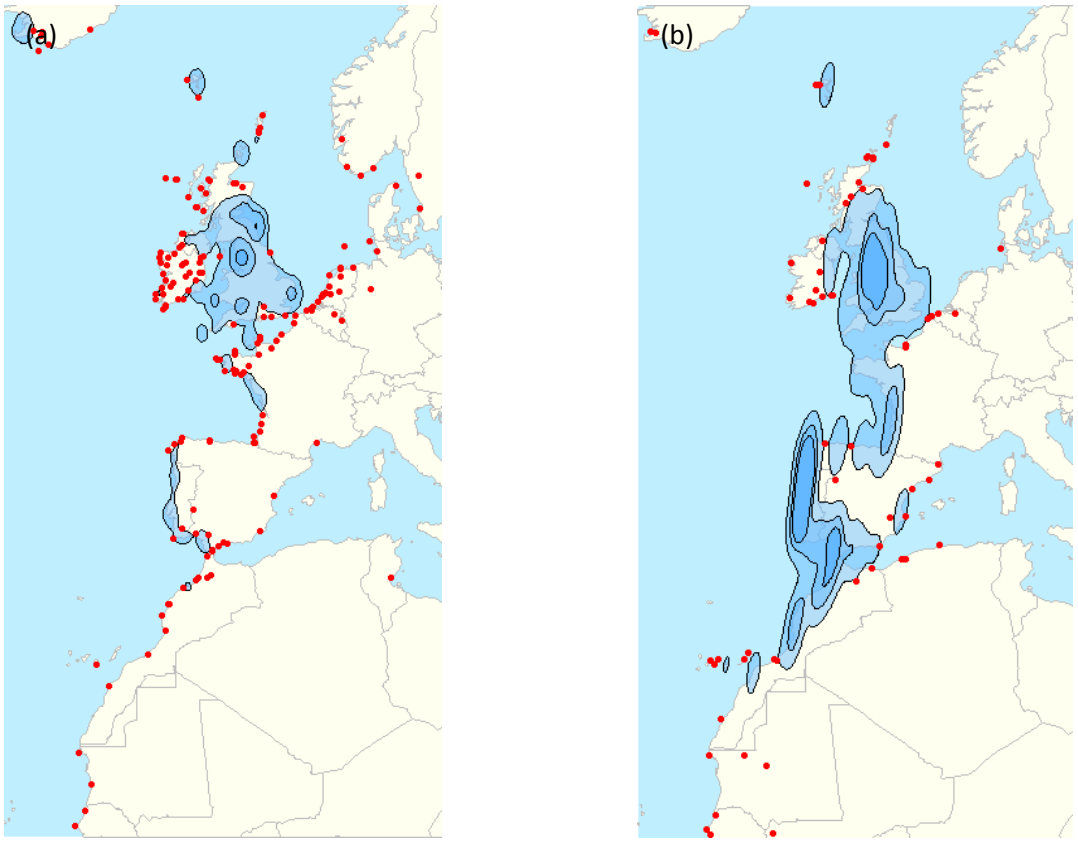

Figure 4 Kernel maps of dead Lesser Black-backed Gulls ringed as pulli for the subspecies *Larus fuscus graellsii* found during the (a) breeding season (April-July, 3,906 birds) and (b) winter (October-February, 1,414 birds). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries, only those outside the 90% kernel are shown.

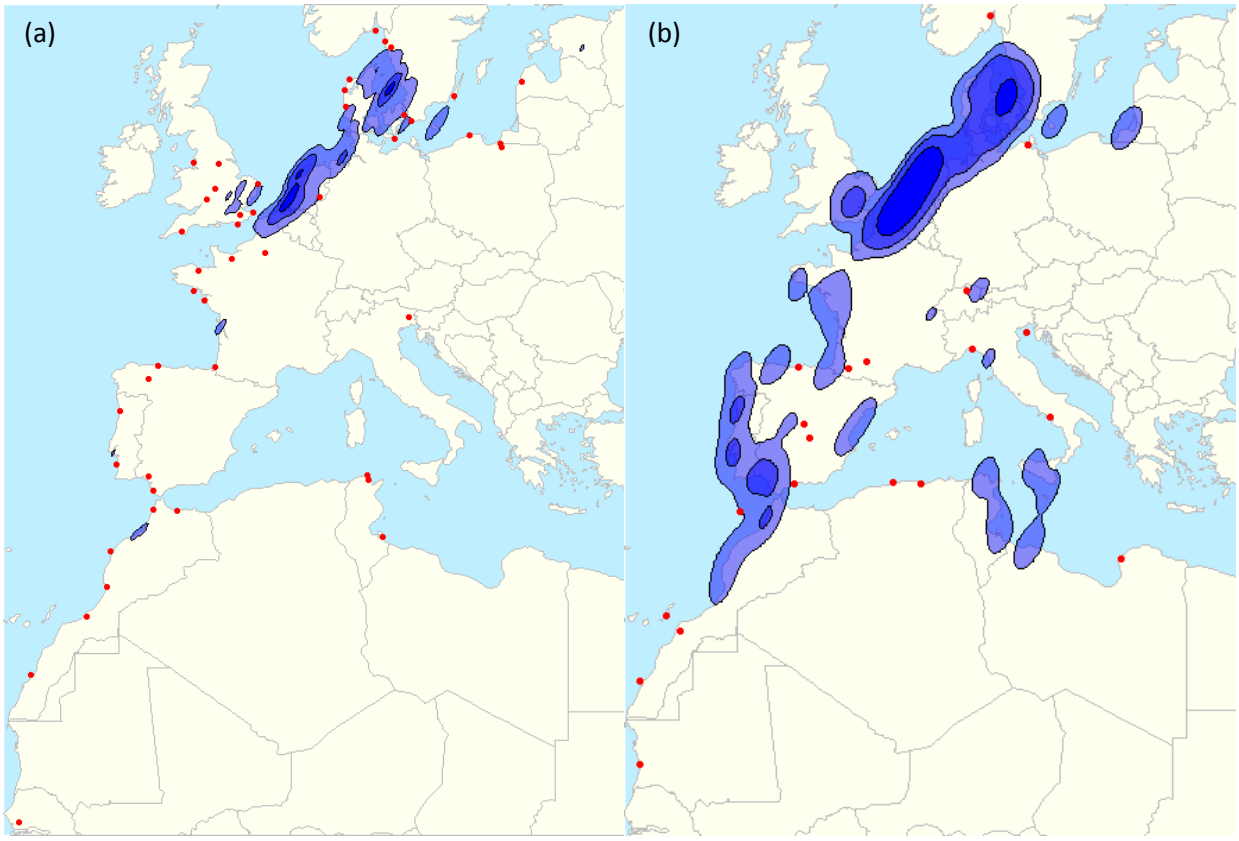

Figure 5 Kernel maps of dead Lesser Black-backed Gulls ringed as pulli for the subspecies *Larus fuscus intermedius* found during the (a) breeding season (April-July, 990 birds) and (b) winter (October-February, 499 birds). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries, only those outside the 90% kernel are shown.

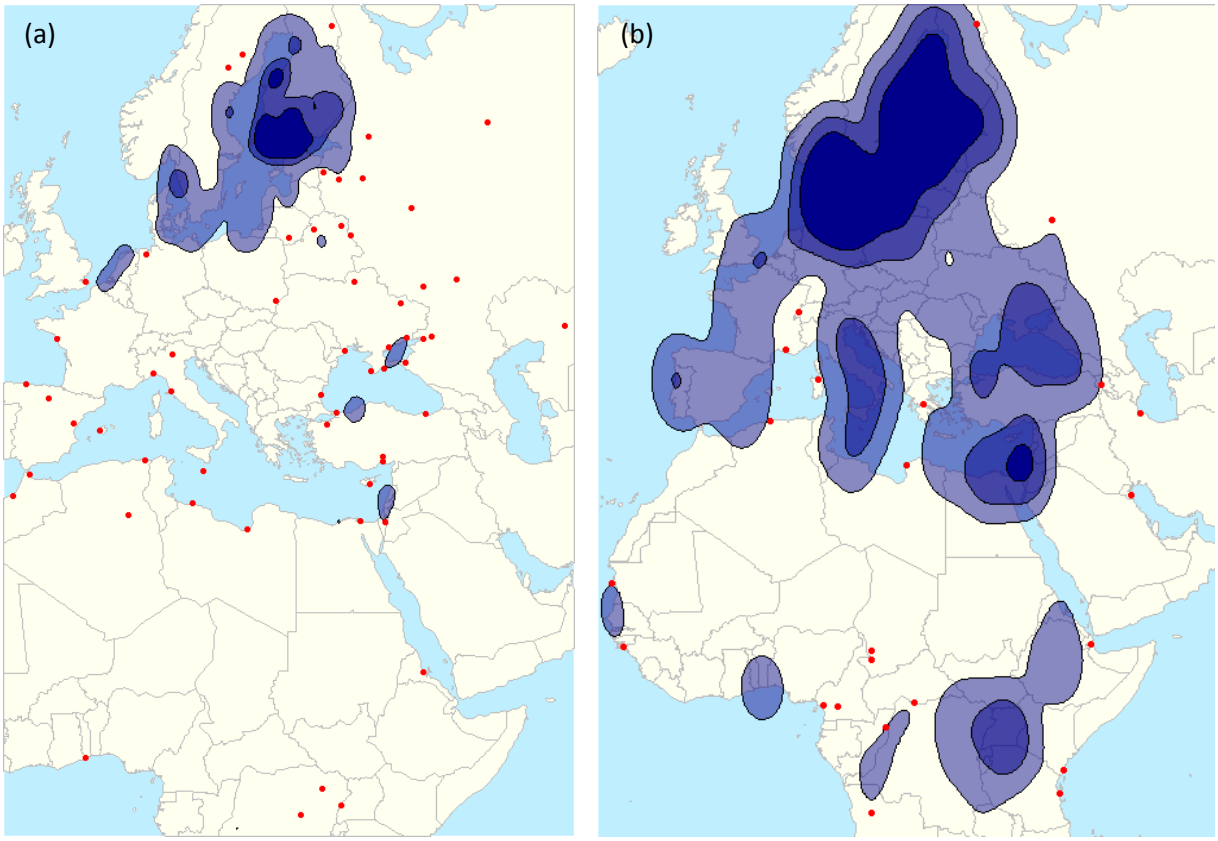

Figure 6 Kernel maps of dead Lesser Black-backed Gulls ringed as pulli for the subspecies *Larus fuscus fuscus* found during the (a) breeding season (April-July, 1,181 birds) and (b) winter (October-February, 524 birds). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries, only those outside the 90% kernel are shown.

These maps show considerable overlap between the breeding and wintering range of the Lesser Black-backed Gull, especially for the *graellsii* subspecies. In all cases, the winter range is larger than the breeding range, but this appears to be particularly true for *fuscus*.

3.1.2.1 Dead recoveries of birds ringed as pulli, split by age at finding

Records were divided into separate age classes per subspecies (Table 5) and kernel density plots produced of finding sites for each, to compare breeding (Figures 7-8) and winter distributions (Figures 9-10) across and between ages and subspecies (for *fuscus*, see Appendix 1).

Season	Subspecies	Age			
		Pulli	1st year	Subadult	Adult
Breeding	*Graellsii*	172	326	585	2,843
Winter		55	648	325	386
Breeding	*Intermedius*	284	130	123	454
Winter		96	252	81	70
Breeding	*Fuscus*	170	126	316	569
Winter		26	336	111	51

Table 5 The number of individual Lesser Black-backed Gulls ringed as pulli and recovered dead, split by age class and subspecies.

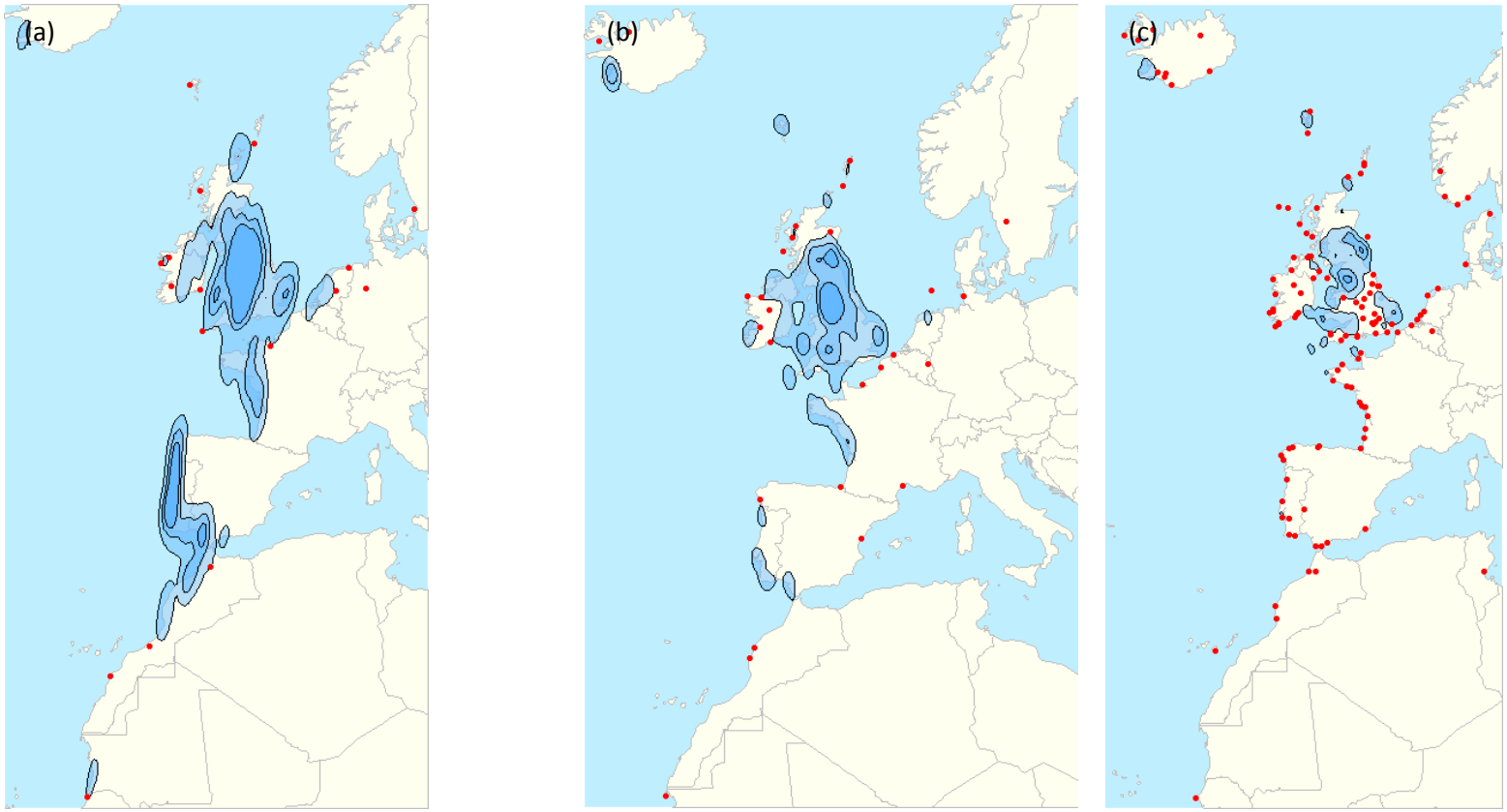

Figure 7 Kernel maps of Lesser Black-backed Gulls ringed as pulli, recovered dead during the breeding season (April-July) for *Larus fuscus graellsii* split by age (a) first years (326 birds) (b) subadults (585 birds) and (c) adults (2,843 birds). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries, only those outside the 90% kernel are shown.

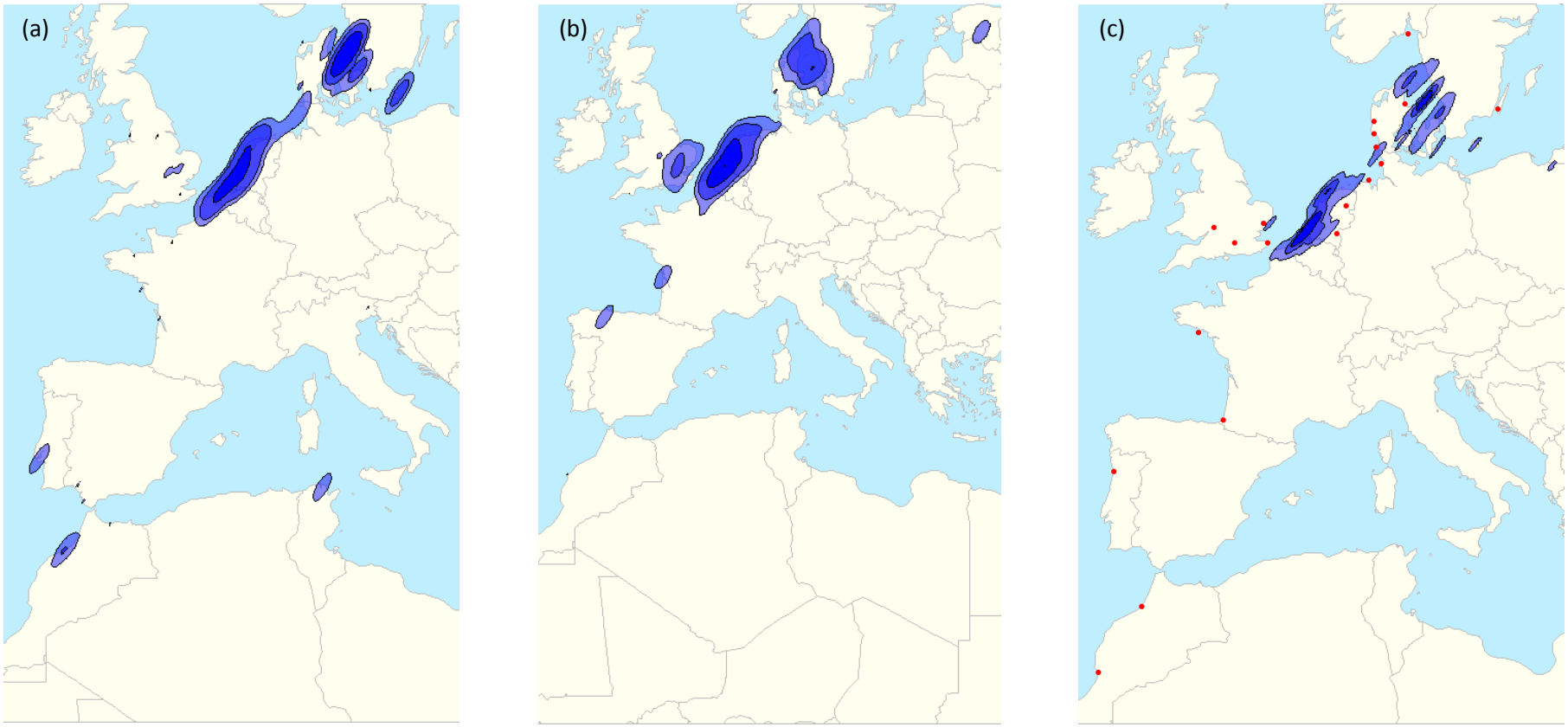

Figure 8 Kernel maps of birds ringed as pulli, recovered dead during the breeding season (April-July) for *Larus fuscus intermedius* split by age (a) first years (130 birds) (b) subadults (123 birds) (c) adults (454 birds). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries, only those outside the 90% kernel are shown.

Figures 7 and 8 show how adult birds have a tighter range that is more concentrated around breeding colonies during the breeding season than younger birds do for each subspecies. First years and subadults are apparently more likely to be found on the wintering grounds in the breeding season than adults are, especially in the case of *graellsii*.

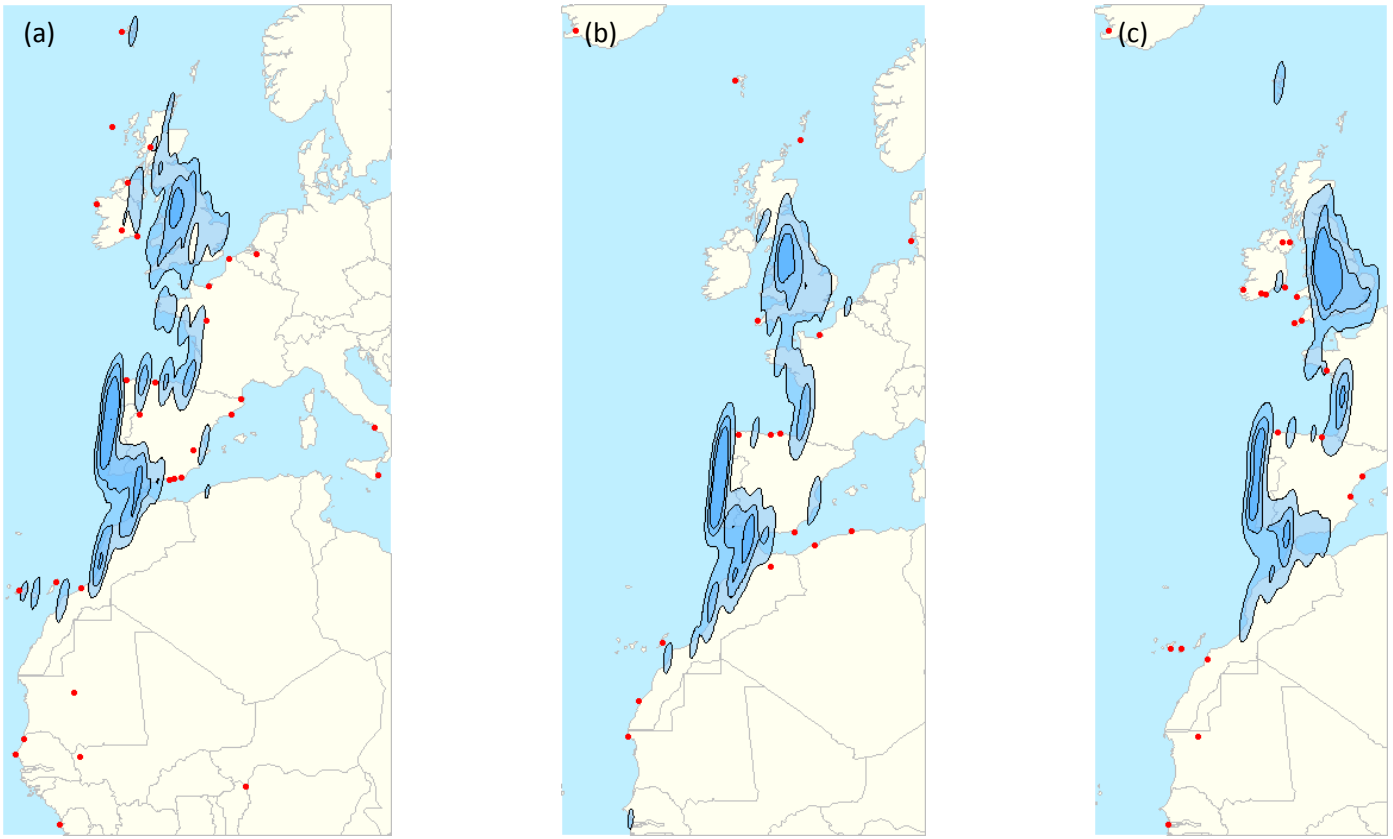

Figure 9 Kernel maps of birds ringed as pulli, recovered dead during the winter (October-February) for *Larus fuscus graellsii* split by age (a) first years (648 birds) (b) subadults (325 birds) (c) adults (386 birds). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries, only those outside the 90% kernel are shown.

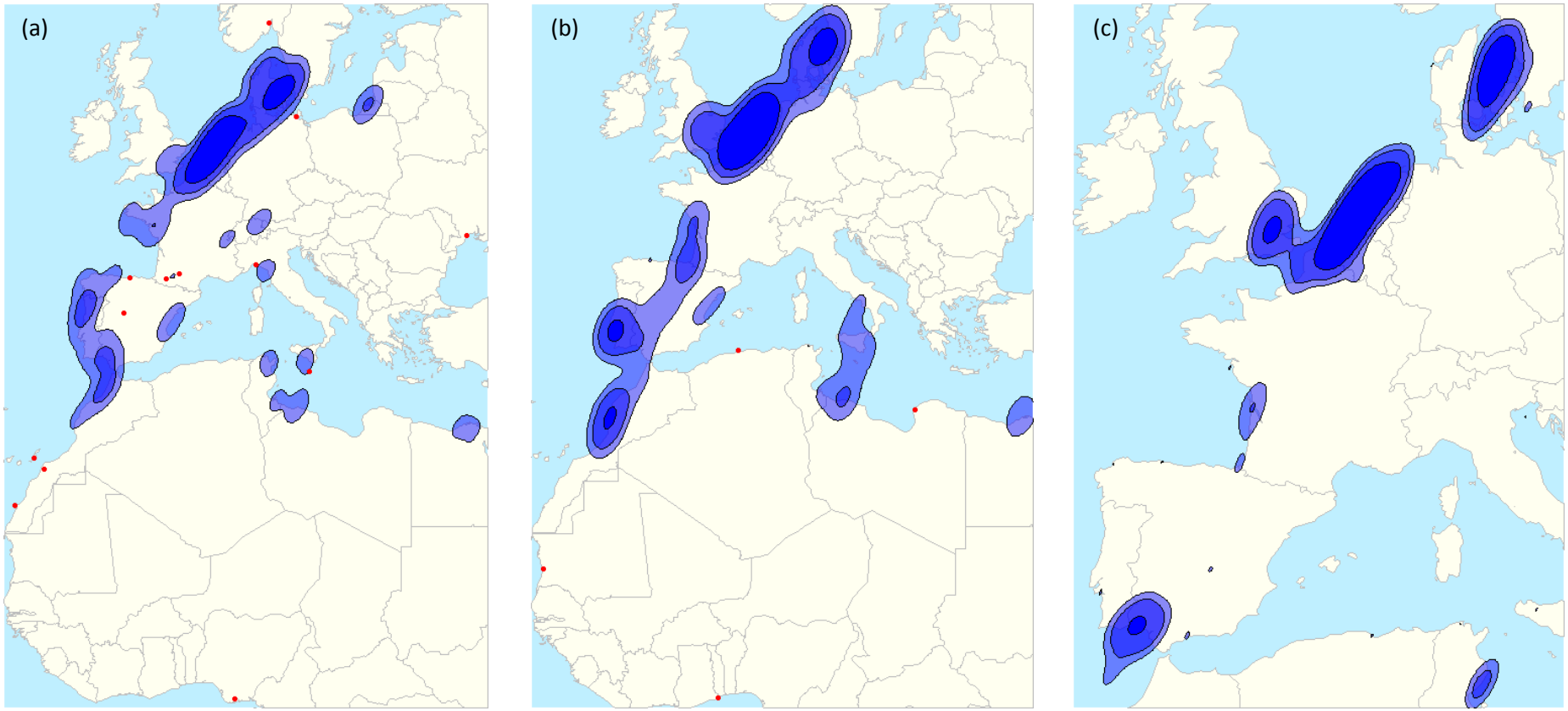

Figure 10 Kernel maps of birds ringed as pulli, recovered dead during the winter (October-February) for *Larus fuscus intermedius* split by age (a) first years (252 birds) (b) subadults (81 birds) (c) adults (70 birds). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries, only those outside the 90% kernel are shown

Figures 9 and 10 illustrate how for each Lesser Black-backed Gull subspecies, adults have a smaller wintering range than the younger age classes. This difference is least marked in *graellsii* and most pronounced for *fuscus* (see Appendix 1). For each subspecies, the first year and subadult wintering range extends further south than the adult range, and spans a wider longitudinal range.

3.1.2.2 International movements of the breeding population from recoveries of birds found dead

There were relatively few records of birds ringed as pulli in one country that were subsequently found dead at breeding age during the breeding season in a different country. At the subspecies level, there were 99 records for *graellsii* (birds ringed between 1927 and 2006, found between 1932 and 2012), 86 for *intermedius* (ringed 1929 to 2006, found 1934 to 2013) and 61 for *fuscus* (ringed 1937 to 2005, found 1943 to 2013) (Figure 11). Eighty-seven birds that were ringed as pulli in Britain were found dead as adults during the breeding season in other countries, while 12 birds that were ringed as pulli elsewhere in Europe were found dead as adults in the breeding season in Britain.

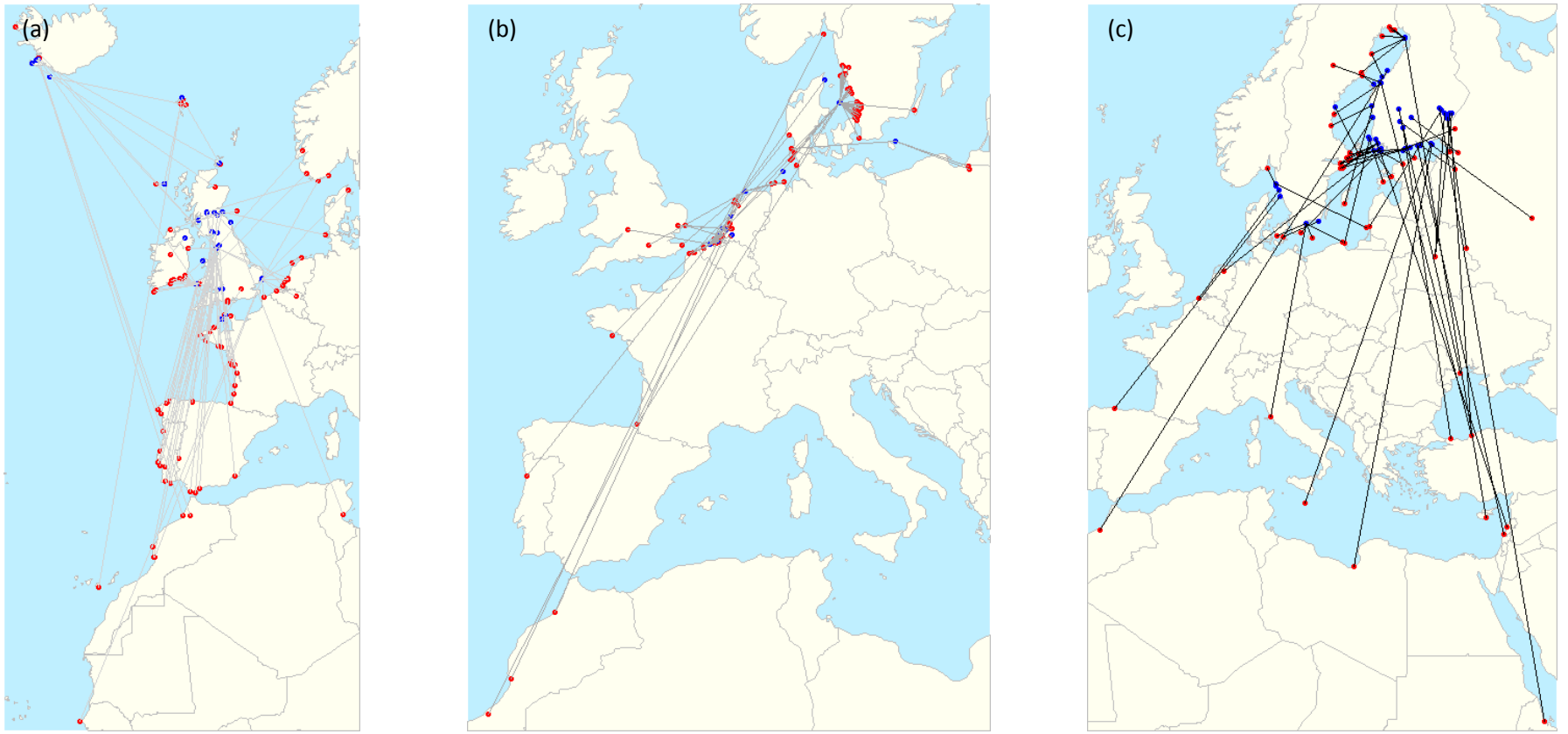

Figure 11 Ringing (blue dots) and recovery locations (red dots) of dead (a) *Larus fuscus graellsii*, (b) *Larus fuscus intermedius* and (c) *Larus fuscus fuscus* found during the breeding season (April-July) at least four calendar years after they were ringed as pulli. All these birds were reported dead in a different country to that in which they were ringed.

3.1.2.3 Changes in dead recovery trends

The distance between where birds of known age (ringed as pulli) and origin were recovered dead (excluding those birds that were deliberately killed) and where they were ringed varied significantly with many factors. In the breeding season (April-July), this distance varied significantly with birds' age classes (GLM, $F_{3,4265} = 132.66$, $p < 0.001$) (Figure 12), countries of origin (GLM, $F_{8,4265} = 3.22$, $p = 0.001$), subspecies (GLM, $F_{2,4265} = 9.00$, $p < 0.001$) and the decade in which they were recovered ($F_{10,4265} = 4.94$, $p < 0.001$) (Figure 13).

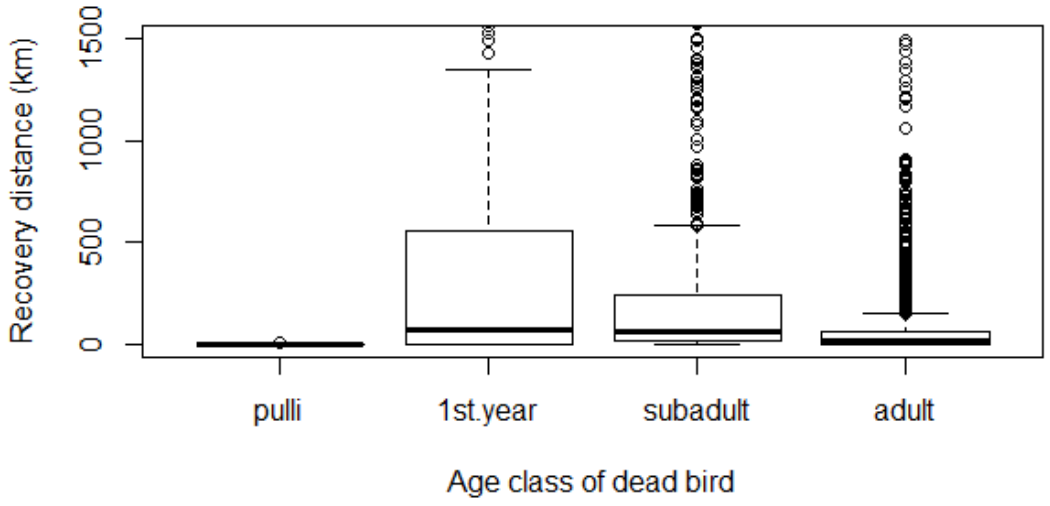

Figure 12 Variation in recovery distance with age class for Lesser Black-backed Gulls ringed as pulli and found dead (excluding birds deliberately killed) during the breeding season (April-July).

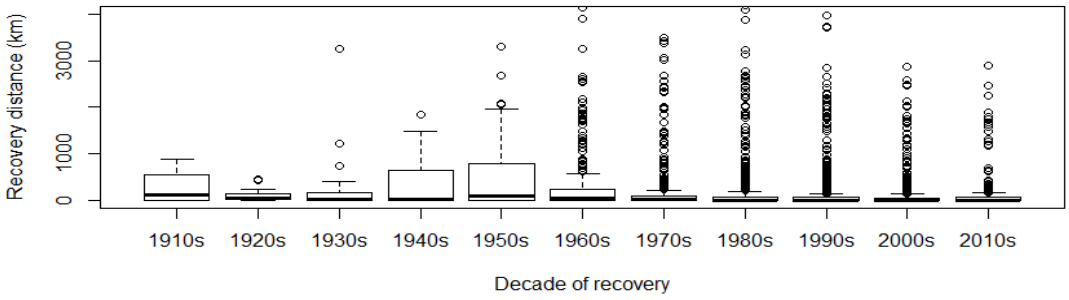

Figure 13 Variation of distance between ringing and recovery destination per decade for Lesser Black-backed Gulls ringed as pulli and found dead (excluding birds deliberately killed) during the breeding season (April-July).

Similar patterns were found when considering birds recovered dead during the winter (October-February), with distance varying significantly with age class (GLM, $F_{3,1673} = 54.96$, $p < 0.001$) (Figure 14), subspecies (GLM, $F_{2,1673} = 66.64$, $p < 0.001$), country of origin (GLM, $F_{9,1673} = 6.32$, $p < 0.001$) and the decade in which birds were reported (GLM, $F_{10,1673} = 3.05$, $p < 0.001$) (Figure 15).

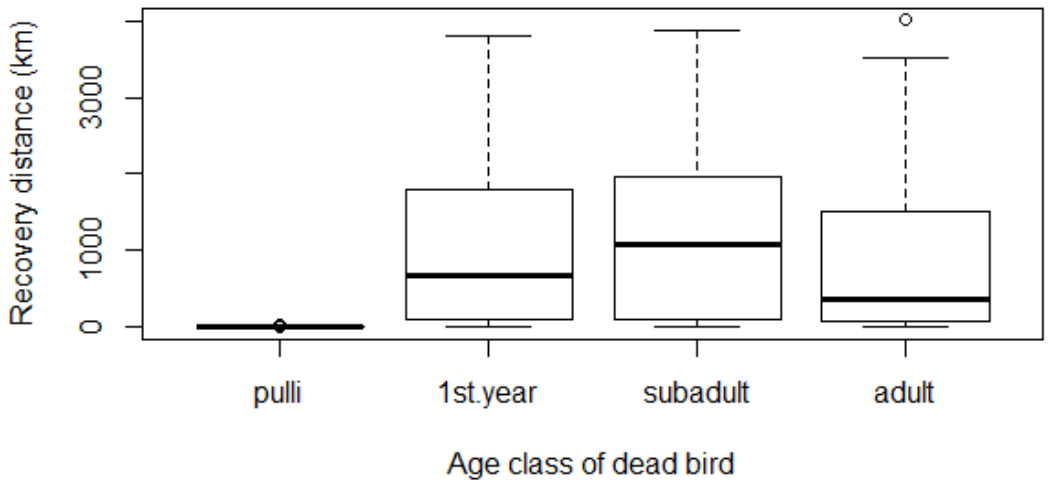

Figure 14 Variation in recovery distance with age class for Lesser Black-backed Gulls ringed as pulli and found dead (excluding birds deliberately killed) during the winter (October-February).

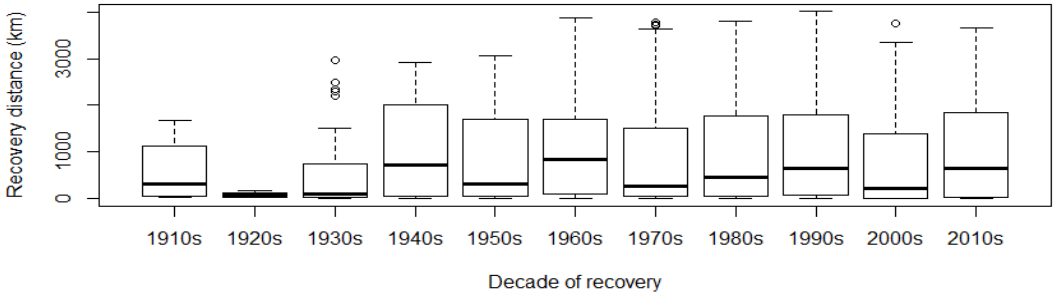

Figure 15 Variation of distance between ringing and recovery destination per decade for Lesser Black-backed Gulls ringed as pulli and found dead (excluding birds deliberately killed) during the winter (October-February).

3.2.1 Recoveries of birds reported alive (resightings and recaptures)

There were 20,009 records of individual Lesser Black-backed Gulls ringed as pulli or as subadults and adults during the breeding season that were subsequently found recaptured or resighted between the years 1910 and 2014 (Table 6). Many birds were recovered alive on more than one occasion. The number of recoveries rose sharply in the late-Twentieth Century, partly as a result of the introduction of Lesser Black-backed Gull colour ringing, which makes birds' rings easier to read in the field, an increase in the number of observers specifically searching for colour-marked gulls (pers. obs.) and more records of such reports being processed by ringing schemes as they moved to computerised systems.

Decade recovered	Number of birds
1910s	1
1920s	3
1930s	17
1940s	23
1950s	30
1960s	65
1970s	107
1980s	534
1990s	10,242
2000s	79,778
2010s	13,824

Table 6 Number of Lesser Black-backed Gulls ringed as pulli or as subadults and adults during the breeding season recaptured or resighted per decade reported.

3.2.1.2 Living recoveries of birds ringed as pulli

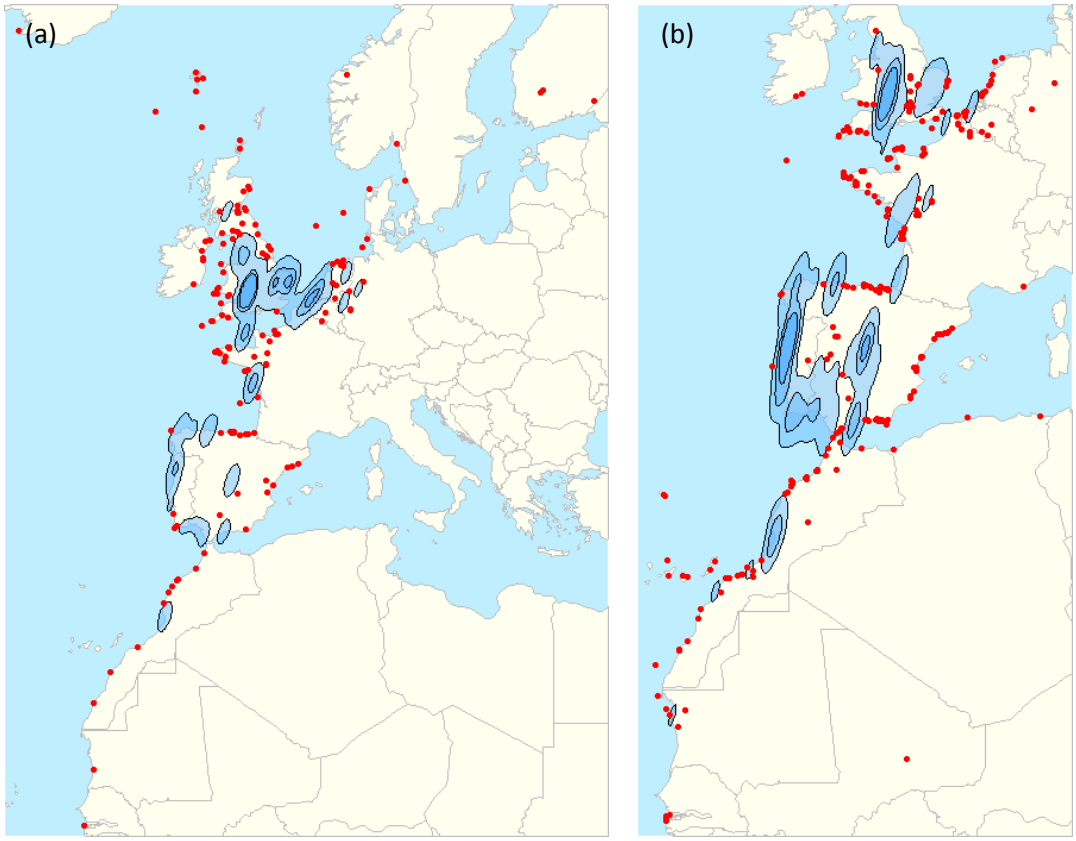

Figure 16 Kernel maps of resighted and recaptured Lesser Black-backed Gulls ringed as pulli for the subspecies *Larus fuscus graellsii* reported during the (a) breeding season (3,675 sightings of 2,751 birds, April-July,) (b) winter (October-February). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries outside the 90% kernel.

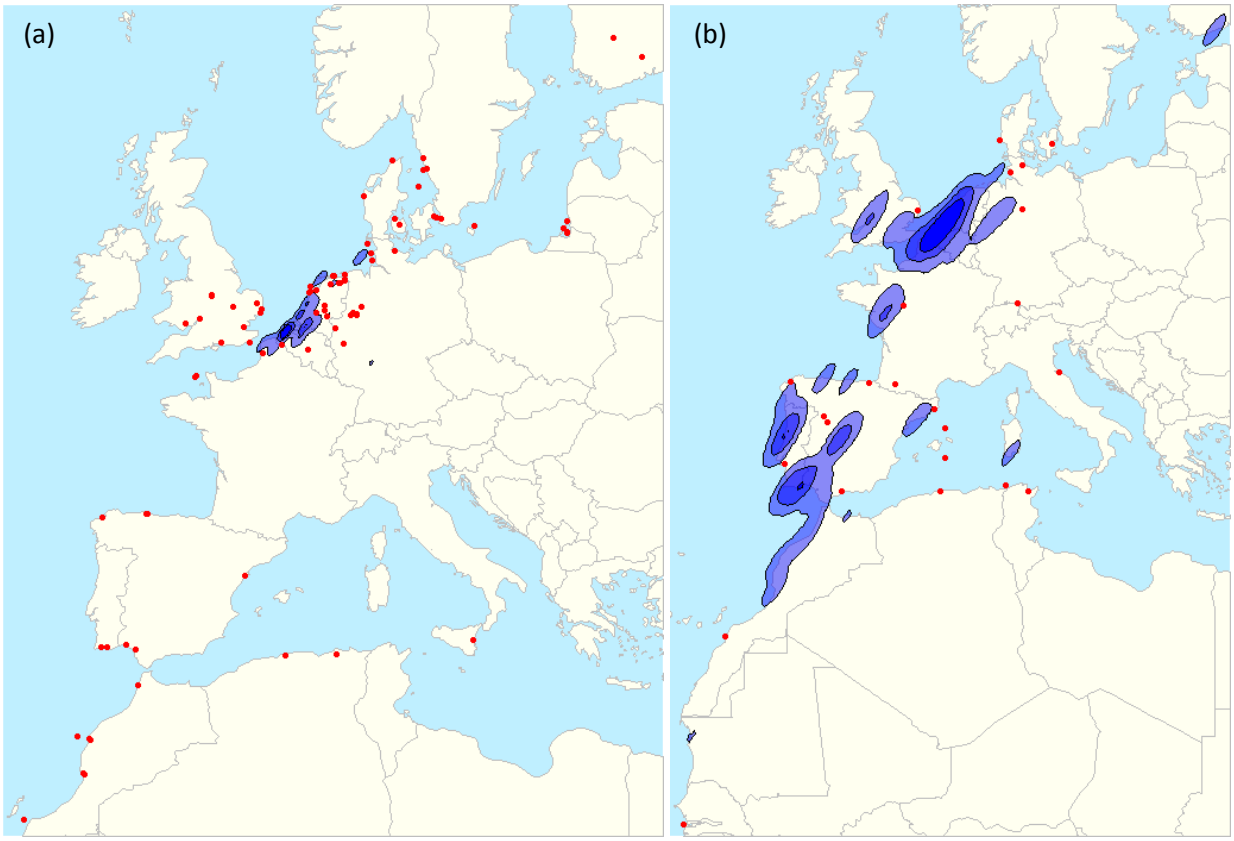

Figure 17 Kernel maps of resighted or recaptured Lesser Black-backed Gulls ringed as pulli for the subspecies *Larus fuscus intermedius* reported during the (a) breeding season (2,463 sightings of 1,688 birds, April-July) (b) winter (October-February). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries outside the 90% kernel.

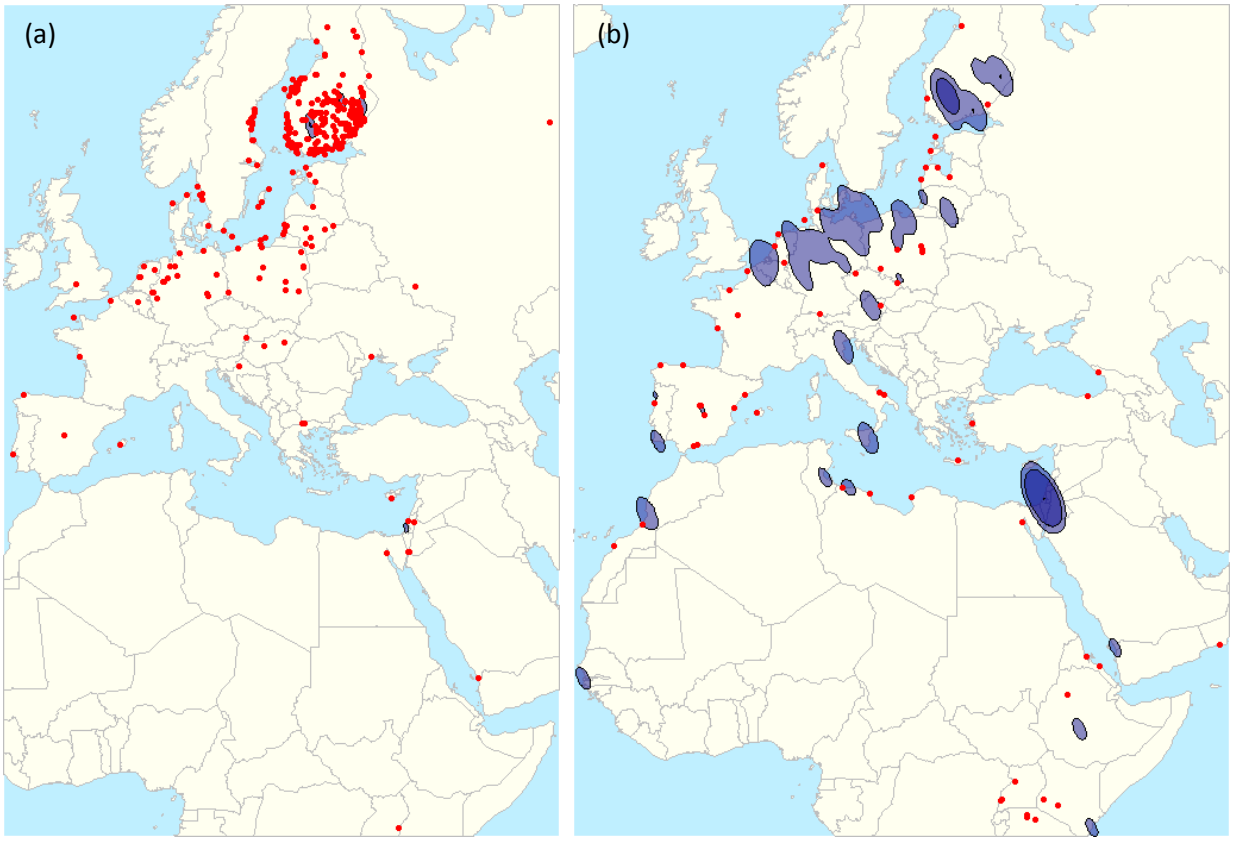

Figure 18 Kernel maps of resighted and recaptured Lesser Black-backed Gulls ringed as pulli for the subspecies *Larus fuscus fuscus* reported during the (a) breeding season (55,827 sightings of 4,361 birds, April-July) (b) winter (October-February). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries outside the 90% kernel.

Figures 16-18 demonstrate how reports of living Lesser Black-backed Gulls are much more biased by observer effort than reports of dead birds. This can be seen in the large number of narrow, discrete kernels centred on spots where people specifically go to look for ringed gulls, such as the Algarve, compared to the larger kernels that are a result of chance encounters on the equivalent maps of dead recoveries (Figures 4-6).

3.2.2.2 Recoveries of birds ringed as pulli and reported alive (resightings and recaptures), split by age

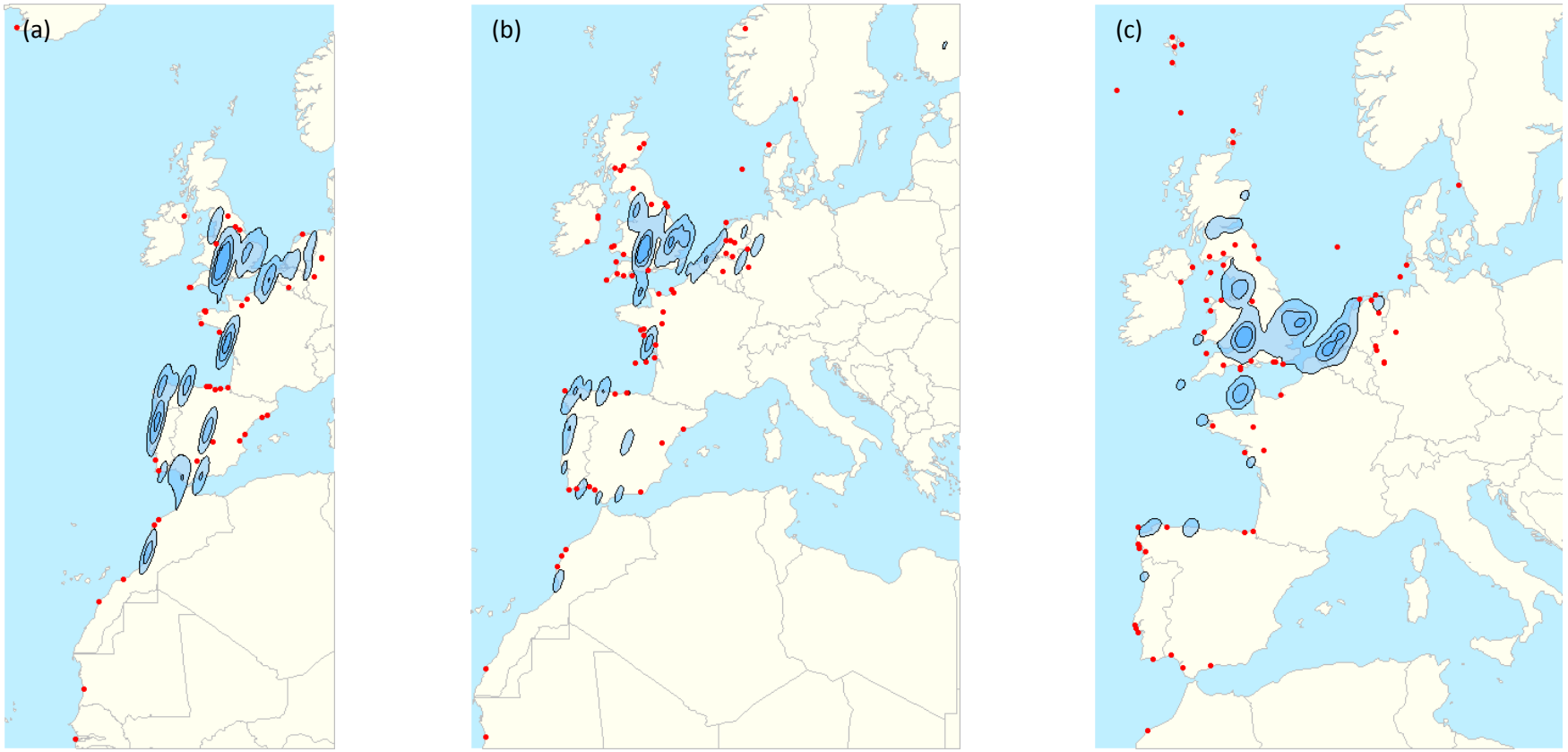

Figure 19 Kernel maps of birds ringed as pulli, resighted or recaptured during the breeding season (April-July) for *Larus fuscus graellsii* split by age (a) first years (919 sightings of 838 birds) (b) subadults (1,310 sightings of 1,167 birds) (c) adults (1,446 sightings of 1,073 birds). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries outside the 90% kernel.

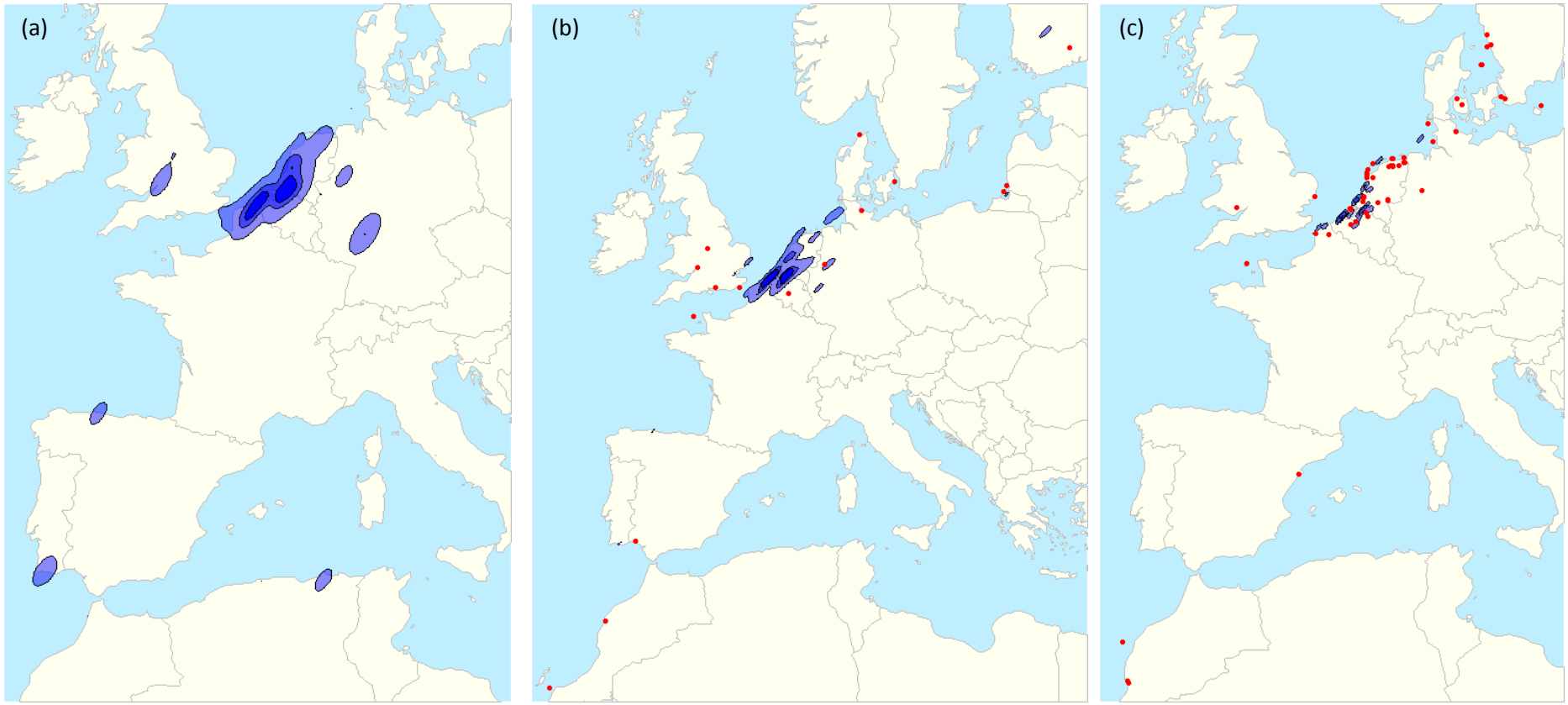

Figure 20 Kernel maps of birds ringed as pulli, resighted or recaptured during the breeding season (April-July) for *Larus fuscus intermedius* split by age (a) first years (188 sightings of 164 birds) (b) subadults (389 sightings of 325 birds) (c) adults (1,886 sightings of 1,265 birds). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries outside the 90% kernel.

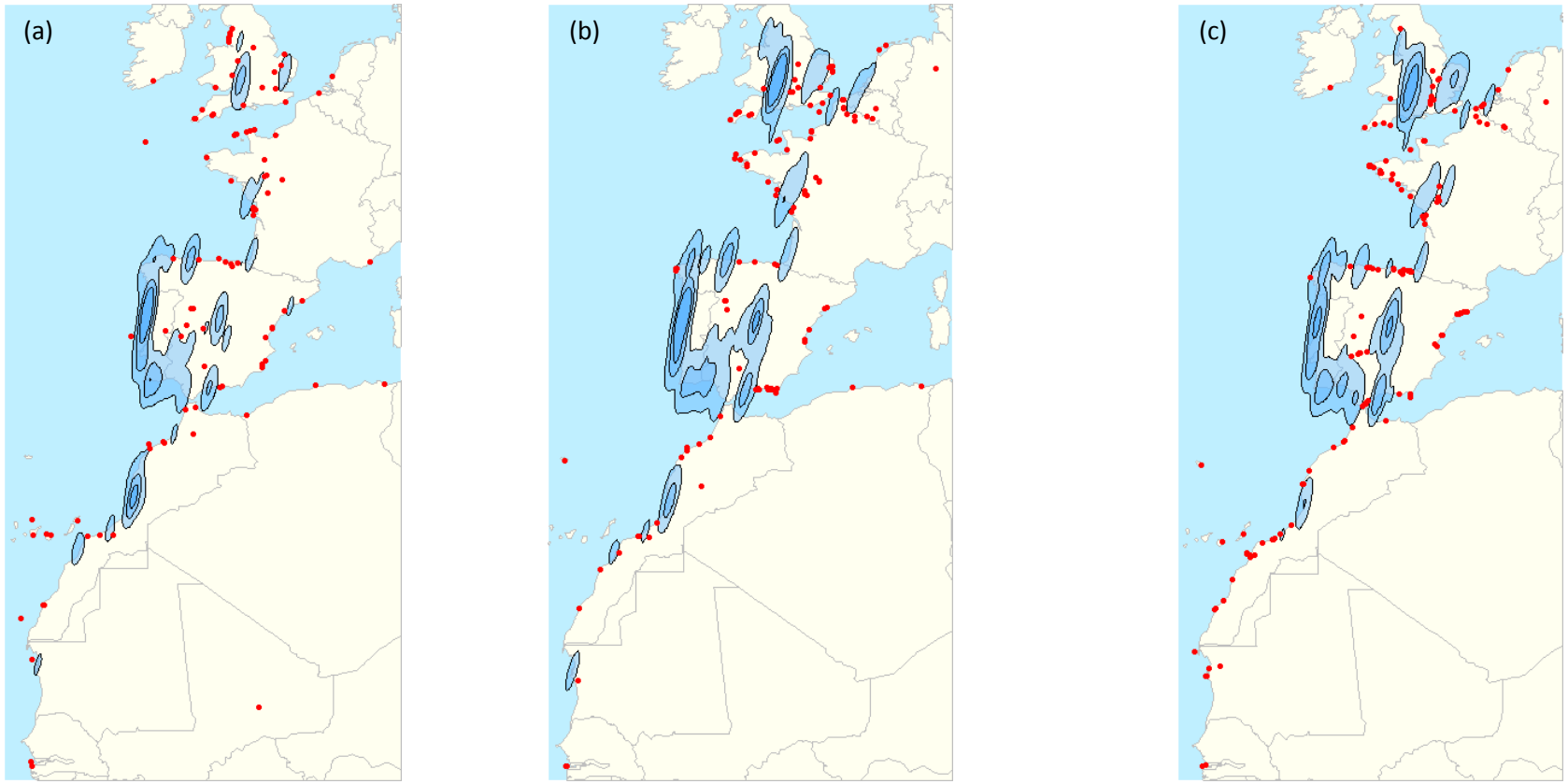

Figure 21 Kernel maps of birds ringed as pulli, resighted or recaptured during the winter (October-February) for *Larus fuscus graellsii* split by age (a) first years (2,469 sightings of 2,146 birds) (b) subadults (3,504 sightings of 2,601 birds) (c) adults (4,471 sightings of 2,511 birds). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries outside the 90% kernel.

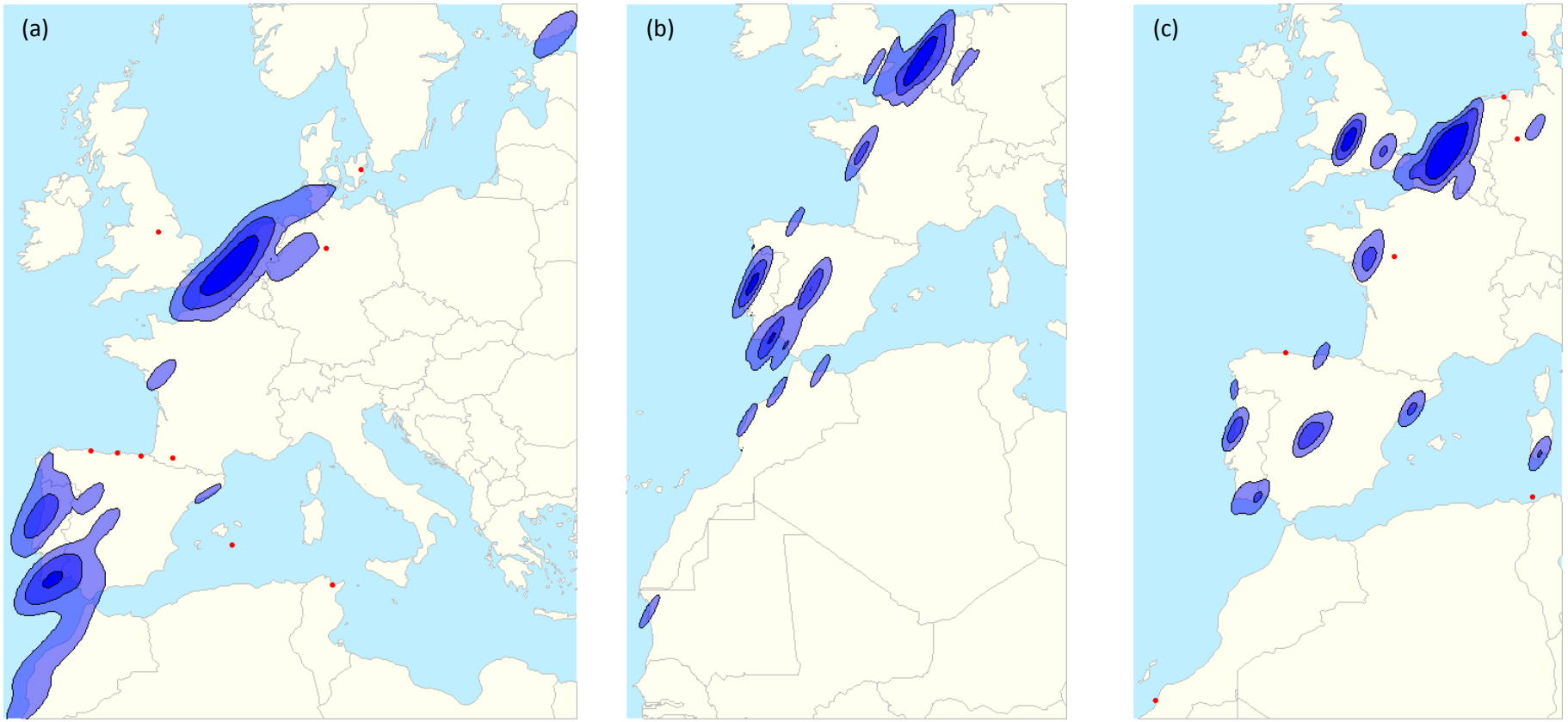

Figure 22 Kernel maps of birds ringed as pulli, resighted or recaptured during the winter (October-February) for *Larus fuscus intermedius* split by age (a) first years (201 sightings of 170 birds) (b) subadults (169 sightings of 140 birds) (c) adults (139 sightings of 106 birds). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries outside the 90% kernel.

3.2.2.3 International movements of the breeding population from recoveries of birds ringed as pulli, resighted or recaptured during the breeding season

As with dead recoveries, there were relatively few records of birds ringed as pulli in one country that were subsequently resighted or recaptured at breeding age during the breeding season in a different country. At the subspecies level, there were 462 records of 264 individuals for *graellsii* (birds ringed between 1961 and 2007, found between 1976 and 2012), 271 records of 188 individuals for *intermedius* (ringed 1973 to 2009, found 1986 to 2013) and 601 records of 284 individuals for *fuscus* (ringed 1971 to 2008, found 1987 to 2013) (Figure 23). 259 birds that were ringed as pulli in Britain were recaptured or resighted as adults during the breeding season in other countries, while only five birds that were ringed as pulli elsewhere in Europe were recaptured or resighted as adults in the breeding season in Britain.

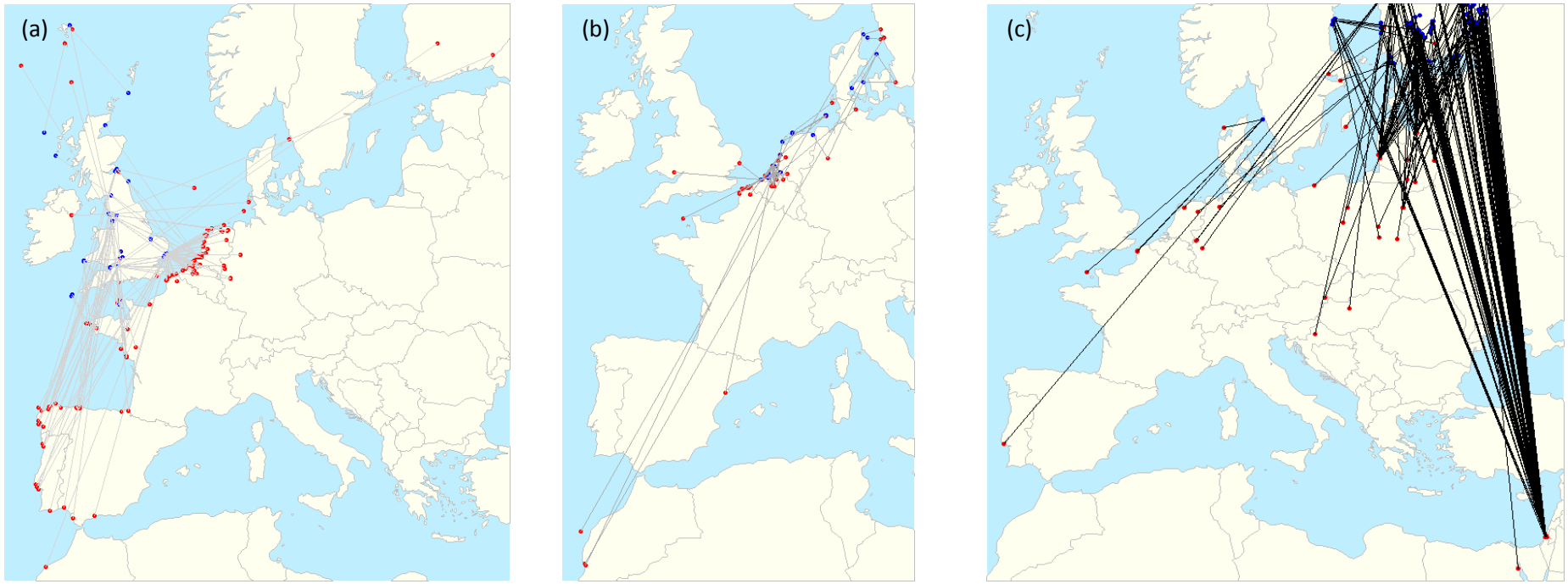

Figure 23 Ringing (blue dots) and recovery locations (red dots) of (a) *Larus fuscus graellsii*, (b) *Larus fuscus intermedius* and (c) *Larus fuscus fuscus* resighted or recaptured during the breeding season (April-July) at least four calendar years after they were ringed as pulli. All these birds were reported in a different country to that in which they were ringed

4 DISCUSSION

4.1 Breeding Distribution

The breeding distributions of the three subspecies are contiguous but do not show much evidence of overlap. As birds were assigned subspecies on the basis of the country in which they were ringed (and most of these were ringed as pulli), this result suggests that the majority of Lesser Black-backed Gulls recruit to the areas that are typically used by their subspecies, confirming the natal philopatry widely reported in the literature (e.g. O'Connell 1995; Wanless et al. 1996; Camphuysen 2013; Rock & Vaughan 2013; Ross-Smith *et al*. 2014b). A relatively small number of birds were recovered at breeding age in countries other than those in which they were ringed as pulli. This was notable for resightings and recaptures of *fuscus*, indicating movement between countries around the Baltic, perhaps due to birds recruiting to new colonies in response to the widespread breeding failure and colony declines this subspecies has experienced in recent decades (Hario *et al*. 1994; Hario *et al*. 2004). There was also evidence of movement of *intermedius* from the Netherlands to Belgium, and of *graellsii* moving between different parts of its range in Britain, Ireland and North-West France.

Interestingly, there was limited evidence of birds recruiting to countries where a different subspecies to their own normally breeds. This is seen more clearly in recoveries of living birds than those of dead, where a number of *graellsii* ringed as pulli in British colonies were later seen or recaptured in the Netherlands, Belgium and northeast France. It is possible that some of these resightings and recaptures represent birds that have not yet returned to their breeding grounds (i.e. records from early-April), or birds that have finished breeding (i.e. records from late-July), or even breeding birds taking long foraging trips to different countries, as has been demonstrated by data from GPS-tagging studies (Camphuysen, *unpublished data*, Ross-Smith*, unpublished data*). However, it seems likely that some of these birds have recruited to colonies outside Britain, possibly as a response to collapses at the colonies in which they hatched. For example, a number of recoveries of living birds in Belgium and the Netherlands in recent years originated from Orford Ness, where there has been a catastrophic decline in Lesser Black-backed Gull breeding numbers in recent years (Ross-Smith *et al*. 2014a).

The analyses of distances moved by birds found dead in the breeding season suggests that breeding birds have moved smaller distances from their natal colonies since the mid-Twentieth Century, perhaps suggesting that Lesser Black-backed Gulls have become more likely to recruit at or close to their natal colonies than they were previously, and/or that adult birds have to travel less far to forage during the breeding season than they did before this time. This change would also coincide with the exponential population growth reported for this species at this time. However, the extent of this effect could be confounded by the advent of culling programmes at around this time, which often targeted breeding birds at their colonies (e.g. O'Connell 1995). This could have disrupted the movements breeding birds would have made if undisturbed (as reported elsewhere, e.g. Sellers & Shackleton 2011). It is also possible that drop in distance travelled could also be an artefact of an intensification in the study of Lesser Black-backed Gulls at particular colonies and the advent of colour ringing, meaning that birds were more likely to be recovered in the vicinity of their nest sites than previously. The finding that the maximum distance birds travel has not changed (Figure 13) supports the idea that the overall behaviour of this species might not have changed.

4.2 Wintering Distribution

The western part of the wintering range of *fuscus* overlaps with that of *intermedius* and *graellsii*, but there is very little overlap between *fuscus* and the other two subspecies elsewhere in the wintering

range. There is evidence of *intermedius* visiting parts of the central and eastern Mediterranean (Tunisia, Libya, Sicily, Egypt) that falls in the *fuscus* wintering range, but these areas are relatively small and discrete, and do not appear to connect to more southerly wintering areas. Wintering *intermedius* also overlap with *fuscus* in southern Scandinavia, suggesting that some birds of both subspecies spend some or all of the winter months close to their breeding grounds, although these could also be a result of some birds leaving their wintering grounds late or returning early. The overall population of *fuscus* is declining faster than that of *intermedius* and *graellsii*, and this is thought to be linked in part to poisons ingested on the birds' wintering grounds in eastern and central Africa that affect chick survival once adults head back north to breed (Hario *et al*. 2004, Hario & Nuutinen 2011). It would be interesting to investigate whether the survival and productivity of birds that winter in the western part of the range is more similar to that of *intermedius* and *graellsii*.

The kernel maps show substantial overlap between the wintering ranges of *intermedius* and *graellsii* in southern Britain, western France, Spain, Portugal and Morocco. The winter range of *graellsii* spans the narrowest longitude of any of the three subspecies. The latitudinal range of *graellsii* is greater than that of *intermedius*, stretching from the Faroes to the Canary Islands/Western Sahara for *graellsii* and southern Sweden to Morocco for *intermedius*.

There is evidence that all three subspecies are found in Britain during the winter, although there are regional differences in their strongholds. The results suggest that Britain is not an important wintering area for *fuscus*, although birds do visit much of southern, central and eastern England, perhaps on passage to southwest Europe and North Africa. Dead recoveries suggest southeast England is an important wintering area for *intermedius*. Britain is also an important wintering area for *graellsii*, although the stronghold appears to be further west and north than that of *intermedius*, in northern and western England, Wales and southern Scotland. Despite the regional differences, the wintering distributions of the three subspecies suggest individuals from each are likely to visit the same areas and could mix during the winter months. This could provide opportunities for cultural transmission of information and behaviour.

4.3 Changes with Age

The results support those from previous studies showing how Lesser Black-backed Gull range contracts as birds mature, probably as a result of adult birds wintering closer to their breeding grounds than younger individuals (e.g. Marques *et al*. 2010; Jorge *et al*. 2011; Ross-Smith *et al*. 2014b), although the dataset used here was larger than that of other studies and encompassed all subspecies over much of the breeding range. The contraction in wintering range with age appeared more marked for *intermedius* and *fuscus* than for *graellsii*. For all subspecies, there was also evidence of first year and subadult birds remaining outside the breeding grounds in the breeding season, as has been widely reported elsewhere (e.g. Wernham *et al*. 2002).

4.4 Conservation Implications

Figures 11 and 23 might indicate that the population declines reported at important colonies of *graellsii* in Britain are accompanied by a redistribution of birds from these colonies to other countries, including those that fall into the breeding range typically thought to be occupied by the *intermedius* subspecies. This supports previous work suggesting that there could be a metapopulation of Lesser Black-backed Gulls across the southern North Sea, taking in eastern England and the Netherlands (Ross-Smith *et al*., 2014b). The numbers of birds involved also indicate that birds hatched in Britain might become breeding birds in other countries more often than birds from abroad breed in Britain, but the values are so small that this statement cannot be made with any confidence. Nevertheless, this provides circumstantial evidence of gene flow between *graellsii* and *intermedius*, which are already known to be very similar to one another genetically (Collinson *et al*. 2008). This study suggests that such redistribution is relatively rare. However, firm conclusions cannot be drawn about the extent to which such movements may mean that national-scale population declines (such as those reported in the UK) are simply the result of birds moving to other parts of their range.

Acknowledgements

This report would not have been possible without the work of many ringers and volunteers resighting living birds and reporting dead ones. Thanks to Penny Mitchell (BTO) for all her work on the tender document. Alex Banks and Tim Frayling (Natural England) provided helpful comments at all stages of this work.

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Appendix 1

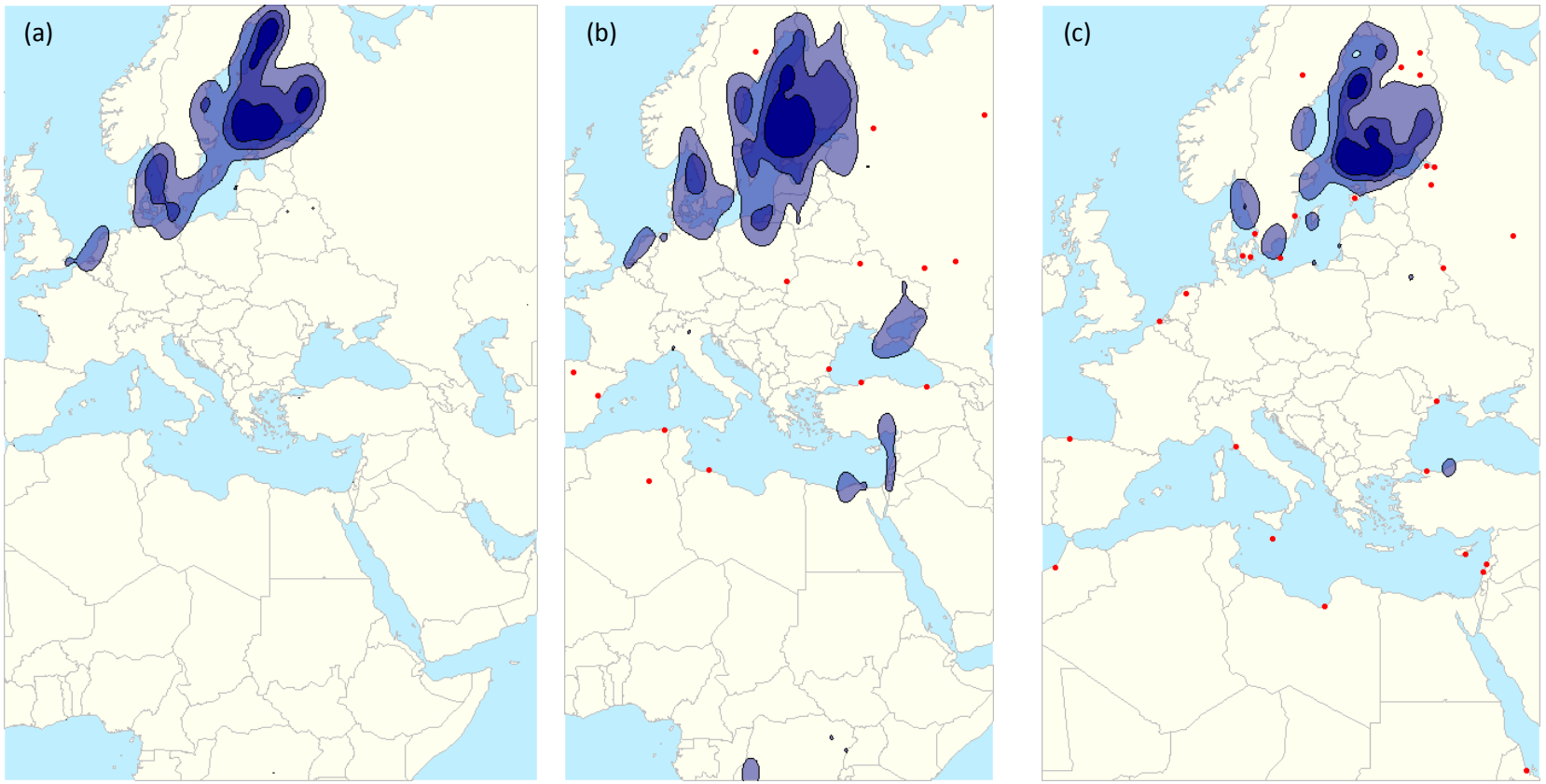

Figure A1 Kernel maps of birds ringed as pulli, recovered dead during the breeding season (April-July) for *Larus fuscus fuscus* split by age (a) first years (126 birds) (b) subadults (316 birds) (c) adults (569 birds). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries, only those outside the 90% kernel are shown.

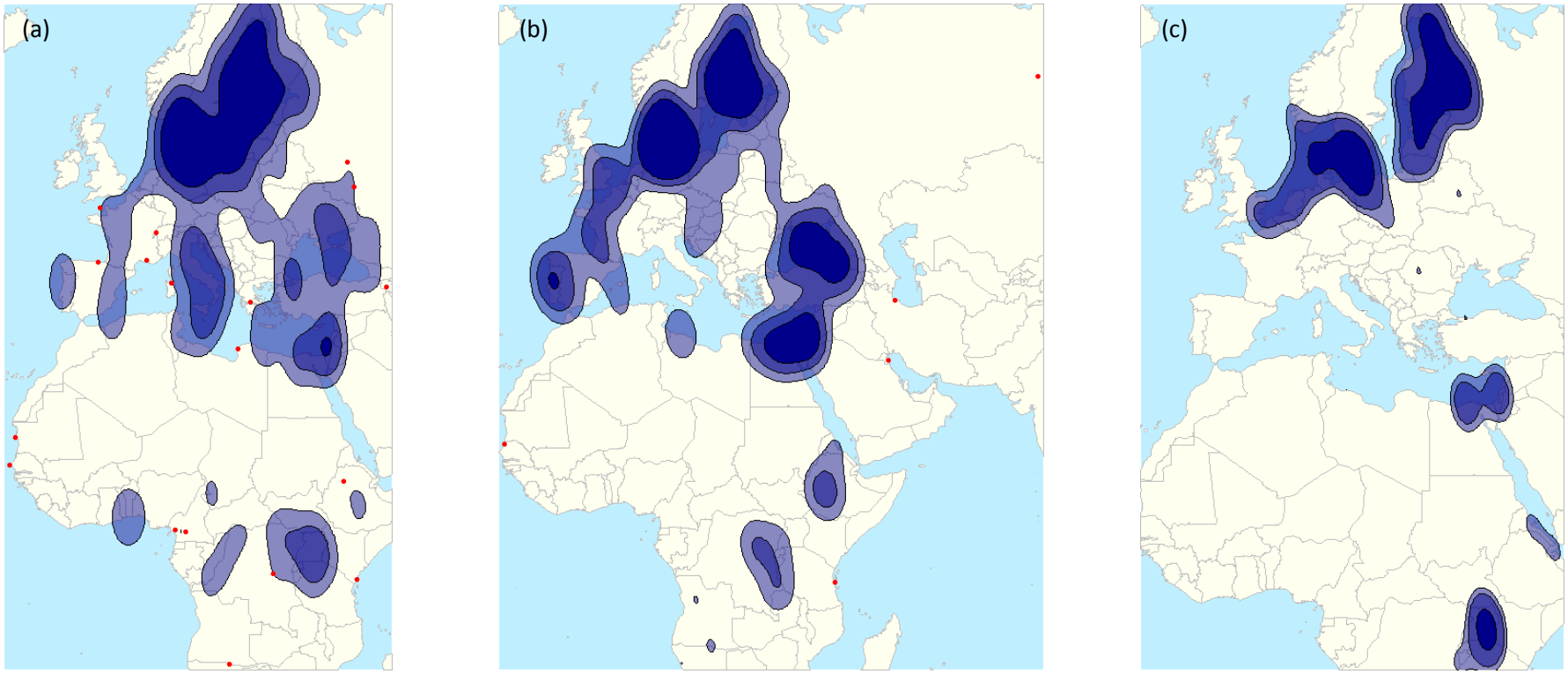

Figure A2 Kernel maps of birds ringed as pulli, recovered dead during the winter (October-February) for *Larus fuscus fuscus* split by age (a) first years (336 birds) (b) subadults (111 birds) (c) adults (51 birds). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries, only those outside the 90% kernel are shown.

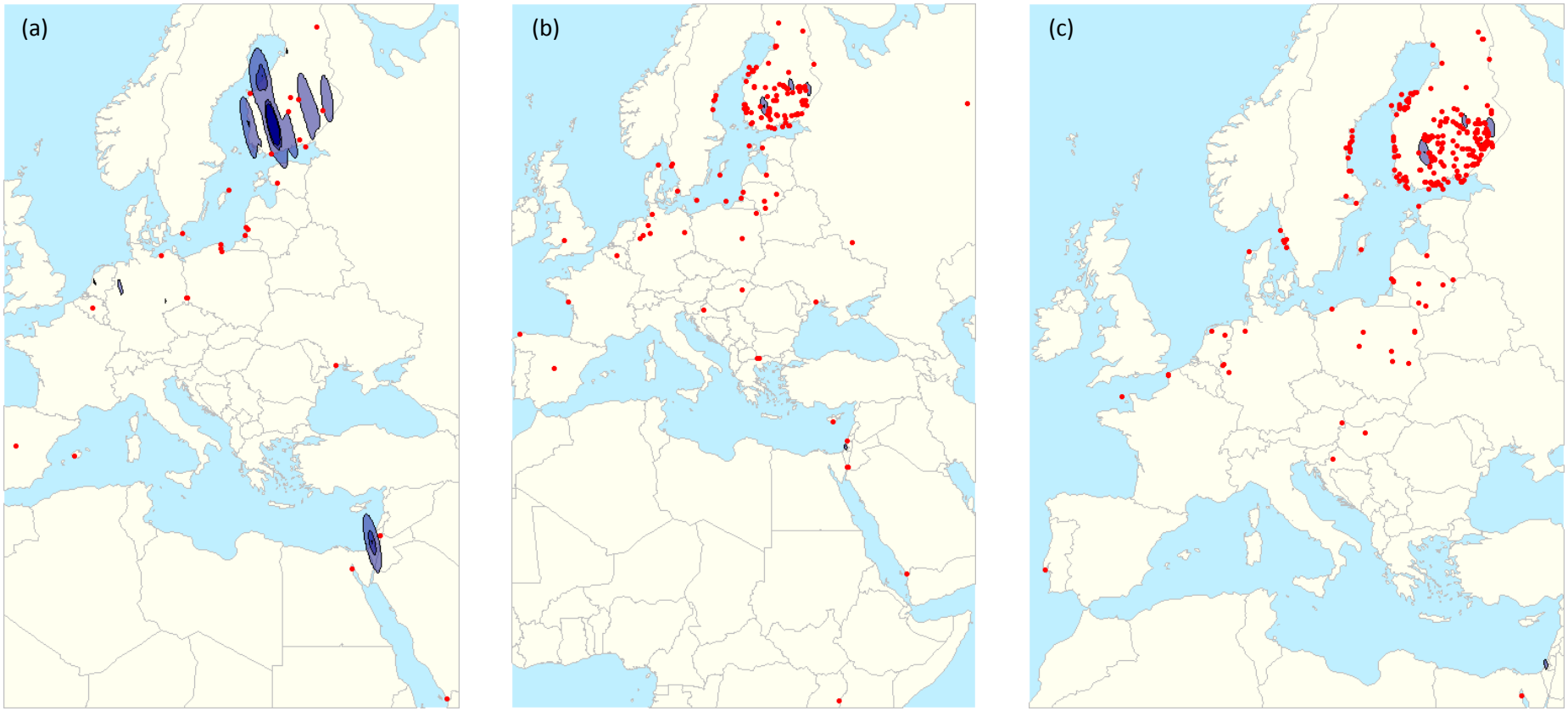

Figure A3 Kernel maps of birds ringed as pulli, resighted or recaptured during the breeding season (April-July) for *Larus fuscus fuscus* split by age (a) first years (895 sightings of 506 birds) (b) subadults (17,367 sightings of 2,601 birds) (c) adults (37,565 sightings of 2,735 birds). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries outside the 90% kernel.

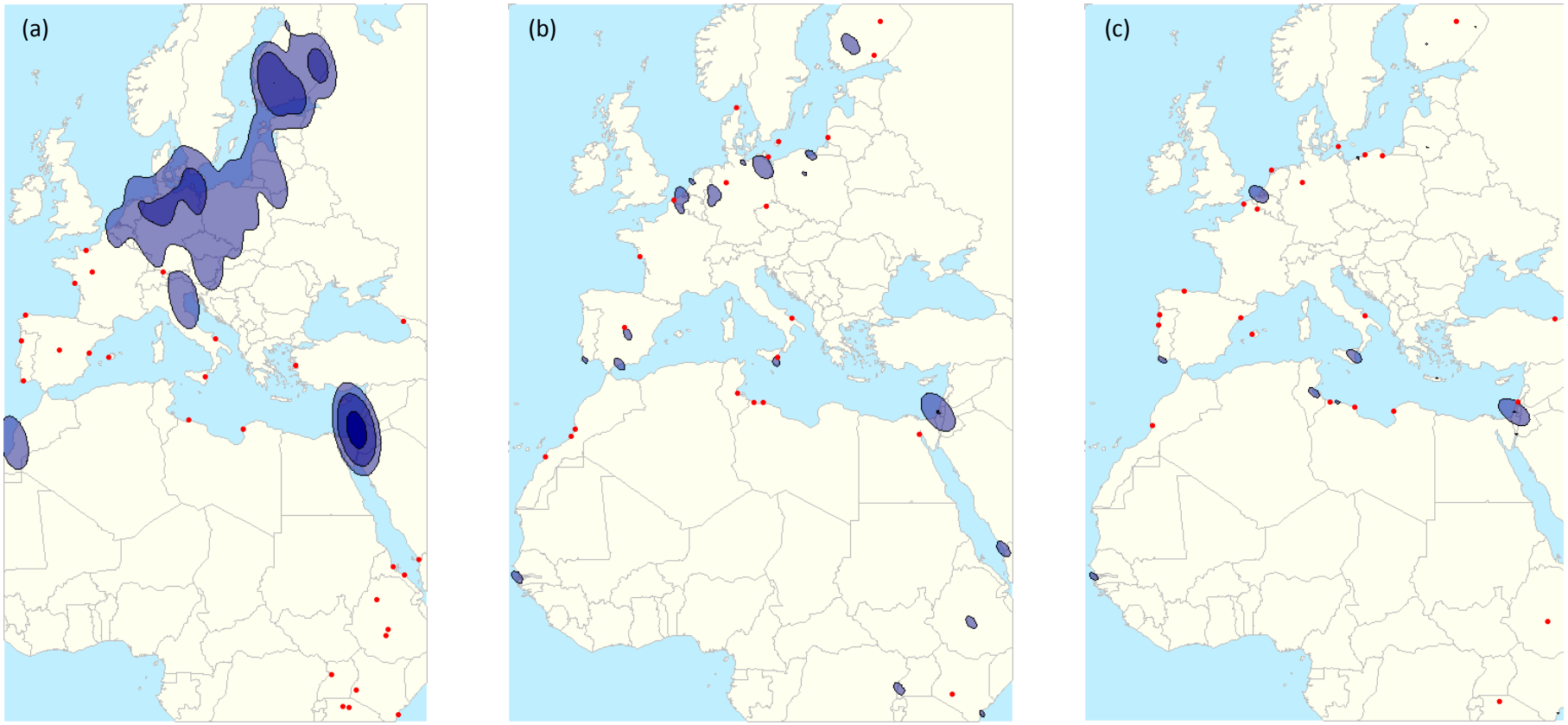

Figure A4 Kernel maps of birds ringed as pulli, resighted or recaptured during the winter (October-February) for *Larus fuscus fuscus* split by age (a) first years (539 sightings of 302 birds) (b) subadults (466 sightings of 159 birds) (c) adults (532 sightings of 173 birds). Smoothed kernels enclose 50% (darkest), 75% and 90% (lightest) of recoveries. Dots are actual site of recoveries outside the 90% kernel.