



# Interspecific variation in non-breeding aggregation: a multi-colony tracking study of two sympatric seabirds

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**ABSTRACT:** Migration is a widespread strategy for escaping unfavourable conditions during winter, but the extent to which populations that segregate during the breeding season aggregate during the non-breeding season is poorly understood. Low non-breeding season aggregation may be associated with higher likelihood of overlap with threats, but with fewer populations affected, whereas high aggregation may result in a lower probability of exposure to threats, but higher overall severity. We investigated non-breeding distributions and extent of population aggregation in 2 sympatrically breeding auks. We deployed geolocation–immersion loggers on common guillemots *Uria aalge* and razorbills *Alca torda* at 11 colonies around the northern UK and tracked their movements across 2 non-breeding seasons (2017–18 and 2018–19). Using 290 guillemot and 135 razorbill tracks, we mapped population distributions of each species and compared population aggregation during key periods of the non-breeding season (post-breeding moult and mid-winter), observing clear interspecific differences. Razorbills were largely distributed in the North Sea, whereas guillemot distributions were spread throughout Scottish coastal waters and the North, Norwegian and Barents Seas. We found high levels of aggregation in razorbills and a strong tendency for colony-specific distributions in guillemots. Therefore, razorbills are predicted to have a lower likelihood of exposure to marine threats, but more severe potential impact due to the larger number of colonies affected. This interspecific difference may result in divergent population trajectories, despite the species sharing protection at their breeding sites. We highlight the importance of taking whole-year distributions into account in spatial planning to adequately protect migratory species.

**KEY WORDS:** Migration · Non-breeding · Populations · Seabirds · Spatial planning · Light-level geolocation · *Alca torda* · *Uria aalge*

## 1. INTRODUCTION

In animals breeding in temperate and polar regions, migration is a strategy commonly used to overcome challenging winter conditions, such as depressed food availability and poor weather, at the

breeding site (Dingle & Drake 2007). Understanding seasonal migration is critical since peak mortality typically occurs in the non-breeding season, with implications for population dynamics (Jansson et al. 1981, Bartmann 1984). At the meta-population scale, a key question is the extent to which populations that

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are segregated during the breeding season aggregate during the non-breeding season. Such aggregation could arise if there are hotspots of high food availability that attract individuals from multiple breeding locations. Alternatively, breeding populations may remain segregated throughout the annual cycle if migration distances are restricted by intrinsic constraints, or if food is less concentrated. The extent of aggregation is thus important in establishing the risk to meta-populations from anthropogenic threats (Webster et al. 2002). Where breeding populations overlap extensively in the non-breeding season, the probability (or 'likelihood') of encountering a threat at a specific location will be lower than for segregated populations, as aggregated populations are more concentrated. However, should overlap with a threat occur, the absolute impact (or 'severity') is predicted to be higher than for segregated populations, as more breeding populations would be affected. There is widespread evidence in nature for both non-breeding aggregation (Baker et al. 1990, Reppert et al. 2010) and segregation (Als et al. 2011, Hewson et al. 2016). However, we currently have limited understanding of the variation in the extent of non-breeding aggregation of sympatrically breeding species. This is a key knowledge gap, because such variation could result in shared environmental drivers of demography during the breeding season only, with implications for population dynamics and conservation (Lahoz-Monfort et al. 2011). Therefore, whilst a single conservation management approach may be effective for protecting multiple species at breeding localities, this protection may not be appropriate for the rest of the annual cycle.

Seabird species breeding in temperate and polar regions have a clearly defined annual cycle (or biennial cycle, for some larger species) and have recently been the subject of much research on migration strategies (e.g. Meier et al. 2017, Frankish et al. 2020). During the breeding season, they are constrained to forage within a certain distance of their breeding site in order to make frequent visits to their nest (Daunt et al. 2002, Wakefield et al. 2013). During the non-breeding season, these central place constraints are relaxed, allowing seabirds to migrate to areas with potentially more favourable conditions; yet, as with many temperate and polar species, mortality is highest at this time of the year (Acker et al. 2021). Seabirds may be exposed to a wide range of marine threats, such as extreme weather events, fisheries by-catch, harvesting, hunting, oiling events and marine renewable developments, which vary across both spatial and temporal scales (Dias et al. 2019). Many

of these threats are localised, and the probability of individuals from multiple populations encountering them during the non-breeding season will depend on the extent of aggregation at this time. Shortly after completing breeding, most seabirds initiate feather moult, a process with high energetic requirements and in some volant species a period of flightlessness, limiting the ability of individuals to move between locations and away from threats (Bridge 2006). Following the moult period, seabirds may experience challenging winter conditions, with individuals exposed to prolonged periods of poor weather (Morley et al. 2016), lower food availability (Osborn et al. 1984) and shorter daylight hours in which to forage (Daunt et al. 2006, Moe et al. 2021). The moult and mid-winter periods are therefore key parts of the annual cycle when individuals may experience more hostile environmental conditions and/or energetic constraints (Burke & Montevecchi 2018), making their populations more vulnerable to other marine threats.

Tracking studies have vastly improved our understanding of seasonal migration in seabirds, as they enable the location of individuals from known breeding colonies to be recorded throughout the annual cycle. Several single-species tracking studies have investigated the levels of non-breeding season aggregation across multiple breeding populations. These studies have demonstrated a wide range of aggregation levels, from low in Atlantic puffins *Fratercula arctica* (Fayet et al. 2017) and Brünnich's guillemots *Uria lomvia* (Gaston et al. 2011), moderate in common guillemots *Uria aalge* (McFarlane Tranquilla et al. 2013) and high in black-legged kittiwakes *Rissa tridactyla* (Frederiksen et al. 2012). However, to our knowledge, only 2 studies have investigated the non-breeding season movements of multiple populations of sympatrically breeding species. Linnebjerg et al. (2018) mapped the non-breeding distributions of 3 populations of common and Brünnich's guillemots and razorbills *Alca torda* breeding sympatrically in Iceland. The distributions suggest varying levels of population aggregation between the species (high in razorbills and moderate in common and Brünnich's guillemots), but the extent of overlap was not formally quantified (Linnebjerg et al. 2018). Merkel et al. (2021) used an extensive dataset of common and Brünnich's guillemots tracked from 16 colonies across the Northeast Atlantic between 2007 and 2017 and found fairly low levels of aggregation in both species. However, they analysed a large region extending from the northern UK to Iceland, Svalbard and western Russia (mean nearest colony distance: 667.2 km), and potential for

aggregation at these scales could be constrained by the physiological limitation on migration distances in auks, associated with their high flight costs (Elliott et al. 2013). Accordingly, there is a need to undertake a multi-colony study of sympatrically breeding species at a scale where individuals from all populations have the potential to aggregate during the non-breeding season, maximising the ability to investigate the likelihood and severity of encountering marine threats.

Here, we tracked 2 sympatrically breeding auk species, the common guillemot (hereafter ‘guillemot’) and razorbill, at 11 northern UK breeding colonies. These colonies are located sufficiently close to one another (mean nearest colony distance: 100.3 km) that there is the potential for both species to exhibit complete population aggregation or segregation, based on our understanding of the migration potential of breeding adults (Harris et al. 2015, Merkel et al. 2021). During the breeding season, adults operate as central-place foragers with restricted foraging ranges (guillemot:  $37.8 \pm 32.3$  km; razorbill:  $23.7 \pm 7.5$  km; Thaxter et al. 2012). As such, there is segregation of foraging locations between colonies in each species (Wakefield et al. 2017), but marked overlap in spatial foraging distribution and shared environmental drivers of demography between species at each colony (Lahoz-Monfort et al. 2013). Accordingly, colony-based conservation protection and management typically support both species simultaneously during breeding, but it is unclear whether the 2 species vary in the extent to which multiple breeding populations aggregate during the non-breeding season. Understanding this is central to determining what drives variation in population dynamics between breeding populations and what conservation approaches are required in the face of a suite of marine threats across their range.

We focused on 2 key periods during the non-breeding season: post-breeding moult and mid-winter. Guillemots and razorbills breed from late March to late June/early July in the UK. Following the breeding season, successful males continue to provide parental care of chicks for up to 2 mo (Gaston & Jones 1998), and all adults of both species moult their primary and secondary feathers for a period of 4 to 6 wk during August and September, rendering them flightless (Birkhead & Taylor 1977, Harris & Wanless 1990). These species may be particularly vulnerable to marine threats during moult because they are unable to respond rapidly to disturbance and are already expending energy on moult and/or parental care. During mid-winter, auks are more likely to experience poor weather conditions, high energetic costs, and

limited food availability (Burke & Montevecchi 2018). Our study had 2 aims: (1) to identify the core moult and mid-winter distributions of guillemots and razorbills from our study colonies; and (2) to compare the level of between-colony aggregation during these key periods in these sympatrically breeding species.

## 2. MATERIALS AND METHODS

### 2.1. Data collection

We deployed geolocation-immersion loggers (hereafter ‘geolocators’) on 473 common guillemots and 339 razorbills during 2 field seasons (June–July 2017 and 2018) at 11 breeding colonies around the north of the UK (Fig. 1). Two brands of geocator were used: Biotrack model MK3006 and Migrate Technology Intigeo models C65, F100 and C65-Super. These geolocators measure light levels, saltwater immersion and sea surface temperature (SST), from which daily locations are estimated. They are sufficiently small to be deployed on a leg ring (maximum mass of the geocator plus colour ring: guillemots = 4.8 g; razorbills = 4 g) and can remain operational for up to 5 yr, making them well suited for studying year-round distribution.

Individuals were caught by hand or using a noose pole or leg hook at the nest during late incubation or chick rearing (mid-June to early July). Birds were fitted with a unique metal leg ring (if not already present) and a geocator (on the other leg) mounted on a

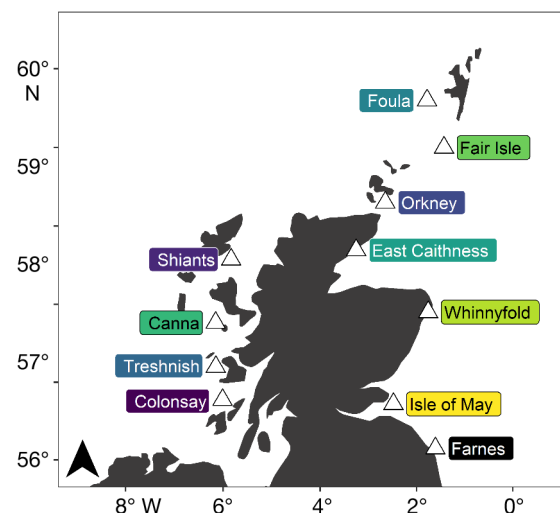


Fig. 1. Common guillemot and razorbill breeding colonies (triangles) where geolocators were deployed, with labels following the same colour scheme as used in Figs. 2 & 3, and in Figs. S1 & S2 in the Supplement

plastic colour ring by a cable tie. Deployments were made under licence by the British Trust for Ornithology. Breeding adults were recaptured during the 2018, 2019 and 2020 field seasons using the same capture method, resulting in a deployment duration of 1, 2 or 3 yr; however, as geolocators were retrieved from fewer colonies during 2020, we included data from 2017–18 and 2018–19 in our analyses, but excluded data from 2019–20 (Table 1). In all cases, handling times did not exceed 10 min. Total number of deployments and retrievals at each colony and year are presented in Table 1.

## 2.2. Device effects

Guillemots and razorbills are wing-propelled divers, and leg-mounted devices have relatively low impacts on species with this foraging mode (Geen et al. 2019). In addition, the maximum mass of the geocator plus colour ring (see Section 2.1) comprised 0.63% (guillemots) and 0.79% (razorbills) of the minimum body mass recorded in breeding adults of the 2 species in Britain (guillemots: 765 g; razorbills: 505 g; Wagner 1999, Harris et al. 2000). This is consistent with recommendations that logger mass be as small as possible (Bodey et al. 2018). Any disturbance caused to the individuals through the catching and tagging method appeared to be short-lived. Although we did not systematically record post-release behaviour, in order to avoid further disturbance, incidental sightings suggested that individuals returned quickly to normal breeding behaviour. We were unable to quantify the potential effect of carrying the logger on foraging efficiency and demographic rates such as productivity and survival. However, a recent study on Manx shearwaters *Puffinus puffinus* found no significant difference in foraging efficiency, trip duration or breeding success between individuals deployed with a geocator and those which were untagged (Gillies et al. 2020). Although Manx shearwaters have a different flight and foraging behaviour to auks, both forage through wing-propelled diving; thus it is likely they would experience similar levels of drag underwater from a leg-mounted geocator.

## 2.3. Data processing and analysis

MK3006 geolocators recorded light levels every minute, with the maximum light recorded for each 10 min period. Saltwater immersion was sampled every 3 s, with the number of samples that were wet

recorded every 10 min. Temperature was recorded for each 20 min period during which the device was consistently wet (no dry periods of more than 3 s). Intigeo geolocators (all models) sampled light every minute and recorded the maximum light every 5 min. C65-Super sampled saltwater immersion every 30 s, recording the number of samples that were wet every 10 min. Temperature was sampled for each 20 min period during which the device was consistently immersed in saltwater, with the minimum, maximum and mean temperatures (when immersed) determined across each 8 h period. C65 and F100 sampled saltwater immersion every 30 s, recording the number of samples that were wet and the maximum conductivity every 4 h. Temperature was sampled every 5 min (irrespective of whether the logger was dry or saltwater immersed), with the maximum and minimum values recorded every 4 h in both models, along with mean temperature in F100s.

Locations were derived from light data. We used the R package 'GeoLight' (Lisovski & Hahn 2012) to convert light readings to twilight events using the threshold method (Hill 1994, Ekstrom 2004). Both species had high quality light curves throughout the non-breeding season, with the majority of transitions clearly identifiable. We then used 'probGLS' (Merkel et al. 2016) to determine locations, a method shown to reduce the generally large error associated with geolocation (Phillips et al. 2004, Halpin et al. 2021). This method incorporates remotely-sensed environmental data, such as SST, with light, activity and saltwater temperature recorded by the logger. 'ProbGLS' is particularly useful at reducing location error during the equinox periods, during which daylight lengths are equal across all latitudes. Within our study region, SST is sufficiently variable spatially to be a reliable additional predictor of geocator location (Frederiksen et al. 2007). Because SST was key for determining locations, it was important to ensure that all temperatures included in the analysis were measurements of SST. As MK3006 and C65-super models only sampled temperatures when the device had been immersed in saltwater for 20 min, we adjusted temperature data from the C65 and F100 loggers to only be included when the device was continuously wet for a 20 min period. We ran the 'prob\_algorithm' function using 100 iterations, following Dunn et al. (2020). The resolution was set to the sampling rate of the wet-dry sensor of the geocator (30 s for Migrate Technology models and 3 s for the Biotrack model). We did not use land masks, but as SST was incorporated into the predictive algorithm (where available), points were generally lo-

Table 1. Deployed, retrieved and processed geolocators by year, along with sample sizes for each breeding colony and species. Retrieval rates are calculated for the total number of geolocators deployed and retrieved for each species and breeding colony. (-) no data

Colony	Latitude (°N)	Longitude (°W)	Species	Deployed		Retrieved		Processed		Sample size				
				2017	2018	2018	2019	2020	Total	2017-18	2018-19	Total		
Colonsay	56.07	6.21	Guillemot	-	30	-	14	10	24	80	24	-	24	24
			Razorbill	-	9	-	1	-	1	11	11	1	-	1 <sup>b</sup>
Treshnish Isles	56.49	6.43	Guillemot	-	20	-	12	2	14	70	14	-	14	14
			Razorbill	-	20	-	12	1	13	65	12 <sup>a</sup>	-	-	12
Canna	57.06	6.54	Guillemot	90	40	35	25	-	60	46	60	44	24	68
			Razorbill	20	22	4	16	-	20	48	19 <sup>a</sup>	9	15	24
Shiant Islands	57.90	6.35	Razorbill	-	20	-	13	-	13	65	13	-	13	13
			Guillemot	40	-	13	-	-	13	33	13	13	-	-
Foula	60.14	2.07	Razorbill	10	-	1	-	-	1	10	1	1b	-	0
			Guillemot	25	-	10	5	-	15	60	15	15	15	5 <sup>b</sup>
Fair Isle	59.53	1.63	Razorbill	21	-	9	2	-	11	52	11	11	2 <sup>b</sup>	11
			Guillemot	30	22	4	10	-	14	27	14	8	10	10
Orkney	58.79	2.95	Razorbill	40	40	20	27	9	56	70	51 <sup>a</sup>	22	32	54
			Guillemot	30	30	13	7	2	22	37	21	15	8	23
East Caithness	58.16	3.56	Razorbill	40	40	24	27	4	55	69	54 <sup>a</sup>	30	28	58
			Guillemot	20	19	2	8	-	10	26	10	5	8	13
Whimnyfold	57.40	1.87	Razorbill	30	34	12	23	7	42	66	39 <sup>a</sup>	17	27	44
			Guillemot	30	30	11	11	-	22	37	21 <sup>a</sup>	11	10	21
Isle of May	56.19	2.55	Razorbill	4	-	1	-	-	1	25	1	1 <sup>b</sup>	-	0
			Guillemot	6	-	3	1	-	4	67	4	4 <sup>b</sup>	1 <sup>b</sup>	0
Farne Islands	55.63	1.63	Razorbill	-	-	-	-	-	-	-	-	-	-	0
			Guillemot	-	-	-	-	-	-	-	-	-	-	-
Total			Guillemot	473	280	271	141	149	290	59	141	149	149	290
			Razorbill	339	131	127	59	76	135	39	59	76	76	135
			Combined	812	411	398	200	225	51	398	200	225	425	

<sup>a</sup>n = 12 geolocators failed to record a full non-breeding season of data and were removed

<sup>b</sup>Removed following bootstrapping analyses



cated in the sea. To obtain more accurate locations, 'probGLS' calculates the travel speed between adjacent fixes when the logger was wet (individual assumed to be swimming) or dry (individual assumed to be flying) and limits subsequent fixes to be within a maximum distance based on this specified speed value (values presented in Table S1 in the Supplement at [www.int-res.com/articles/suppl/m684p181\\_supp.pdf](http://www.int-res.com/articles/suppl/m684p181_supp.pdf); taken from Thaxter et al. 2010). We then smoothed all remaining implausible locations that suggested individuals had travelled more than 500 km by sea in 1 d, by replacing each with the mean of the previous and next location: 7834 fixes; 2.93 % of total location points (McFarlane Tranquilla et al. 2013).

To address our first aim, we determined 50 % kernel density contours (representing core distributions used) during the post-breeding moult and mid-winter for each species by breeding colony and year tracked (i.e. 2017–18 and 2018–19), hereafter referred to as a dataset. We defined post-breeding moult as 31 d from 16 August to 15 September inclusive, with the aim to capture the core dates in which most individuals would be undertaking flight feather moult (generally throughout August and September; Birkhead & Taylor 1977, Harris & Wanless 1990). We attempted to identify individual-level moult periods from geolocation-immersion data, but were unable to do so, as (1) UK guillemots and razorbills fly relatively little during the first part of the non-breeding season, so it was not possible to extract clear periods of low movement that could be interpreted as the moult period; (2) periods of dry are recorded by the loggers throughout the non-breeding period, including moult, because auks regularly tuck 1 leg into the plumage whilst sitting on the water, so it was not possible to identify the moult period using activity data; and (3) successful males do not fly at all from chick fledging until moult completion, including an extended period when they are capable of flying, as they are providing continued parental care to flightless chicks. Mid-winter was defined as 31 d between 6 December and 5 January inclusive, with the winter solstice (21 December) as the mid-point. We calculated kernel density for these periods for each dataset using the 'kernelUD' function in the R package 'adehabitatHR' (Calenge 2006), using bivariate normal kernels, ad hoc smoothing ('href') and a grid cell size of 1000 m<sup>2</sup>. Core colony distributions (delineated by 50% density contours) were then extracted using the 'getverticeshr' function in 'adehabitatHR'.

To determine whether our sample sizes for each dataset were sufficient to capture colony- and year-specific distributions during the moult and mid-

winter periods, we conducted a bootstrapping procedure. We calculated 50 % kernel density contours for each dataset, following the above methods, using randomly sampled selections of birds and allowing individual replacement, starting with a sample size of 1 bird and increasing until the total number of birds for that dataset had been reached (adapted from Bogdanova et al. 2020). This step was repeated 1000 times. We then determined the point where the increase in the median kernel contour area used (km<sup>2</sup>) levelled off for each dataset, suggesting that further addition of individuals would not result in a substantial increase in the size of the core colony distribution (Soanes et al. 2013). We eliminated any datasets where this point was not reached, indicating we did not have confidence that the sample size of tracked birds was sufficient to reliably estimate the core distribution of individuals from that breeding colony for that period in the given year. Where the median kernel contour area levelled off or peaked and started to decline, we included the dataset for further analyses.

To address our second aim, we only included years at a colony where both species were tracked to ensure that the results were not affected by different breeding colonies of each species being tracked in a given year. We first determined similarity between core moult and mid-winter distributions of different colonies by calculating Bhattacharyya's affinity (BA; Fieberg & Kochanny 2005). Points for each dataset were clipped to the corresponding 50 % kernel density contour, calculated as above, and BA was calculated for these points using the 'kerneloverlap' function within the 'adehabitatHR' package in R (Calenge 2006). We then calculated mean and standard error of pairwise BA scores for each period, year and species. Following this, we investigated levels of core colony distribution overlap and locations of aggregations. We estimated the overlap in core distributions between different colonies for each dataset by converting the 50 % kernel density contours into grids with 2 km<sup>2</sup> resolution and determining the number of colonies present in each grid cell.

All processing and analyses were conducted within R (version 3.6.3; R Core Team 2019).

### 3. RESULTS

#### 3.1. Retrievals and processed datasets

In total, 411 geolocators were retrieved from 11 colonies during 3 breeding seasons (2018–2020),

comprising 280 from common guillemots and 131 from razorbills (Table 1). Overall retrieval rate was 51% (guillemots: 59%; razorbills: 39%; range between colonies: guillemots 25–80%; razorbills 10–67%; Table 1). Retrieval rate was lower on average in razorbills because their nesting locations on boulder beaches or cliff crevices make capture more challenging than at the open ledges favoured by guillemots. Variation in retrieval rate between colonies occurred due to differences in colony accessibility and ability to coincide retrieval effort with the narrow window of opportunity in these species. Geolocators varied in their length of deployment, with 246 guillemot and 116 razorbill deployments spanning 1 non-breeding season and an additional 68 guillemot and 30 razorbill deployments spanning 2 non-breeding seasons, in total resulting in 382 guillemot years and 176 razorbill years across our sampling period of 2017–2019. Geolocators that failed ( $n = 5$ ), produced corrupted data ( $n = 3$ ) or failed prior to the end of mid-winter during the first year of deployment ( $n = 4$ ) were removed, as were years when a geocator failed prior to the end of mid-winter during the second year of deployment ( $n = 5$ ). Data from all remaining geolocators were then included in the bootstrapping analysis. This analysis showed that the size of the median core area did not level off with increasing sample size of individuals (up to the total sample size) in any Colonsay and Foula razorbill dataset, Fair Isle razorbills during both moult and mid-winter 2018–19, and all datasets from the Farne Islands, so these were removed (Table 1; Figs. S1 & S2). This resulted in a final sample size of 290 guillemot and 135 moult and mid-winter razorbill distributions (Table 1).

### 3.2. Core moult and mid-winter colony distributions

#### 3.2.1. Moult

Core colony distributions (50% kernel density contours) of guillemots during the post-breeding moult were located in waters off the west and north coasts of Scotland, in the central North Sea and in the Norwegian and Barents Seas (Fig. 2a,c). Two areas were commonly used by multiple colonies of guillemots during this period: off the north coast and off the west coast of Scotland (Fig. 2a,c). In each year, the north coast area was populated by all of the northern (Fair Isle and Foula) and eastern (East Caithness, Whinnyfold and the Isle of May) colonies tracked, and the west coast area was populated by all of the western

colonies tracked (Colonsay, Treshnish and Canna). A small number of fixes were located in the Barents Sea during the post-breeding moult for the Isle of May in 2018 and Canna during both 2017–18 and 2018–19, but fell outside of the core colony distribution for these datasets (Figs. S3 & S4).

During the post-breeding moult, razorbill core colony distributions were located throughout the coastline of mainland Scotland, around Orkney and into the central North Sea (Fig. 2b,d). During the post-breeding moult of both years, 2 commonly used areas were identified: one, located in the northern North Sea, was used by birds from all tracked colonies (Fig. 2b,d). The other, located off the west coast of Scotland, was used by birds from west coast colonies (Treshnish, Canna and the Shiant; Fig. 2b,d). No razorbill fixes were recorded in the Barents Sea (Figs. S5 & S6), but a small number of fixes from Fair Isle in 2017 were located off the south-west coast of Iceland, though again these fell outside of the core colony distribution for these datasets (Fig. S5).

#### 3.2.2. Mid-winter

During mid-winter, core colony distributions of guillemots were located around the coasts of Scotland, throughout the North Sea, off the south-west coast of England and in the Norwegian Sea (Fig. 3a,c; Figs. S7 & S8). Three commonly used areas were apparent: off the north-west coast of Scotland and in the northern and central North Sea, with additional core distributions located in the vicinity of their breeding colonies.

In mid-winter, core colony distributions of razorbills were located off the north coast of Scotland, in the central North Sea and in the English Channel (Fig. 3b,d; Figs. S9 & S10). There were 2 commonly used areas, off the north coast of Scotland and in the central North Sea. The area in the central North Sea was used by individuals from all colonies (Fig. 3b,d).

### 3.3. Species comparison of population aggregation

Across the 5 colonies simultaneously tracked for both species, similarity of core colony distributions was higher in razorbills than in guillemots, as indicated by higher mean BA scores during both moult and mid-winter across both years (Fig. 4). Accordingly, overlap of core distributions was higher in

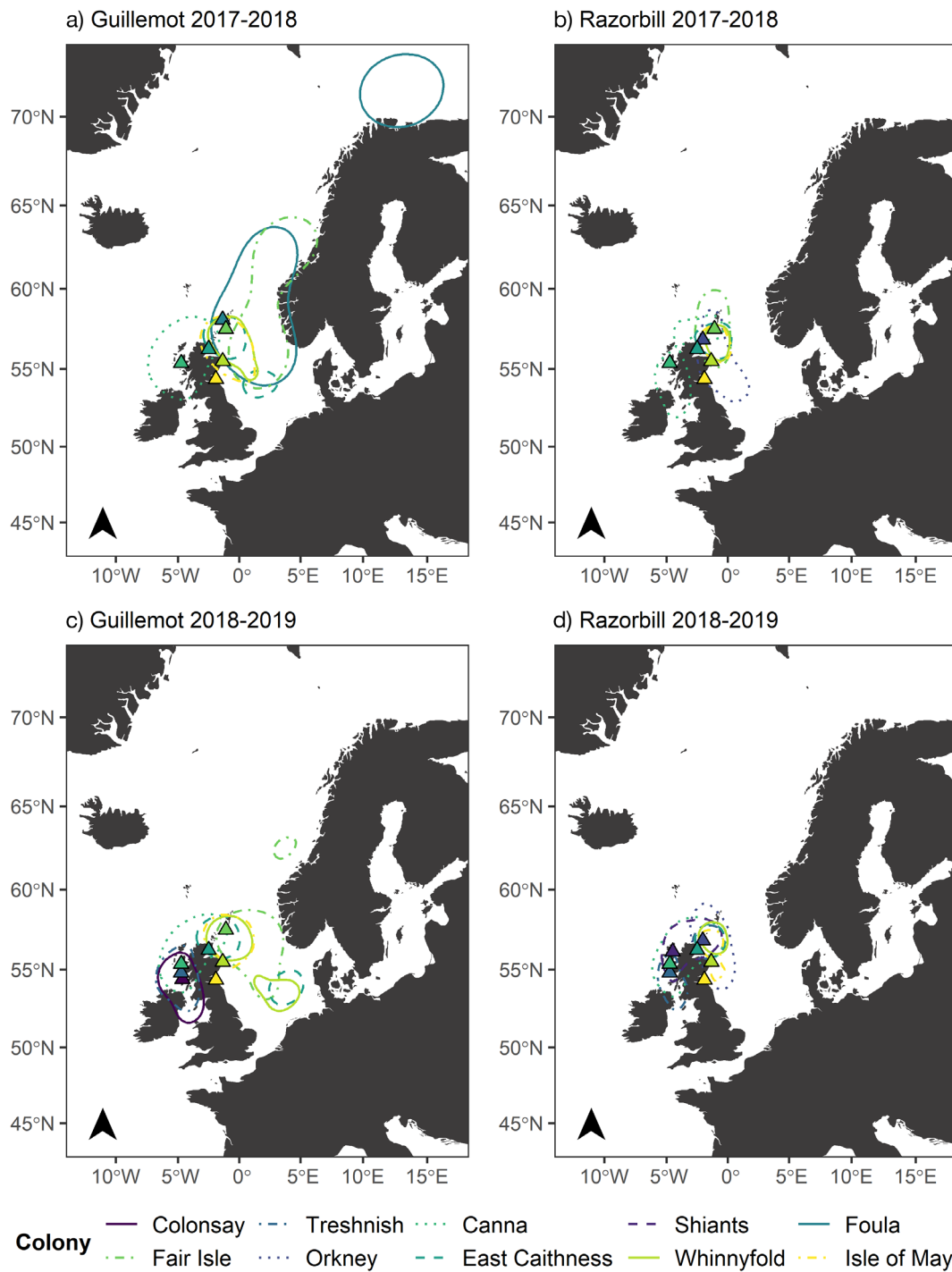


Fig. 2. Core colony distributions (50% kernel density contour outlines) of common guillemots and razorbills during post-breeding moult (16 August–15 September). Colony locations are depicted by triangles, with colours matching the distributions

razorbills than in guillemots. This pattern was clear across all periods and years, with all 5 razorbill core colony distributions consistently overlapping in a single area in the northern North Sea during post-breeding moult (Fig. 5b,d) and the central North Sea

during mid-winter (Fig. 6b,d). In contrast, in guillemots, 4 core colony distributions overlapped during each post-breeding moult (Fig. 5a,c), and there was a maximum of 4 and 3 distributions overlapping during each mid-winter tracked (Fig. 6a,c).



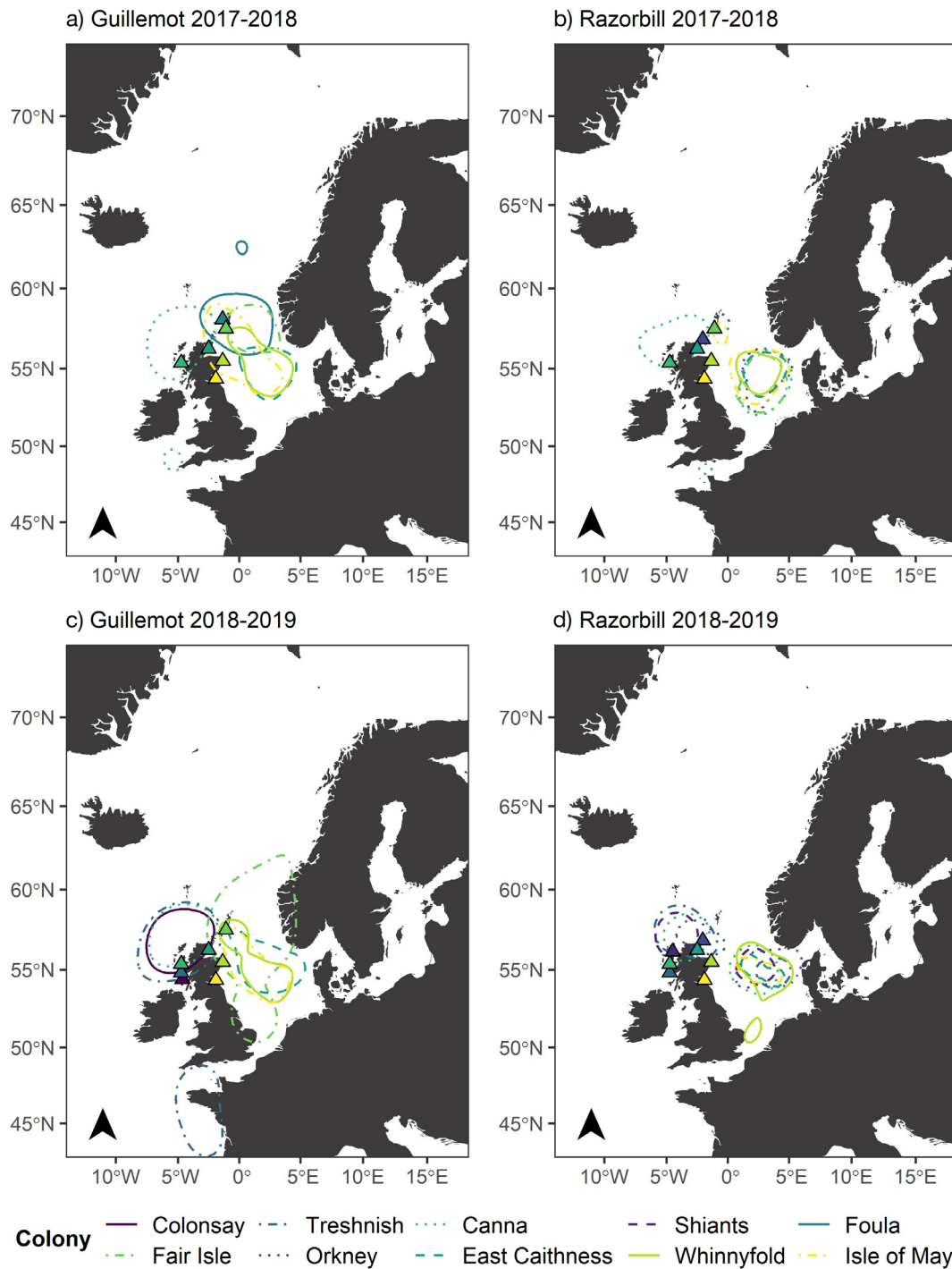


Fig. 3. Core colony distributions (50% kernel density contour outlines) of common guillemots and razorbills during mid-winter (6 December–5 January). Colony locations are depicted by triangles, with colours matching the distributions

#### 4. DISCUSSION

In this study, we present core distributions of multiple populations of common guillemots and razorbills during 2 key periods of the non-breeding sea-

son, post-breeding moult and mid-winter, and compare population aggregation between species. During the post-breeding moult, guillemots had a broad distribution extending through the Scottish coastal waters and the North, Norwegian and Barents Seas,

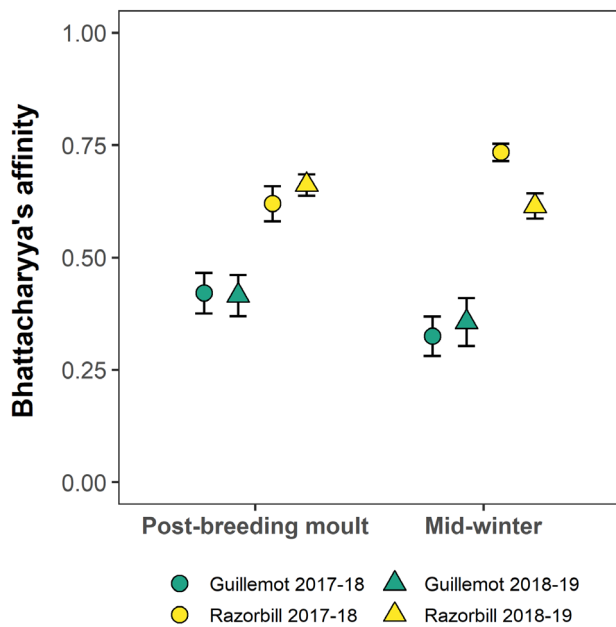


Fig. 4. Similarity in core distributions between populations during post-breeding moult (16 August–15 September) and mid-winter (6 December–5 January) for each species (common guillemot and razorbill) and year (mean  $\pm$  SE pairwise Bhattacharyya's affinity score). Colonies are included where both species were tracked in the same year (see Table 1)

whereas razorbills largely remained in Scottish coastal waters. During mid-winter, guillemots were mostly distributed coastally, whereas razorbills were concentrated in the central North Sea. Crucially, razorbills showed higher levels of population aggregation than guillemots, with all razorbill population distributions overlapping in a single area during both post-breeding moult and mid-winter. Contrastingly, fewer guillemot populations mixed, particularly during mid-winter.

Differences in the level of population aggregation between species are likely due to difference in prey preference and winter colony attendance behaviour. Previous studies have found that guillemots displayed more variable foraging behaviours across the non-breeding season than razorbills (Dunn et al. 2019) and have a more varied non-breeding diet (Ouweland et al. 2004, St. John Glew et al. 2018). In addition, guillemots have been recorded attending nest sites from October onwards at a number of colonies (Mudge et al. 1987, Harris et al. 2006, Harris & Wanless 2016, Merkel et al. 2019). The prevalence of non-breeding colony attendance varies between guillemot populations (Mudge et al. 1987, Harris et al. 2006, Harris & Wanless 2016) and is an energetically costly strategy (Dunn et al. 2020), so is most

likely driven by local prey availability at the breeding site (Harris & Wanless 2016). Conversely, razorbills do not frequent the breeding colony during the non-breeding season (Harris & Wanless 1990) and instead alter their distribution based on prey locations between years (St. John Glew et al. 2019). This may be due to a lower flexibility in diet in razorbills, causing multiple razorbill populations to aggregate at prey hotspots. Similar patterns have been observed in other north-east Atlantic seabirds. Few other studies have been able to test this question robustly because of challenges associated with distances between study colonies limiting the potential for aggregation in winter. However, in one key study, black-legged kittiwake populations aggregated west of the Mid-Atlantic Ridge during the non-breeding season, which is likely due to the high productivity of this region (Frederiksen et al. 2012).

Quantifying levels of aggregation of multiple breeding populations has important implications for understanding impacts of marine threats. In particular, where aggregation is high, there is a lower likelihood of encountering a threat, but if a threat were to overlap with the area of high aggregation, the severity would potentially be higher, since more breeding populations would be affected. Within our study region, there are multiple threats to seabirds, such as marine pollution (Greenwood et al. 1971), extreme weather and marine renewable energy developments. Although the frequency of oil spills has decreased over the last 50 yr in the North Sea, and despite multiple measures in place to reduce these events, they continue to occur (Carpenter 2019) and can have drastic consequences for auks (Greenwood et al. 1971, Ouweland et al. 2004). Furthermore, the volume of marine litter present in the North Sea continues to increase (Gutow et al. 2018), and guillemots and razorbills are vulnerable to entanglement or ingestion (Battisti et al. 2019). Extreme weather events during the non-breeding season can cause high levels of mortality for seabirds such as auks, with multiple wrecks in our study region in recent decades (Harris & Wanless 1984, 1996, Heubeck et al. 2011, Morley et al. 2016), and it is predicted that frequencies of such events will increase under climate change (IPCC 2018). Furthermore, within our study region, there are large-scale plans for marine development of wind energy in northern European waters over the next decade, with coastal Scottish waters and the southern North Sea being key areas for development (The Scottish Government 2020, The Crown Estate 2021). Both of these areas are commonly used by the auk populations in this study, and

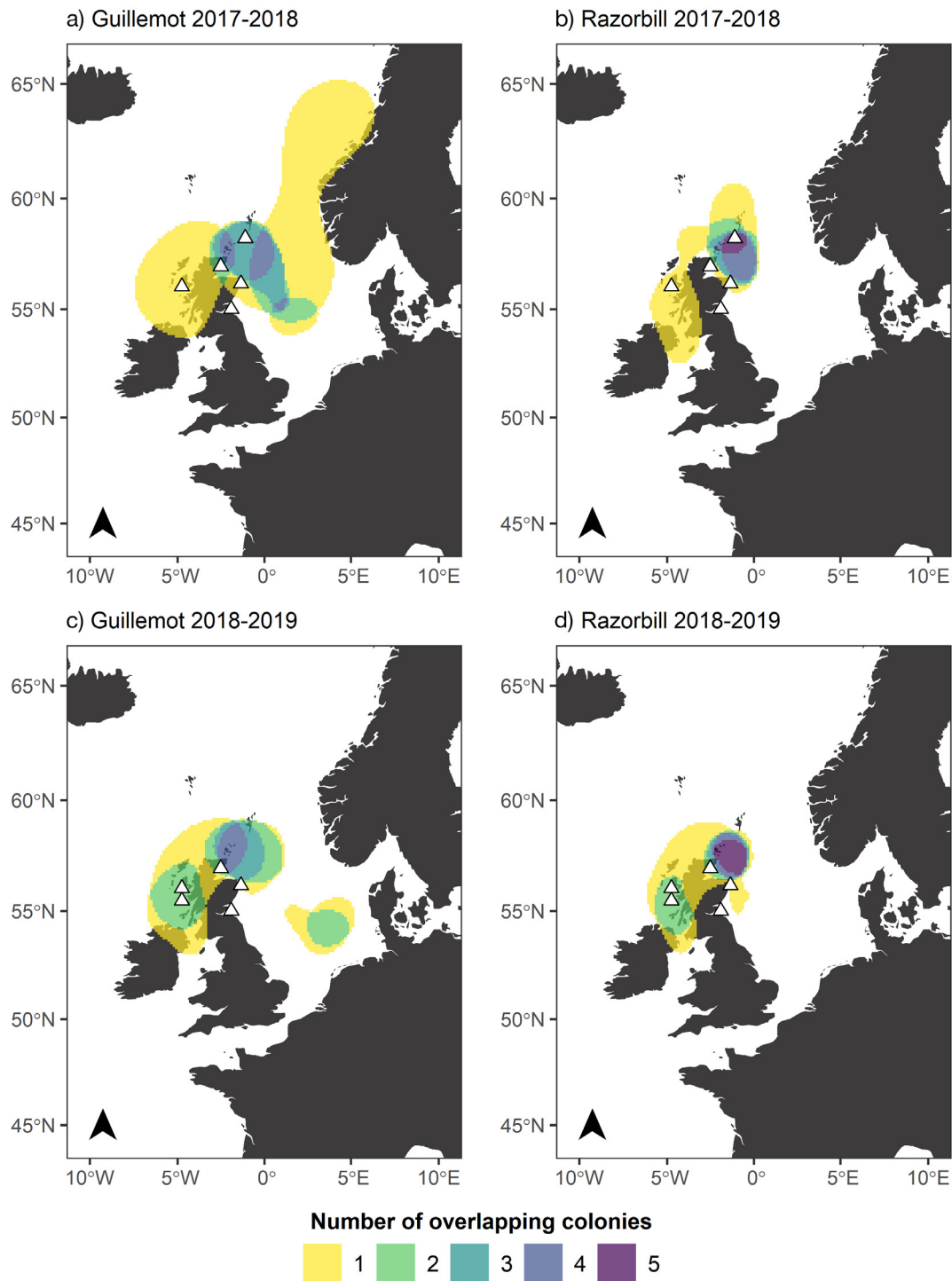


Fig. 5. Overlap in core colony distributions (50% kernel density contours), represented as the number of overlapping colonies within each species (common guillemot and razorbill), during post-breeding moult (16 August–15 September) for colonies where both species were tagged in the same year. Colony locations are depicted by white triangles

guillemots and razorbills are vulnerable to displacement from offshore wind farms (Furness et al. 2013, Peschko et al. 2020). As guillemot breeding populations were more segregated than those of razorbills,

the non-breeding UK guillemot population as a whole has a higher likelihood of encountering a marine threat in the study region, but a lower severity is expected, since fewer breeding populations would

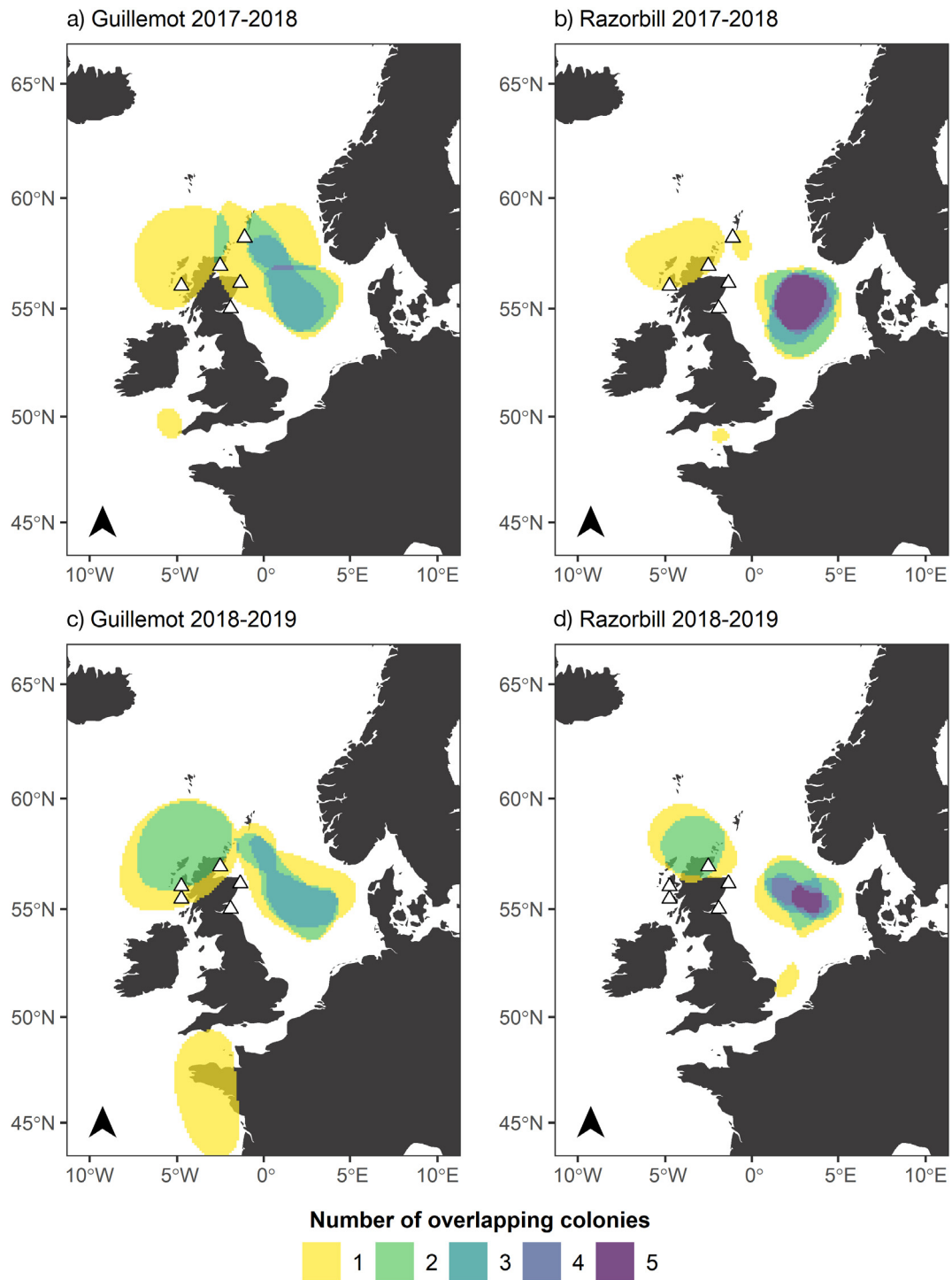


Fig. 6. Overlap in core colony distributions (50% kernel density contours), represented as the number of overlapping colonies within each species (common guillemot and razorbill), during mid-winter (6 December–5 January) for colonies where both species were tagged in the same year. Colony locations are depicted by white triangles

be affected by a threat. In contrast, the likelihood of the razorbill non-breeding population overlapping with a threat is lower due to their more concentrated area, but should overlap occur, then the severity is

likely to be higher, since a greater number of breeding populations would be affected. This is the case for both of the key periods of the non-breeding season that we investigated: the post-breeding moult,

when individuals are less able to move freely, and mid-winter, when environmental conditions are harsh, capping energetic resources.

Our findings support the need for incorporating movements and behaviour throughout the annual cycle when developing conservation plans and estimating vulnerability for migratory species. Interspecific differences in population trends could arise in species sharing breeding locations because of heterogeneity in winter distribution. For multiple populations of a given species, site-based conservation protection, commonly used with seabird colonies, must be accompanied by protection of these populations outside the breeding season, which may require a different approach based on the level of aggregation between populations and location of hotspots. Previous meta-analysis indicates that non- or partially-migratory avian species may be more resilient than fully migratory species (Gilroy et al. 2016), perhaps as they are protected by breeding site-based conservation plans for more of the annual cycle. In addition, it is likely that we observed greater population-level aggregation in razorbills partly due to their more specialised feeding habits than guillemots. Studies of diet specialisation, such as through stable isotope analyses of feathers (Wiley et al. 2019, Barrionuevo et al. 2020), may therefore be useful in predicting levels of non-breeding population aggregation and therefore vulnerability to marine threats in other seabird species or unstudied populations of our study species, which could be of great use to seabird conservation as it may highlight situations where multi-colony tracking studies are required.

Moult migrations, such as the long post-breeding migrations to the Barents Sea that we observed in several guillemot populations, have previously been described in other seabird species and are generally made in order to reach time-limited prey hotspots (Jessopp et al. 2013, Gaston et al. 2017). Although this behaviour has previously been recorded for a single individual guillemot breeding on the Isle of May (Harris et al. 2015), our study is the first to demonstrate moult migrations to the Barents Sea in breeding adult guillemots from other UK populations (Canna, Foula and Fair Isle). The Barents Sea is a highly productive region and an important area for multiple seabird species throughout the annual cycle (Anker-Nilssen et al. 2000). In addition, the Barents Sea is a known important moulting area for guillemots breeding in Norway (Lorentsen & May 2012), so it is likely that this area provides sufficient prey resources to outweigh the high costs of such a long

migration by flight in this species (Elliott et al. 2013). We did not observe a high proportion of razorbill populations undertaking extensive moult migrations, with razorbills from only 1 colony (Fair Isle) migrating to Iceland prior to the post-breeding moult. It is possible that razorbills exhibit this behaviour less than guillemots, as razorbills begin their post-breeding moult earlier and therefore have less time available in which to fly after completing breeding (St. John Glew et al. 2018). This finding also corresponds with Linnebjerg et al. (2018), who found that razorbills were distributed in coastal waters and travelled less far during both moult and mid-winter than guillemots. Post-breeding moult distributions are likely to vary with sex, as successful males of both guillemots and razorbills provide extended parental care to flightless chicks for up to 2 mo following the breeding season (Gaston & Jones 1998). Males may therefore be less able to perform extensive moult migrations (Burke et al. 2015, Dunn et al. 2019). However, we have no reason to believe that the sex ratio was unbalanced in our sampled birds across the different colonies we tracked. Furthermore, guillemots and razorbills have similar differences between sexes during the post-breeding period, so we believe that our comparison of the extent of aggregation between species during moult is robust despite not factoring sex into our analyses.

It is likely that our study took place during favourable environmental conditions for razorbills but not guillemots, as the return rates of each species as measured at one colony, the Isle of May, were above and below average for each species, respectively (razorbills: 2017–18: 0.923; 2018–19: 0.872; average 1986–2016: 0.842; guillemots: 2017–18: 0.891; 2018–19: 0.833; average 1982–2016: 0.904). Return rates are the proportions of uniquely marked individuals resighted during a breeding season that were alive during the previous season and are a reliable indicator of true survival rate during the intervening winter in site-faithful seabirds (Harris et al. 2005, Pollet et al. 2017). St. John Glew et al. (2019) demonstrated that Isle of May razorbills adjust their winter distributions in response to environmental conditions, based on differences in distribution in 2 years of contrasting adult survival, and indeed razorbills in our study aggregated in a similar area to that used during the year of high survival highlighted by St. John Glew et al. (2019). As razorbill survival rate is linked to fish abundances during the non-breeding season, locations of the razorbill aggregation distributions are likely to shift during years of poor survival (Heubeck et al. 2011, St. John Glew et al. 2019),



with locations most likely driven by SST (Fort et al. 2012, Johns et al. 2020), areas of high productivity (Fort et al. 2012, Linnebjerg et al. 2018) or adverse weather conditions (Heubeck et al. 2011). Guillemot distributions also appeared relatively consistent between the 2 years tracked, but it is not known if the non-breeding distributions of guillemots breeding in the north-eastern UK differ between years of good and poor survival. A study examining interannual variation in non-breeding distribution in a larger number of years would be informative in establishing whether the species differences we observed are consistent across a wider range of environmental conditions.

The locations we have highlighted are broadly in line with previous ring recovery data (Harris & Swann 2002, Merne & Mitchell 2002), but give much more detail on non-breeding movements. However, we recorded more northerly core distributions in guillemots during moult and mid-winter, and our distributions were more constrained than in previous studies from the Isle of May (Harris et al. 2015, St. John Glew et al. 2018, 2019, Dunn et al. 2020). These studies were conducted in different years to ours, but logger types and analytical methods also differed. In particular, our combined analysis of light, activity and SST means that our location estimates are likely to be more precise, constraining our ability to compare our results with these studies, but allowing us to robustly identify core areas and compare population level aggregation between the species. In addition, we present the core areas (50% kernel density contours) for each colony, whereas some of the other studies presented wider distributions. We have identified a location of aggregation in razorbills in the central North Sea, which is not clearly evident from at-sea densities of auks in winter based on survey data from 1980–2018 (Waggitt et al. 2020). Although it is well-known that there are high levels of error associated with locations derived from geolocators, our methods of processing the data followed current best practice for minimising that error (Halpin et al. 2021). Further, we extracted 50% kernel density contours from relatively high sample sizes of individuals from each colony, so we believe that our findings are reliable. It is possible that discrepancies between our findings and at-sea survey data arose because our data were derived from breeding adults from a sample of colonies, whereas at-sea survey data comprise individuals from all age classes and potentially from colonies outside our study region, such as Norway (Hestem 2019) or Iceland (Linnebjerg et al. 2018). A second possible explanation is that the methods dif-

fered between studies. Here, we derived kernel distributions from locational fixes, whereas Waggitt et al. (2020) present predicted distributions from habitat association models. As our colonies included many of the major breeding sites for these species and were well distributed, we are confident that our findings of interspecific variation in levels of aggregation would be consistent for colonies within this range (Fig. 1).

## 5. CONCLUSIONS

In this study, we describe differences in interspecific variation in non-breeding aggregation between 2 sympatrically breeding seabird species. The differences we observed are likely driven by diet, prey distribution and behavioural differences and have clear and contrasting risk impacts from marine threats for each species. Because of this, each species may have different population trajectories despite shared protection at breeding sites. We therefore highlight the need for management plans to take into account year-round distributions in order to adequately protect migratory species.

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