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Four sympatrically nesting auks show clear resource segregation in their foraging environment

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ABSTRACT: Auks share ecological similarities and are often found in sympatrically nesting assemblages at suitable nesting sites. It is expected that co-existing species would have evolved strategies to reduce niche overlap in response to resource competition. The presence of Atlantic puffins *Fratercula arctica*, razorbills *Alca torda*, thick-billed murres *Uria lomvia* and common murres *U. aalge* at the Gannet Islands, Labrador, is an opportunity to study interspecific interactions in a major seabird community. We compared the foraging movements of adult breeding birds and the diet of the birds inferred through (1) stable isotopes in the blood of adults, and (2) prey delivered to the chicks, as dimensions in the foraging niche among these 4 auks. Our results revealed that puffins and thick-billed murres headed offshore to forage, while razorbills and common murres were more coastal, heading towards mainland Labrador. The patterns of spatial segregation found among coastal and pelagic birds were mirrored by their stable isotope ratios, with one group of species foraging at a higher trophic level of an inshore food web and the other foraging on a lower trophic level of an offshore, pelagic food web. The 'pelagic' species segregated by prey choice for their chicks while differential alternate prey selection was the source of segregation between the 'coastal' species. Our research highlights the importance of segregation patterns in both spatial and diet dimensions of the foraging niche among the 4 auks—a potential mechanism for reducing interspecific competition among ecologically similar seabirds and explaining the persistence of such seabird assemblages through time.

KEY WORDS: Seabird · Foraging distribution · Niche overlap · Diet · Isotopic niche

INTRODUCTION

Seabirds forage in an environment regulated by bottom-up processes that influence the availability of their prey (Frederiksen et al. 2006). The patchy distribution of food resources, characteristic of such environments, may have led to the evolution of seabird coloniality (Clode 1993, Rolland et al. 1998). However, colonial breeding could increase costs for central-place foragers because resources will become depleted closer to larger seabird colonies as a result of intraspecific competition (i.e. the Storer-Ashmole halo theory; Storer 1952, Ashmole 1963). Furthermore, prey availability near the colony regulates colony size, and birds breeding in larger colonies will go farther to forage (Gaston et al. 2007, Elliott et al. 2009b). Despite the enhanced competitive interaction between individuals nesting in large colonies and evidence supporting the Storer-Ashmole halo theory, larger colonies persist and assemblages of ecologically similar species of seabird regularly occur. Co-existing species have evolved strategies that reduce niche overlap in response to resource competition by differential use of the available resources (Gause 1934). Moreover, plasticity of individual strategies through individual specialization might reduce competition when changes occur in preferred resources given that inter- and intraspecific competition are likely affected by the availability of each species' preferred prey (Furness &

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Birkhead 1984, Barger & Kitaysky 2012). In most systems, ecological segregation between sympatric seabirds is observed and resources are partitioned in one or more dimensions of the foraging niche (Cherel et al. 2008, Weimerskirch et al. 2009, Masello et al. 2010, Linnebjerg et al. 2013, Navarro et al. 2013, Robertson et al. 2014).

The Alcidae (subsequently called auks) is one of the most diverse families of seabirds. While most of the diversity is in the Pacific Ocean, 6 species occur in the North Atlantic Ocean. Except for the planktivorous dovekie *Alle alle*, the Atlantic puffin *Fratercula arctica*, black guillemot *Cepphus grylle*, razorbill *Alca torda* and the 2 *Uria* species (common and thick-billed murres; *U. aalge* and *U. lomvia*, respectively), are all mainly piscivorous, pursuit-diving seabirds during the breeding season (Gaston & Jones 1998). Colonies made of an assemblage of these auk species can be found in the North Atlantic Ocean west from the United Kingdom to Canada (Birkhead & Nettleship 1987, Thompson et al. 1999, Linnebjerg et al. 2015, Shoji et al. 2015). One of the most important, multi-auk species colonies in eastern Canada is located at the Gannet Islands, Labrador (Robertson & Elliott 2002, Irons et al. 2015). This site hosts the largest colony of razorbills in North America (NA; 10 000 pairs), the third largest Atlantic puffin colony in NA and thousands of common murres and thick-billed murres (Robertson & Elliott 2002). The chick diet of these 4 species, as well as the diving behaviour of the razorbill and thick-billed murre, have been characterized and compared at this site since the 1980s. At that time, resource partitioning in chick diet was apparent (Birkhead & Nettleship 1982, 1987); clear differences in diving depth were subsequently observed between the razorbill and thick-billed murre (possibly driven by these prey preferences; Paredes et al. 2008), and thick-billed and common murres are known to be deep-diving seabirds exploiting the water column at similar depth (Hedd et al. 2009, Burke et al. 2015). Diving patterns of razorbills and Atlantic puffins observed in Europe were similar (Shoji et al. 2015), while at the Gannet Islands the chicks' diet somewhat overlapped (Birkhead & Nettleship 1982, 1987), especially in years of low capelin *Mallotus villosus* availability during which Atlantic puffins switched to sand lance *Ammodytes* sp. (Baillie & Jones 2004). Since the decline of capelin stocks in the 1990s (Carscadden & Nakashima 1997, Carscadden et al. 2001, Buren et al. 2014), a major forage prey for seabirds of the Newfoundland-Labrador area (Carscadden et al. 2002), it is possible that the segregation previously observed in the chicks' diet has changed, as well as their foraging behaviour in response to variation in the availability of their preferred prey (Burger & Piatt 1990, Davoren 2000). Due to interspecific interactions, assemblages of closely related seabirds may respond differently to environmental changes compared to single-species colonies. The presence of the 4 species at this site provides an opportunity to study segregation patterns and complement existing literature about the interactions found among ecologically similar seabirds.

Given the diving niche of these species (Paredes et al. 2008, Hedd et al. 2009, Burke et al. 2015, Shoji et al. 2015) and chick diet preferences previously studied at this site (Birkhead & Nettleship 1982, 1987), the niche partitioning theory of co-existing species suggests that, if overlap occurs in a dimension of the foraging niche, divergence in another dimension should be apparent, preventing direct competition for the resource (Gause 1934). To test these ideas, we compared 2 dimensions in the foraging niche between sympatrically nesting Atlantic puffins (hereafter 'puffins'), razorbills, common and thick-billed murres during one breeding season. Foraging areas have never been assessed for the 4 species at the Gannet Islands, nor has the isotopic niche of breeding adults. Moreover, since the 1980s, simultaneous assessment of the chick diet for the 4 species has not been done. Thus, we first compared the foraging movements of adult birds during late incubation or chick-rearing. Second, we compared the diet of birds through direct observation of the prey composition of the chick diet and of the adult diet inferred from stable isotope ratios in the blood of breeding adults. We predicted that (1) given the known similarity in the diving behaviour of razorbills and puffins, and of common and thick-billed murres, those 2 groups would segregate in either their trophic and dietary preference or spatially in their foraging range, and that, (2) considering multiple dimensions of their foraging niche, the 4 co-existing species would differentiate from one another. Along with this, we compared the chick diet of the species with previous studies at this site to understand the larger context of prey availability throughout the years.

MATERIALS AND METHODS

Study area

The project was conducted at the Gannet Islands (53° 56′ 32″ N, 56° 30′ 40″ W), a group of 7 islands

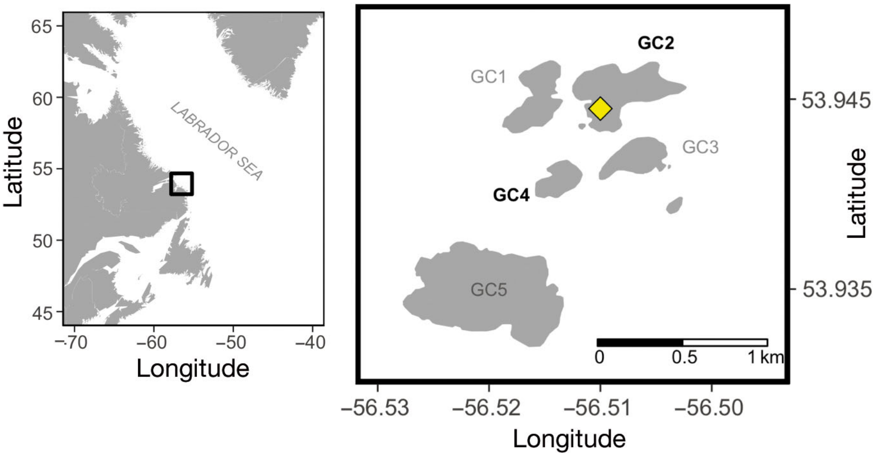

Fig. 1. Location of the Gannet Islands (53.94° N, 56.51° W) off the Labrador coast and close-up of the Gannet Cluster, with the main cabin indicated by a yellow diamond. GC2 and GC4 were the main research islands

located about 50 km east of Cartwright, Labrador, in the Labrador Sea (Fig. 1). Work was conducted between 16 July and 22 August 2015 on 2 islands named GC2 (puffins and razorbills) and GC4 (murres); the 2 islands are only 300 m apart.

Foraging movements

Breeding birds were banded, weighed and equipped with an unpackaged 14.5 g GPS logger (i-gotU GT 120; Mobile Action Technology) or a GPS-UHF Uria logger (Ecotone Telemetry; 8 and 12 g loggers). Once unpackaged, the i-gotU loggers were sealed in heat-shrink plastic tube and attached on the lower back feathers of the bird using waterproof Tesa© tape (no. 426), which we expected would be lost by the bird about 10 d after deployment or during the next moult if the individual could not be recaptured (Linnebjerg et al. 2013, Shoji et al. 2015). Two razorbills and 3 thick-billed murres were captured at the end of incubation; all the other birds equipped with tracking devices were rearing chicks (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m572p243_supp.pdf). The total mass of the i-gotU loggers with tubing and tape was 17 g, corresponding to 3.8% of the lightest individual's body mass for puffins, 2.5% for razorbills, 2.2% for thick-billed murres and 2% for common murres. However, we did not recover any i-gotU devices from puffins and do not recommend the use of this device, as we believe it is too heavy or bulky to track that species. The Uria loggers, already waterproofed, were attached using the same technique. The i-gotU loggers were set to record a GPS location at 3 min intervals and the Uria loggers at 2 min intervals. Since Atlantic puffins may be prone to nest desertion after capture (Rodway & Montevecchi 1996), only individuals rearing young chicks that were at least 7 d old were selected. The birds were recaptured after at least 2 d of data collection according to the battery life of the loggers and our capacity to recapture the birds. During the second capture, the loggers were removed and blood was collected for stable isotope analysis.

A total of 86 loggers were deployed (11 puffins, 25 common murres, 24 razorbills, 26 thick-billed murres). A fraction of the i-gotU loggers deployed were recovered: 1 puffin, 4 common murres, 5 razorbills and 13 thick-billed murres, while no Uria loggers were recovered (although data were remotely downloaded from these units). Out of the recovered i-gotU loggers, one recorded very little data (razorbill), while the data in 6 others were lost due to corrosion from the lithium battery acid (1 common murre, 1 puffin, 4 thick-billed murres). We believe that the loggers' batteries were damaged during the drastic pressure change that occurred during very deep dives, leading to leakage of the battery acid onto the logger's electronic parts. It appears that the i-gotU loggers packaged in shrink-wrap are not suitable for use on deep-diving seabirds. Another factor contributing to low logger recovery was rough seas, making one of our sampling sites often inaccessible. For puffins and razorbills, which are smaller birds seemingly more sensitive to disturbance, the small, reliable Uria GPS units with remote download were an optimal choice. We summarize our tracking sample sizes in Table S1 in the Supplement.

Chick diet

Chick diet observations consisted of watching a group of birds for a minimum of 2 h while recording every adult bird observed with food at the colony or flying by. The observations were made at the main thick-billed murre cliff for this species but at various locations for the other species, not always at the same area of the colony or on the same island. For each individual bird observed, we recorded the species as well as the number and species of fish carried. We also recorded opportunistic feeding observations to add to the data, which were recorded while doing other tasks not specific to the feeding observation bouts.

Blood sampling

Blood was collected from the brachial vein with a butterfly needle (23 or 25 gauge) attached to a syringe. We obtained ~2 ml of blood for a variety of projects, although only a few drops were required for our research. Blood was collected from chick-rearing individuals as well as from tracked individuals that were recaptured. Blood was placed in a freezer a maximum of 5 h after sampling and kept frozen in an Eppendorf tube for stable isotope analyses (SIA; $\delta^{13}C$ and $\delta^{15}N$). Frozen samples were shipped or taken back to Acadia University and stored frozen. To prepare the samples for analysis, we dried them for 24 h at 60°C and then crushed each sample into a fine powder. The samples were sent for analysis to SINLAB at the University of New Brunswick, where isotopes were determined using continuous flow isotope ratio mass spectrometry without lipid extraction. Data are reported as differences in isotopic ratios, for which the units are parts per thousand (‰), compared to Pee Dee Belemnite for carbon and atmospheric air for nitrogen. During analyses, SINLAB ran 3 secondary standards; nicotinamide ($\delta^{15}N$: 0.02 ± 0.05‰ [SD]; $\delta^{13}C$: −34.56 ± 0.07‰, n = 6), bone liver standard ($\delta^{15}N$: 7.15 ± 0.08‰; $\delta^{13}C$: −18.72 ± 0.09‰, n = 6) and muskellunge *Esox masquinongy* muscle standard ($\delta^{15}N$: 14.01 ± 0.07‰; $\delta^{13}C$: −22.31 ± 0.07‰, n = 14). Check standards were also run to assess analytical accuracy: protein ($\delta^{15}N$: 6.08 ± 0.07‰; $\delta^{13}C$: −27.17 ± 0.13‰, n = 6), N_2 ($\delta^{15}N$: 20.30 ± 0.05‰, n = 2) and CH_7 ($\delta^{13}C$: −32.16 ± 0.01‰, n = 2).

Prey item collection

We collected various prey items at the colony, by either actively forcing a bird to drop its bill load, or by collecting prey that were opportunistically found on the ground. The prey items were preserved frozen and used for SIA ($\delta^{13}C$ and $\delta^{15}N$) without lipid extraction following the protocol described above. The back muscles (fish) or the whole organism (amphipod) were used for the SIA.

Data analysis

Spatial distribution

All spatial analyses were performed in R 3.3.1 (R Core Team 2016) using the package 'adehabitatLT 0.3.21' and 'adehabitatHR 0.4.14' (Calenge 2006). The tracking data were first resampled at 6 min intervals to allow comparison between the 2 types of loggers. We excluded from the analyses locations within 700 m of the colony, which corresponded to a major drop in the number of locations in relationship to distance from the colony. We felt locations within 700 m were strongly under the influence of the colony; the islands are about 300 m apart, and birds in between the cluster and around the islands were washing off, preening and resting, but not foraging (authors' pers. obs.). We identified individual foraging trips and filtered foraging locations based on a speed of ≤5 km h^{-1} between successive locations (Shoji et al. 2014); trips with less than 20 locations were also excluded from the analysis. We acknowledge that the categorization of foraging locations solely based on speed will also include locations associated with resting behaviour at sea. Because auks perform diving bouts interspersed with resting bouts while sitting on the water (Croll et al. 1992, Jodice & Callopy 1999; Elliott et al. 2009a, Shoji et al. 2014), it was not possible to differentiate those 2 states without a dive sensor, but we considered that locations associated with resting state at sea likely represent potential foraging areas as well. Because the number of foraging locations varied greatly across individuals (Table S1), we randomly selected 25 locations ind.$^{-1}$ to perform further analyses of foraging range. This was done to limit potential within-individual correlation in the data (i.e. some individuals made more than one foraging trip), and to give the same weight to all individuals in the kernel foraging analyses. Thus, the foraging range obtained would not be representative of only one or few individuals over-weighted by their higher number of foraging locations. Following this, we performed bivariate normal kernel density analyses ('kernelUD' function) to obtain the utilization distribution (UD) of the foraging locations for each species. To allow comparison between species, we used a fixed smoothing factor (*h*) of 2000 m. This smoothing factor was visually chosen in order to limit the amount or overlapping area between the species kernel and the mainland. We estimated the degree of overlap between the species' foraging range by using the HR (home range overlap) method of the 'kerneloverlap' function. HR measures the proportion of the foraging range of one species covered by the foraging range of another:

$$\mathrm{HR}_{i,j} = \frac{A_{i,j}}{A_i} \qquad (1)$$

where $A_{i,j}$ is the area of overlap between species *i* and *j*, and A_i is the area of the foraging range of species *i*. The estimation of foraging overlap was done 1000 times from a sample of 25 randomly selected locations per individual to calculate the mean foraging range overlap among species.

Given our small sample sizes (Table S1), we compared our mean observed foraging range overlaps to the overlaps of 4 null groups (the 4 species) obtained through a randomization procedure. This test was performed to assess if our observed results were smaller (segregation) or larger (clustered) than expected by chance. After randomly selecting 25 foraging locations per individual, as previously stated, we randomly assigned a species to each individual and not to individual locations, to reflect the real spatial covariation among locations and individual variation, and proceeded with the kernel analysis procedures calculating the overlap based on the HR method. We completed that procedure 1000 times, creating a distribution of 1000 null overlaps of kernels. For each species pairwise comparison, we then assessed if the mean observed overlap in the foraging range (95% UD) was smaller than that expected by chance. To do so, we calculated a p-value as the proportion of randomized overlaps that were smaller or equal to the mean observed overlap value for each pairwise comparison of species (null test). We used a significance value of $\alpha = 0.05$ for 1-way pairwise comparisons. Following the null test above, if $p \geq 0.95$, it would indicate that the real observed value was at the other end of the randomized distribution (on the right-end tail) indicating significant clustering, or 2 species overlapping more than expected by chance.

Chick and adult diet

Each bill load is a meal for the growing chick, and thus individual bill load proportions of various prey items should give a better account of the actual diet of the chick in comparison to the absolute frequency of individual prey items in the diet. This is particularly relevant for multi-prey loading species like puffins and razorbills, but not for murres, which carry a single fish at a time. Thus, to characterize and compare the chick diet in 2015, instead of total prey frequencies, we calculated the percentage of bill loads containing specific prey items, which could lead to a total percentage for each individual above 100.

For each species, we determined prey diversity in the chick diet using the Shannon-Weaver diversity index (H') following the equation:

$$H' = -\sum_{i=1}^{s} p_i \log p_i \qquad (2)$$

where *p* is the proportion of prey species *i* in the diet (based on absolute frequencies) and *s* is the total number of species in the diet. A larger index value indicates a greater diversity of prey. We also compared chick diet observed in 2015 with previous studies done at the Gannet Islands. To enable comparison among years, we calculated the proportion of individual prey items landed at the colony; a method that likely biases the percentage observed towards smaller prey items, especially for puffins that can carry many items in a single bill load as mentioned previously.

We performed multivariate analysis of variance (MANOVA Wilks' lambda) to compare the isotopic ratios in adult blood among species. If differences were found following the MANOVA model ($p \leq 0.05$), we fitted a generalized linear model (GLM) with no intercept on each response variable (δ^{13}C and δ^{15}N) separately and compared the fitted means followed with a Tukey contrasts test. We used stable isotopes Bayesian ellipses in R (SIBER) from the package 'SIBER' (Jackson et al. 2011) to calculate the isotopic niche width of each species and their degree of overlap using respectively posterior Bayesian estimates of simulated standard ellipse area ($\mathrm{SEA_b}$) and standard ellipse area corrected for small sample sizes ($\mathrm{SEA_c}$).

RESULTS

Spatial distribution

Based on the methods described, we used a total of 43 individual trips from 3 puffins (7 trips), 5 razorbills (10), 5 common murre (11) and 7 thick-billed murres (15) (Fig. S1 in the Supplement). Puffins and thick-billed murres displayed considerable overlap in their foraging areas (95% UD; mean ± SD = 24 ± 8 and 44 ± 9%, respectively, for one species area over the other), and to a lesser extent, so did razorbills and common murres (21 ± 10 and 18 ± 4%, respectively) and puffins and common murres (14 ± 7 and 19 ± 6%, respectively) (Table 1). Otherwise, segregation was observed, especially between thick-billed and com-

Table 1. Mean ± SD observed overlap of the foraging range (95% utilization distribution, UD) obtained following 1000 iterations of 25 randomly selected foraging locations per individual between the 4 studied species: Atlantic puffin (ATPU, n = 3), common murre (COMU, n = 5), razorbill (RAZO, n = 5) and thick-billed murre (TBMU, n = 7) at the Gannet Islands in 2015, and mean ± SD randomized overlap obtained following 1000 iterations of randomly assigned species to individual trips. The proportion of random overlaps that is smaller or greater than the observed mean overlap is presented as the p-value. The lack (segregation) or predominance of overlap (clustering) that are significant ($\alpha \leq 0.05$) are indicated in **bold** with the direction of the interaction based on the position of the observed value in the randomized distribution (left-tail = segregation; right-tail = clustering)

Pairwise interaction	Foraging range (95% UD) Observed overlap %	Random overlap %	p	Direction of interaction
ATPU				
COMU	14 ± 07	20 ± 22	0.52	–
RAZO	08 ± 07	19 ± 23	0.23	–
TBMU	24 ± 08	20 ± 22	0.85	–
COMU				
ATPU	19 ± 06	23 ± 17	0.27	–
RAZO	18 ± 04	23 ± 13	0.35	–
TBMU	**06 ± 03**	**22 ± 12**	**0.02**	Segregation
RAZO				
ATPU	14 ± 11	23 ± 17	0.30	–
COMU	21 ± 10	24 ± 14	0.45	–
TBMU	12 ± 11	23 ± 13	0.11	–
TBMU				
ATPU	44 ± 09	28 ± 16	0.84	–
COMU	**08 ± 03**	**28 ± 12**	**0.03**	Segregation
RAZO	**12 ± 04**	**28 ± 12**	**0.05**	Segregation

mon murres, and thick-billed murres and razorbills (Fig. 2). Thick-billed murres, and to a limited extent puffins, headed offshore to forage in the pelagic zone, while the razorbills were more coastal, heading towards mainland Labrador for the majority of their trips. Common murres were more variable, but mainly shared the coastal preference of razorbills (Fig. 2).

The randomization procedure (Fig. 3) showed that, despite an apparent overlap within the pelagic species (puffins and thick-billed murres) and within the coastal species (razorbills and common murres), none of the overlap observed in the foraging range appeared to be larger than would be expected by chance ($p > 0.35$; Table 1). In other words, the overlap in the observed foraging distribution of the 4 species was not different than the ones obtained following the random species assignment. However, the lack of overlap observed between the 2 spatially segregated groups (i.e. pelagic vs. coastal foragers) was significant between thick-billed murres and common murres ($p = 0.03$) and thick-billed murres and razorbills ($p = 0.05$; Table 1). Therefore, thick-billed murres were statistically different in their foraging range from razorbills and common murres, while puffin foraging ranges were not detectably different from either common murres or razorbills (Table 1).

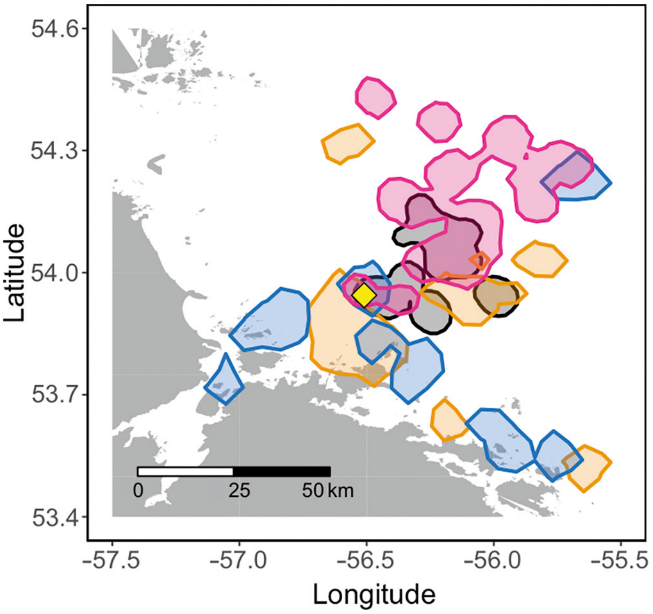

Fig. 2. Utilization distribution contours (95% UD) of the foraging locations of the 4 auks (blue: razorbill, n = 5; orange: common murre, n = 5; black: Atlantic puffin, n = 3; pink: thick-billed murre, n = 7) breeding at the Gannet Islands (yellow diamond) in 2015. A total of 25 locations were randomly selected per individual of each species

Isotopic niche of breeding adults

MANOVA analysis indicated segregation among the species in their stable isotope ratios ($F_{3,6} = 15.79$, $p < 0.001$; Table 2). Razorbills (n = 13) and common murres (n = 12) were similar, and both fed higher in the trophic chain (δ^{15}N) and close to shore (δ^{13}C; both Tukey $p > 0.48$; Fig. 4). Puffins (n = 19) and thick-billed murres (n = 22) had lower δ^{13}C and δ^{15}N than razorbills and common murres (both Tukey > |5.53|, $p < 0.001$), consistent with feeding at a lower trophic level and offshore, and differed from each other in their δ^{13}C (Tukey $z = 2.57$, $p = 0.05$) and δ^{15}N (Tukey $z = 3.64$, $p = 0.001$), although a small degree of overlapping in their trophic niche was revealed by the SEA$_c$ (see below).

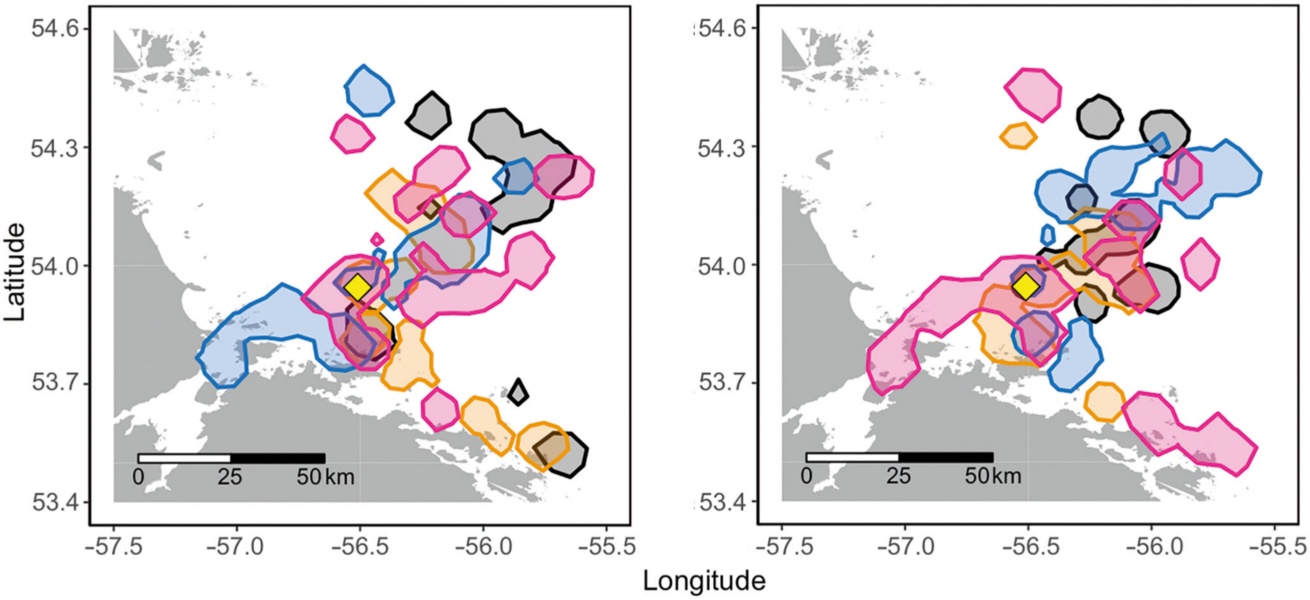

Fig. 3. Examples of randomized distribution obtained from 2 permutations after species was randomly assigned to each individual. The observed sample size was kept the same for each random assignment. Utilization distribution contours (95% UD) of the permutation are shown (blue: razorbill, n = 5; orange: common murre, n = 5; black: Atlantic puffin, n = 3; pink: thick-billed murre, n = 7). Yellow diamond: the breeding colony on the Gannet Islands

Table 2. Blood isotopic values of the 4 auks breeding at the Gannet Islands in 2015 and of their prey items (muscle) collected at the colony. Mean and standard deviation are presented

Species	n	$\delta^{13}C$	$\delta^{15}N$	C:N
Atlantic puffin	19	−19.74 ± 0.11	13.52 ± 0.17	3.41 ± 0.05
Razorbill	13	−19.40 ± 0.11	14.53 ± 0.17	3.41 ± 0.03
Common murre	12	−19.44 ± 0.07	14.67 ± 0.37	3.42 ± 0.04
Thick-billed murre	22	−19.65 ± 0.12	13.77 ± 0.25	3.38 ± 0.05
Capelin	4	−20.76 ± 0.20	12.39 ± 0.26	3.84 ± 0.34
Sand lance	4	−20.58 ± 0.52	10.80 ± 0.50	3.71 ± 0.21
Fish doctor	1	−18.82	14.78	3.38
Daubed shanny	1	−18.42	13.42	3.46
Fish larvae[a]	2	−21.65 ± 0.55	10.54 ± 0.47	4.18 ± 0.14
Atlantic wolffish (juvenile)	1	−21.13	11.09	4.29
Amphipod[b]	2	−22.49 ± 0.52	8.88 ± 0.25	5.54 ± 0.32

[a]2-pooled sample of 8 items, [b]2-pooled sample of 4 items

The segregation between coastal and pelagic species was also found following the SIBER analysis. It was clear that the coastal birds segregated from the more pelagic ones in their diet as showed by the SEA_c (Fig. 4), although there was overlap within the coastal (54%) and pelagic (14%) groupings (Fig. 4). All species had small and similar isotopic niche widths (SEA_b between 0.06 and 0.09‰, $p > 0.1$; see Fig. S2 in the Supplement).

Chick diet

The proportion of preferred prey per species has varied since 1981 (Table 2). In the 1990s, there were low numbers of capelin landed at the colony by puffins, common murres and thick-billed murres. However, this proportion appeared higher in 2015 for the common murre compared with the 1990s (52% [n = 114] compared to 12% [n = 373 in 1996]; $\chi^2 = 109.09$, $p < 0.001$). Razorbills had previously shown consistent preferences for sand lance (80 to 90%); however, an important drop occurred in 2015 (37% [n = 62] compared to 90% [n = 110 in 1996]; $\chi^2 = 52.19$, $p < 0.001$), during which capelin were mostly fed to razorbill chicks (57%). Daubed shanny *Leptoclinus maculatus* has been an important prey item in the diet of the thick-billed murre chicks (33 to 97%) since 1983 and has always been present in the common murre chick diet. Fish larvae were an important part of puffin chick diet in the 1980s and in 2015.

In 2015, based on the composition of prey loads, capelin was the main prey item fed to razorbill (73%,

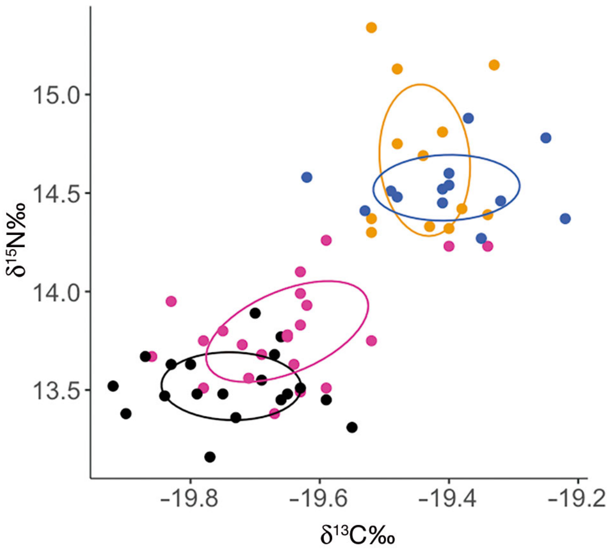

Fig. 4. Isotopic niche based on δ^{13}C and δ^{15}N values in blood of adult birds sampled during chick-rearing at the Gannet Islands in 2015. Standard ellipses (40% credible interval) following Jackson et al. (2011) are represented. Black: Atlantic puffin (n = 19); orange: common murre (n = 12); blue: razorbill (n = 13); pink: thick-billed murre (n = 22)

Table 3. Percentage (%) of bill loads containing different prey items among the 4 auks at the Gannet Islands in 2015. 'Other' includes squid, stout eelblenny, fish doctor, first year Atlantic wolffish and Atlantic cod. Note that more than one type of prey can be found in razorbill and puffin bill load, explaining the sum of each species percentages above 100. Also presented is the index of diversity of prey (*H'*) assessed for each species' chick diet based on total frequencies of prey items

	Atlantic puffin	Razorbill	Common murre	Thick-billed murre
Capelin	39	73	52	12
Sand lance	10	30	9	5
Daubed shanny	0	0	35	83
Fish larvae	55	3	1	0
Other	1	0	3	0
n	174	37	114	40
H'	1.27	0.71	1.13	0.59

n = 37) and common murre chicks (52%, n = 114), while it was the second most important food item in the puffin chicks' diet (39%, n = 174). Daubed shanny contributed most to the thick-billed murre chick diet (83%, n = 40), which also had the lowest diversity of prey (Table 3). Daubed shanny was also an important part of the common murre chick diet (35%). Puffins provided their chicks with significant quantities of fish larvae in 2015 (55%) and a higher diversity of prey (Table 3). In general, sand lance was not found to be a major prey item, even for the razorbill (30%; Table 3), despite its past importance at this site (Table 4).

DISCUSSION

Among the 4 species, we found differences in chick diet and distinct patterns of spatial segregation that were clearly reflected in the isotopic niche of the adult birds.

Spatial segregation

Segregation occurred in the foraging range (95% UD) between 2 groups of species: one group being more coastal (razorbills and common murres) and another mainly pelagic (thick-billed murres and puffins). We observed overlap, to differing extents, in the core foraging area within each spatially segregated group between larger, single prey-loading murres and the multi-prey loading auks. However, all the overlap observed could have been obtained by chance and was unlikely to result in increased competitive interaction in this spatial dimension of their foraging niche. Piatt (1990) suggested that resource segregation is more pronounced between smaller and larger auk species because body size has an influence on species-specific diving behaviour in response to prey dispersion within a foraging area. Finer-scale segregation in space has been observed among murrelets, which avoid foraging close to larger murres (Ronconi & Burger 2011). Such fine-scale segregation is likely associated with differences in diving behaviour and has been observed previously among the 4 auk species (Paredes et al. 2008, Burke & Montevecchi 2009, Shoji et al. 2015). Fine-scale mechanisms of segregation could effectively minimize the interaction between species sharing a preference for the same foraging area. The observed spatial segregation in foraging range was partly supported by the randomization test, and relates strongly to segregation revealed by the stable isotope ratios. We note, however, that individual foraging decisions are likely to change among breeding stages (Navarro et al. 2009, Delord et al. 2016), but our small sample size was insufficient to detect any differences between the few individuals sampled at incubation and the chick-rearing birds (see Fig. S1 in the Supplement). Nonetheless, clear patterns of segregation in both dimensions of the foraging niche

Table 4. Percentage (%) of prey items delivered to chicks by number and per species at the Gannet Islands during different years of study. 'Other' includes squid, stout eelblenny, fish doctor, first year Atlantic wolffish, Atlantic and Arctic cod. '–' prey item not looked for; '0' prey item looked for, but not found; na: sample size not reported

Atlantic puffin	1981[a]	1982[a]	1983[a]	1996[b]	1997[b]	1998[b]	2015
Capelin	14	29	7	0.5	8	7	8
Sand lance	26	12	2	6	16	6	4
Fish larvae	0	0	0	72	68	82	88
Other	60	59	91	18	9	5	0.005
n	1347	318	5910	470	279	1219	867
Razorbill	1981[c]	1996[d]	1981–1983, 1997[e]	2000–2003[f]	2003–2006[d]		2015
Capelin	11	3	19	8	17		57
Sand lance	80	90	80	85	80		37
Daubed shanny	0	1	1	6	3		0
Fish larvae	6	–	–	–	–		–
Other	9	6	1	1	0		0
n	409	na	941	1685	na		62
Common murre	1981[c]	1982[g]	1983[g]	1996[h]	1997[h]		2015
Capelin	78	76	75	12	45		52
Sand lance	7	1	2	2	1		9
Daubed shanny	14	9	15	84	53		35
Other	1	14	9	4	2		4
n	294	2085	1646	373	380		114
Thick-billed murre	1981[c]	1982[g]	1983[g]	1996[h]	1997[h]	2000–2003[f]	2015
Capelin	45	20	13	2	6	10	12
Sand lance	20	5	0	0	0	–	5
Daubed shanny	33	72	66	97	94	83	83
Other	2	3	5	1	1	7	0
n	91	241	409	110	149	956	40

[a]Baillie & Jones (2004), [b]Baillie & Jones (2003), [c]Birkhead & Nettleship (1982), [d]Lavers & Jones (2007), [e]Lavers et al. (2009), [f]Paredes et al. (2008), [g]Birkhead & Nettleship (1987); fish larvae were included in 'other prey items' for these years, [h]Bryant et al. (1999)

imply that, despite our modest tracking sample sizes, the spatial patterns observed may represent the population.

Trophic segregation

From the SIA, the coastal birds were foraging at a higher trophic level of an inshore food web and the pelagic birds on a lower trophic level of an offshore and pelagic food web. This pattern was mostly driven by difference in δ^{13}C. Inshore and benthic food webs are characterized by higher ^{13}C occurrence compared to offshore and pelagic food webs (France 1995). The spatial overlap observed between the razorbill and the common murre was mirrored by their significantly higher carbon isotopic values, both suggesting a coastal preference, compared to the pelagic species. The differences found in δ^{15}N between the 2 groups suggest that they feed on different levels of the trophic chain and/or that the contribution of different prey items in their diet varies (Hobson et al. 1994).

All of the species had a small isotopic niche width. This could be expected in a system where seabirds are foraging in a relatively restricted area around their colony, which is exemplified during the energy-demanding period of chick-rearing (Ceia et al. 2014). The small variation in δ^{13}C values we observed remains significant and still differentiated the coastal from the pelagic species, consistent with the distribution patterns of the 4 auks at sea.

Dietary segregation and historical perspective

We observed a substantial proportion of daubed shanny in the chick diet of both murre species. However, their trophic levels were highly segregated, and common murres provisioned their chicks with a higher proportion of capelin and more diverse landings. Such prey selection, along with the spatial segregation observed, led to major partitioning of the foraging resource between the 2 murre species. As for common murre and razorbill, capelin was the main prey landed at the colony. The 2 species, however, exploited different alternative prey for their chicks; common murre provisioned their chicks with daubed shanny, a resource absent in the razorbill chicks' diet. Daubed shanny could be an accessible prey to the deep-diving common murres (dive up to 140 m; Hedd et al. 2009) which were also feeding their chicks a higher diversity of prey than the razorbills (dive up to 36 m; Paredes et al. 2008). Such differences in selected alternative prey for the chicks, likely influenced by their diving behaviour, must contribute to resource segregation between these 2 auk species despite their preference for the coastal zone and their similar isotopic niche.

Sand lance, which has been regarded as a major prey item provisioned to the razorbill chicks (Birkhead & Nettleship 1982, Lavers & Jones 2007), was less important in 2015. In contrast, the proportion of capelin in the landings we observed were not as low as recorded in the 1990s (especially 1996), suggesting that this keystone species is now more available than it was in recent decades. In the 1990s, the capelin stocks declined or shifted their spawning season, inducing a mismatch with the phenology of seabird predators (Carscadden et al. 2001, Carscadden et al. 2002, Regular et al. 2009, Buren et al. 2014). Less information is available concerning the sand lance, a non-commercial fish, but inter-annual variation in environmental conditions could affect its availability or its synchronicity with seabird breeding phenology. Such changes in preferred prey have been observed in Northern Europe, with a switch in the chick diet of auks towards alternative prey after sandeel and capelin declined (Barrett & Furness 1990, Barrett 2002, Anderson et al. 2014). Decline in sand lance availability could explain the lesser importance of this fish in the razorbill chick diet in 2015, and the resulting prey selection overlap found between the razorbill and common murre for capelin. Phenotypic plasticity and the capacity of individuals of each species to adjust their foraging behaviour when facing different foraging conditions (Barger & Kitaysky 2012, Cherel et al. 2014, Sommerfeld et al. 2015, Jakubas et al. 2016) could mediate resilience for the cost associated with inter-annual variation in prey abundance, as has been demonstrated for the common murre (Burger & Piatt 1990, Harding et al. 2007).

Contrasting with the coastal species, in 2015 the pelagic puffin and thick-billed murre differed in the prey they delivered to their chicks. Thick-billed murres almost exclusively fed daubed shanny to their chicks, while this species was completely absent in provisioning by puffins. The pelagic behaviour of the thick-billed murre along with its ability to dive to great depths (up to 110 m; Paredes et al. 2008) enables it to exploit this demersal fish (which can be found deep in the water column; Coad & Reist 2004) compared to the puffin, which dives to shallower depths (up to 48 m; Shoji et al. 2015). Puffins returned to the colony mostly bringing fish larvae mixed with amphipods, 2 sources of prey that also contributed to their adult diet. Despite the pelagic preference and similarities in the adult isotopic niche between puffins and thick-billed murres, clear differences in the prey items provisioned to their chicks support niche segregation between these 2 species.

CONCLUSION

Our research highlights the importance of segregation patterns in both the spatial and diet dimensions of the foraging niche among Atlantic puffins, razorbills, common murres and thick-billed murres nesting in sympatry. Each species appeared to prefer either coastal or pelagic habitats, a dichotomy that was reflected in their isotopic niche. Even if species were sharing a spatial preference, their overlap was limited, or divergence in other dimensions of their foraging niche such as chick diet, adult trophic ecology, or diving behaviour as reported in the literature was prevalent, potentially limiting the degree of competitive interaction among them. Our results highlight that by examining at-sea distribution, isotopic niche of adults and chick diet, we can reveal the patterns that differentiate sympatric and ecologically similar species, explaining the persistence of such seabird assemblages through time.

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LITERATURE CITED

Anderson HB, Evans PGH, Potts JM, Harris MP, Wanless S (2014) The diet of common guillemot *Uria aalge* chicks provides evidence of changing prey communities in the North Sea. Ibis 156:23–34

Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. Ibis 103b:458–473

Baillie SM, Jones IL (2003) Atlantic puffin (*Fratercula arctica*) chick diet and reproductive performance at colonies with high and low capelin (*Mallotus villosus*) abundance. Can J Zool 81:1598–1607

Baillie SM, Jones IL (2004) Response of Atlantic puffins to a decline in capelin abundance at the Gannet Islands, Labrador. Waterbirds 27:102–111

Barger CP, Kitaysky A (2012) Isotopic segregation between sympatric seabird species increases with nutritional stress. Biol Lett 8:442–445

Barrett RT (2002) Atlantic puffin *Fratercula arctica* and common guillemot *Uria aalge* chick diet and growth as indicators of fish stocks in the Barents sea. Mar Ecol Prog Ser 230:275–287

Barrett RT, Furness RW (1990) The prey and diving of seabirds on Hornoy, North Norway after a decrease in the Barents Sea capelin stocks. Ornis Scand 21:179–186

Birkhead TR, Nettleship DN (1982) Studies of alcids breeding at the gannet clusters, Labrador, 1981. OLABS Program Report, Canadian Wildlife Service, Darmouth

Birkhead TR, Nettleship DN (1987) Ecological relationships between common murres, *Uria aalge*, and thick-billed murres, *Uria lomvia*, at the Gannet Islands, Labrador. III. Feeding ecology of the young. Can J Zool 65:1638–1649

Bryant R, Jones IL, Hipfner JM (1999) Responses to changes in prey availability by common murres and thick-billed murres at the Gannet Islands, Labrador. Can J Zool 77: 1278–1287

Buren AD, Koen-Alonso M, Pepin P, Mowbray F and others (2014) Bottom-up regulation of capelin, a keystone forage species. PLOS ONE 9:e87589

Burger AE, Piatt JF (1990) Flexible time budgets in breeding common murres: buffers against variable prey abundance. Stud Avian Biol 14:71–83

Burke CM, Montevecchi WA (2009) The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. J Zool (Lond) 278:354–361

Burke CM, Montevecchi WA, Regular PM (2015) Seasonal variation in parental care drives sex-specific foraging by a monomorphic seabird. PLOS ONE 10:e0141190

Calenge C (2006) The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519

Carscadden JE, Nakashima BS (1997) Abundance and changes in distribution, biology, and behavior of capelin in response to cooler waters of the 1990s. In: Forage fishes in marine ecosystems: proceedings of the international symposium on the role of forage fishes in marine ecosystems. University of Alaska Sea Grant College Program, Anchorage, AK, p 457–615

Carscadden JE, Frank KT, Leggett WC (2001) Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. Can J Fish Aquat Sci 58:73–85

Carscadden JE, Montevecchi WA, Davoren GK, Nakashima BS (2002) Trophic relationships among capelin (*Mallotus villosus*) and seabirds in a changing ecosystem. ICES J Mar Sci 59:1027–1033

Ceia FR, Paiva VH, Garthe S, Marques JC, Ramos JA (2014) Can variations in the spatial distribution at sea and isotopic niche width be associated with consistency in the isotopic niche of a pelagic seabird species? Mar Biol 161: 1861–1872

Cherel Y, Corre M, Jaquemet S, Ménard F, Richard P, Weimerskirch H (2008) Resource partitioning within a tropical seabird community: new information from stable isotopes. Mar Ecol Prog Ser 366:281–291

Cherel Y, Connan M, Jaeger A, Richard P (2014) Seabird year-round and historical feeding ecology: blood and feather $\delta^{13}C$ and $\delta^{15}N$ values document foraging plasticity of small sympatric petrels. Mar Ecol Prog Ser 505: 267–280

Clode D (1993) Colonially breeding seabirds: Predators or prey? Trends Ecol Evol 8:336–338

Coad BW, Reist JD (2004) Annotated list of the Arctic marine fishes of Canada. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2674, Fisheries and Oceans Canada, Winnipeg

Croll DA, Gaston AJ, Burger AE, Konnoff D (1992) Foraging behavior and physiological adaptation for diving in thick-billed murres. Ecology 73:344–356

Davoren GK (2000) Variability in foraging in response to changing prey distributions in rhinoceros auklets. Mar Ecol Prog Ser 198:283–291

Delord K, Pinet P, Pinaud D, Barbraud C and others (2016) Species-specific foraging strategies and segregation mechanisms of sympatric Antarctic fulmarine petrels throughout the annual cycle. Ibis 158:569–586

Elliott KH, Woo KJ, Gaston AJ (2009a) Specialization in murres: the story of eight specialists. Waterbirds 32:491–506

Elliott KH, Woo KJ, Gaston AJ, Benvenuti S, Dall'Antonia L, Davoren GK (2009b) Central-place foraging in an Arctic seabird provides evidence for Storer-Ashmole's halo. Auk 126:613–625

France RL (1995) Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Mar Ecol Prog Ser 124:307–312

Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S (2006) From plankton to top predators: bottom-up control of a marine food web across four trophic levels. J Anim Ecol 75:1259–1268

Furness RW, Birkhead TR (1984) Seabird colony distributions suggest competition for food supplies during the breeding season. Nature 311:655–656

Gaston AJ, Jones IL (1998) The auks: Alcidae, 1st edn. Oxford University Press, Oxford

Gaston AJ, Ydenberg RC, Smith GEJ (2007) Ashmole's halo and population regulation in seabirds. Mar Ornithol 35: 119–126

Gause GF (1934) Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. Science 79:16–17

Harding AMA, Piatt JF, Schmutz JA, Shultz MT, Van Pelt TI, Kettle AB, Speckman SG (2007) Prey density and behavioral flexibility of a marine predator: the common murre (*Uria aalge*). Ecology 88:2024–2033

Hedd A, Regular PM, Montevecchi WA, Buren AD, Burke CM, Fifield DA (2009) Going deep: common murres dive into frigid water for aggregated, persistent and slow-moving capelin. Mar Biol 156:741–751

Hobson KA, Piatt JF, Pitochelli J (1994) Using stable isotopes to determine seabird trophic relationships. J Anim Ecol 63:786–798

Irons D, Petersen A, Anker-Nilssen T, Arturhin Y and others (2015) Circumpolar seabird monitoring plan. Conservation of Arctic Flora and Fauna (CAFF) monitoring report No. 17, CAFF International Secretariat, Akureyri

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—stable isotope Bayesian ellipses in R. J Anim Ecol 80:595–602

Jakubas D, Wojczulanis-Jakubas K, Boehnke R, Kidawa D, Blachowiak-Samolyk K, Stempniewicz L (2016) Intra-seasonal variation in zooplankton availability, chick diet and breeding performance of a high Arctic planktivorous seabird. Polar Biol 39:1547–1561

Jodice PGR, Collopy MW (1999) Diving and foraging patterns of marbled murrelets (*Brachyramphus marmoratus*): testing predictions from optimal-breathing models. Can J Zool 77:1409–1418

Lavers JL, Jones IL (2007) Impacts of intraspecific kleptoparasitism and diet shifts on razorbill *Alca torda* productivity at the Gannet Islands, Labrador. Mar Ornithol 35:1–7

Lavers J, Hipfner JM, Chapdelaine G (2009) Razorbill (*Alca torda*). In: Rodewald PG (ed) The birds of North America online. Cornell Lab of Ornithology, Ithaca, NY. http://bna.birds.cornell.edu/bna/species/635 (accessed 6 June 2016)

Linnebjerg JF, Fort J, Guilford T, Reuleaux A, Mosbech A, Frederiksen M (2013) Sympatric breeding auks shift between dietary and spatial resource partitioning across the annual cycle. PLOS ONE 8:e72987

Linnebjerg JF, Reuleaux A, Mouritsen KN (2015) Foraging ecology of three sympatric breeding alcids in a declining colony in southwest Greenland. Waterbirds 38: 143–152

Masello JF, Mundry R, Poisbleau M, Demongin L, Voigt CC, Wikelski M, Quillfeldt P (2010) Diving seabirds share foraging space and time within and among species. Ecosphere 1:art19

Navarro J, Forero MG, González-Solís J, Igual JM, Bécares J, Hobson KA (2009) Foraging segregation between two closely related shearwaters breeding in sympatry. Biol Lett 5:545–548

Navarro J, Votier S, Aguzzi J, Chiesa J, Forero M, Phillips R (2013) Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels. PLOS ONE 8: e62897

Paredes R, Jones IL, Boness DJ, Tremblay Y, Renner M (2008) Sex-specific differences in diving behaviour of two sympatric Alcini species: thick-billed murres and razorbills. Can J Zool 86:610–622

Piatt JF (1990) The aggregative response of common murres and Atlantic puffins to schools of capelin. Stud Avian Biol 14:36–51

R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Regular PM, Shuhood F, Power T, Montevecchi WA and others (2009) Murres, capelin and ocean climate: interannual associations across a decadal shift. Environ Monit Assess 156:293–302

Robertson GJ, Elliott RD (2002) Population size and trends of seabirds breeding in the Gannet Islands, Labrador. Technical Report Series No. 393, Canadian Wildlife Service, Atlantic Region, Mount Pearl

Robertson GS, Bolton M, Grecian WJ, Wilson LJ, Davies W, Monaghan P (2014) Resource partitioning in three congeneric sympatrically breeding seabirds: foraging areas and prey utilization. Auk 131:434–446

Rodway MS, Montevecchi WA (1996) Sampling methods for assessing the diets of Atlantic puffin chicks. Mar Ecol Prog Ser 144:41–55

Rolland C, Danchin E, de Fraipont M (1998) The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. Am Nat 151:514–529

Ronconi RA, Burger AE (2011) Foraging space as a limited resource: inter- and intra-specific competition among sympatric pursuit-diving seabirds. Can J Zool 89: 356–368

Shoji A, Owen E, Bolton M, Dean B and others (2014) Flexible foraging strategies in a diving seabird with high flight cost. Mar Biol 161:2121–2129

Shoji A, Elliott K, Fayet A, Boyle D, Perrins C, Guilford T (2015) Foraging behaviour of sympatric razorbills and puffins. Mar Ecol Prog Ser 520:257–267

Sommerfeld J, Kato A, Ropert-Coudert Y, Garthe S, Wilcox C, Hindell MA (2015) Flexible foraging behaviour in a marine predator, the masked booby (*Sula dactylatra*), according to foraging locations and environmental conditions. J Exp Mar Biol Ecol 463:79–86

Storer RW (1952) A comparison of variation, behavior and evolution in the sea bird genera *Uria* and *Cepphus.* Univ Calif Publ Zool 52:121–222

Thompson DR, Lilliendahl K, Solmundsson J, Furness RW (1999) Trophic relationships among six species of Icelandic seabirds as determined through stable isotope analysis. Condor 101:898–903

Weimerskirch H, Shaffer S, Tremblay Y, Costa D and others (2009) Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. Mar Ecol Prog Ser 391: 267–278

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