



Spatiotemporal and isotopic niche overlap among Atlantic puffins, razorbills, and common murres during the non-breeding season in the Northwest Atlantic

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ABSTRACT: Little is known about the spatial and dietary overlap of seabird species during the non-breeding season, when scarce and patchy marine food resources could lead to interspecific competition. We aimed to quantify spatiotemporal and isotopic niche overlap among common murres *Uria aalge*, razorbills *Alca torda*, and Atlantic puffins *Fratercula arctica* outside the breeding season by combining data from geolocators and stable isotope ratios ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) of belly, secondary, and head feathers collected in 2017–2020 from birds breeding in coastal northeastern Newfoundland, Canada. Seasonal utilization distributions of each species indicated generally low spatial overlap during most of the non-breeding period, with exceptions immediately post-breeding and with variability in movement paths among puffins. Stable isotope analysis revealed a broader isotopic niche (1.5 to 3 \times) for puffins than other species, matching their greater spatial variation. There was no isotopic niche overlap among the 3 species, except during flight feather molt of razorbills and murres. Individual puffins located in the same area as razorbills or murres had lower $\delta^{15}\text{N}$ values, suggesting a lower trophic position. The minimal overlap of these 3 alcid species during an understudied phase of their annual cycle suggests that they segregate spatially and partition resources, implying that different spatial planning and ecosystem conservation strategies should be applied to each of these 3 species.

KEY WORDS: Seabird · Interspecific competition · Distribution · Stable isotope · Geocator · North Atlantic · Alcid

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1. INTRODUCTION

The patchy prey distribution in the ocean brings foraging seabirds together in areas of higher prey density (Hunt et al. 1999). If prey resources are not limited in these patches, species could co-occur without detriment to foraging success, and facilitative interactions could even enhance prey capture rates (e.g. Harrison et al. 1991, Silverman et al. 2004). Alternately, co-occurring species may compete if shared prey resources are limited at these patches when foraging tactics overlap in

space and time (Lack 1944). These circumstances create the opportunity for interspecific interactions and the evolution of niche partitioning. Sympatric seabird species have many ways to minimize competition for limited prey resources through niche differentiation, including spatial segregation (McFarlane Tranquilla et al. 2015), foraging depth differences (Ballance et al. 1997), prey specialization (Mancini et al. 2014), and phenological differences (Navarro et al. 2013).

When breeding seabirds are concentrated in space and time at multi-species colonies, there is ample

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opportunity for competition (Ashmole 1963), but species interactions are also possible during low productivity winter periods in the patchy ocean environment (May & MacArthur 1972, Hutchinson 1978; see also Haury et al. 1978). There is a higher potential for competition among seabird species if they forage in the same prey-limited patches on similar prey types during the winter than if they are not in the same location and are foraging on dissimilar prey types.

Niche overlap may be more likely between closely related species that obtain prey in a similar manner, as their shared ancestor evolved while relying on a comparable pool of resources (Wiens & Graham 2005). Atlantic puffins *Fratercula arctica*, razorbills *Alca torda*, and common murres *Uria aalge* are wing-propelled pursuit diving Alcidae that are characterized by stout body shape and high wing loading (body mass/wing area; Gaston & Jones 1998). All 3 species breed sympatrically across the North Atlantic during the boreal summer, where they forage predominantly on locally abundant, small forage fish (e.g. Barrett & Furness 1990, Scopel et al. 2019, Jenkins & Davoren 2020). Common murres (hereafter, sometimes, 'murre') are the largest and heaviest of the 3 alcids and can dive the deepest (maximum 180 m; Piatt & Nettleship 1985) and longest (41 to 212 s; Wanless et al. 1988, Hedd et al. 2009, Ainley et al. 2020). Razorbills are of intermediate size and dive capabilities (140 m, 19 to 49 s; Wanless et al. 1988, Lavers et al. 2020), while Atlantic puffins (hereafter, sometimes, 'puffins') are the smallest of the 3 species with the shallowest maximum dive depths (68 m) and shortest dive duration (20 to 30 s; Wanless et al. 1988, Lowther et al. 2020). This size variation can lead to spatial partitioning of prey resources during the breeding season, perhaps because larger body size might impart a competitive advantage and ability to exploit the highest quality prey patches while excluding similar smaller bodied birds (Piatt 1990, Wanless et al. 1990, Linnebjerg et al. 2013). Spatial and diet segregation among the 3 alcids has been observed within foraging ranges of colonies during breeding, but both spatial and dietary overlap increase when and where prey is abundant (Wanless et al. 1990, Pratte et al. 2017, Jenkins & Davoren 2020, Lescure 2021, Petalas et al. 2021). Pre- and post-breeding, sympatric alcids are more spatially dispersed; however, there is evidence of high dietary similarity (Linnebjerg et al. 2013). Increased spatial segregation during non-breeding may allow these alcids to feed on similar prey types, but it is also possible that both spatial and dietary overlap remain high.

Tracking technology has increased understanding of the non-breeding movement patterns of North-

west Atlantic alcids (e.g. McFarlane Tranquilla et al. 2013, Burke et al. 2015, Baran et al. 2022). During non-breeding, Atlantic puffins are thought to disperse widely and gradually move off the continental shelf (Hedd et al. 2010, Fayet et al. 2017, Lowther et al. 2020). Newfoundland common murres do not appear to disperse far from breeding colonies (McFarlane Tranquilla et al. 2013, Burke & Montevecchi 2018, Ainley et al. 2020), while Newfoundland razorbills stay near the coast or in shallow areas (Lavers et al. 2020). Male razorbills and murres are limited to areas within swimming distance from colonies during the fall molt, when they are flightless and attending flightless, post-fledging offspring. The distribution and movements of all 3 species may depend strongly on environmental conditions (Oedekoven et al. 2001, Veit & Manne 2015, Diamond et al. 2020) and prey predictability (Skov et al. 2000), and may also be influenced by the density and distribution patterns of other species. As only a few studies have examined species-specific seasonal variation in distributional patterns in a multi-species context (e.g. Buckingham et al. 2022), spatial overlap among species during the non-breeding season remains unclear.

Although overlap in alcid diet is difficult to assess during non-breeding, when they are not accessible at colonies, Atlantic puffin, razorbill, and common murre winter diets have been studied in a few parts of their range. Winter stomach contents from all 3 species include both fish (e.g. capelin, herring) and invertebrates (e.g. euphausiids, squid) of various types and proportions depending on location. Most studies found that common murres consume a higher proportion of fish in the winter than the other 2 species (Ainley et al. 1996, Rowe et al. 2000), and Atlantic puffins often consume a higher proportion of invertebrates (Falk et al. 1992, Hedd et al. 2010, Harris et al. 2015), although species-specific diets vary among regions (Blake 1984, Huettman et al. 2005). Stable isotope analysis of feathers can provide insight into non-breeding diet (Karnovsky et al. 2012), with $\delta^{15}\text{N}$ generally indicating prey trophic levels and $\delta^{13}\text{C}$ generally indicating spatially varying ecosystem baselines (Hobson et al. 1994, Bond & Jones 2009, Shipley & Matich 2020). Although there are shared prey species among the 3 alcids, different proportions of higher and lower trophic level prey consumed during feather growth will be reflected in the isotopic niche. Recent research using feather stable isotope analysis in the North Sea showed that the 3 alcids have different diets during fall, winter, and spring, suggesting that trophic segregation coupled with spatiotemporal

differences could reduce interspecific competition (St. John Glew et al. 2018).

Our objective was to determine the spatiotemporal and isotopic niche overlap during the non-breeding season among Atlantic puffins, razorbills, and common murres that breed sympatrically in the Northwest Atlantic. Based on previous single-species studies in this region (e.g. Hedd et al. 2010, Burke & Montevicchi 2018), we hypothesized that non-breeding alcid species would vary in their spatial and isotopic niche during different seasonal stages of the non-breeding season. We predicted some shared space use among the 3 species occurring during initial dispersal in the fall and return to the breeding colony during spring, but generally low spatial overlap of species-specific core use areas during the remainder of the non-breeding period. Specifically, we predicted that razorbills would be distributed closer to the coast, puffins mostly off the continental shelf, and murres on the Grand Banks. Isotopic niche overlap among the species was expected to be minimal, especially when spatial overlap was high.

2. MATERIALS AND METHODS

2.1. Tag deployment and feather sampling

Logger deployment and feather sampling took place during the breeding season on 2 colonies on the northeastern Newfoundland coast (Fig. 1): James Island (49.58° N, 53.78° W), where razorbills (~3000 pairs) and Atlantic puffins (~16 000 pairs) breed sympatrically (E. Jenkins et al. unpubl.), and, 47 km to the east-northeast, Funk Island (49.76° N, 53.18° W), the largest breeding colony of common murres in the Atlantic (~470 000 pairs; Wilhelm et al. 2015, Ainley et al. 2020). On James Island, puffins and razorbills were hand captured from burrows or nest crevices during chick-rearing and predominantly between midnight and sunrise to reduce disturbance. On Funk Island, breeding murres were captured with telescopic noose poles at breeding sites or nets on long poles while returning to breeding sites during daylight. We measured tarsus length (mm), wing chord (mm), and body mass (g) of each individual. Fieldwork was conducted in accor-

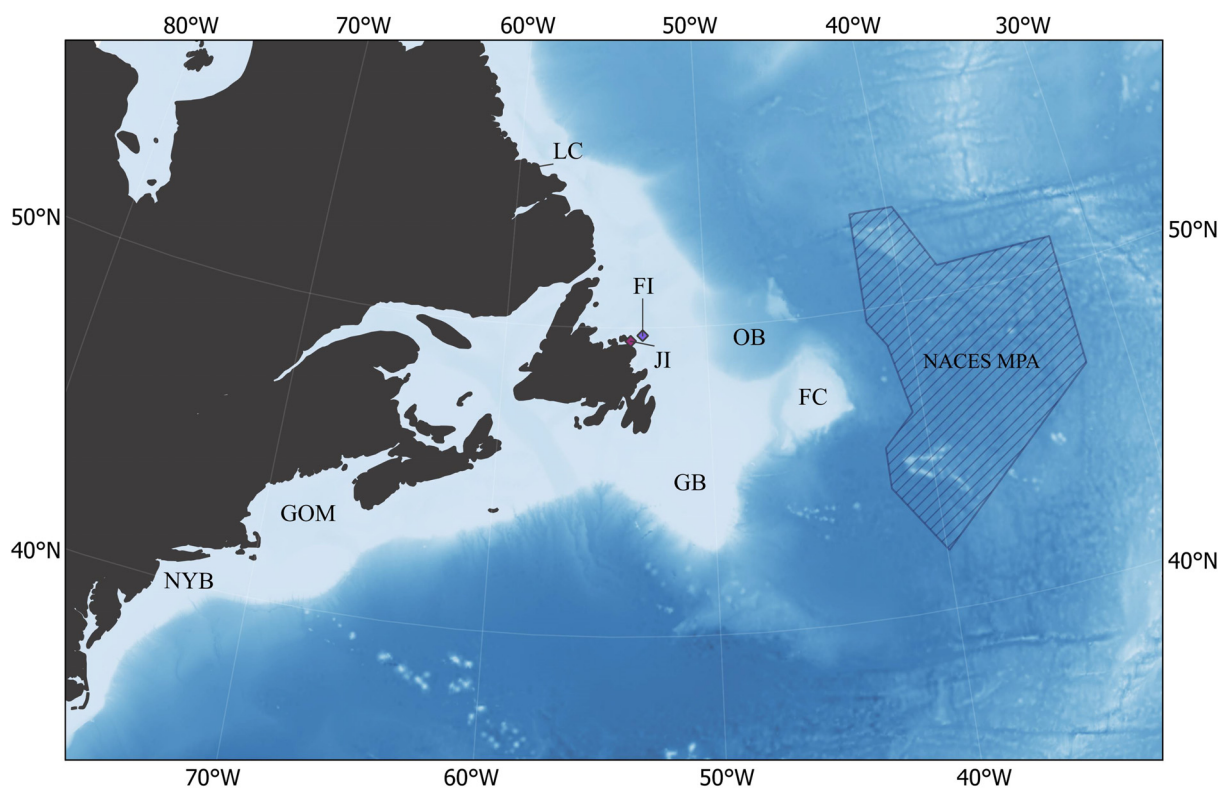


Fig. 1. Study area in the northwest Atlantic, indicating the breeding colonies of Funk Island (FI) and James Island (JI) off the northeastern Newfoundland coast, along with other referenced oceanographic and political locations: The New York Bight (NYB), Gulf of Maine (GOM), Labrador Coast (LC), Grand Banks (GB), Orphan Basin (OB), Flemish Cap (FC), and North Atlantic Current and Evlanov Sea basin Marine Protected Area (NACES MPA). Depth information is from Blue Earth Bathymetry, a GEBCO (www.gebco.net) derived product, the MPA boundaries are provided by OSPAR (www.ospar.org), and the land boundaries are from Natural Earth (www.naturalearthdata.com)

dance with the Canadian Council on Animal Care (University of Manitoba Protocol F16-017/1/2/3, F20-017/1; Memorial University of Newfoundland 19-01-WM) and Canadian Bird Banding Office (Banding Permits 10873 and 10332).

During 2019 and 2020, we deployed 10 to 25 light-level geolocators per species per year with immersion switches and temperature loggers (Migrate Technology C330 and C65+ on razorbills and puffins, Biotrack MK3006 on murres; see Table 1). The geolocators were attached to plastic leg bands with cable ties for year-round deployments and retrieval the following breeding season. Most loggers and bands were <1% of the birds' weight at the time of attachment (except 4 on puffins that were <1.25%), minimizing the potential for device effects during long-term deployment (Bodey et al. 2018, Geen et al. 2019). To examine possible device effects, we compared the mass:wing chord ratios of birds upon deployment and upon retrieval (as in Baran et al. 2022) and found that individual body condition did not differ (paired *t*-test: $t = 2.04$, $df = 30$, $p = 0.56$). Low recapture rates of common murres (Table 1) were primarily due to murres breeding on flat rock (in contrast with the crevice- and burrow-nesting puffin and razorbill) and, thus, flushing upon researcher approach. Slightly different data were collected and recorded by the 2 brands of geolocators. The Biotrack MK 3006 loggers, deployed as part of the SEATRACK project (Strøm et al. 2021), measured light intensity every 60 s and recorded the maximum of these light intensity values every 10 min, along with salt water immersion status every 3 s and recorded counts of 'wet' samples every 10 min. Temperature (°C) was also measured every 4 h, when 2 samples were taken and recorded 20 min apart, after the logger had been continually immersed for 20 min. Both Migrate Technology models measured light intensity every 60 s and recorded the maximum of

these light intensity values every 5 min, along with immersion status every 30 s and recorded counts of 'wet' status every 10 min. When the tags were immersed continuously for 20 min, temperature was measured once, and the maximum, minimum, and mean temperature every 8 h were recorded. Before deployment of the Migrate Technology geolocators, we performed a 3 to 8 d rooftop light-level calibration. Upon retrieval, we also conducted a simulated *in situ* light-level calibration where the geolocators were suspended below a plastic common murre decoy at the depth of the foot and moored at known coordinates for 5 to 8 d.

Samples of head (3 to 5 feathers) and first secondary (2 cm² snips) feathers were collected to quantify stable isotope ratios of carbon and nitrogen from 20 untagged chick-rearing individuals per species per year during 2017–2019. In 2020, fewer birds were sampled (17 puffins and murres, 14 razorbills) and belly feathers (3 to 5 feathers) were also collected. These birds were captured on the colony typically on 1 day each year. Head, first secondary, and belly feather samples were also collected from birds with geolocators upon recapture, with the exception of a secondary from one puffin in 2020 and head feathers from another in 2021. Reported molt schedules of these alcid species vary (Harris & Yule 1977, Thompson et al. 1998, Pyle 2009, St. John Glew et al. 2018, Lowther et al. 2020), though a commonality is that they are timed relative to the regional breeding season. Adjusting that relative annual molt timing based on the breeding schedule on the northeastern Newfoundland coast, we estimated murre and razorbill secondaries were molted during September to November and all 3 species molt head feathers during March to May. The timing of puffin secondary feather molt, however, may be highly variable (Harris & Yule 1977, Howell & Pyle 2005, Darby et al. 2022). Belly

Table 1. Summary of deployments of light-level geolocators on Atlantic puffins (ATPU), razorbills (RAZO), and common murres (COMU) during 2019 and 2020, including the number of Migrate Technology C330 and C65+ and Biotrack MK3006 model geolocators used in each year for each species, the number of geolocators retrieved in each year (2020 and 2021), the overall retrieval rate during this project, and summarized arrival and departure dates. Dates are given as mo/d

| Species | Quantity and models deployed | | Quantity retrieved | | Retrieval rate | Median (range) dates of non-breeding period boundaries | |
|---------|------------------------------|-----------|--------------------|------|----------------|--|-----------------|
| | 2019 | 2020 | 2020 | 2021 | | Departure | Arrival |
| ATPU | 10 C330 | 15 C65+ | 3 | 11 | 0.56 | 9/6 (8/28–9/13) | 5/13 (5/8–5/26) |
| RAZO | 10 C330 | 15 C330 | 5 | 8 | 0.52 | 8/13 (8/2–9/14) | 5/12 (5/5–5/31) |
| COMU | 25 MK3006 | 25 MK3006 | 3 | 5 | 0.16 | 8/12 ^a | 5/6 (5/3–7/02) |

^aThe geolocators deployed on murres were programmed to start recording between late July and mid-August, so all murre departure dates were set to August 12, a reasonable estimate for when many individuals have left the colony based on the typical breeding schedule

feather molt timing of all 3 species is also uncertain, with a fall molt potentially supplemented by additional body feather replacement later in the non-breeding season.

2.2. Spatial analysis

Arrival and departure dates from the colony for puffins and razorbills were determined based on the first or last day during an appropriate seasonal window (razorbills: June 15 to September 1 and May 15 to June 15; puffins: August 30 to September 12 and April 15 to June 15) when daytime light measurements dropped below a species-specific threshold, indicating burrow or nest crevice attendance. As the geolocators deployed on murre were programmed to start recording between late July and mid-August, all murre departure dates were set to August 12. This date is a reasonable estimate for when many individuals have left the colony based on the typical breeding schedule. Murre arrival dates were set as the first time during an appropriate seasonal window (May 1 to June 15) that the immersion sensor was dry for 6 h continuously during daylight, suggesting dedicated colony attendance, as long flights are unlikely in this and other alcid species (Elliott & Gaston 2014, Dunn et al. 2020). Murres in Newfoundland are not known to visit the colony during non-breeding, as they do in other regions (e.g. Bennett et al. 2022), thus this 6 h 'dry' threshold for murres avoids excluding data before the likely onset of incubation.

Geolocator data processing followed commonly used methods (Lisovski et al. 2012) in R version 4.0.3 (R Core Team 2020). Twilights were detected and extracted from the non-breeding, logged light data with 'TwGeos' (Lisovski et al. 2016) using a visually confirmed light threshold of 0.9. Location estimates were determined using 'ProbGLS' (Merkel et al. 2016), by incorporating light, immersion, and temperature data into a probabilistic model that estimated 2000 possible locations based on each twilight time, and weighted those locations by possible flight distances, based on the immersion data, species-specific flight speeds, and environmental characteristics. Combining these data, 100 iterations were then computed of the most likely movement paths, and the geographic median track for each individual was reported. The flight speeds used were based on estimates by Pennycuick (1987), adjusted to be more conservative (Buckingham et al. 2022), given that the activity data are based on immersion sensors, which register as dry when alcids sitting on the water's surface are leg tucking, a more common

occurrence than long flights in alcids (Dunn et al. 2020). Environmental variables included land cover, ice cover, and sea surface temperature (SST) obtained from the NOAA High-resolution Blended Analysis of Daily SST and Ice, a 0.25 degree resolution interpolation of observations from different platforms (Reynolds et al. 2007). We set a range of solar angles as input parameters (−6 to −3) based on values calculated with 'GeoLight' (Lisovski & Hahn 2012) using data from the 2 calibration methods. A list of all input parameters is provided in Table S1 in the Supplement at www.int-res.com/articles/suppl/m739p241_supp.pdf.

Spatial data (i.e. GLS location estimates) were projected in a Lambert Azimuthal Equal Area centered on James Island. Bivariate normal kernel density of core (50%) utilization distributions were calculated for each species in successive 2 mo periods (August to September, October to November, December to January, February to March, April to May) with 'ade-habitatHR' 0.4.19 (Calenge 2006). Smoothing factors for all periods and all species were set to a bandwidth of 150 km, based on reasonable assumptions about geolocator spatial precision (mean \pm SD; 186 \pm 114 km: Phillips et al. 2004; 304 \pm 413 km: Halpin et al. 2021), with an extent of 1 and grid cell size of 25 km, approximately the same resolution as the environmental data supporting the location estimates. Pairwise comparisons of the spatial overlap between species within each 2 mo period were quantified with the utilization distribution overlap index (UDOI) of the 50% kernels (Fieberg & Kochanny 2005). The UDOI represents niche overlap and shared space use because the concentration of occurrences within the kernels is considered together with the overlap of the kernels. For 50% kernel density estimates, a UDOI of 0 indicates no overlap, while a UDOI of 0.25 indicates a complete overlap and uniform distribution of occurrences throughout. UDOI values are often between 0 and 0.25, indicating that even where kernels overlap, species occurrences are not concentrated in the same places; however, UDOI values >0.25 could result from varying overlap of kernels but high overlap of concentrated occurrences of 2 species within the kernels (Fieberg & Kochanny 2005). Although there was some variation in UDOI depending on grid cell size, the relative amount of overlap among species pairs remained the same (Table S2).

2.3. Stable isotope analysis

Feathers were cleaned of dirt and oils by rinsing twice with 0.25 M sodium hydroxide (NaOH) solution for 30 s,

followed by rinsing twice with distilled water for 30 s (Bearhop et al. 2002). All feather samples ($n = 609$) were dried in uncapped glass scintillation vials in a warm oven for a minimum of 2 h, or in a room-temperature sheltered space with low humidity for a minimum of 48 h. Samples were sent to the GLIER Stable Isotopes Lab at the University of Windsor, Ontario, Canada, where they were homogenized, and sub-samples of 0.7 to 1 mg were analyzed with a continuous-flow isotope ratio mass spectrometer (Thermo Delta V) to quantify stable carbon and nitrogen isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$). The measured ratios of sample values relative to the ratios of universal standards (Vienna Pee Dee Belemnite for carbon, and atmospheric N_2 for nitrogen) are presented in standard δ notation in units of parts per mil (‰; Bond & Jones 2009). These are calculated as:

$$\delta^H X = \left[\left(\frac{R_{\text{Sample}}}{R_{\text{Standard}}} - 1 \right) \right] \times 1000 \quad (1)$$

where X is the element (C or N), H is the heavy isotope mass of that element, and R is the ratio of the heavy to the light isotope for the element ($^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$). Precision was measured as $\leq 0.48\text{‰}$ for $\delta^{15}\text{N}$ and $\leq 0.17\text{‰}$ for $\delta^{13}\text{C}$ using the standard deviation of replicate analyses of 4 standards: NIST1577c, tilapia muscle, USGS 40 and urea ($n = 60$ for all). Instrument accuracy, based on the certified values of USGS 40 ($n = 60$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analyzed throughout runs showed a difference from the certified value of 0.08‰ for $\delta^{15}\text{N}$ and 0.11‰ for $\delta^{13}\text{C}$.

We inspected the stable isotope data visually with multivariate histograms and determined that there were no large departures from multivariate normality. A Bayesian multivariate mixed model with Gaussian error was fit to the data. The response variables were the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, with species and feather type as fixed predictors, and individual and year as random intercepts. Individuals were nested within years. We ran the model using 13 000 iterations, 3 chains, a thinning rate of 10, and a burn-in of 3000 (R package 'MCMCglmm', Hadfield 2010). A minimally informative normal prior was used for the means, and the broadest possible inverse-Wishart distribution was used as a prior for the covariance matrices. Model fit was assessed with visual inspection of trace plots and a posterior predictive check. As the model estimated the covariances between the 2 response variables and fit different regression slopes for each of the predictor–response combinations in a Bayesian framework, it allows for direct comparison of estimates of the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values among species for each feather type, based on maximum *a posteriori* (MAP) and 90% credible intervals. The MAP is

the most probable value for $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ (i.e. the mode of the posterior distribution), and the credible intervals provide a 90% probability that the $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ value is within the given range. MAP and 90% credible intervals (CrI) for other model parameters of interest are also reported, along with additional probabilities derived from our posterior distribution estimates. For example, to determine the probability that the effect of year was close to 0, we calculated the proportions of iterations for which the coefficient for each year was higher/lower than 0 and reported the maximum.

Species-specific standard ellipse areas corrected for small sample size (SEA_c) were calculated using the R package 'SIBER', to visually represent isotopic niche breadth for each species and feather type (Jackson et al. 2011). To describe the variability in our estimates of niche breadth and niche overlap, Bayesian standard ellipse areas (SEA_b) and 90% CrI were also calculated for each species and feather type with a minimally informative normal prior for the mean and inverse-Wishart prior for the covariance matrices, using a burn-in of 1000, 20 000 iterations, 2 chains, and a thinning rate of 10 (Jackson et al. 2011). Following Jackson (2023), probabilities for pairwise comparisons of niche breadth (p_c) between species within feather types or feather types within species were calculated as proportions of iterations for which SEA is higher/lower for one species/feather type than another. Isotopic niche overlap between species pairs for each feather type was calculated by dividing the area of the portion that overlaps by the total niche area occupied by the 2 species (Jackson et al. 2011) for the first 1000 draws from the SEA_b ellipses. Overlap MAP and 90% CrI are reported.

3. RESULTS

3.1. Spatiotemporal analyses

We recovered 35 geolocators over the 2 years of tracking (Table 1). The geolocators from 2 murres and 1 puffin malfunctioned and did not have usable data, and 5 birds were tracked for 2 years (2 puffins, 2 razor-bills, 1 murre); thus our dataset represents 37 bird-years total. Based on our interest in examining core space use of each species and overlap among species, we used all the available data in our analysis. Every core area polygon (i.e. kernel density) was always based on at least 4 and a maximum of 13 individuals.

In August to September, core use areas (50% kernel density estimates) overlapped to some extent among

all 3 species in the waters off eastern Newfoundland (Fig. 2A), but this overlap generally decreased throughout the non-breeding season (Fig. 2B–E). As razorbills and murres departed the colony around mid-August, while puffins departed around mid-September (Table 1), there may be less overlap during August to September than presented (Fig. 2A), depending on how quickly birds disperse from the colony vicinity. During August to September, razorbills ranged over a wide area, with some individuals mov-

ing farther north (around 60°N, Fig. 2A), perhaps because of sex-based differences and/or differences in nest success (Wanless & Harris 1986). After this period, there was no shared core area space use (i.e. UDOI = 0) of murres and razorbills (October to March; Fig. 2B–D) until the April to May period (Fig. 2E), when returning to the colony. By contrast, puffins were more widely dispersed than murres and razorbills throughout the non-breeding period, which led to varying degrees of overlap with both species

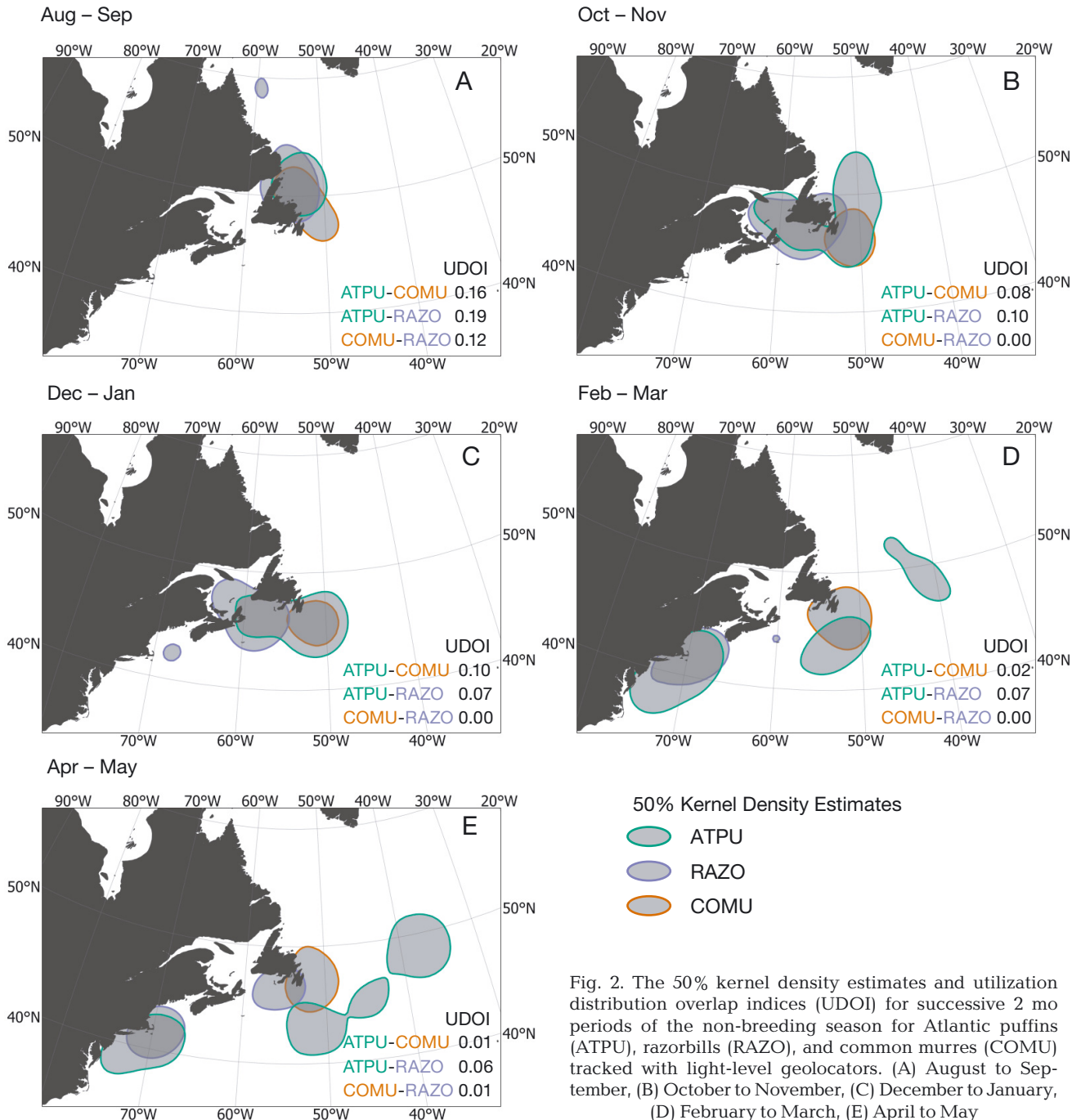


Fig. 2. The 50% kernel density estimates and utilization distribution overlap indices (UDOI) for successive 2 mo periods of the non-breeding season for Atlantic puffins (ATPU), razorbills (RAZO), and common murres (COMU) tracked with light-level geolocators. (A) August to September, (B) October to November, (C) December to January, (D) February to March, (E) April to May

(Fig. 2B–E). In October to November and December to January, spatial overlap of puffins with the other species decreased (Fig. 2B,C), which continued in February to March (Fig. 2D). By February to March, puffins had split into 3 distinct core use areas: east of the shelf break, over the Grand Banks where they overlapped with murres, and towards the Gulf of Maine and US coast where they overlapped with razorbills. During April to May, all 3 species moved back towards the breeding colonies (Fig. 2E).

3.2. Isotopic analyses

The Bayesian multivariate generalized linear mixed model converged successfully, based on visual inspection of trace plots and density plots of the posteriors. For all feather types, the probability that $\delta^{13}\text{C}$ for puffins was higher than that of both of the other 2 species was 0.75, while $\delta^{15}\text{N}$ differed more among species, with a 0.95 probability that murre $\delta^{15}\text{N}$ was more enriched than that of razorbills, and a 0.99 probability that razorbills were more enriched than puffins (Fig. 3). The estimates of covariance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ centered on 0 (MAP = -0.02 , 90% CrI: -0.57 to 0.60), indicating no detectable linear relationship between the 2 response variables in our data. Year did not affect model results (90% CrI included 0, the probability that the effect was either $>$ or $<$ 0 was under 0.71, MAP range: -0.20 to 0.13), except for 2021, when $\delta^{13}\text{C}$ was comparatively much higher than the other years (MAP = 0.46 , 90% CrI: -0.30 to 1.30 , the probability that the effect was >0 was 0.90). As feathers were only collected from tagged (geolocator)

birds in 2021, sample sizes from all 3 species were lower that year ($n = 71$) and, thus, we pooled data from 2017–2020 (i.e. excluded 2021) for subsequent niche breadth and overlap analyses.

During secondary feather molt, there was 39% isotopic niche overlap of murres and razorbills (90% CrI: 16 to 60%), but no overlap of puffins with murres (90% CrI: 0 to 1%) or razorbills (90% CrI: 0 to 2%; Fig. 4). Murres had a narrower niche breadth (SEA_b) than razorbills ($p_c > 0.99$), although both were less than one-third of the puffin niche breadth ($p_c > 0.97$; Table 2, Fig. 4). During belly feather molt, murre isotopic niche expanded relative to secondary feather molt ($p_c > 0.97$), while razorbill niche breadth stayed consistent ($p_c = 0.66$) and that of puffins contracted ($p_c = 0.96$), although puffin niche breadth was still broader than for either of the other 2 alcids ($p_c > 0.94$; Table 2, Fig. 4). The narrow niches of murres and razorbills during this molt was associated with a large range in the estimates of overlap (90% CrI: 0 to 48%), but there was a 0.93 probability that the overlap was $<15\%$. Puffins had similarly minimal isotopic niche overlap with murres (MAP = 0%, 90% CrI: 0 to 32%) and razorbills (MAP = 0%, 90% CrI: 0 to 17%) during belly feather molt. During head feather molt (Fig. 4), the isotopic niches of these alcids differentiated on the $\delta^{15}\text{N}$ axis, with minimal overlap between only razorbills and puffins (MAP = 0%, 90% CrI: 0 to 6%). Razorbill niche breadth expanded by more than 50% during this molting period compared to the other 2 molt periods ($p_c > 0.93$), while murre niche breadth was similar to during belly feather molt ($p_c = 0.49$) and puffin niche was broader than during body molt but narrower than during secondary feather molt ($p_c > 0.96$).

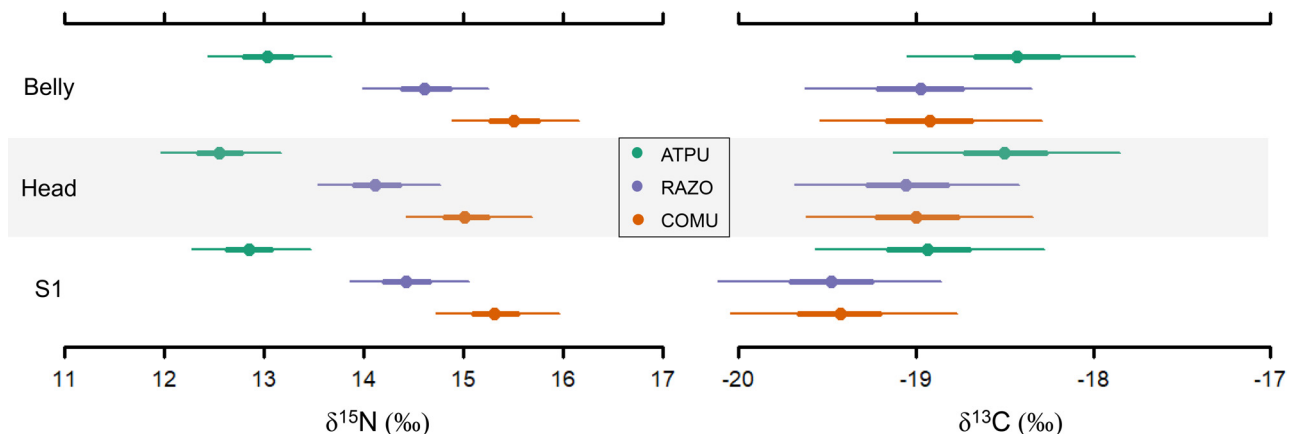


Fig. 3. Posterior distributions from a Bayesian multivariate generalized linear mixed model on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of feathers collected in 2017–2021. Maximum *a posteriori* (MAP) estimates (points), and 50% (thick line) and 90% (thin line) credible intervals for all combinations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, belly, head, and first secondary (S1) feather types, and species: Atlantic puffin (ATPU), razorbill (RAZO), and common murre (COMU). MAP is the most probable value for the isotope ratio (i.e. the mode of the posterior distribution), and credible intervals provide a 90% or 50% probability that the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ value is within the given range

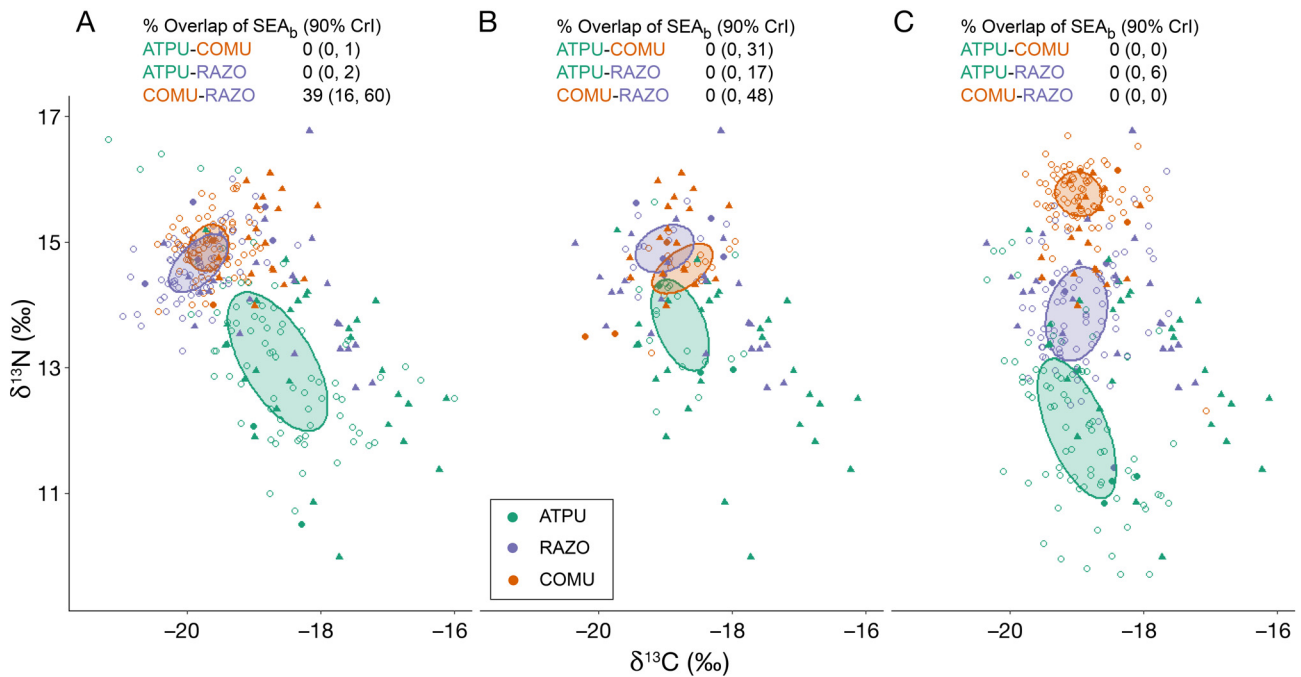


Fig. 4. Isotopic niche breadth (SEA_c) and isotopic niche overlap (% overlap of SEA_b MAP, 90% CrI) of Atlantic puffin (ATPU), razorbill (RAZO), and common murre (COMU) (A) first secondary (S1), (B) belly, and (C) head feathers. Calculated SEA_c ellipses are plotted for visualization of overlap. The matching calculations of overlap are based on SEA_b, to provide an indication of variability. The MAP is the most probable value for the % overlap (i.e. the mode of the posterior distribution), and credible intervals provide a 90% probability that the overlap is within the given range. SEA and overlap calculations were based on feathers collected in 2017–2020 and included untagged birds (open circles) and geolocator-tagged birds (solid circles). Feathers collected from geolocator-tracked birds in 2021 (solid triangles) are presented but were not included in SEA or overlap calculations

3.3. Combining spatial and isotopic data

The feather isotope ratios from geolocator tagged birds were used to visually assess whether variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was due to spatial baseline shifts or diet, when the approximate timing of a particular feather molt was known. Carbon isotope ratios ($\delta^{13}\text{C}$) of tagged birds did not show much variation in any of the feather molt periods (ranges of 3.17 to 4.08‰; Table 2, Fig. 4) and no apparent geographic gradient (Fig. S1), suggesting minimal baseline shifts within the distributional range of all 3 species. Therefore, we focused on examining $\delta^{15}\text{N}$ values to determine whether species located in the same general area during a molting period occupied different trophic positions. During fall (September to November), when murres and razorbills molt secondary feathers, all tracked murres and razorbills had $\delta^{15}\text{N}$ ratios within 1.98‰

of each other (Fig. 4), suggesting minimal variation as to trophic position. We could not include puffins in this comparison because of uncertainty and variability as to when (and therefore where) they molt secondary

Table 2. Stable isotope ratios (mean \pm SE) of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) along with estimates of isotopic niche breadth, including the standard ellipse area corrected for small sample sizes (SEA_c), and the maximum *a posteriori* estimates of the Bayesian standard ellipse area (SEA_b) and associated 90% credible intervals (90% CrI) from Atlantic puffin (ATPU), razorbill (RAZO), and common murre (COMU) head, belly, and first secondary (S1) feathers collected during July to August 2017 to 2020 on the northeast coast of Newfoundland

| Feather type | Species | SEA _c (‰ ²) | SEA _b (‰ ²) | 90% CrI | | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) |
|--------------|---------|------------------------------------|------------------------------------|---------|-------|---------------------------|---------------------------|
| | | | | lower | upper | | |
| S1 | ATPU | 2.88 | 2.85 | 2.41 | 3.47 | -18.63 \pm 0.10 | 13.15 \pm 0.14 |
| | RAZO | 0.71 | 0.69 | 0.59 | 0.86 | -19.81 \pm 0.06 | 14.66 \pm 0.06 |
| | COMU | 0.46 | 0.45 | 0.38 | 0.56 | -19.66 \pm 0.04 | 14.90 \pm 0.05 |
| Belly | ATPU | 1.24 | 1.12 | 0.85 | 1.83 | -18.73 \pm 0.11 | 13.69 \pm 0.19 |
| | RAZO | 0.66 | 0.60 | 0.45 | 0.94 | -18.98 \pm 0.11 | 14.91 \pm 0.09 |
| | COMU | 0.73 | 0.69 | 0.52 | 1.08 | -18.83 \pm 0.12 | 14.49 \pm 0.12 |
| Head | ATPU | 2.17 | 2.15 | 1.81 | 2.62 | -18.99 \pm 0.07 | 12.05 \pm 0.14 |
| | RAZO | 1.41 | 1.39 | 1.17 | 1.69 | -18.95 \pm 0.06 | 13.90 \pm 0.10 |
| | COMU | 0.74 | 0.73 | 0.61 | 0.88 | -18.92 \pm 0.05 | 15.70 \pm 0.06 |

feathers. During spring (March to May), when all 3 species molt head feathers, all tracked birds had $\delta^{15}\text{N}$ ratios that ranged $\sim 5.30\text{‰}$ (Fig. 5). The range of murre $\delta^{15}\text{N}$ values was 0.82‰ , but the $\delta^{15}\text{N}$ values of puffins varied by 3.30‰ and those of razorbills by 3.64‰ . There was no clear geographic gradient in $\delta^{15}\text{N}$ values during this molting period, with variation in $\delta^{15}\text{N}$ among closely spaced individuals of the same species apparently greater than the differences between individuals farther apart (Fig. 5). The differences in $\delta^{15}\text{N}$ among species in the same general area (Fig. 5) reflected the patterns seen in Fig. 4, suggesting that murre were feeding at a higher trophic position, razorbills were intermediate, and puffins were at a lower trophic position.

4. DISCUSSION

As predicted, we generally found minimal spatio-temporal and isotopic niche overlap during the non-breeding season among sympatrically breeding Atlantic puffins, razorbills, and common murre, with a few exceptions during certain times of year. Spatial overlap of species-specific core use areas was low among the 3 species, with 2 exceptions: overlap was

higher just after and before the breeding season, and variability in puffin distributions was associated with some spatial overlap with the other 2 species at other times. Isotopic niche overlap among the 3 species was also usually low, especially during head feather molt in the spring, thereby supporting our prediction that isotopic niche overlap would be low when spatial overlap is high. Our results suggest that these species either have always had separate niches (i.e. always relied on different resources in different places, often referred to as 'the Ghost of Competition Past') during non-breeding, or have co-evolved niche partitioning to allow coexistence (Connell 1983).

One exception to the minimal niche overlap was the high isotopic niche overlap between murre and razorbills during secondary feather molt in the fall, when they also overlapped spatially. Spatial overlap was not surprising during this period, as male razorbills and common murre are limited to swimming-speed movements while flightless during wing molt and the 1 to 2 mo period of post-fledging parental care of flightless offspring (Gaston & Jones 1998). This leaves both species highly vulnerable to certain anthropogenic threats in this area, e.g. vessel traffic, oil spills, or chronic oil pollution (Wiese & Ryan 2003, Wilhelm et al. 2009, Lieske et al. 2020). Additionally,

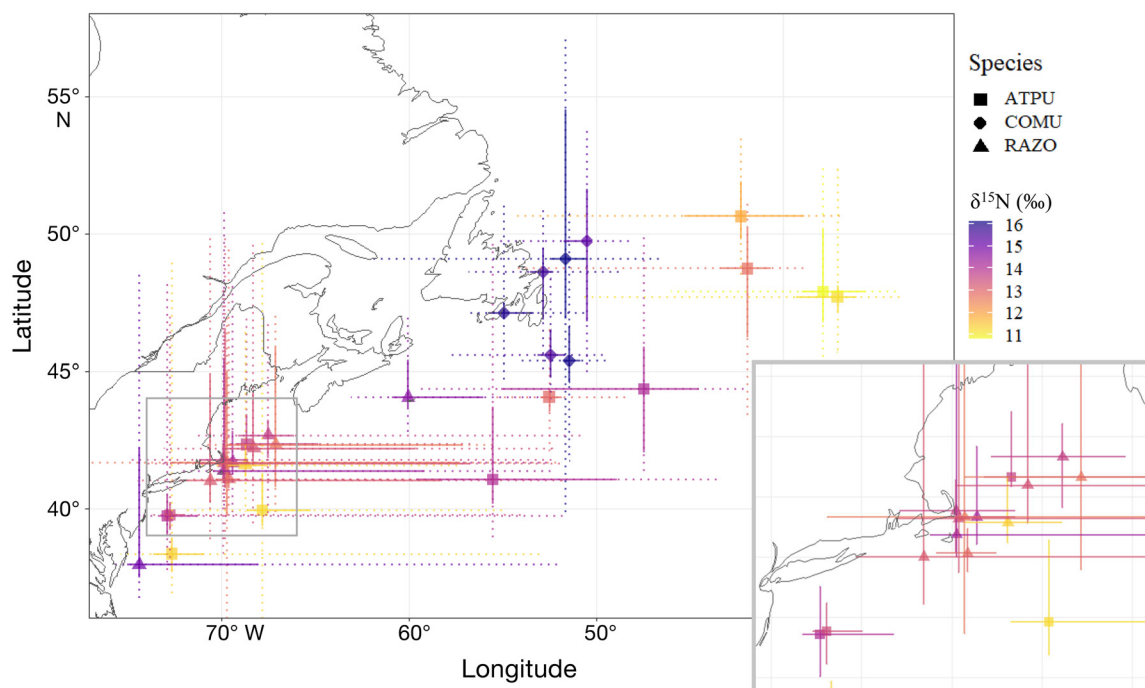


Fig. 5. Head feather $\delta^{15}\text{N}$ of individual geolocator-tagged Atlantic puffins (ATPU), razorbills (RAZO), and common murre (COMU) at their estimated geographic median locations during March to May, the time of year when head feathers are molted. Solid error bars: 25th to 75th quantiles of latitude and longitude estimates; dotted lines: entire range of latitude and longitude estimates during this period

the Newfoundland turr hunt, a regulated coastal harvest of murres (Montevecchi et al. 2007), begins in Labrador in September and off northeast Newfoundland in October (ECCC 2023), when razorbills in the area could easily be incorrectly identified as murres (Lavers et al. 2009) and, thus, mistakenly hunted during this period of spatial overlap. The high isotopic niche overlap could be partly because both species rely on available prey near the colony. Interestingly, while all the murres stayed in the same area during September and October, some razorbills, perhaps females or failed breeders (Wanless & Harris 1986), dispersed far to the north, along the Labrador coast. Future research could determine if females or individuals not caring for offspring have different isotopic niches from males performing parental care during flight feather molt (e.g. Burke et al. 2015).

It is difficult to disentangle the effect of different sources of variation on isotopic niche overlap. The spatially varying, basal primary productivity predominantly determines $\delta^{13}\text{C}$ ratios, while $\delta^{15}\text{N}$ ratios mostly increase with trophic position (Hobson et al. 1994, Fry 2006), but both stable isotope ratios incorporate trophic, spatial, environmental, temporal, and physiological variability (Newsome et al. 2007, Shipley & Matich 2020) that we could not control for in this study. Any of these sources of variation may underlie the low isotopic niche overlap among these 3 alcid species, as we largely do not know when or where certain feather types are molted, nor the physiology of molting in alcids (Pyle 2009). Distribution differences alone could result in low isotopic niche overlap, as there are gradients of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ baselines associated with major water masses such as the Gulf Stream in the northwest Atlantic (McMahon et al. 2013). For feather types where a reasonable molt timespan could be estimated, variation in the feather nitrogen isotope ratios of species occurred in an area where there was little baseline variation, which suggests that differences in $\delta^{15}\text{N}$ values represent occupation of different trophic positions (Hobson et al. 1994). Isotopic niche segregation while co-located during breeding has previously been documented among all 3 species in northeast Newfoundland (Jenkins & Davoren 2020, Lescure 2021) and other regions (Linnebjerg et al. 2013, Pratte et al. 2017, Petalas et al. 2021), with puffins consistently feeding at a lower trophic position while razorbills and murres overlap to varying extents. Our isotope results also align with non-breeding diet studies showing that puffins have a generalist diet with a high proportion of invertebrates (Falk et al. 1992, Hedd et al. 2010, Harris et al. 2015), murre diet contains large proportions of fish (Ainley

et al. 1996, Rowe et al. 2000), and razorbills consume both invertebrates (Huettman et al. 2005) and fish (Blake 1984, Ouwehand et al. 2004). As patterns of spatial and dietary overlap are further confounded by individual variation in when a particular feather was grown, the reason for low isotopic niche overlap remains uncertain.

Species-specific spatial patterns match previous knowledge about non-breeding distribution patterns of birds from Newfoundland colonies. Similar to our tracked birds, Newfoundland common murres do not appear to disperse far from breeding colonies during non-breeding, remaining mostly on the Grand Banks and Orphan Basin and returning toward their colony in late winter (McFarlane Tranquilla et al. 2013, Burke & Montevecchi 2018), where capelin *Mallotus villosus* and sand lance *Ammodytes dubius* are distributed during this period (Morrison 2021, DFO 2021). Newfoundland razorbills stay near the coast, in shallow areas, but move much farther south than murres (Lavers et al. 2020) and likely cover even larger distances when winter feeding conditions are poor (Diamond et al. 2020), similar to razorbills in other regions (St. John Glew et al. 2019). The razorbills we tracked also moved south along the US coast, where the dominant forage fish are sand lance, herring *Clupea harengus*, and Atlantic menhaden *Brevoortia tyrannus* (Anstead et al. 2021, Suca et al. 2021). Puffins used some of the same areas as razorbills and murres throughout non-breeding, eventually overlapping mostly along the US coast and on the Grand Banks, but, as documented previously, they were also found farther from the coast (Hedd et al. 2010, Fayet et al. 2017) and towards the mid-Atlantic (Fayet et al. 2017). During late winter, some puffins moved over the Flemish Cap and then towards the Mid-Atlantic Ridge, a recently described hotpot that is used by puffins from eastern Atlantic colonies (Davies et al. 2021b). While this hotspot has been designated as the North Atlantic Current and Evlanov Sea basin Marine Protected Area (NACES MPA, Fig. 1; Davies et al. 2021a), the low spatial overlap among the 3 alcids underlines the value of establishment and management of functional networks of protected areas to maintain ecosystem processes (Game et al. 2009).

The high spatial variation and broad isotopic niche of puffins during non-breeding could result from displacement from high-quality foraging areas and/or prey types to avoid competitive interactions with larger alcids (e.g. Shealer & Burger 1993, Maniscalco et al. 2001, Carvalho et al. 2020). Puffins are displaced from high-quality prey patches by larger alcids during breeding in coastal Newfoundland (Piatt 1990),

and, on a larger scale, they often migrate longer distances from the colony and coast than other sympatrically breeding larger alcids throughout their range (Jessopp et al. 2013, Fayet et al. 2017). The lower trophic position of puffins when spatially overlapped with the other 2 species suggests displacement from higher trophic level prey. Additionally, puffins occupying the mid-Atlantic had similarly low $\delta^{15}\text{N}$ values, possibly indicating large-scale displacement from high-quality foraging locations occupied by murres and razorbills (e.g. US coast, Grand Banks), or displacement from higher trophic level prey by other species within another known high-quality foraging area, the NACES MPA (Davies et al. 2021a,b). Although the broad secondary feather isotopic niche of puffins may be due to individual variability in the timing and, thus, location of feather growth (Harris & Yule 1977, Howell & Pyle 2005, Darby et al. 2022), this variability in molt patterns may also have evolved to reduce overlap of this energetically demanding period with other species. High isotopic variability during belly and head feather molt was possibly related to variation in migration patterns and baselines encountered, but there was also more variation within puffins in the same general area during head feather molt. Despite this evidence for displacement, it is possible that puffins simply exploit different resources to murres and razorbills, exhibiting greater non-breeding diet flexibility (e.g. St. John Glew et al. 2019) or targeting alternative prey types because their dive depth is comparatively constrained.

The low spatiotemporal and isotopic niche overlap among these alcids during the non-breeding season suggests that different localized threats will impact each species, although there are key exceptions. Murres and puffins that remain on the Grand Banks are likely at increased risk of oil exposure, due to chronic and accidental discharges along high-traffic shipping routes and around offshore oil platforms (Hedd et al. 2011). This would likely affect a greater proportion of the murre population, as many of the tracked puffins left this area, but most of the tracked murres stayed. The US coast, specifically the Gulf of Maine and New York Bight, where extensive offshore wind development is planned (Stenhouse et al. 2020, Moriarty 2023, NROC 2023), is an important area for puffins and razorbills from northeast Newfoundland in mid-winter and early spring. Although alcids have low risk of collision with turbine blades, due to low flight heights (Johnston et al. 2014), there is evidence that alcids are vulnerable to displacement by offshore wind installations (Vanermen et al. 2015, Welcker & Nehls 2016, Kelsey et al. 2018). Displacement can

potentially have population-level impacts (Busch & Garthe 2016, Peschko et al. 2024), but the magnitude of these barrier effects is site specific (Dierschke et al. 2016). Although the consequences of this loss of habitat are unknown, it could increase the spatial overlap between puffins and razorbills. Declines in prey abundance on the US coast or Grand Banks could also be particularly detrimental to puffins (Scopel et al. 2019), especially if they are displaced from high-quality resources in this area of overlap with razorbills.

By combining tracking and stable isotopes, we found evidence of differences in space and resource use during the low-productivity, non-breeding period, in line with predictions based on niche theory. However, remaining knowledge gaps hamper understanding of species interactions during non-breeding. Uncertainty around molt timings, especially for puffin flight feathers, limits our ability to interpret variability in isotope ratios even when combined with tracking. Further studies should focus on this basic aspect of natural history (Pyle 2009), possibly employing compound specific isotope analysis of amino acids (CSIA-aa) to parse out isotopic baseline shifts from trophic position independent of location (McMahon et al. 2015, Ohkouchi et al. 2017). Additionally, multi-colony tracking studies over a wider geographic area (e.g. Buckingham et al. 2022) and analysis of migratory connectivity (e.g. Merkel et al. 2021) would provide a broader picture of important non-breeding foraging areas for alcids in this region.

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