



Multidimensional niche differentiation of chick-rearing sympatric auks in the Gulf of St. Lawrence

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Abstract

Niche theory predicts that similar species cannot occupy the same geographical space when resources are limited. Sympatric seabirds, such as auks, are ideal models for investigating niche differentiation because they share life history traits and form breeding colonies that rely on common prey items. Auk differentiation may be driven by variations in body mass and wing size, diving capacity, and visual acuity leading each species to forage at different distances, depths, or times of day, respectively. However, previous auk studies have produced diverse results, leaving us with an incomplete understanding of their foraging differentiation across spatial, environmental, and temporal dimensions. In 2021, we tested niche differences at the Mingan Archipelago National Park Reserve, Québec, Canada (50°11' N, 63°13' W) by utilizing GPS and time and depth recorders to track the positions of breeding Atlantic puffins (*Fratercula arctica*), razorbills (*Alca torda*), and common murres (*Uria aalge*), which were then paired with environmental data. There was high niche overlap in geographical foraging areas, with auk wing size and mass not appearing to influence their foraging distance. Instead, auk foraging was partitioned over different depths and times of day. Although razorbills and puffins generally exploited shallow foraging areas, puffin foraging activity occurred in deeper waters and at different times of day than razorbills. Murres foraged in the deepest benthic areas and were the only species to forage at night. Our study therefore suggests that auks could be facilitating their coexistence by exhibiting temporal and spatial differences in their foraging behaviours and locations.

Keywords Foraging ecology · Ecological segregation · Interspecific competition · Biologging · Temperature-depth recorders · Central place · Alcidae

Introduction

Sympatric species competing for limiting resources can create environments of unstable competition (Pianka 1973). To mitigate competitive exclusion, niche theory predicts that similar species are expected to coexist within a community by differentiation in one or more dimensions of their ecological niche (Gause 1934; Hardin 1960). An ecological niche refers to all the factors that an organism needs to exist, including the resources it uses and the environment in which

it lives (Hutchinson 1957, 1978). Seabirds are particularly relevant to test niche theories as they share life history traits and aggregate into dense mixed species breeding assemblages (Gochfeld 1980). Competition increases during chick-rearing when individuals are constrained to the vicinity of the colony and need to supplement themselves and their chicks, creating the strongest partitioning (Orlans and Pearson 1979; Gaston et al. 2007; Barger et al. 2016). Indeed, intraspecific competition in seabirds leads to patterns consistent with direct prey depletion during that period (Elliott et al. 2009; Patterson et al. 2022). Broad niche differentiation patterns within seabird communities have been established since the 1970s (Cody 1973; Jessopp et al. 2020). Seabirds may differentiate in their foraging strategies by exploiting different prey resources, geographical spaces (areas, depths, and environmental conditions), and/or peak foraging times of day (Robertson et al. 2014; Shoji et al. 2015; Connors et al. 2015). Nonetheless, niche differentiation will become

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unnecessary in cases of resource abundance (Weimerskirch et al. 2012; Calado et al. 2018).

Diving seabirds face an evolutionary trade-off between flight and diving capabilities, typically dictated by wing area relative to body mass (wing-loading hypothesis; Thaxter et al. 2010). Species that dive with greater propulsion will often be high wing-loaders with elevated energy costs during flight (Elliott et al. 2013). Members of the family Alcidae (hereafter, auks) are wing-propelled pursuit divers and have morphological differences, influencing their wing-loading (Piatt and Nettleship 1985; Delord et al. 2020). Sympatric breeding auks exhibit different flight and diving capabilities, influenced by their aerobic dive limits (based on oxygen stores), which may have evolved to diverge aspects of their niches to maximize prey energy gain (Elliott et al. 2013). Chick-rearing auks tend to segregate using different foraging strategies (Table 1). Auk studies report varying degrees of horizontal overlap among all species, where larger species (with higher wing-loading and oxygen stores) tend to dive deeper, segregating from smaller species in the vertical dimension. While evidence for partitioning among congeneric murrelets is available (Table 1; Takahashi et al. 2021), there is limited understanding regarding how partitioning may occur across the entire family, including auks from different genera. Notably, previous auk studies have made valuable contributions by exploring specific aspects of spatial foraging encompassing vertical, horizontal, temporal (i.e., time of day), and environmental characteristics. Building upon this foundation, there is a need for research to explore these aspects concurrently across multiple auk species at fine spatial scales, providing a comprehensive examination of their foraging strategies (Bonnet-Lebrun et al. 2021).

A multi-species auk colony in eastern Canada is located within the Gulf of St. Lawrence on Ile à Calculot des Betchouanes (hereafter, Betchouanes). Three auk species, which primarily feed on forage fish, inhabit this site and share a common breeding range in the Atlantic: Atlantic puffins (*Fratercula arctica*, hereafter puffins), razorbills (*Alca torda*), and common murrelets (*Uria aalge*, hereafter murrelets, Gaston and Jones 1998). In 2019, Petalas et al. (2021) characterized the horizontal foraging movements during incubation and chick diets of these auks at Betchouanes. Despite sharing two common prey species, namely capelin (*Mallotus villosus*) and sand lance (*Ammodytes sp.*), the three auks exhibited clear niche partitioning in their horizontal foraging strategies during incubation. Therefore, Betchouanes provides an opportunity to further investigate the foraging ecology of closely related auk species during chick-rearing, allowing comparisons between breeding stages and with the existing body of literature on niche differentiation (Table 1).

We examined whether niche differentiation was occurring among chick-rearing auks using Global Positioning System (GPS) loggers and Temperature-Depth Recorders (TDR) at

Betchouanes. We evaluate the extent of niche partitioning by applying a four-dimensional approach: (1) quantifying overlap in foraging areas during chick-rearing and determining whether there are differences in horizontal (latitude and longitude) characteristics, (2) determining differences in foraging depth, (3) identifying environmental characteristics (i.e., seafloor depth and sea temperature) where foraging occurred, and (4) determining differences in the time of day of foraging events. We hypothesize limited overlap in the ecological niche spaces (Table 1). As dive depth and duration tend to increase with body size in auks (Elliott et al. 2013), we predict that larger murrelets, with high wing-loading and greater flight energy expenditure, will have increased dive capacity relative to intermediate-sized razorbills and smaller puffins. We predict that murrelets would be foraging closer to the colony in the deepest and coldest waters relative to razorbills and puffins (Fig. 1a). Further, we predict that murrelets will exhibit a greater specialization for nocturnal diving due to wing-loading differences and their higher visual acuity (Elliott and Gaston 2015; Gulka and Davoren 2019). Thus, we predict that murrelets will be diving the most during the night, razorbills will have more crepuscular diving, and puffins (with lower visual acuity) will dive more during the day (Fig. 1a).

Materials and methods

Study area

We collected data at Betchouanes Island (50°11' N, 63°13' W), located in the Mingan Archipelago National Park Reserve (in the Côte-Nord region). Betchouanes, a small Migratory Bird Sanctuary (≈10.22 ha/9.83 km², maximum altitude ≈15 m), is situated ≈2.6 km south of the mainland. The topography is characterized by a central plateau covered in dense herbaceous vegetation. Betchouanes consists of 11 breeding species including three auks. In 2015, approximately 468 puffins, 724 murrelets, and 1323 razorbills were nesting on Betchouanes (Rail 2021). Morphology varies among murrelets (mass 800–1125 g, wingspan 64–71 cm, wing-loading 205 N/m², Elliott et al. 2013; Ainley et al. 2020), razorbills (mass 570–880 g, wingspan 63–68 cm, wing-loading 167 N/m², Elliott et al. 2013; Lavers et al. 2020), and puffins (mass 404–538 g, wingspan 47–63 cm, wing-loading 108 N/m², Elliott et al. 2013; Lowther et al. 2020).

Fieldwork

During the chick-rearing period in 2021, we deployed tracking devices at Betchouanes between the 4th to 8th of July. We captured 11 adults from each species by hand in rock

Table 1 Summary of studies that have directly studied niche differentiation among chick-rearing breeding auks using biologists

Common name	Island Colony	Horizontal segregation pattern (using GPS)	Vertical segregation pattern (using TDR)	Environmental segregation pattern	Foraging time of day segregation pattern	Source
Thick-billed murre Razorbill	Gannet, Islands, Canada	Not investigated	Murres exploited deeper diving depths than razorbills	Not investigated	Both murres and razorbills foraged more during the daytime	Paredes et al. (2008)
Common murre Razorbill Thick-billed murre	Kitsissut Avallit, Greenland	All species foraged close to the colony	Both murres exploited deep diving depths, but razorbills dove shallow	Not investigated	Not investigated	Linnebjerg et al. (2013)
Common murre Razorbill Thick-billed murre	Kitsissut Avallit, Greenland	Thick-billed murres foraged close to the colony, whereas common murres and razorbills foraged farther	Both murres exploited deep diving depths, but razorbills dove shallow	Not investigated	Razorbills and common murres foraged more at night than thick-billed murres that foraged more during daytime	Linnebjerg et al. (2015)
Razorbill Atlantic puffin	Skomer Island, Wales	Not investigated	Both razorbills and puffins exploited shallow dives	Not investigated	Both razorbills and puffins foraged during the daytime	Shoji et al. (2015)
Common murre Thick-billed murre	Bogoslof Island, USA	Not investigated	Diving depths did not differ between the murres, but diving depth was different with the time of day between species: common murres diving shallower during the day and deeper at night compared to thick-billed murres	Common murres foraged in colder water compared to thick-billed murres	Thick-billed murres performed more dives at nighttime compared with common murres	Barger et al. (2016)
Common murre Thick-billed murre	St. George Island, USA	Not investigated	Diving depths did not differ between the murres, but diving depth was different with the time of day between species: common murres diving deeper in the day and shallower at night compared to thick-billed murres	Both murres exploited similar water temperatures	Both murres foraged more during the daytime	Kokubun et al. (2016)
Common murre Thick-billed murre Razorbill Atlantic puffin	Gannet Islands, Canada	Puffins and thick-billed murres overlapped in pelagic foraging areas, whereas razorbills and common murres overlapped in a more coastal area	Not investigated	Not investigated	Not investigated	Pratte et al. (2017)

Table 1 (continued)

Common name	Island Colony	Horizontal segregation pattern (using GPS)	Vertical segregation pattern (using TDR)	Environmental segregation pattern	Foraging time of day segregation pattern	Source
Common murre Thick-billed murre	Látrabjarg, Iceland	Both murre species foraged far from the colony	Both murre species foraged to shallow/intermediate depths	Both murre species foraged in the same intermediate sea floor depths, but Thick-billed murre foraged in colder waters than common murre	Both murre species foraged throughout the day	Bonnet-Lebrun et al. (2021)
Common murre Thick-billed murre	Grimsey Island, Iceland	Both murre species foraged close to the colony	Both murre species foraged to shallow/intermediate depths	Thick-billed murre foraged in deeper water columns compared to common murre, while both murre species exploited similar water temperatures	Common murre species foraged throughout the diel cycle, while Thick-billed murre species foraged more at nighttime hours	Bonnet-Lebrun et al. (2021)
Common murre Razorbill Atlantic Puffin	Bethouanes Island, Canada	All species foraged close to the colony	Murre species exploited deep diving depths, but razorbills and puffins dove shallow	Razorbills foraged in shallower water columns compared to puffins and murre species, but puffins foraged in warmer waters than murre species	Murre species foraged more during the night and in the afternoon than razorbills and puffins that foraged throughout the day	This study

Biologgers included in this table to investigate the horizontal and vertical dimensions were GPS = Global Positioning Systems and TDR = temperature-depth recorders, respectively

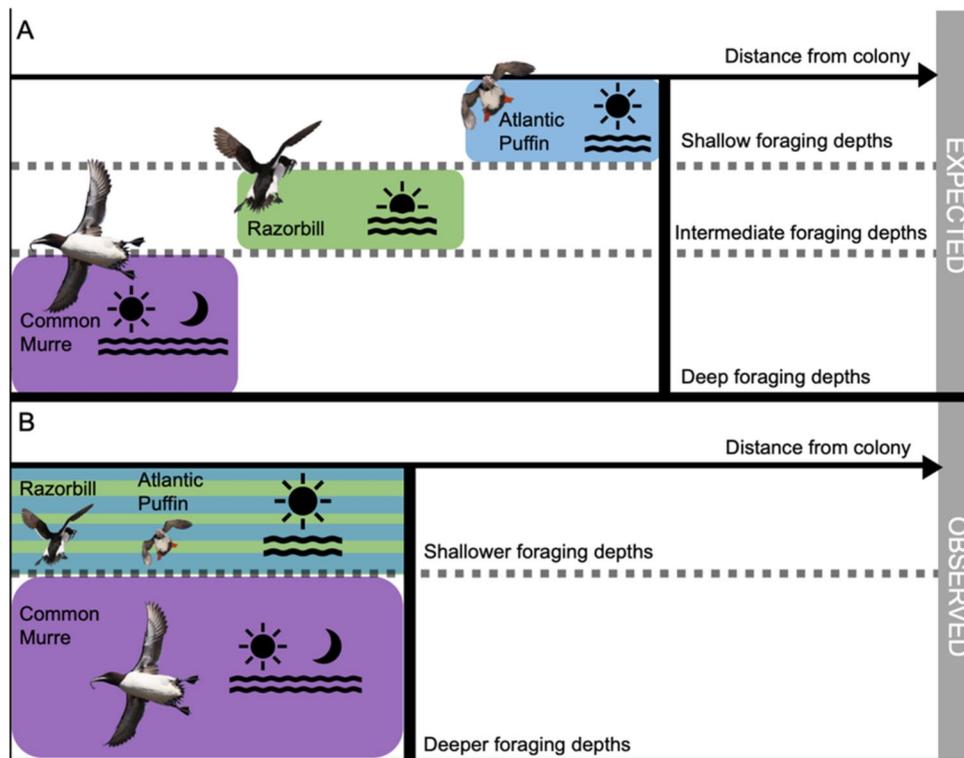


Fig. 1 **a** Conceptual diagram driving foraging niche partitioning among breeding competing auk species, and **b** summary results found in the present study. Common murres have the highest wing loading among seabirds and are thus expected to forage deepest and closest to the colony. Also, murres are low-light specialists, and we expect them to forage more frequently during the night (*purple square* represents the hypothesized realized niche in panel **a**) and observed in panel **b**), nighttime foraging is represented by the moon icon). Razorbills, with intermediate wing-loading, are expected to forage at intermediate depths and distances during crepuscular hours (*green square* represents the hypothesized realized niche in panel **a**) and observed in panel **b**), crepuscular foraging is represented by the sun rising/setting icon). Atlantic puffins, a low wing-loading species, are expected to forage at the shallowest depths and farthest distances during daylight (*blue square* represents the hypothesized realized niche in panel **a**) and observed in panel **b**), daytime foraging is represented by the sun icon). We found that all three auk species foraged at the same distance from the colony but at different maximum depths and/or periods of the day (panel **b**)

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crevices (razorbills and murres) or in burrows (puffins) that had chicks present at the nest. By capturing breeding individuals during the chick-rearing period, we increased our chances that adults would not abandon their nesting attempt after being tagged (Sun et al. 2020). We equipped each bird

with a ‘Uria’ GPS-TDR logger (see Table 2) from Ecotone® Telemetry (Gdynia, Poland). We attached GPS loggers to feathers on the middle of the back using Gorilla tape, tie wraps, and UV adhesive glue. Logger mass corresponded to <1.5% of adult body mass (puffins 1.4% ± 0.1, murres

Table 2 Model, weight, and number of GPS (Global Positioning Systems) units installed on Atlantic puffins, razorbills, and common murres during the 2021 field season on Betchouanes Island

Species	Model of GPS	GPS Weight (g)	Installed	Mean no. of days tracked	No. of recorded positions	No. of recorded trips	No. of recorded dives
Atlantic puffin	Ecotone UR1A-70 with TDR	6	11	21.7	131,105 (12,347.0)	223 (20.3)	39,618 (3601.6)
Common murre	Ecotone UR1A-100 with TDR	8.5	11	6.4	46,767 (4402.2)	64 (5.8)	3941 (358.3)
Razorbill	Ecotone UR1A-100 with TDR	8.5	11	21.4	123,748 (11,658.8)	205 (18.6)	24,371 (2215.5)

Summary of the mean total number of foraging trips and dives obtained after cleaning. Averages across individuals are in parenthesis

0.9% \pm 0.0, and razorbills 1.2% \pm 0.1 of body mass). All adults were banded using standard metal bands issued by Environment and Climate Change Canada (ECCC). The handling time of birds was always <20 min. After handling, the birds were released within the vicinity of their breeding site. Puffins were put back into their burrows.

We programmed the loggers to record GPS positions every 15 min and TDRs to record temperature and pressure, and hence dive depth, every 1 s, while submerged. The loggers had solar panels to recharge batteries and a remote download function to a base station through an Ultra High Frequency (UHF) link. The base station automatically downloaded data when loggers were within a 200 m radius. Recording stopped when in range of the base station. All animal handling and tagging procedures were approved by the Eastern Wildlife Animal Care Committee, ECCC, and followed all relevant guidelines and regulations for handling live vertebrates. We received all appropriate permits.

Auks, prone to abandonment post-logger installation (Symons and Diamond 2019), exhibited prompt return and seemingly normal behavior in response to our camera traps placed at GPS-equipped individuals' nests throughout the chick-rearing season. Our use of small light loggers (Table 2) aimed to mitigate potential alterations in seabird foraging patterns with biologging equipment (Harris et al. 2012) and influences on chick provisioning, such as frequency and prey loading (Robinson and Jones 2014). This could partly explain the seemingly normal behavior after tagging.

Interspecific segregation in space: GPS, depth, and temperature data

We performed spatial analyses using R software (version 4.0.5, R Core Team 2021). We checked for potential spatial and temporal duplicates and removed unrealistic data points according to ground speed. We defined a foraging trip as a movement away from the island where a bird departed and returned from the colony (using a ground speed cut-off of 88 km/h). After cleaning, the foraging trip was further determined by creating a 500 m "splashdown" buffer around the island, as foraging is unlikely to occur close to the island where auks often stop to preen and rest before and after foraging trips (authors' pers. obs., Brisson-Curadeau et al. 2018). We removed all trips that were <3 data points, <1 total km or that had a time difference between two consecutive points in a trip >3 h. We then calculated the following metrics for each complete foraging trip: maximum distance from the colony (km), foraging path distance (km), and trip duration (h).

Dive data were analyzed to determine the maximum dive depth and diving duration for all dives deeper than 0.5 m and >0.5 s (Kokubun et al. 2016). This was done to exclude

shallow dives unrelated to feeding while accounting for the inaccuracy of the depth recorders at the sea surface. We removed any erroneous noise within the diving data following the visual inspection of diving profiles. To estimate foraging locations, we used simple linear interpolation using the previous GPS location and time before a dive took place.

We determined sea temperature ($^{\circ}$ C) when foraging (henceforth 'foraging temperature'), which was the minimum temperature recorded during each dive. Due to the lag time in temperature sensor inertia registered by TDRs, resulting in warmer temperatures at maximum depths, we offset temperatures using a calculated time constant of 0.04 1/s. We then were able to calculate temperatures using the formula in Daunt et al. (2003), accounting for the time delay in the depth loggers (Text S1).

Interspecific segregation in environmental characteristics: seafloor depth

We were interested in whether seafloor depth was influencing the observed species foraging distributions. We extracted seafloor depth for each GPS location from the General Bathymetric Chart of the World (15-arc second dataset at a resolution of 0.05 $^{\circ}$, GEBCO 2020 Grid 2020). Values were then extracted for dive locations to determine the mean underlying seafloor depth when foraging. We computed a 'relative depth' percentage, which was the depth reached during each dive divided by the seafloor depth at that foraging location.

To determine whether there were differences in the types of dives performed between species, we distinguished between mid-water (within the water column) and benthic (performed near the sea floor) dives. Relative depths that were >0.8 (exploiting more than 80% of the water column; maximum depth (m)/seafloor depth (m)) were considered benthic and the remaining dives were classified as mid-water (Baylis et al. 2015).

Interspecific segregation in time of day: daily foraging activities

We considered a variable related to diving behaviour: the foraging time of day. This variable was derived by extracting the hour of the day when each dive started. Subsequently, we compared the proportion of dives performed per hour of the day across different species. This was done by summarizing from all dives, for each species, the proportion of dives per hour of the day, aiming to elucidate any variations in foraging timing. Daytime, twilights, and nighttime periods were found using the 'getSunlightTime' function within the 'suncalc' package for the 15th of July, 2021 (Thieurmél and Elmarhraoui 2019).

Statistical analysis

Using foraging locations, we obtained spatial distributions using the package ‘adehabitatHR’ (Calenge 2006) to calculate bivariate normal fixed kernel density estimations using the ‘kernelUD’ function (Worton 1989). We employed a smoothing factor h to obtain utilization distributions (UDs) of foraging locations for each species. To achieve a similar degree of smoothing for each species, we calculated a common reference smoothing parameter ($href$) based on the average bandwidth between all species. Parameters were set to $h = 0.068^\circ$ and $grid = 200$. We calculated both the 95% utilization distribution, representing the broad foraging range (the area of broad active use), and the 50% utilization distribution, representing the core foraging range (Ford and Krumme 1979).

The estimated extent of overlap in foraging ranges between species was assessed using two different methods within the ‘kerneloverlapR’ function: (1) the utilization distribution overlap index (UDOI) and (2) Bhattacharyya’s Affinity index (BA) (Fieberg and Kochanny 2005). The UDOI measures the degree of spatial overlap between two species under the assumption that they use space independently (i.e., different shapes of UD between species). A UDOI of 0 indicates non-overlapping UD, while a value of 1 represents perfect overlap with uniform UD of similar shapes. A value greater than 1 indicates a high overlap with non-uniform UD of different shapes (Fieberg and Kochanny 2005). A BA index indicates overall similarity between two distributions ranging from 0 (if there was 0% overlap) to 1 (if there was 100% overlap). We then used a randomization procedure to test the null hypothesis that there would be no difference in foraging spatial distribution between species for both UDOI and BA measures. If true, the size of the observed overlap between species would not be significantly different from the size of overlap expected by chance (Breed et al. 2006). We generated our null hypothesis by randomly assigning each species to a foraging trip to calculate a randomized permuted overlap index for both UDOI and BA methods. We ran 1000 randomizations of our dataset. We calculated a P value for each species pairwise comparison based on the proportion of randomized overlap indices that were smaller than the observed overlap index (50/1000 models = 0.05, Clay et al. 2016; Delord et al. 2020). A $P \leq 0.05$ would indicate whether the species in either the core or broad foraging range were segregating more than expected by chance. P values were subsequently corrected for multiple comparisons using a Bonferroni correction (here $0.05/3 = 0.016$). As UDOI methods are considered the most appropriate measure of overlapping space use (Fieberg and Kochanny 2005), the results of UDOI indices are found in Table 3, whereas BA indices can be found in the supplementary materials (Table S2).

Table 3 Observed and randomly permuted overlap indices (Utilization distribution overlap indices, UDOI) characterizing spatial foraging 95 and 50% utilization distributions (UDs) of Atlantic puffin (puffin), razorbill, and common murre (murre) during the chick-rearing breeding stage on Betchouanes island in the Mingan Archipelago National Park Reserve, Quebec, in 2021

Overlap between	Observed overlap	Randomized permuted overlap	P value
<i>95% UD</i>			
Murre ~ Razorbill	0.96	1.40	0.06
Murre ~ Puffin	1.49	1.61	0.30
Puffin ~ Razorbill	1.16	1.42	0.06
<i>50% UD</i>			
Murre ~ Razorbill	0.05	0.13	0.03
Murre ~ Puffin	0.08	0.16	0.02
Puffin ~ Razorbill	0.05	0.14	0.02

P values represent the proportion of randomized permuted overlaps (obtained from averaging a distribution of overlaps from 1000 permutations) that were smaller or equal to the observed overlap. Significant segregation (at $\alpha = 0.016$; Bonferroni corrected) was identified by estimating the proportion of randomized permuted overlaps that were smaller than the observed overlap. Overlaps are of the 95 and 50% utilization distributions (UD)

Linear mixed effect models (LMMs) using multiple restricted maximum likelihoods (REMLs) were used to determine the effect of species on different foraging metrics within the horizontal (foraging trip characteristics), vertical (maximum diving depths, dive durations, and foraging temperatures), and environmental dimensions (seafloor depth and relative depth) using the package ‘lme4’ using the ‘lmer’ function (Venables and Ripley 2002; Bates et al. 2018). We used LMMs to consider non-independence in our data because it allows for repeated measures per individual. Thus, in each model, the foraging metric was the response variable, individual was added as a random effect, while species was included as a fixed effect. Models were checked for deviations from assumptions and when residuals were not normally distributed, we log-transformed the raw data (all horizontal metrics). Finally, we used ANOVA-based model selection to assess the significance of explanatory variables compared to the null LMM using likelihood ratio tests (LRTs) using the ‘anova’ function. Post-hoc pairwise comparisons between species were performed for significant explanatory variables using the ‘emmeans’ function from the emmeans package with Tukey adjustment for multiple testing and using Kenward-Roger approximated degrees of freedom (Gulka et al. 2019; Lenth et al. 2018).

We compared benthic and mid-water diving frequencies among the three species using chi-squared tests on the proportion of benthic dives performed. The significance level was set at 0.05 unless a Bonferroni correction was applied (see below).

To assess pairwise comparisons in foraging time of day between the species, we used a Kolmogorov–Smirnov (K–S) two-sample test to test differences in the frequency of dives performed per hour of the day. We quantified the distance between two distribution functions using the ‘*ks.test*’ function within the ‘*dgof*’ package (Arnold and Emerson 2011). We also compared nighttime (both night and twilight hours) and daytime diving proportions among the three species using chi-squared tests. *P* values were subsequently corrected for multiple comparisons using a Bonferroni correction corresponding to the chosen alpha (here, $0.05/3 = 0.016$).

Results

Interspecific foraging segregation: horizontal distribution

We recovered data from all GPS-equipped individuals ($n = 33$, Table 2). During the chick-rearing period, the broad foraging ranges (95% kernel distributions) of puffins, razorbills, and murres overlapped considerably (Table 3). The foraging activity was concentrated relatively close to the colony (under 20 km, Fig. 2). The overlap between puffins and murres (95% UDOI: 1.53) and between puffins and razorbills (95%

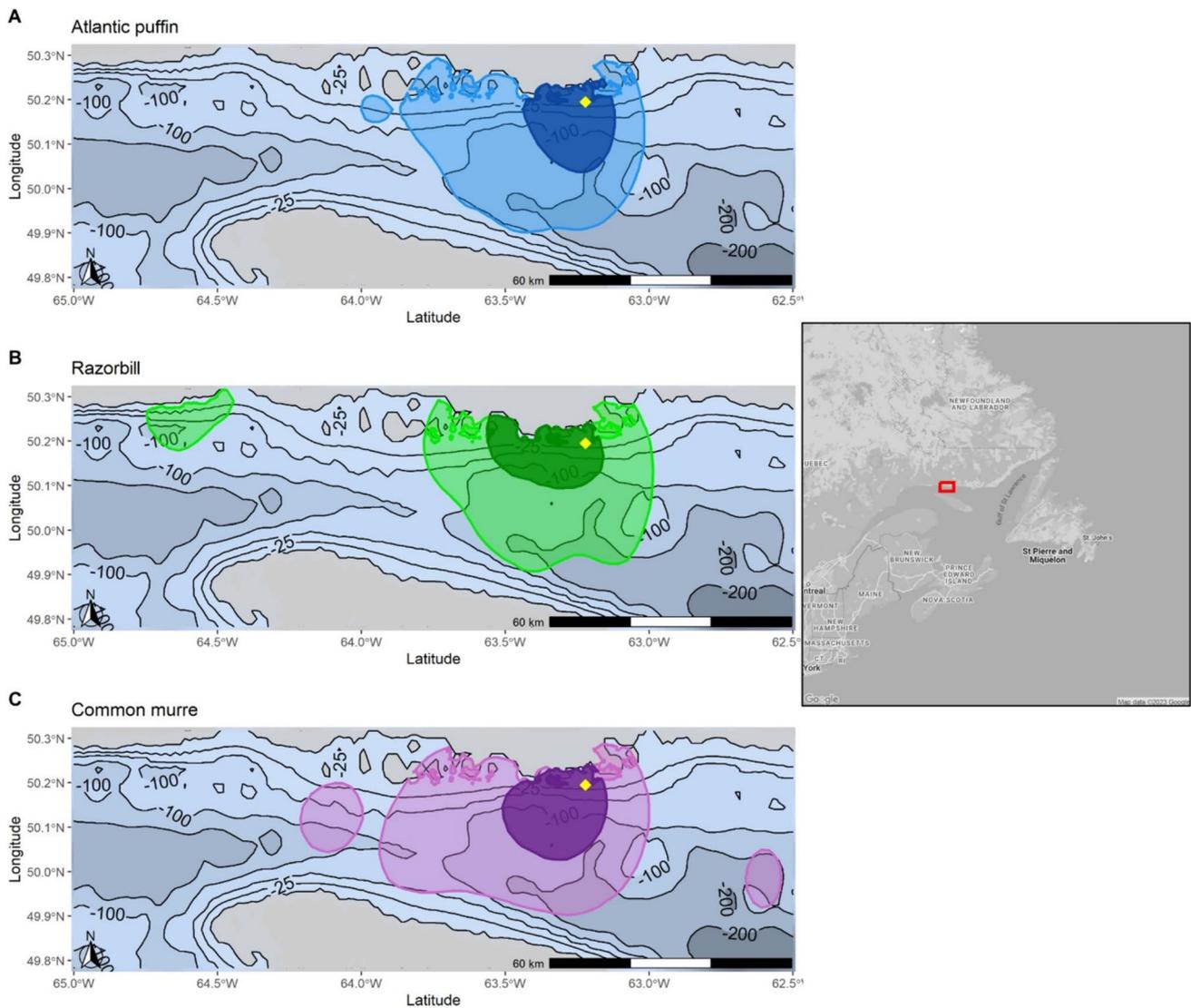


Fig. 2 Foraging areas used by **a** Atlantic puffins, **b** razorbills, and **c** common murres, around Betchouanes island (yellow diamond) during the 2021 chick-rearing breeding stage. The broad foraging range (95% kernel density estimate, KDE) is indicated by lighter contours, and

the core foraging range (50% KDE) is indicated by darker contours. Black lines show bathymetric contours with corresponding depths. Land is represented in grey. Smoothing parameter $h = 0.068^\circ$ and grid = 200

UDOI: 1.17) was higher than the overlap between razorbills and murres (95% UDOI: 0.96). Segregation was higher between all species' core foraging ranges (50% kernel distributions, UDOI < 0.1, Fig. 2). However, our randomization procedure showed that the observed UDOI indices (50 and 95% UD) for both broad and core foraging ranges among all auk species were not significantly different from the randomly permuted overlaps (Table 3). None of the horizontal foraging trip parameters differed between the auk species (maximum distance from the colony, foraging path distance, and foraging trip duration; Table 4).

Interspecific foraging segregation: vertical and environmental distribution

We found a clear difference in diving pattern between murres and the other auk species, with murres diving significantly deeper ($33.2 \text{ m} \pm 0.8$ 95% confidence intervals (CI) and for longer dive durations ($67.9 \text{ s} \pm 1.2$ 95% CI, $P < 0.0001$). Diving depths and durations did not differ between razorbills and puffins (Table 4, Table S1).

The relative depths of the dives for each species differed significantly ($P < 0.0001$, Table 4). Puffins dove on average 29.8% of the relative depth of the water column, which was significantly shallower than both razorbills (average 78.8%, $P < 0.0001$) and murres (average 65.1%, $P = 0.001$). Murres were not exploiting significantly different relative depths than razorbills, where they foraged in over 60% of deep and shallow water columns, respectively (Table S1).

The proportion of mid-water and benthic dives was significantly different between murres and both razorbills ($\chi^2 = 23,103$, $P < 0.0001$) and puffins ($\chi^2 = 31,187$, $P < 0.0001$). Murres performed a higher proportion of benthic dives (61.1% reached the benthic area). These

proportions also showed a significant difference between puffins and razorbills ($\chi^2 = 47,552$, $P < 0.0001$), where puffins conducted more mid-water dives (94.0%) than razorbills (50.26%).

Auks also foraged in areas with significantly different seafloor depths (Fig. 3; Table 4). Although seafloor depths ranged on average from 0 to 210 m across all species, razorbills foraged in areas of significantly shallower depths than both puffins and murres ($P < 0.0001$). Murres foraged in marginally significantly deeper water columns than puffins who foraged in more intermediate water columns ($70.3 \text{ m} \pm 1.4$ 95% CI and $55.8 \text{ m} \pm 0.5$ 95% CI, respectively, $P = 0.05$).

Puffins, on average, foraged in the warmest sea temperatures ($12.2 \text{ }^\circ\text{C} \pm 0.03$ 95% CI), which were significantly different from murres and razorbills that foraged in colder waters ($P < 0.0001$ and $P < 0.03$, respectively). Razorbills foraged in sea temperatures that did not significantly differ from murres (Table S1; Fig. S3).

Interspecific segregation in time: daily time budgets

The proportion of dives per hour for each auk species was influenced by the time of day (Fig. 4), with foraging occurring during all hours except from 22:00 to 1:00. During these nighttime hours, the auks were primarily resting on the water away from the colony (Fig. S4). Murres showed a significant difference from both razorbills and puffins in terms of the distribution of their diving activity (K-S: $D = 0.7$, $P = 0.0001$, $D = 0.7$, $P < 0.0001$, respectively). Razorbills and puffins were not significantly different from each other. Puffins showed a relatively uniform distribution in foraging activity throughout most hours of the day (3:00–20:00), whereas razorbills exhibited a higher

Table 4 Mean spatial horizontal and vertical foraging characteristics of Atlantic puffins, razorbills, and common murres breeding on Betchouanes island in the Mingan Archipelago National Park Reserve during the chick-rearing breeding stage

Metric	Atlantic puffin	Razorbill	Common murre	χ^2	P value
<i>Horizontal distribution</i>					
Maximum distance from the colony (km)	12.9 ± 1.0	16.0 ± 1.3	16.4 ± 1.3	2.56	0.28
Foraging path distance (km)	34.0 ± 2.8	43.0 ± 3.5	41.5 ± 3.5	2.17	0.34
Foraging trip duration (h)	8.2 ± 0.6	10.4 ± 0.7	10.2 ± 0.6	3.49	0.17
<i>Vertical distribution</i>					
Maximum dive depth (m)	8.7 ± 0.1^a	8.4 ± 0.1^a	33.2 ± 0.8^b	60.21	***
Dive duration (s)	31.9 ± 0.2^a	29.1 ± 0.2^a	67.9 ± 1.2^b	45.08	***
Foraging temperature ($^\circ\text{C}$)	12.2 ± 0.0^a	10.6 ± 0.0^b	8.2 ± 0.1^b	15.62	***
<i>Environmental distribution</i>					
Seafloor depth (m)	55.8 ± 0.5^a	33.2 ± 0.5^b	70.3 ± 1.4^c	21.49	***
Relative depth (%)	29.8 ± 0.6^a	78.8 ± 1.7^b	65.1 ± 2.2^b	26.30	***

Values for each species include mean \pm 95% confidence intervals. Differences among species were tested using LMM models controlling for an individual as a random effect with a level of significance indicated as *** $P < 0.001$. Different superscript letters within each parameter indicate significant pairwise differences between species determined using Tukey post hoc testing ($P < 0.05$)

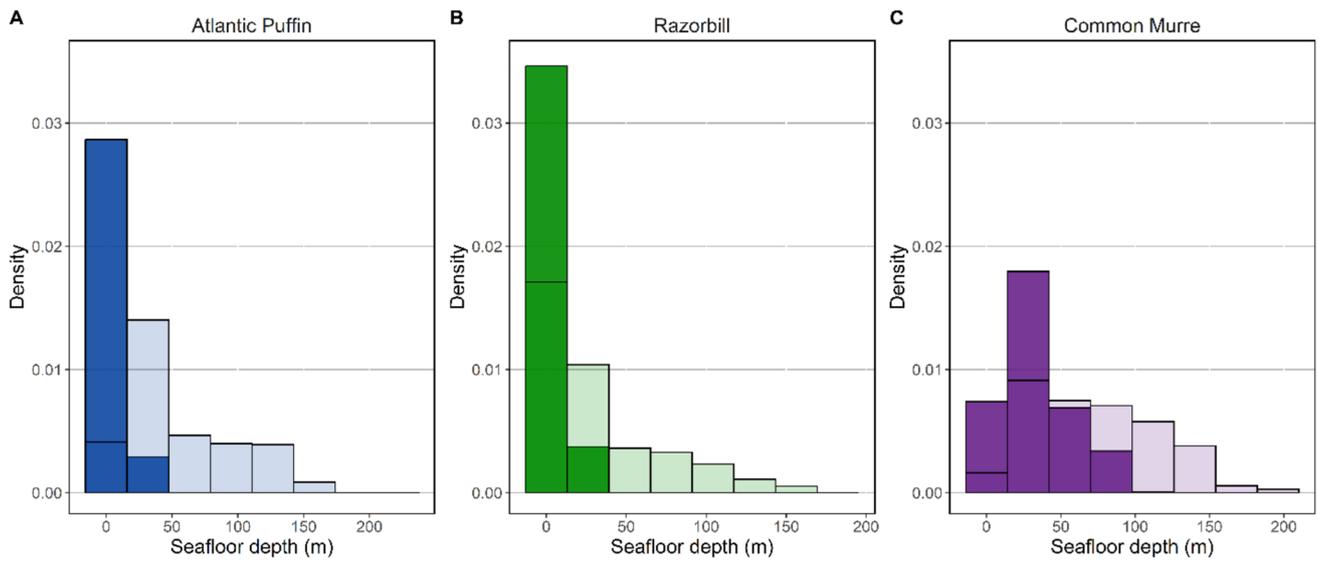


Fig. 3 Density histograms each panel represents the maximum seafloor depth when each species foraged (*lighter shaded bars*), and the maximum depths exploited (*darker shaded bars*) for chick-rearing Atlantic puffins, razorbills, and common murres on Betchouanes in 2021

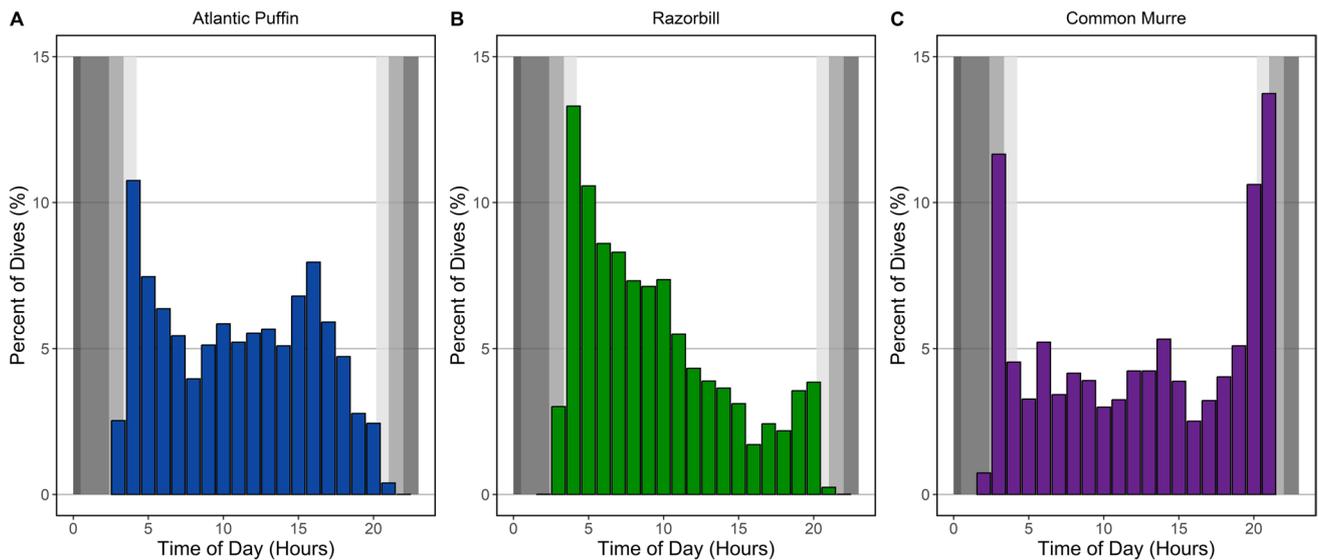


Fig. 4 Percent frequency of dives by the time of day (h) during the chick-rearing breeding stage for Atlantic puffins, razorbills, and common murres. *Shaded rectangles* reflect periods of darkness where gradients go as follows: night (23:45–00:50), astronomical twilights

(00:50–2:38 and 21:59–23:45), nautical twilights (2:38–3:36 and 21:02–21:59), civil twilights (3:36–4:23 and 20:19–21:02), and day (4:23–20:19). Local time (Eastern Daylight Savings) is UTC-5 h

concentration of foraging during the early morning hours (4:00) which decreased as the day progressed. Murres exhibited two peak concentrations of foraging activity during the late night (21:00) and early morning (3:00).

The proportion of nighttime dives to daytime dives varied significantly between murres and both razorbills ($\chi^2 = 2667$, $P < 0.0001$) and puffins ($\chi^2 = 3713$, $P < 0.0001$), where murres performed a higher proportion of dives at nighttime. These counts also differed between puffins and razorbills

($\chi^2 = 21$, $P < 0.0001$). Specifically, murres foraged on average at ~13:00 h and performed 29% of their foraging activity during twilight and nighttime hours. Puffins foraged during the late morning (on average at ~11:00 h), while razorbills foraged during the morning (on average at ~9:00 h). Both puffins and razorbills concentrated foraging activity primarily during the day and had less foraging activity, from 20:19 to 4:23, during twilight and nighttime periods (3 and 4%, respectively, Fig. 4a and b).

Discussion

By combining GPS, TDR, and environmental data, we show foraging niche differentiation along multiple dimensions among three species of chick-rearing auks as predicted by ecological theory and prior work on auk partitioning (Abrams 1990, Table 1). Per our predictions, breeding auks partitioned in diving depth, environment characteristics, foraging time of day, or a combination of these. Contrary to our predictions, auks foraged within overlapping geographical areas, while conducting similar trips of comparable durations and distances from the colony (Fig. 1b). These similarities were found regardless of differences in wing-loading and the potential increase in competitive interactions during this stage. Thus, we refute the generality of wing-loading as a mechanism for partitioning in auks (Thaxter et al. 2010), at least at Betchouanes, as we found that differences in wing loads and the associated flight costs may not be an important factor in determining partitioning. Instead, the foraging ecology of auk species may have been influenced by their aerobic dive limits and visual acuity, resulting in segregation based on depth, environmental characteristics, and/or time of day. Although these differences in auk foraging ecology may be more subtle, they contribute to the overall niche differentiation patterns.

The auk species tended to stay close to their colony, causing a lack of horizontal segregation. Species overlapped considerably in their broad foraging ranges (95% kernel distributions), although some segregation did occur in the core foraging ranges (50% kernel distributions, Fig. 2; Table 3). Likewise, horizontal foraging characteristics between all three auks were similar (Table 4; Fig. S1c). Thus, auk wing-loading at Betchouanes as a mechanism for geographical partitioning did not seem to be driving horizontal foraging strategies, consistent with findings elsewhere with population sizes similar to Betchouanes (Thaxter et al. 2010; Linnebjerg et al. 2013). In contrast, previous studies on auk chick-rearing in larger-sized colonies have identified horizontal segregation and foraging behaviour occurring far away from the colony (Table 1). For instance, Pratte et al. (2017) found that murre (higher wing-loading) had a different core foraging range compared to puffins and razorbills (lower wing-loading), in Labrador (~66,000 pairs). The absence of horizontal segregation in our study may be attributed to the colony's relatively small size. In smaller colonies, segregation may occur in subtler dimensions, constrained more by morphology, such as aerobic dive limits constraining diving depths (Fig. S2). Therefore, given the high costs of flight in auks, horizontal segregation may only become apparent when a larger colony size is reached (Table 1; Wakefield et al. 2017). However, the

presence of horizontal segregation in larger colony sizes is not always consistent (Bonnet-Lebrun et al. 2021).

Differences in breeding auk foraging areas can be driven by differences in prey preferences and the distributions of such prey (Dehnhard et al. 2020; Fayet et al. 2021). Such environmental differences among sympatric auks may illustrate the likely role of local conditions, such as oceanography influencing prey distribution and availability, in mediating foraging strategies. The Mingan islands feature wind-driven upwellings, tidal mixing, and heightened biological productivity (Koutitonsky and Bugden 1991). This dynamic coastal ecosystem, influenced by rivers, relies on nutrient-rich water, with the interplay of environmental factors becoming crucial in years of poor productivity, impacting prey abundance and potentially foraging strategies of the auks (Senneville et al. 2018). Thus, a superabundance of prey may have enabled overlapping niches in the horizontal dimension. For instance, Barger and Kitaysky (2012) found that when resources were abundant, two murre species relied on common prey items and occupied similar geographical niche spaces. Lynnes et al. (2002) found that sympatric penguins exhibited significant spatial differentiation when prey availability was low, whereas they overlapped in a year when availability was high. As prey abundance at our study site is unknown and our findings are based on a single breeding season, it's important to recognize the extent of auk niche partitioning we observed could vary. This variation is likely influenced by competition levels, which, in turn, may be affected by the availability of prey. Given the lack of horizontal segregation around Betchouanes, it does not appear that major resource limitations occurred in our year of study. It would be valuable for future studies to quantify changes in prey availability around the studied colony (e.g., through acoustic sampling), while also considering fluctuations in colony sizes (Weimerskirch et al. 2012; Jenkins and Davoren 2021). This approach would offer context for understanding the observed foraging ecology of the auk species.

During the 2019 incubation stage on Betchouanes, murre exhibited a broader foraging range from the colony compared to razorbills (Petalas et al. 2021). In contrast, our 2021 findings during chick-rearing did not reveal clear horizontal niche partitioning. For example, incubating murre in 2019 had foraging trip durations averaging 18 ± 2.4 h, contrasting with 10.2 ± 0.6 h during chick-rearing in 2021. These differences in seabird foraging strategy between incubation and chick-rearing align with past observations (Davoren and Burger 1999; Harding et al. 2007; Ito et al. 2010), suggesting that the increased constraints of foraging trip length and the high energy demands during chick-rearing force a shift in foraging strategies (Ricklefs 1983). Therefore, differences between the two breeding stages could be partially attributed to changes in requirements at the colony.

Murres at Betchouanes demonstrated different vertical foraging behaviour compared to razorbills and puffins (Fig. S1a and b), consistent with previous studies (Paredes et al. 2008; Thaxter et al. 2010; Shoji et al. 2016; Linnebjerg et al. 2013; 2015). Specifically, murres were deep-diving (~72 m), exploiting 65.1% of the relative depth of the water column. In addition, they performed the highest number of benthic dives and foraged in deeper and/or colder waters when compared to razorbills and puffins. We expect larger-sized murres to exploit deeper depths than smaller auks, as there is a positive correlation between body size, oxygen stores, and dive capacities (Gulka et al. 2019; Piatt 1990). Furthermore, murres had different peak foraging times relative to both razorbills and puffins and performed foraging during the night (Fig. 4c). Deep-diving murres, with the highest aerobic dive limits, may be specializing in a particular range of depths with a greater tolerance for very low-light conditions (Paiva et al. 2010). This is in contradiction with the assertion that murres, such as all auks, are visual predators adapted primarily to diurnal foraging (Regular et al. 2010). However, despite the decrease in available light for foraging, increasing findings, including ours, suggest that murres are well-suited for nocturnal diving, contradicting previous assumptions (Kokubun et al. 2016; Gulka et al. 2019). Regular et al. (2011) concluded that breeding murres in Newfoundland showed great plasticity in their foraging strategy, adjusting their diving patterns in response to the vertical migration of prey throughout the day and night. The exceptional diving capabilities of murres, combined with their environmental tolerance and temporal flexibility, serve as mechanisms to increase efficiency in prey energy gain and capture rate. Ultimately, these adaptations contribute to optimizing murre chick-provisioning by obtaining energy-dense prey and minimizing interspecific competition. However, as we were only able to capture approximately one-third of the breeding period for the murres (with chicks fledging after ~20 days, Table 2), these patterns may not fully represent the murre foraging dynamics throughout the entire chick-rearing season.

The diving depths of razorbills were not different from those of puffins, contrasting to predictions based on wing-loading and oxygen stores in auks (Table 4; Thaxter et al. 2010; Elliott et al. 2013). Razorbills and puffins were diving primarily to shallow depths (~8 m) where both hardly exceeded their aerobic dive limits (Fig. S2). Similar findings have been found elsewhere, showing that for chick-rearing razorbills and puffins, most dives reach mid-water depths and do not exceed 10–15 m (Shoji et al. 2015; Watanuki et al. 2006; Benvenuti et al. 2001). Puffins and razorbills can reach deeper foraging depths than what they exploited during this study (Elliott et al. 2013). Optimal foraging strategies of multi-prey loaders may be to forage within shallower depths when competing

with larger deep-diving murres that are exploiting a more benthic area. Alternatively, single-prey loading murres may be constrained to forage in areas where they do not compete with the other multi-prey loading species to capture high-quality prey suitable for single-prey loading. Thus, the shallow dives for puffins and razorbills may be attributed to the ease of visually tracking schooling fish close to the surface (Shoji et al. 2015).

Although both razorbills and puffins foraged at similar depths, razorbills tended to exploit shallower waters (33 m) than puffins (55 m), despite being larger (Fig. 3). Studies have reported that when coexisting with other auks, razorbills tend to forage in shallow waters (Chimienti et al. 2017; Linnebjerg et al. 2015; Shoji et al. 2015; Thaxter et al. 2010), while foraging at deeper depths when breeding alone (Isakkson et al. 2019). At Betchouanes, the razorbills were exploiting a narrow range of bathymetric depths, with most of their dives occurring in shallow water, exploiting approximately 79% of the water column (similar to the foraging temperatures and relative depths of the murres in deep waters). Razorbills also never reached their aerobic dive limits during even their deepest dives (Fig. S2). Razorbills, when coexisting with other auks, may segregate by specializing in prey patches located in shallower waters and consistently exploiting a broader range of the water column, despite having the capability to forage in intermediate depths. In contrast, puffins may target prey aggregations that are distributed more variably throughout deep waters.

Puffins performed the greatest number of dives per hour during the morning and evening, coinciding with findings by Büche et al. (2013) and Shoji et al. (2015). Razorbills dove mostly during daylight hours as found in other studies (Dall'Antonia et al. 2001; Thaxter et al. 2010; Shoji et al. 2015). Thus, smaller puffins and razorbills both exploited shallow depths (0–30 m in the water column) within the same area around the colony (10 km) but are segregated in terms of their foraging strategies by exploiting different environmental conditions at different hours of the day (Fig. 1b, S3).

In 2019, murres foraged on varied prey species on Betchouanes (Petalas et al. 2021). Murre chick diet had the highest diversity, including benthic prey items. Our study aligns with these findings, indicating that, unlike razorbills and puffins, murres are foraging in benthic cold zones. Contrastingly, razorbills and puffins differentiated by targeting different sizes of capelin and sand lance, potentially at similar mid-water depths. However, puffins were foraging in significantly warmer waters. Capelin, a major resource of the auks in past years (Petalas et al. 2021), responds to temperature gradients by concentrating within specific thermal zones and avoiding colder waters within the St. Lawrence (Marchand et al. 1999). Oceanographic variability, like temperature of the water column, may thus influence prey species distributions, enabling differentiation

in the vertical dimension among the auks, despite horizontal overlap (Pratte et al. 2017).

Auk species breeding on Betchouanes appear to be differentiating aspects of their niche spaces across multiple foraging dimensions during a constraining period of the breeding season (Birt et al. 1987; Cairns et al. 1987). The complex nature of the marine environment emphasizes the importance of studying a combination of dimensions of a species' ecological niche. Consistent with previous findings on chick-rearing auks, our results suggest that the wing-loading hypothesis did not determine flight distances on Betchouanes (Table 1). Instead, similar to other auk studies, we found that vertical segregation was present between smaller and larger auks. Among smaller auks, segregation occurred in terms of foraging environment characteristics and time of day (Fig. 1). Future work should be conducted over many years across multiple niche dimensions and include the diet of the species and prey abundance around the colony. By understanding the processes that maintain competitive interactions, we can determine the stability of these assemblages and gain a comprehensive appreciation of how colonial organisms persist.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding author upon request.

Declarations

Conflict of interests The authors have no relevant financial or non-financial interests to disclose.

Ethics approval All applicable institutional guidelines for the care and use of animals were followed. This work was carried out with permits to capture, band, and handle birds from #10711 bird banding permit. All animal experimentation met the Canadian Council for Animal Care wildlife guidelines for the ethical treatment of animals (authorization

from the Easter Wildlife Animal Care Committee, Environment and Climate Change Canada, #21RL01). Access to the site was permitted by Parks Canada (MIN-2021-39198) and Canadian Wildlife Service (access to Migratory Bird Sanctuary, #RE-70).

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