Ecological niche partitioning in two Pacific puffins

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ABSTRACT: Ecological theory predicts that closely related species can coexist if they segregate in space, time, or diet to reduce competitive overlap when resources are limited. These differences in ecological niche are presumably driven by concomitant differences in morphology. The link between form and functional segregation may only occur at 1 period of the year, and while examining behavioural differences among closely related species across the whole annual cycle can answer this question, it is rarely tested. Here, we investigated niche partitioning between sister species within the puffin clade: tufted puffins *Fratercula cirrhata* with high wing loading and rhinoceros auklets *Cerorhinca monocerata* with low wing loading, breeding in sympatry on Middleton Island, Alaska. We collected data for horizontal movement, dive depth, and trophic ecology. Tufted puffins dived deeper, foraged closer to the colony during breeding, and migrated shorter distances relative to rhinoceros auklets. Examination of allometric patterns further revealed that puffins exceeded the predicted dive duration limit with exceptionally long dives. However, isotopic niches of the 2 species were very similar. Rhinoceros auklet breeding phenology was about 3 wk earlier than tufted puffin phenology, and breeding success during the study period was always higher for auklets than puffins. We conclude that the 2 species of sympatric puffin partitioned both in space and time throughout the annual cycle, illustrating how such partitioning can facilitate the coexistence of seabirds sharing apparently similar space.

KEY WORDS: Annual cycle · Biologging · Stable isotope analysis · Diet · Competition · Seabirds

1. INTRODUCTION

Understanding the factors that drive species distributions and abundance is a fundamental goal in the field of population ecology. Competition among organisms for limited resources is central in shaping community structure and processes (Hutchinson 1957). Niche theory predicts that sympatric species with similar ecological requirements should exhibit niche partitioning to reduce competition (Gause 1934, Ricklefs & Miller 1999, Putman & Flueck 2011). Niche partitioning typically occurs along spatial, temporal, or trophic niche axes (MacArthur 1958,

Pianka 1969), has been observed in a wide range of taxa in both terrestrial and marine ecosystems (Ainley et al. 2009, Masello et al. 2010), and is often associated with morphological differentiation (Hutchinson & MacArthur 1959). However, most studies focus on niche partitioning during either the breeding season or non-breeding season in seabirds (Thiebot et al. 2012, Shoji et al. 2015). While each brings valuable insight into intra- and/or inter-specific competition, examining a single season does not allow us to understand the whole picture of the mechanisms driving niche partitioning. Generally, niche partitioning during the non-breeding season is not well

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documented, even though there is potential for strong resource limitation during this time when high densities of competitors share wintering habitat (Nishizawa et al. 2020). As a result, the factors shaping the distribution of species across the entire annual cycle, the ways in which animals manage to mitigate competition between species, and whether these affect breeding success remain prominent topics in ecology.

The mechanisms underlying species distributions and competition are particularly relevant for species with high energetic costs in movement, because individuals are constrained in their ability to increase foraging and migration distances. Determining drivers of animal distributions is critical to understanding their ecology, but also the evolution of different species under different selective pressures due to variation in morphology and mode of locomotion, as shown in mammals (Avgar et al. 2014), birds (Weber & Houston 1997), and fish (Alerstam et al. 2003). Furthermore, animals may exploit resources vertically as they fly, climb, or swim, and this may lead to interspecific niche segregation that goes undetected if a study does not consider altitude or depth. Distinct niche use raises questions about the control of niche segregation, particularly where these may make species more vulnerable to changes in their habitat. Thus, studies should examine both horizontal and vertical movement to understand how morphological differences contribute to niche partitioning.

In this study, we focus on the entire annual cycle of 2 closely related puffin species that both dive for prey and breed in sympatry in the North Pacific: tufted puffins *Fratercula cirrhata* (hereafter puffins) with high wing loading (1.90 g cm^{-2}; Johnsgard 1987) and rhinoceros auklets *Cerorhinca monocerata* (hereafter auklets) with low wing loading (1.33 g cm^{-2}; Elliott et al. 2013). Although we refer to each species by their English names to easily distinguish them, both species are closely related and in the puffin clade, and only distantly related to true *Aethia* auklets (Friesen et al. 1996). Central place foragers are expected to increase their foraging range only if net energy gain increases with distance from the central place (e.g. colony), and thus species with high wing loading are less likely to extend their foraging distance (Houston & McNamara 1985, Cuthill & Kacelnik 1990, Waite & Ydenberg 1996). Similarly, migration ranges decrease with wing loading in flapping flight species (Watanabe 2016). We examined puffin and auklet habitat use, breeding phenology, and trophic ecology across the annual cycle in order to quantify their ecological niches in time, space, and diet. Seabird communities present an excellent model system to examine niche

theory because several species coexist in large colonies and feed on similar prey (Cody 1973, Bédard 1976, Gaston & Jones 1998), and they are central-place foragers that hunt in close proximity to the colony and thus each other. Furthermore, puffins are diving seabirds and spatial niche segregation may occur in 3 dimensions (latitude, longitude, depth; Navarro et al. 2015). We combined state-of-the-art miniature biologging devices to track 3-dimensional niche use of these 2 species year-round and test for spatial niche segregation.

We then tested for body mass–dive relationships across the alcid species to examine whether dive behaviours of puffins or auklets at our study site depart from allometric relationships. We investigated potential segregation in adult (poorly known) diet within and outside the breeding season by using stable isotope analytical approaches on feather samples, supplemented by prey items collected from adults provisioning young. We monitored breeding phenology to examine temporal niche segregation, which could reduce inter-specific competition, and test whether puffins and auklets reduce temporal overlap during breeding, when parents must meet high energy requirements for themselves and offspring. While temporal niche segregation can reduce inter-specific competition, this may result in temporal mismatch between predators and prey (Hipfner 2008), which may lead to differences in reproductive success between species. To test this idea, we measured breeding success to explore the potential consequences of niche differences for reproductive output. Our study provides novel insights into the mechanisms of niche partitioning and their associations with differences in form and function between sympatric species, a central question in ecology, while also shedding new light on the at-sea behaviour of puffins, known to be useful as marine ecosystem sentinels (Gjerdrum et al. 2003).

2. MATERIALS AND METHODS

The study was carried out on Middleton Island, Gulf of Alaska, at a puffin colony (59° 4′ N, 146° 3′ W) and an auklet colony (59° 25′ N, 146° 19′ W), from June to mid-August over 4 years (2016 to 2019). Puffins and auklets are both medium-sized, sexually monomorphic, burrow-nesting auks with biparental provisioning of young. Puffins feed their young twice or more per day, typically in the morning and evening. Auklets feed their young only once per day, always at night. Both species are multiple prey-

loaders, but puffins tend to carry smaller fish than auklets. Puffins and auklets are known to be particularly sensitive to handling, therefore we minimised handling and nest visits, and sampled mostly during chick-rearing to reduce disturbance (Sun et al. 2020). All work was conducted with ethical approval from the McGill University Animal Care Committee (permit number: 2015-7599).

2.1. Reproductive monitoring and food load collection

Burrows within monitoring plots were followed throughout the breeding season, from egg-laying to fledging, to obtain colony-level breeding phenology and breeding success of both species. To reduce disturbance, marked burrows were examined once a week during incubation and chick-rearing. Thus, we used the first date that a chick was observed as a proxy for hatch date. At each colony, breeding success was determined using marked burrows found during incubation (puffins: 71–82 burrows per year; auklets: 39–62 burrows per year). We calculated breeding success as the proportion of active nests (defined as a nest in which an egg was laid) that successfully raised a chick. Concurrently, we sampled prey items carried in the bills of adult birds ('bill loads') to feed chicks in the colony as part of an ongoing long-term diet study. To sample prey items, birds that landed in the colony while carrying prey were captured by hand along trails in the colony at night (auklets) or at their nest site during the day (puffins). Prey sample collection campaign efforts began in 1978 and we combined all available prey data brought to puffin and auklet chicks to examine niche partitioning. Samples were identified to species level.

2.2. Biologging methods during the breeding season

In 2016 and 2017, birds were hand-captured either at the nest or at the 'landing strips' during late incubation or brood guard for device deployment and retrieval during the day (puffin) or at night (auklets). No individual was tracked more than once. Global positioning system (GPS; ECOTONE Telemetry Logger ALLE-60 GPS-UHF, 26 × 16 × 10 mm, 4.5 g) devices were configured to record a location every 15 min, either remote download (puffins) or archival (auklets). The GPS devices would turn off automati-

cally when unable to acquire satellite signals and when the birds were diving. Time-depth recorders (TDRs; LAT 1500, Lotek Wireless, 8 [diam.] × 32 mm, 3.4 g) with a nominal depth resolution of 4 cm were configured to record depth at 1 Hz. Devices were attached to dorsal mantle feathers, or tail feathers (2016), using TESA® marine cloth tape (GPS) or to a leg ring using a cable tie (TDR). We deployed 30 devices (GPS: 4 puffins and 6 auklets; TDR: 11 puffins and 9 auklets). In 2016, both GPS and TDR were attached to 3 puffins, while only a GPS was attached to 1 puffin. Similarly, both GPS and TDR were attached to 6 auklets, while only a TDR was attached to 3 auklets. In 2017, a TDR alone was attached to all puffins. Total weight of both GPS and TDR deployments weighed <9 g (<1.8% of body mass). To minimise disturbance, bird handling was minimised to <10 min for all deployments and we used remote-download GPS devices, thereby not requiring recapture for puffins. For auklets, there was no significant mass loss before versus after deployment, suggesting no physiological tag effect. GPS tags, however, are known to affect prey delivery rate and abandonment rates in alcids (Elliott et al. 2007), including rhinoceros auklets (Sun et al. 2020). Therefore, foraging behaviour may have been affected.

As seabirds are limited by the oxygen store capacity in the respiratory and circulatory systems and muscles, there must be a dive duration (aerobic dive limit: ADL) beyond which accumulated blood lactate is metabolised during surface recovery. Examining whether wing loading correlates with flight costs leading to niche separation allows us to test whether ADL may contribute, in part, to niche separation. Many studies of dive behaviour in auks do not provide these metrics along with wing-loading data. Given that flight costs increase with wing loading while dive depth increases with body mass because of higher oxygen stores in flapping flight seabirds (Elliott et al. 2013), we used body mass and wing loading to examine whether flight costs are associated with niche separation in puffins and auklets. Based on 2 previous auk studies (Shoji et al. 2016, Cunningham et al. 2018), the ADL was estimated as 130 s for puffins and 92 s for auklets (see Fig. 2B, dashed vertical lines). To develop an allometric relationship across alcids, we retrieved diving metrics (maximum dive duration and maximum dive depth) for 8 species from Shoji et al. (2016; their Table 1) and included data from puffins and auklets at Middleton Island from this study (Table 1, see Fig. 3). We then compared wing loading with dive metrics.

Table 1. Alcid average body mass, wing loading, maximum dive depth, and maximum dive duration. Data collected during this study and earlier studies

Species	Scientific name	Average mass (g)	Wing loading (g cm^{-2})	Maximum dive depth (m)	Maximum dive duration (s)
Ancient murrelet[a]	*Synthliboramphus antiquus*	197	0.81	37	70
Atlantic puffin[a]	*Fratercula arctica*	400	1.10	36	123
Cassin's auklet[a]	*Ptychoramphus aleuticus*	171	0.76	28	101
Common guillemot[a]	*Uria aalge*	985	2.31	73	166
Brünnich's guillemot[a]	*Uria lomvia*	1000	2.20	123	168
Razorbill[a]	*Alca torda*	600	1.38	28	93
Dovekie[a]	*Alle alle*	150	0.90	33	85
Black guillemot[a]	*Cepphus grylle*	430	1.02	29	111
Rhinoceros auklet[b]	*Cerorhinca monocerata*	503	1.33	29	98
Tufted puffin[b]	*Fratercula cirrhata*	813	1.90	75	169

[a]Data from Shoji et al. (2016; their Table 1). Wing loading data from Elliott et al. (2013; their supporting information) and unpubl. data
[b]Data collected in this study

2.3. Biologging methods during the non-breeding season

In 2017 and 2018, birds were caught for device deployment either at their nest by hand (puffins) or on a landing strip by net (auklets) during late incubation or brood guard during the day (puffins) or night (auklets). No birds were tracked during breeding and only 1 logger was deployed on each bird. Birds were weighed, ringed, and fitted with a geolocator (hereafter GLS, Biotrack MK4083, 15 × 10 × 6 mm, 1.5 g; or Migrate Technology Intigeo-C65, 14 × 8 × 6 mm, 1.0 g) attached with lightweight cable ties to a tarsus-mounted plastic ring. Devices were retrieved in the year following each deployment.

2.4. Spatial and behavioural analysis

Population-level spatial occupation kernels of 95% and 50% utilisation distributions of GPS locations (breeding period) and geolocator-derived location estimates (non-breeding period) were calculated with adehabitatHR (Calenge 2006). For GPS data, trips <2 km away from the colony were excluded because puffins and auklets were likely on land or rafting on the water rather than foraging during these short trips. Trip duration was calculated as the time between the last location before leaving the 2 km radius around the colony and the first subsequent location within the same radius. Maximum foraging range was calculated as the straight line distance between the colony and the farthest location of the foraging trip outside of the 2 km radius. For TDR

data, individual dives were determined using a Microsoft Excel macro with dives as >2 m in depth, to ensure dives were for foraging purposes (Kuroki et al. 2003). Maximum and average dive depth and duration were extracted for each individual over an entire deployment. For GLS data, 27 complete tracks were collected from unique individuals. Light data were decompressed and processed using the BASTrack software suite (British Antarctic Survey). A sun elevation angle of 4.0° was chosen based on the position of ground truth. Positions were filtered using speed and equinox filters following methods in Fayet et al. (2016), and data corresponding to the breeding season were excluded (1 April to 31 August to encompass breeding for both species). We calculated 2 d median positions for all tracks and filtered out those with high SE (SE$_{longitude}$ > 150 km, SE$_{latitude}$ > 150 km) or unrealistic locations (latitude <20°, longitude >180° or <120°). We estimated distance from the colony as the great-circle distance between the colony and each position. Mean and total distance covered was calculated for each track by summing the great-circle distances from 1 September to 31 March.

2.5. Environmental data

Sea surface temperature (SST, °C) and chlorophyll *a* concentrations (chl *a*, mg m^{-3}), proxies for prey resource availability (Henson & Thomas 2007), were obtained from the NASA OceanColor website (https://oceancolor.gsfc.nasa.gov/) using data from the MODIS Terra and Aqua satellites. The spatial grid of variables was 1° in accordance with the geolocation

technique accuracy and the temporal resolution was 8 d. Each location from the dataset was assigned an SST and chl *a* value. To test whether environmental conditions were potential drivers of at-sea behaviour, each track was assigned an SST and chl *a* value averaged over the whole track, and average values were calculated for each species.

2.6. Stable isotope analysis

Isotopic compositions of seabird feathers reflect diet and foraging locations during the moulting period (Rubenstein & Hobson 2004) because the isotopes in feather keratin become metabolically inert after synthesis, thereby recording the trophic niche of seabirds at the time of growth (Thompson & Furness 1989, Hobson & Clark 1992). Feathers are particularly useful because the timing of feather moult differs among feather types, therefore different feather types contain information on diet and habitat at different temporal scales (Hobson & Clark 1992). Two types of feathers (3 cm tips of flight feathers [P10] and 2 to 3 body feathers) were collected with scissors for stable isotope analyses. We minimised the number of feathers taken to limit possible adverse effects on the birds. These tissues were selected to reflect diet during different periods in the annual cycle: flight feathers represent diet during the breeding season (flight feathers are grown soon after the breeding season), while body feathers represent the non-breeding diet (body feathers are grown before breeding in auks; Pyle 2009, Sorensen et al. 2010, Gaston & Dechesne 2020, Piatt & Kitaysky 2020). Stable isotope ratios for nitrogen (δ^{15}N) and carbon (δ^{13}C) in feathers were used as proxies for trophic level and foraging habitat, respectively.

After collection, feathers were kept frozen at −20°C in the field freezer, and then at −60°C in a lab freezer until analysis. Feathers were prepared, washed, and pulverised prior to subsampling. Pulverised feather samples (0.40 to 0.60 mg) were placed in a tin capsule, sealed, and deposited for combustion. The samples of δ^{15}N and δ^{13}C values were measured using an Isotope Ratio Mass Spectrometer System (ANCA-GSL and Hydra 20-20, Sercon). Stable isotope ratios are reported in δ (delta) notation as parts per thousand (‰) deviation from the international standards δ^{13}C PDB and δ^{15}N air according to $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X is ^{13}C or ^{15}N, and R_{sample} and $R_{standard}$ are the corresponding ratios ^{13}C/^{12}C or ^{15}N/^{14}N of samples and international standards, respectively. Replicate measurement of an internal laboratory standard (L-alanine) indicated measurement errors were ±0.28‰ for N and ±0.11‰ for C. Samples were analysed at the Meijo University Stable Isotope Facility.

2.7. Statistical analysis

Data processing and analysis were performed in R (4.1.1.; R Core Team 2021). To test for differences between species in breeding phenology, mean maximum foraging range, and mean total trip distance, we used a chi-square test, while for breeding success, we used a paired *t*-test. To test for differences in spatial and behavioural metrics between species for data averaged per bird, we used linear models. Response variables were log transformed to meet assumptions of normality and homoscedasticity where necessary. Due to small sample sizes, we pooled data across years. Values are given as means ± SD in the text.

3. RESULTS

Puffin breeding phenology was later than that of auklets (Table 2). The mean hatch date was 16 July ± 6 d (n = 4 years) for puffins and 22 June ± 3 d for auklets, thus auklets bred about 3 wk earlier than puffins (χ^2_7 = 37.2, p < 0.001). Breeding periods were estimated as May to August for puffins and April to July for auklets based on breeding phenology (Table 2). Puffins were heavier (813 ± 49 g) than auklets (503 ±

Table 2. Summary of reproductive monitoring data collected from auks on Middleton Island, Alaska, during the 4 year study period (2016 to 2019). Average indicates averages across all 4 study years

Year	Eggs laid (n)	Eggs hatched (n)	Fledged (n)	Breeding success (%)	First chick observed (mean ± SD)
Tufted puffin					
2016	82	26	20	24	8 July ± 4 d
2017	71	17	12	17	17 July ± 6 d
2018	73	35	31	42	15 July ± 7 d
2019	60	20	19	32	23 July ± 7 d
Average	72	25	21	29	16 July ± 6 d
Rhinoceros auklet					
2016	62	39	31	50	22 June ± 6 d
2017	62	40	30	48	25 June ± 6 d
2018	61	35	33	54	19 June ± 6 d
2019	39	28	23	59	23 June ± 5 d
Average	56	36	29	53	22 June ± 3 d

27 g). Breeding success during the study period was always higher for auklets than puffins (paired t-test, $t = -5.79$, p < 0.05). Deployment and retrieval information is provided in Table 3. Annual tag recoveries for puffins averaged 100% of those deployed for GPS, 33% for TDR, and 63% for GLS, and those for auklets averaged 83% of those deployed for GPS, 78% for TDR, and 37% for GLS. Annual sample sizes were 4 to 5 birds for GPS, 1 to 7 birds for TDR, and 9 to 24 birds for GLS.

Table 3. Annual sample sizes of tags deployed and retrieved from tufted puffins and rhinoceros auklets. Values in parentheses are the number of geolocators retrieved that contained useable data and were used in this study. GLS: geolocator; TDR: time-depth recorder

Type	Species	Year tracked	No. of birds tagged	No. of tags retrieved
GPS	Tufted puffin	2016	4	4
	Rhinoceros auklet	2016	6	5
TDR	Tufted puffin	2016	3	1
		2017	8	4
	Rhinoceros auklet	2016	9	7
GLS	Tufted puffin	2017–2018	15	9 (6)
		2018–2019	26	15 (4)
	Rhinoceros auklet	2017–2018	36	24 (15)
		2018–2019	53	9 (2)

3.1. Partitioning during the breeding season

Puffins and auklets showed clear differences in horizontal and vertical space use. Based on 95% occupancy kernels (utilisation distribution), puffins foraged within the auklet foraging area, but closer to the colony (Fig. 1A). The mean maximum foraging ranges were 40.53 ± 16.11 km for puffins (n = 4) and 88.53 ± 33.15 km for auklets (n = 5; $\chi^2_8 = 217.3$, p < 0.001). The mean total trip distances were 361 ± 137 km for puffins (n = 4) and 463 ± 338 km for auklets (n = 5; $\chi^2_8 = 2094.6$, p < 0.001). Puffins exhibited substantially deeper mean maximum dive depth
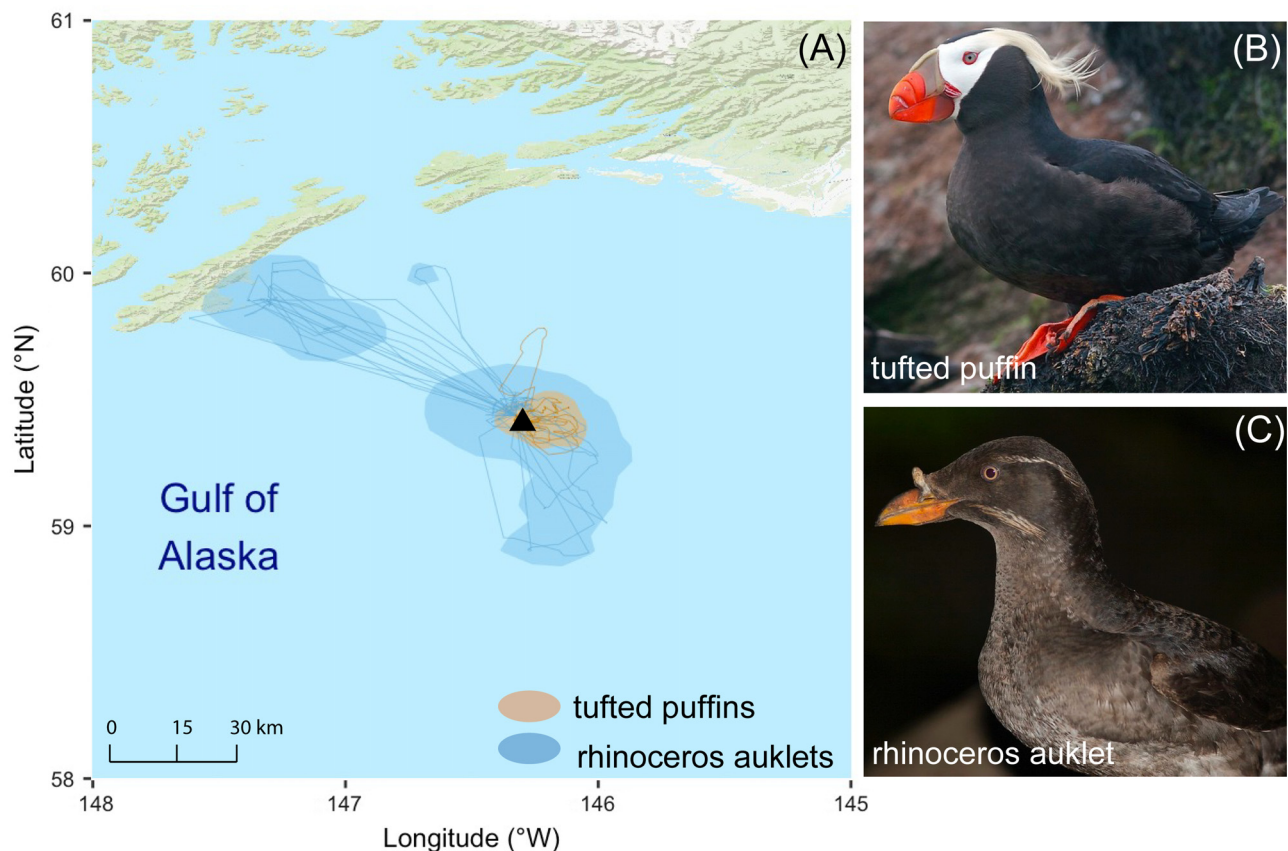

Fig. 1. (A) Foraging distributions of tufted puffins and rhinoceros auklets on Middleton Island, Alaska, USA. (▲) Location of study site, Middleton Island; shaded polygons: 95% utilisation distributions; lines: GPS tracks. (B) Tufted puffin and (C) rhinoceros auklet (photos: K. H. Elliott)

than auklets (puffin: 70 ± 11 m, auklet: 29 ± 9 m, $t_{1,10}$ = −6.82, p < 0.001) and a deeper population mean of individual mean dive depth (puffin: 16 ± 2 m, auklet: 10 ± 5 m, $t_{1,10}$ = −2.72, p = 0.02; Fig. 2A). Puffins dived for longer than auklets, both on average (puffin: 63 ± 8 s, auklet: 40 ± 14 s, $t_{1,10}$ = −3.22, p < 0.01) and via longer maximum dive durations (puffin: 171 ± 16 s, auklet: 98 ± 31 s, $t_{1,10}$ = −4.75, p < 0.01; Fig. 2B). Dive duration increased with dive depth for both puffins ($t_{1,10}$ = 12.02, p < 0.0001; Fig. 2C) and auklets ($t_{1,5}$ = 8.67, p < 0.0001; Fig. 2C).

Across all data, 2 dive metrics, maximum dive duration and maximum dive depth, increased with body mass (max. dive duration: t_8 = 0.48, r^2 = 0.61, p = 0.004; max. dive depth: t_8 = 0.35, r^2 = 0.40, p = 0.002) and wing loading (max. dive duration: t_8 = 0.25, r^2 = 0.67, p = 0.002; max. dive depth: t_8 = 0.10, r^2 = 0.61, p = 0.004; Fig. 3).

3.2. Partitioning during the non-breeding season

Winter distributions differed substantially between species (Fig. 4). Distributions of puffins were more restricted and closer to the colony, relative to auklets; however, both the 95% and 50% (core) utilisation distributions included areas of overlap between the 2 species (Fig. 4). Species differed in the total distance covered over winter, where auklets covered thousands of km more than puffins ($t_{1,25}$ = −4.36, p < 0.001; Fig. 4) and reached, on average, greater distances from the colony ($t_{1,25}$ = −6.72, p < 0.001; Table 4). The 2 species also exhibited temporal segregation during the non-breeding stage based on their breeding phenology and at-sea positional data (Fig. 5). These spatiotemporal differences in individual space use led each species to experience different environmental conditions over the non-breeding stage (Table 4) in terms of SST ($t_{1,25}$ = −5.20, p < 0.001), but not chl *a* ($t_{1,25}$ = −0.38, p = 0.70). Overall, temperature
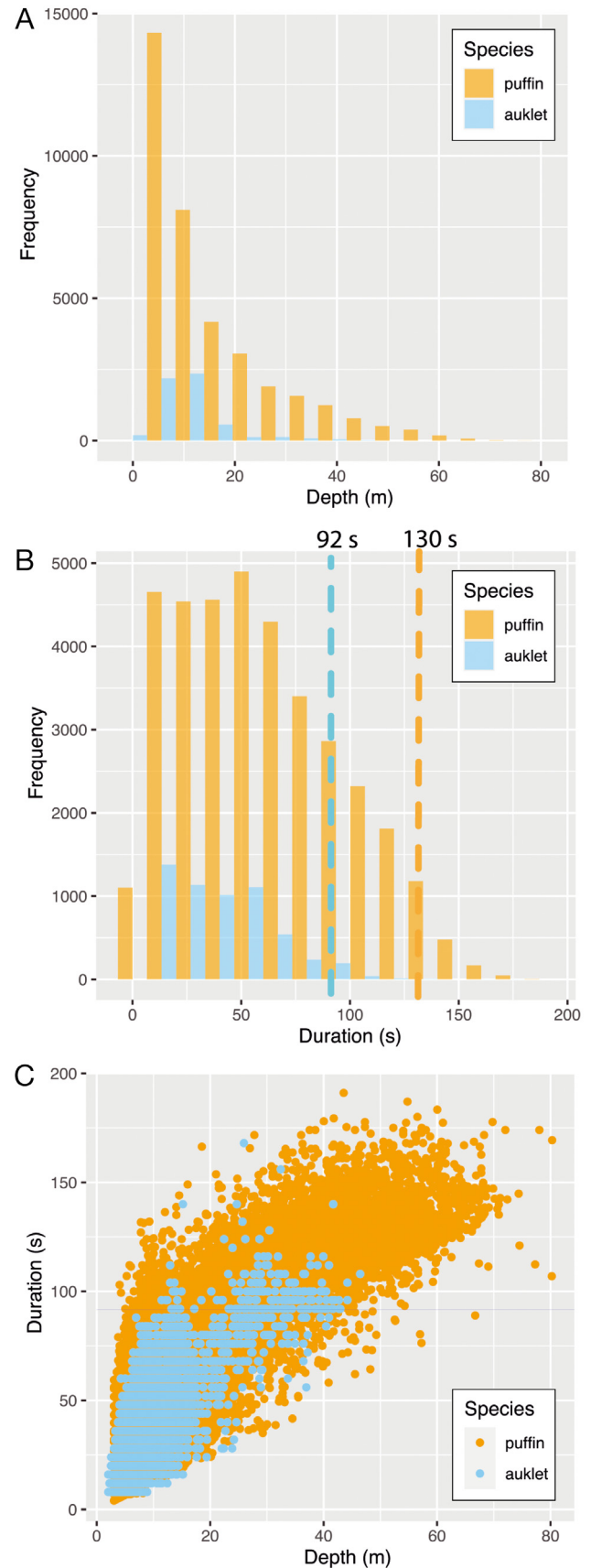

Fig. 2. Patterns of dive depth and duration in tufted puffins and rhinoceros auklets from Middleton Island. (A) Frequency of maximum dive depth. (B) Frequency of dive duration. Based on the aerobic dive limit (ADL) in rhinoceros auklets reported by Cunningham et al. (2018) and myoglobin concentration in alcids being proportional to body mass (M) at $M^{0.36}$ (Shoji et al. 2016), an 813 g alcid is expected to have an ADL of about 130 s (orange dashed vertical line, tufted puffins) and a 503 g alcid is expected to have an ADL of about 92 s (blue dashed vertical line, rhinoceros auklets). In this study, 4% of dives in puffins and 2% of dives in auklets exceeded their ADL. (C) Maximum dive depth and dive duration
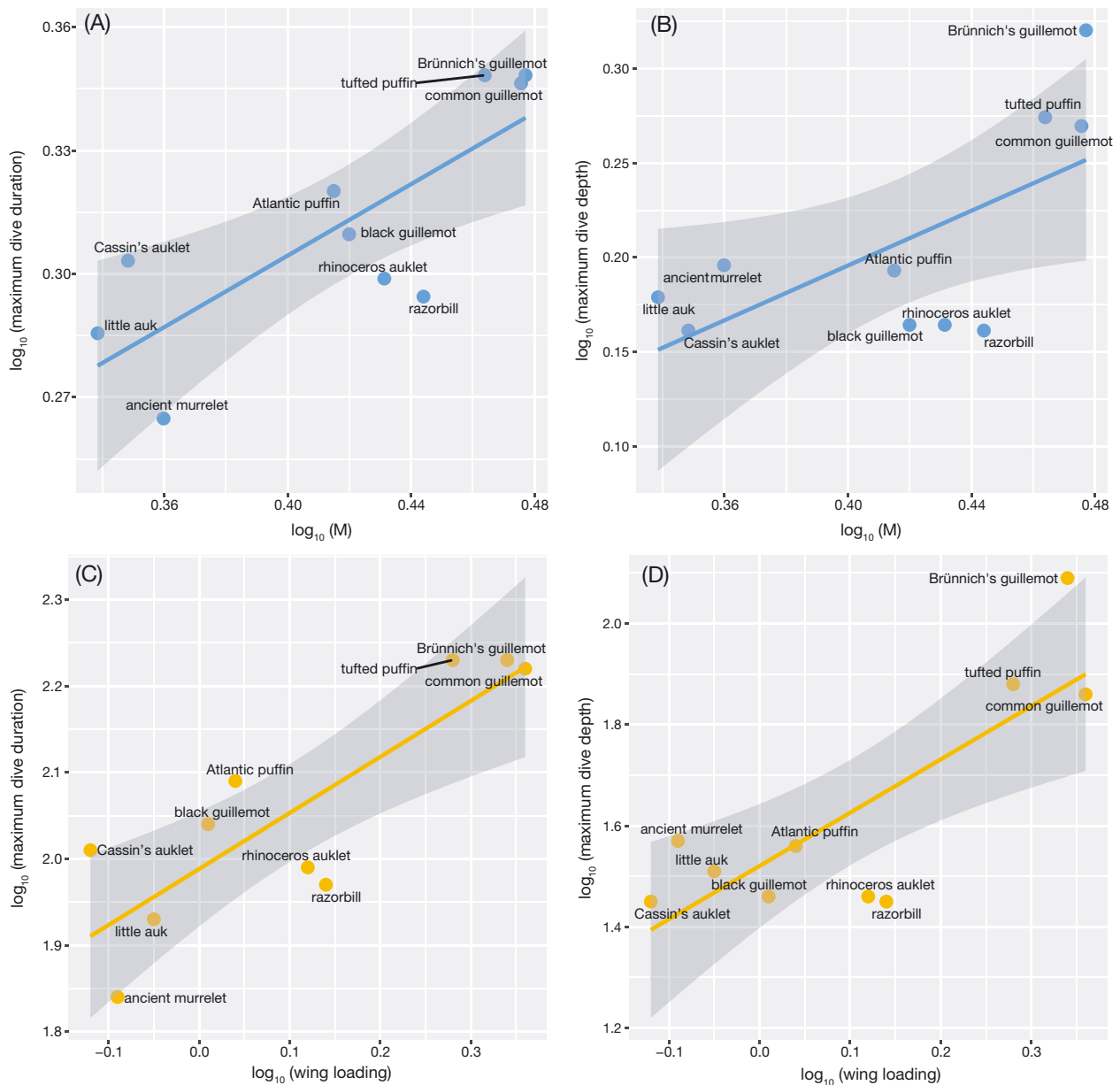
Fig. 3. Allometric relationship between mass (M; g) and (A) maximum dive duration (s) and (B) maximum dive depth (m), and relationship between wing loading (g cm^{-2}) and (C) maximum dive duration (s) and (D) maximum dive depth (m). All values are log$_{10}$ transformed. Data points are from Table 1 and derived from Shoji et al. (2016; their Table 1), Elliott et al. (2013), and data collected from tufted puffins and rhinoceros auklets in this study. Trend lines indicate model predictions from significant linear regressions on a log-log scale (shaded areas indicate 95% confidence intervals)

decreased with latitude ($t_{1,25} = -7.47$, p < 0.001), but not with chl a ($t_{1,25} = 1.15$, p = 0.25).

3.3. Trophic niche

Puffin and auklet feathers showed similar stable nitrogen and carbon isotope values in both flight and body feathers (Table 5), indicating that overall diets may be similar between species and both breeding and non-breeding periods. Prey collected from the 2 species across several decades (1978–2021) revealed that the bill loads of auklets contained primarily Pacific sand lance *Ammodytes personatus* age-0 (29% occurrence), followed by greenling *Hexagrammidae* (23%), Pacific sand lance age-1+ (18%), and Pacific capelin *Mallotus catervarius* (11%), whereas puffins carried mostly Pacific capelin (32%), fol-
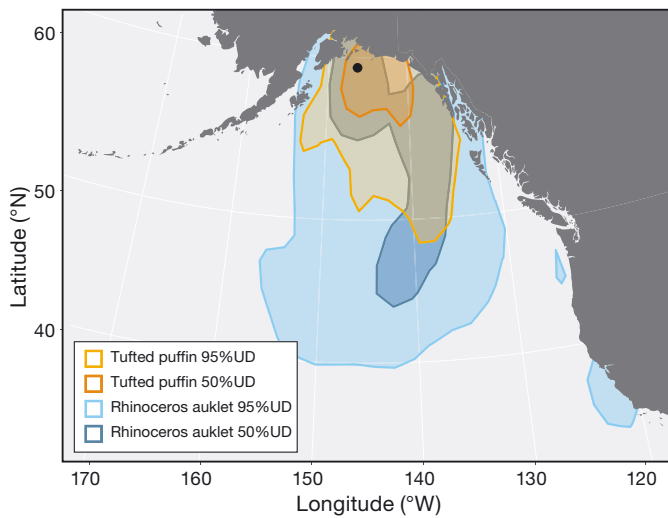
Fig. 4. Wintering distributions of tufted puffins and rhinoceros auklets from Middleton Island. UD: utilisation distribution; black dot: colony

lowed by Pacific sand lance age-0 (26%), and Pacific herring *Clupea pallasii* (19%), but prey were more diverse and smaller (Fisher's exact test: p < 0.0001; Fig. 6, Table 6).

4. DISCUSSION

By combining high-resolution 3-dimensional data with breeding phenology and trophic niche comparisons, our study provides novel insights into the mechanisms driving year-round ecological niche partitioning of 2 closely related sympatric seabirds, tufted puffins and rhinoceros auklets. Despite feeding on prey with similar trophic levels and carbon sources (as determined from stable isotopes), we found clear evidence for spatiotemporal segregation year-round, including during the breeding season, where our sample sizes were relatively small. The 2 species segregated in space along a distance to colony–depth trade-off gradient and this result sup-

Table 4. Spatial and environmental characteristics of tufted puffins (n = 10) and rhinoceros auklets (n = 17) during the non-breeding season after capture on Middleton Island, Alaska

	Tufted puffin (mean ± SD)	Rhinoceros auklet (mean ± SD)
Total distance covered (km)	9816 ± 1396	13460 ± 2398
Average distance from colony (km)	341 ± 137	1161 ± 368
SST (°C)	6.67 ± 0.67	8.53 ± 0.99
Chl *a* (mg m^{-3})	0.81 ± 0.30	0.88 ± 0.53

ports the idea that flight costs associated with wing loading are linked to foraging behaviour and distribution. Tufted puffins, with higher flight costs, used a near-deep strategy, while auklets, with lower flight costs, used a far-shallow strategy, which is consistent with allometry based on their differences in wing loading.

Maximum dive depth and duration in alcids are allometrically related to body mass (Shoji et al. 2016); here, we found that body mass/wing loading–dive relationships across the alcid species were significant for all dive metrics including maximum dive duration (Fig. 3A), maximum dive depth (Fig. 3B), maximum dive duration (Fig. 3C), and maximum dive depth (Fig. 3D). While all dive metrics for puffins fell within the 95% confidence interval of the general alcid trend, values for auklets were lower than expected. Furthermore, puffins had exceptionally long dive durations that were similar to or longer than those of Brünnich's guillemots *Uria lomvia* and common guillemots *U. aalge*, which are both heavier than tufted puffins (Table 1). The mechanism of niche partitioning by spatial segregation has been reported in invertebrates (Connell 1961), mammals (Iwahara et al. 2020) and birds (Thiebot et al. 2012). For instance, when the 2 barnacle species *Balanus balanoides* and *Chthamalus stellatus* sympatrically occur, *C. stellatus* expand their distribution to the upper intertidal zone to mitigate competition with *B. balanoides* (Connell 1961). Similarly, Pacific white-sided dolphins *Lagenorhynchus obliquidens* and Dall's porpoise *Phocoenoides dalli* segregate their spatial distribution when co-existing, with Pacific white-sided dolphins using shallower waters than Dall's porpoises; the authors suggested this difference was partly due to variations in morphology because Dall's porpoises can carry larger oxygen stores, allowing them to dive deeper and mediate competition (Iwahara et al. 2020). Taken together, these findings suggest that the puffin and auklet dive behaviours reflect niche partitioning in both depth and duration, presumably to avoid interspecific competition while breeding in sympatry at Middleton Island.

Our key finding was that the observed partitioning was essentially via spatial and temporal segregations, but isotopic values were identical between species during both the breeding and non-breeding periods. Thus, the trophic levels of prey were similar between species, but this does not necessarily equate to identical diet composition. Bill load data showed an overlap in prey species, but
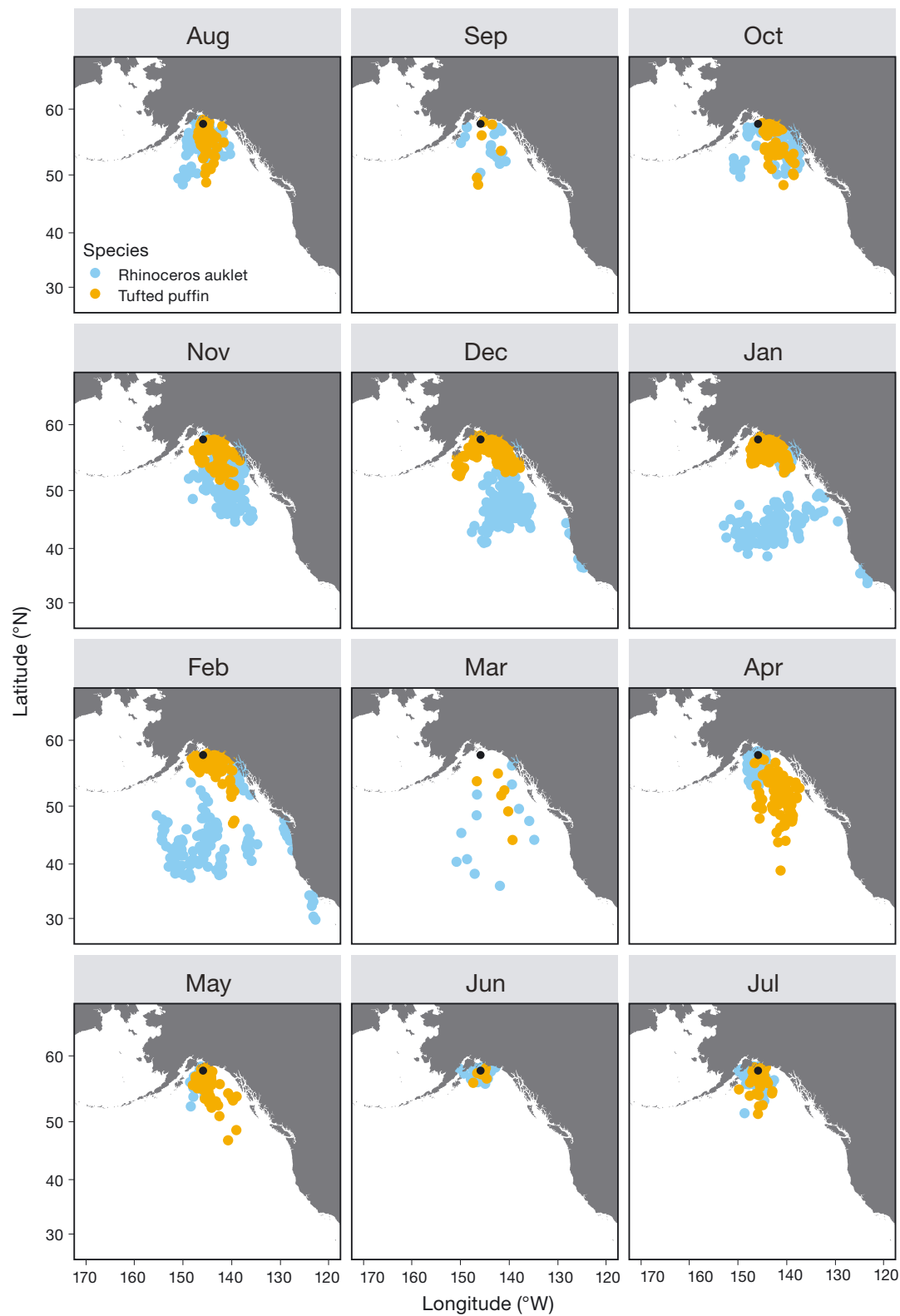
Fig. 5. Monthly year-round positions of tufted puffins and rhinoceros auklets breeding on Middleton Island from 2017 to 2019. Each point represents a 2 d median position after removal of unrealistic positions. Estimated breeding periods of these 2 species were identified as May to August for puffins and April to July for auklets in given years based on breeding phenology. Black dot: colony

Table 5. Mean ± SD $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) values in flight feathers (breeding period) and body feathers (non-breeding period) from tufted puffins and rhinoceros auklets breeding on Middleton Island, Alaska

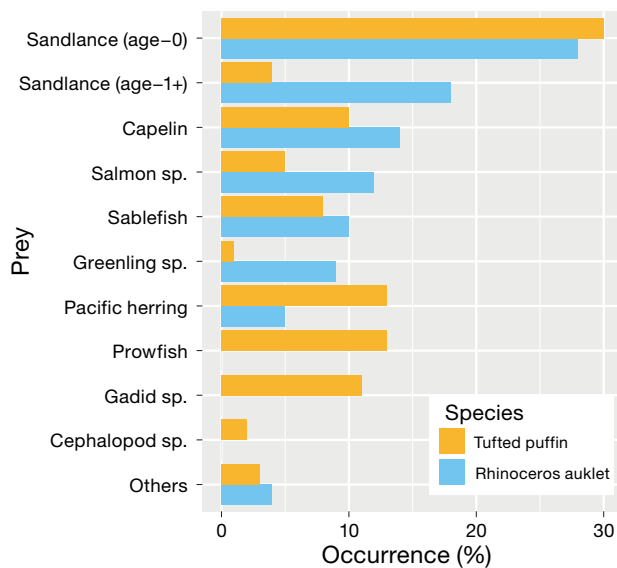| Species	Time period	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Tufted puffin	Breeding	14	−18.9 ± 0.3	16.3 ± 0.7
	Non-breeding	5	−18.6 ± 0.2	16.3 ± 0.5
Rhinoceros auklet	Breeding	57	−18.6 ± 0.6	16.9 ± 0.7
	Non-breeding	27	−18.2 ± 0.7	16.1 ± 1.3

Fig. 6. Overall composition of food samples obtained from chick-rearing rhinoceros auklets (% biomass, July to August) and chick-rearing tufted puffins (% biomass, July to August) on Middleton Island from 1978 through 2021

overall species composition of the diet was substantially different. Indeed, these results suggest dietary segregation where diets are broadly similar in the identity and trophic level of prey, but differ in specific proportions. Processes of spatial segregation may occur either via competitive exclusion (dominant individuals exclude subordinate individuals through direct competition) or niche specialisation (induced by physical capabilities) (Phillips et al. 2004). In this study, we found a clear pattern of segregation as puffins had smaller foraging ranges, deeper dives, and shorter migration distances than auklets, all of which can be explained by inherently higher wing loading. While competitive exclusion may be applicable to our data, the much smaller ranges and deeper dives of puffins suggest the segregation is related to morphological and physiological differences, as greater muscle mass gives more underwater pro-

pulsion and proportionally smaller wing sizes are more efficient underwater (Watanabe 2016, Lapsansky et al. 2022). Higher wing loading improves diving capabilities and indeed puffins have an *a priori* mass advantage for oxygen-storage tolerance — hence a longer aerobic dive limit — than auklets (Yamamoto et al. 2011, Elliott et al. 2013). Higher wing loading, however, increases the energetic costs of flight and therefore generates a trade-off between flight and dive in diving animals (Thaxter et al. 2010). Body size and the degree of wing loading reflect adaptation to wing strokes either under water or above water, and this has been shown in another alcid species (Brünnich's guillemot; Elliott et al. 2013). The extent of horizontal distances travelled can also be restricted due to breeding constraints, because breeding seabirds are extreme central-place foragers (Elliott et al. 2009). Central-place foraging theory predicts that prey items close to the colony are preferred over prey items distant from the colony, which can lead to prey depletion near the colony (the so-called 'Ashmole's halo'; Ashmole 2008). Our results show that puffins have higher dive performance while auklets have higher flight performance, which could be a consequence of segregation by means of indirect competition. While this study shows that rhinoceros auklets on Middleton Island travel long distances to forage, other studies have observed nearshore foraging near colonies (Davoren 2000) or high variation in foraging ranges across colonies and among years (Domalik 2018). Taken together, foraging distances in auklets are clearly flexible during central-place foraging, and part of this variation might be driven by competition with species of similar niche at the same colony site. Whereas variation in foraging distance may be driven by environmental variability — as shown in black-legged kittiwakes *Rissa tridactyla* in the region (Osborne et al. 2020) or in a similar species, Atlantic puffins *Fratercula arctica* (Fayet et al. 2021) — foraging distance at Middleton was remarkably constant across years (2015 to 2022) of considerable environmental variability, including marine heatwaves (Piatt et al. 2020, Arimitsu et al. 2021).

Patterns of spatial segregation were also observed during the non-breeding season when birds were neither central-place foragers nor on parental duty. Again, shorter migration distances in puffins can be explained by higher wing loading, but the similar trophic ecology between the species complicates the interpretation: it remains unclear why auklets extended their range in this case because they were not using more productive waters (similar chl *a* between species). Longer and more varied migration dis-

Table 6. Total length (mm), frequency of occurrence, and mass percent of prey brought to chicks by tufted puffins and rhinoceros auklets breeding on Middleton Island (1978–2021). The data for mass show the pooled mass from all the birds sampled

Prey species	Total length (mm)		Frequency of occurrence				Mass			
	Rhinoceros auklet (mean ± SD)	Tufted puffin (mean ± SD)	Rhinoceros auklet n	%	Tufted puffin n	%	Rhinoceros auklet g	%	Tufted puffin g	%
Pacific sand lance (age-0)[a] *Ammodytes personatus*	85 ± 11	79 ± 10	7923	29	803	26	–	–	–	–
Pacific sand lance (age-1+)[a] *Ammodytes personatus*	133 ± 18	140 ± 21	5067	18	116	4	57687	35	2389	31
Pacific herring *Clupea pallasii*	96 ± 42	54 ± 11	1346	5	593	19	27330	16	1744	23
Prowfish *Zaprora silenus*	–	97 ± 26	42	0	58	2	314	0	872	11
Gadid *Gadidae*	–	64 ± 12	244	1	77	3	818	0	163	2
Pacific capelin *Mallotus catervarius*	108 ± 19	46 ± 15	2925	11	970	32	21325	13	714	9
Sablefish *Anoplopoma fimbria*	106 ± 32	128 ± 21	1369	5	37	1	13573	8	585	8
Oncorhynchus Salmon sp.	119 ± 27	161 ± 21	1233	4	11	0	17960	11	338	4
Cephalopoda Cephalopods	–	25 ± 14	52	0	42	1	235	0	152	2
Hexagrammidae Greenling	73 ± 11	69 ± 7	6411	23	7	0	21781	13	20	0
Others	88 ± 17	65 ± 6	913	3	330	11	5674	3	757	10

[a]Mass of Pacific sand lance for age-0 and age-1+ were combined

tances among auklets, relative to puffins, may be due to either direct intra- and inter-specific competition, or factors unrelated to competition. Concerning direct competition, wintering habitats may contain high densities of competitors (Nishizawa et al. 2020), or segregation into communities comprised of multiple large populations such as seabirds may be driven by density dependence (Ashmole 2008, Wakefield et al. 2013). It is possible that auklets show winter niche segregation due to inter- and intra-specific competition over shared prey. In addition to competition, species-level geographic range limits may be linked to the differences in non-breeding distributions between puffins and auklets. Tufted puffins are primarily a northern species, with the bulk of the global population breeding in high latitudes whereas rhinoceros auklets are primarily a temperate mid-latitude species and Middleton Island is a place of breeding overlap (Gaston & Jones 1998). Both of these alcid species populations became established on Middleton Island relatively recently, after the Alaskan earthquake of 1964 (S. Hatch pers. obs.). If rhinoceros auklets are expanding their breeding range northward, it would not be unexpected for them to

migrate southward to overwinter. Alternatively, wintering movement strategy is often species specific and may be driven by life history or culturally inherent. For instance, Atlantic puffins in Wales show a dispersive pattern of movements during the non-breeding period with a great inter-individual variability in travel distance and direction (Guilford et al. 2011), while a population of auklets from northern Japan consistently exhibits a figure-of-eight migration route (Shoji et al. 2021), suggesting the birds follow seasonal changes in prey availability (Takahashi et al. 2018). Culturally inherited migration as a navigational control is commonly observed in waterfowl, such as swans and geese (Newton 2010), but this phenomenon has rarely been observed in seabirds. In summary, direct and indirect competition may not be mutually exclusive explanations for niche partitioning, and further study is needed to elucidate the mechanisms of spatial segregation during the non-breeding season, perhaps coupling biologging with measures of food availability across years.

In our study, puffins and auklets showed very similar stable isotope signatures with small variance during breeding and non-breeding periods (repre-

sented by flight feathers and body feathers, respectively). Dietary information of adults is scarce for both puffins and auklets, but both species feed on fish and plankton, and puffins tend towards an invertebrate-rich diet while auklet diet contains more vertebrates throughout the year (Gaston & Dechesne 2020, Piatt & Kitaysky 2020). However, in this study, the stable isotope signatures were nearly identical, and thus adult puffins and auklets breeding at Middleton Island are likely feeding on similar prey to each other and throughout the year. On the other hand, bill load composition over years was noticeably different, while the prey species present were similar. Differences in adult and chick diet have been commonly observed in rhinoceros auklets (Davoren & Burger 1999) and other seabirds (Ydenberg 1994, Barrett et al. 2007), and often reflect changing nutritional requirements of growing chicks. However, adults could minimise competition and niche overlap with sympatric species by changing prey delivered to chicks while maintaining prey targeted for self-feeding. Since we did not detect trophic niche segregation in this study, spatiotemporal niche segregation appears to be the primary mechanism for puffin and auklet sympatry.

This is the first information on movements of tufted puffins across the year (see Schaefer et al. 2022 for non-breeding movements), currently a candidate species for listing under the US Endangered Species Act. Populations of puffins have declined in several locations due, in part, to fisheries-associated net mortality, oil pollution, increased predation, harvest, and environmental change (Piatt & Kitaysky 2020, Pearson et al. 2023), and the Japanese population is predicted to be extirpated in the near future (Brazil 2018). Our 3-dimensional approach allowed us to gain insight into potential mechanisms driving population declines, and these results have broad implications for the conservation of other sympatric species. While auklets have relatively constant breeding success among years at Middleton Island, puffins have a boom-and-bust cycle, with only a few years of high breeding success interspersed by many years of low success (Gjerdrum et al. 2003). High wing loading and smaller foraging ranges may cause puffins to be more sensitive to prey availability and distribution, whereas auklets forage over larger areas and thus may be able to find food even in years of reduced prey availability.

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