



Resource partitioning in Atlantic puffins and razorbills facing declining food: an analysis of feeding areas and dive behaviour in relation to diet

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ABSTRACT: Multi-species communities of closely-related seabirds present opportunities to determine how such species coexist. Machias Seal Island (MSI), New Brunswick, Canada, is a migratory bird sanctuary where several seabird species breed, including the largest number of Atlantic puffins *Fratercula arctica* and razorbills *Alca torda* in the Gulf of Maine/Bay of Fundy ecosystem. The species differ in nest sites, body size and wing-loading, as well as life history (specifically post-natal care); they take different proportions of a similar range of prey species, and recent studies show limited overlap in foraging areas at other sites. We wished to expand our understanding of resource partitioning at MSI by measuring differences in foraging areas and behaviour, in the context of recent declines in availability of key prey species and concomitant decreasing breeding success of both species, which suggest that carrying capacity may have been reached. Using GPS loggers in 2 breeding seasons, and long-term chick-diet data collected over 20 yr, we investigated differences in horizontal and vertical foraging distributions and prey that allow these 2 species to breed sympatrically. Logger data collected from puffins ($n = 7$) and razorbills ($n = 8$) revealed that razorbills fed in shallower water than puffins and took shorter foraging trips. Prey brought to chicks at control nests showed higher proportions of high-energy fish in razorbill diet compared with puffins. Foraging behaviour is likely affected by declining availability of high-quality food and increasing temperature since 2010.

KEY WORDS: *Fratercula arctica* · *Alca torda* · Seabird foraging · Resource partitioning · Spatial ecology · Foraging distribution · Auks · Alcids

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1. INTRODUCTION

Seabirds reduce possible competition by partitioning resources through different foraging strategies, though the method of resource partitioning may vary by breeding colony (Masello et al. 2010, Pollet et al. 2014, Chimienti et al. 2017, Wakefield et al. 2017, Jessopp et al. 2020). Strategies to avoid or reduce competition between diving seabirds include partitioning resources horizontally by foraging habitats (Frere et al. 2008, Barger et al. 2016), vertically by foraging depths (Paredes et al. 2008, Elliott et al.

2010, Shoji et al. 2015, Wakefield et al. 2017) and/or by interspecific differences in diet (Thaxter et al. 2010, Linnebjerg et al. 2013, Barger et al. 2016). Understanding their diet and foraging behaviour can provide key insight into how these populations coexist. Seabirds often prey on forage fish that are important to commercial fisheries. The diet of Atlantic puffins *Fratercula arctica* (hereafter puffins) has so far been associated with abundance of capelin *Mallotus villosus*, herring *Clupea harengus* and cod *Gadus morhua* in Norway (Barrett 2002, 2003); sand lance (also known as 'sand eel') *Ammodytes mari-*

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nus, sprat *Sprattus sprattus* and young of various gadoids in Scotland (Harris & Wanless 2011); sand lance in south Wales (Shoji et al. 2015) and south Iceland (Hansen et al. 2021); and spawning capelin and sand lance in Labrador and Newfoundland, Canada (Baillie & Jones 2003). However, in the Bay of Fundy and Gulf of Maine, puffins and other seabirds feed on juveniles of both forage fish whose adult stages are fished commercially (herring, haddock *Melanogrammus aeglefinus* and Acadian redfish *Sebastes fasciatus*) as well as juvenile sand lance *Ammodytes* spp. for which there is no commercial fishery here (Scopel et al. 2018, 2019, Depot et al. 2020). Puffins coexist widely with razorbills *Alca torda* which take similar prey but larger individuals (Barrett 2003, Shoji et al. 2015, Scopel et al. 2019, Major et al. 2021).

Climate change is threatening system-wide change that may affect wildlife in the Bay of Fundy and the Gulf of Maine (Pershing et al. 2021). It is difficult to predict the changes that will occur to oceanographic features through climate change, but we can expect rising sea levels and are already experiencing increasing sea surface temperatures (Mills et al. 2013, Pershing et al. 2015, Diamond 2021, Major et al. 2021) and marine heatwaves (Scannell et al. 2016). These changes could affect the timing and distribution of phytoplankton blooms that are pivotal to the marine food web on which seabirds depend.

Significant changes in marine food webs are already affecting the most important seabird breeding site in New Brunswick, Canada, at Machias Seal Island (MSI). During the breeding season, this island supports 8 seabird species, including regionally important colonies of puffins and razorbills. These 2 species of the auk family coexist sympatrically during the breeding season, occupying similar dietary niches; both species provide mainly juvenile forage fish such as Atlantic herring, sand lance, white hake *Urophycis tenuis* and haddock to their young. Common murre *Uria aalge* also breed but are recent colonists that have been studied less intensively here than puffins and razorbills; they are also plunge-divers that coexist widely with razorbills and puffins, but are not included in this study because no data were retrieved from GPS tags deployed on murre. While breeding, puffins and razorbills are central-place foragers, meaning they are restricted to certain foraging ranges by the need to make several return trips to feed their young or relieve their mate (Orlans & Pearson 1979, Lowther et al. 2002, Lavers et al. 2009, Harris et al. 2012). In recent years, the diet of both species has changed, with a decline in the presence of herring, the highest-energy food (Breton &

Diamond 2014, Kress et al. 2017, Scopel et al. 2019), and there is concern for the future of auks in this region (Diamond 2021, Major et al. 2021). These dietary changes suggest that food resources are becoming more limited, so the need to partition resources may increase and the differences between species become more pronounced.

The purpose of this study was to determine whether and how puffins and razorbills are partitioning food resources when breeding on MSI, focussing mainly on the overlap between foraging areas. We deployed bird-borne GPS loggers on adults while rearing chicks. The potential for competition is likely to be strongest at this time because of the high energy demand of growing chicks. Dive depth and duration both generally increase with body size in auks (Watanuki & Burger 1999), as does wing-loading (Gaston & Jones 1998, Elliott et al. 2013), so we predicted that razorbills would show longer dives than puffins and would feed closer to the colony. Razorbills and puffins at a Labrador colony appear to segregate by prey choice as well as foraging area (Pratte et al. 2017), so we also explored chick-diet data for dietary differences between the 2 focal species.

2. MATERIALS AND METHODS

Logger deployment took place in July and August in 2014 and 2015 at MSI (44° 30' N, 67° 06' W), New Brunswick, Canada. In 2016, this colony hosted 4796 breeding pairs of puffins, 85% of the 4 colonies in the Gulf of Maine, and 2825 pairs of razorbills, 83% of the Gulf of Maine population at 3 colonies (H. Major unpubl. data). Puffins (adult body weight ~450 g) and razorbills (~650 g) are pursuit-diving auks hunting prey tens of metres (maxima ~70 and ~100 m, respectively; Lowther et al. 2002, Lavers et al. 2009) below the surface. Females lay a single egg in a burrow usually excavated in turf-covered soil (puffins) or in rock crevices (razorbills). In both species, both sexes incubate the egg and provide food to the young. The species have different fledging strategies: puffin chicks head out to sea independently after approximately 44 d (Lowther et al. 2002) at about two-thirds of adult body size, whereas razorbill chicks are about one-third adult weight when they leave the land after about 20 d accompanied by the male parent, who takes them to the food (Lavers et al. 2009), rather than continuing to take food to the chick, as puffins do. This difference in life-history means that puffins are constrained by central-place foraging for several weeks longer than razorbills. Razorbill adults

attend the chick in the nest more than puffins do (Harris & Birkhead 1985, Gaston & Jones 1998) so have less time to forage.

In early May each year, 20–25 nest sites of each species were checked by hand for the presence of an egg and/or adult. Burrows containing eggs were checked again before the estimated hatch date (approximately 33 d after lay). Once the hatch date was known, 1 adult from each experimental burrow was targeted for logger attachment during the night once chicks were old enough (20 d in puffins, 15 d in razorbills, established by experiment in 2014; Symons & Diamond 2019). Video cameras were used to assess whether tagged birds continued to bring food to the chick, allowing us to distinguish different spatial foraging patterns for foraging trips where fish was brought back to the chick or not. Video cameras were set up in front of control burrows (similar stage but adults not tagged) once chicks reached 20 d (puffin) or 15 d (razorbill) old (see Supplementary Information in Symons & Diamond 2019), and experimental burrows once the logger was attached to 1 adult. Cameras recorded for an average of 4 d, and the results, including feeding rates, are more fully described by Symons & Diamond (2019).

2.1. Tracking and foraging analysis

Eleven puffins and 12 razorbills (Table 1) were equipped with GPS loggers (Ecotone; ALLE-68, 5 g, dimensions without external antenna 26 × 16 × 10 mm, antenna 52 mm, on puffins, and URI-120, 8 g, dimensions without external antenna 35 × 16 × 11 mm, antenna 70 mm on razorbills) that recorded date, time, latitude, longitude, speed and dive duration by means of a wet/dry sensor. These loggers downloaded remotely to a base station on the colony whenever the bird came within 300 m. Loggers were deployed between 20 June and 18 July 2014, and from 29 June to 1 August 2015, taped to scapular and back feathers. GPS positions were set to record every 30 min, allowing the loggers to record for approximately 4 d (Table 2). The total mass of the device with attachment material was 5.7 ± 1.8 g for puffins and 11.5 ± 5.5 g for razorbills (on average 1.3 and 1.8% of puffin and razorbill body weight, respectively). Although loggers were set to take GPS positions every 30 min, dives were recorded independently of the GPS interval setting; wet/dry dive sensors

recorded the time of diving events but did not collect a GPS location. Therefore, communication between logger and satellites was interrupted while the bird was underwater; this made for longer time lags between points when the bird was diving continuously. Once the bird resurfaced, the 30 min interval continued, but these longer time lags at diving locations resulted in time lags closer to 1–1.5 h on average between GPS locations.

Overall, we retrieved location and dive data from 7 puffins and 8 razorbills and location data only for 2 puffins due to faulty wet/dry sensors. Latitude and longitude recorded to the nearest 10–15 m were used to calculate foraging ranges using autocorrelated kernel density estimates (AKDEs; Fleming et al. 2015). All statistical analyses were performed in R 3.4.0 (R Core Team 2017). The conventional method of estimating range distribution with kernel density estimates (KDEs) assumes that input data are independently and identically distributed (Silverman 1986). GPS data are inherently autocorrelated, especially when sampled in short intervals, violating this assumption. The AKDE accounts for autocorrelation in the data and calculates a better estimate for minimum area, particularly with small sample sizes (Fleming et al. 2015, 2016). The AKDE is especially useful for short observation periods because it uses the autocorrelation (relationships between the past and future movement) to make strong statistical predictions of future movements (Fleming et al. 2015). The area of active use and core area of foraging activity are reported as a percent coverage area (typically 95 and 50%, respectively; Worton 1989, Linnebjerg et al. 2013). We used 90% to represent area of active use, rather than 95%, since the 5% difference in the contours mostly extended over land. Occurrence distributions were calculated using foraging points for each individual to account for differences in the number of GPS locations by individual. Foraging points were GPS locations bounded by foraging dives with speeds less than 15 km h^{-1} . A weighted AKDE was

Table 1. Summary of foraging trips for Atlantic puffins and razorbills on Machias Seal Island, New Brunswick, Canada; n: number of individuals monitored

Species	Year	n	Total number of trips	Total number of GPS fixes	Total number of recording hours
Atlantic puffin	2014	3	9	104	187.8
	2015	4	8	584	343.7
Razorbill	2014	2	27	345	202.7
	2015	6	45	433	553.0

Table 2. Summary of foraging and diving data for Atlantic puffins and razorbills on Machias Seal Island, New Brunswick. 'Short' and 'long' foraging trips are defined as <35 km and >75 km for puffins and ≤10 km and >30 km for razorbills. Data are presented as weighted mean ± SD; n: number of individuals monitored

Year	Atlantic puffins		Razorbills	
	2014 75 (n = 4)	2015 71 (n = 7)	2014 75 (n = 4)	2015 75 (n = 8)
Breeding success (%)				
Foraging data				
Number of individuals	3	4	2	6
Total number of foraging trips	Short	4	16	35
	Long	7	10	27
Trip duration (h)	Short	1.4 ± 1.0	10.4 ± 7.0	0.7 ± 0.1
	Long	24.2 ± 14.0	30.8 ± 11.3	9.7 ± 1.2
Trip length (km)	Short	15.5 ± 8.2	14.1 ± 5.2	1.2 ± 0.2
	Long	116.1 ± 37.0	142.2 ± 22.6	69.8 ± 19.9
Distance from colony (km)	Short	6.1 ± 3.9	8.7 ± 3.9	0.5 ± 0.1
	Long	51.6 ± 13.9	48.6 ± 15.6	29.7 ± 6.8
Prey length (cm)		6.4 ± 2.4	9.0 ± 3.7	9.1 ± 4.4
Diving data				
Number of individuals	0	4	1	6
Number of dives per day	–	290.6 ± 235.7	311 ± 185.2	399.1 ± 233.1
Mean dive duration (s)	–	37.7 ± 6.6	35.4 ± 25.2	28.5 ± 2.0
Mean bathymetry of dive locations (m)	–	103.8 ± 45.1	24.0 ± 12.1	30.2 ± 19.7

then calculated for each species. Overlap, measured as the ratio of the intersecting area to the average species area, was calculated using the overlap function in the R package 'ctmm' (Fleming & Calabrese 2020). This threshold speed was determined from the data: 95.2% of recorded speeds were <15 km h⁻¹. Foraging trips (Table 1) were manually identified from consecutive data points between end points at the colony. We classified chick-feeding trips as foraging trips where the adult returned to the colony with fish, as confirmed by video camera footage. Trips where the adult returned without fish could correspond to foraging locations that have previously been successful. The distribution of trip lengths revealed a large gap in the mid-range distances, indicating that birds alternated between long and short trips, similar to recent findings by Fayet et al. (2021). All puffin trips were <35 or >75 km in length, while razorbills trips were ≤10 or >30 km. Therefore, trips were categorized as short or long for comparison. Separate linear mixed models (LMMs) for long and short trips, with individuals as a random factor (to account for pseudoreplication from the same individual), were used to compare trip length as well as distance from the colony between puffins and razorbills. Trip lengths for long and short data were log transformed, while distances from the colony for short trips and long trips were inverse-square-root transformed and log transformed, respectively, to meet assumptions of normality.

2.2. Dive data analysis

Foraging dives were defined as dives ≥4 s and <120 s. A lower limit of approximately 5 s is commonly used in seabird diving studies (Linnebjerg et al. 2013, Shoji et al. 2015); however, our data showed a clear break at 4 s, and 98.2% of dives (razorbills n = 13 216; puffins n = 3778 dives) were <2 min. Such short dives were likely non-foraging activities; likewise, the upper threshold was used to eliminate possible errors with the wet and dry sensor while birds were rafting. Dive durations recorded by the GPS loggers were used to interpolate dive depths from the relationship between dive depth and duration found by Shoji et al. (2015):

$$\text{Atlantic puffins: Depth in meters} = 0.481 (\text{Duration in seconds}) - 7.69 \quad (1)$$

$$\text{Razorbills: Depth in meters} = 0.427 (\text{Duration in seconds}) - 1.28 \quad (2)$$

Again, we used LMMs with individuals as a random factor to compare dive durations (square-root transformed) between puffins and razorbills. We also used an ANCOVA test to compare dive durations relative to time of day for both species. Multiple comparisons of means (Tukey contrasts) were used to identify significant differences between time of day, holding species constant, as well as differences between species, holding time of day constant. We used 1 km grid cell size resolution bathymetric data

constructed by E. Roworth and R. Signell (<https://pubs.usgs.gov/of/1998/of98-801/bathy/>) to compare the depths at diving locations to the available depths using a *t*-test. To calculate available depth, a random sample of points equal to the number of dive locations per species were populated within the maximum boundary of the GPS data.

2.3. Diet data analysis

Diet data have been collected annually since 1995 in routine monitoring by observing prey brought to burrows through standardized feeding watches (total 1802 (min. = 18, max. = 167, mean = 86) h for puffins, 1165 (min. = 22, max. = 113, mean = 55.5) h for razorbills) using the method described by Breton & Diamond (2014) and Scopel et al. (2019). In 2014 and 2015, there were 147 and 114 h of these feeding watches for puffins and 71 and 72 h for razorbills, respectively. The biomass of each prey taxon was determined by converting lengths observed in the field to mass using formulae in Scopel et al. (2018), Table S3,

their Supplementary Material. Values are presented as means \pm SD, and an alpha level of 0.05 was used to determine significance of all statistical tests.

3. RESULTS

3.1. Foraging areas

Foraging areas of trips not followed by prey delivery to chicks could be failed foraging. Our data for recapture weights of tagged birds are incomplete, but 3 puffins lost 20 g (4.6% of initial weight) over 2 d, 20 g (4.3%) over 8 d and 2 g (0.5%) over 4 d. Three razorbills lost 75 g (10.6%) over 6 d, 30 g (4.6%) over 4 d and 80g (11.1%) over 21 d, while one gained 20 g (3.1%) over 5 d. Loggers may have compromised the ability of the tagged birds to capture prey due to the weight and/or hydrodynamic drag.

Foraging data of puffins and razorbills were segregated in both years (Fig. 1). Although the areas of active use (90% AKDE contour) intersected, puffin foraging trips were twice as long as those of razor-

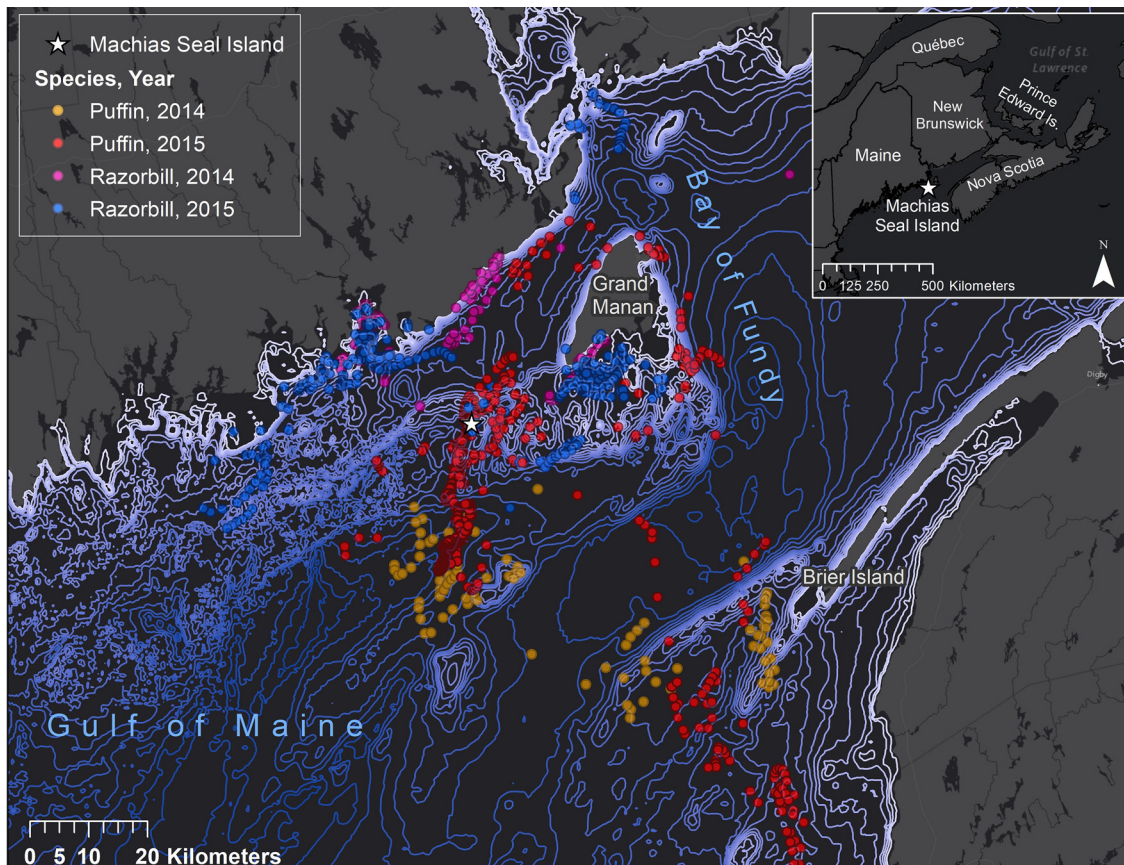


Fig. 1. Bathymetry overlaid with foraging data (GPS locations bounded by foraging dives with speeds less than 15 km h^{-1}) of Atlantic puffins and razorbills breeding at Machias Seal Island, New Brunswick (NB), Canada. Depths in the Gulf of Maine and Bay of Fundy range from 5 (light blue) to 300 m (dark blue)

bills, and they travelled about twice as far from the colony on average (Table 2, Fig. 2). The area of overlap comprised 37.1 and 51.7% of the 90% AKDE contour for puffins and razorbills, respectively. The core foraging areas (50% AKDE contours) intersected within 10 km around the colony, and the overlap corresponded to 8.9 and 18.1% of the puffin and razorbill core foraging areas, respectively. Beyond this 10 km radius, razorbills foraged mainly in coastal waters of Maine and the shoals south of Grand Manan, while puffins fed farther offshore (Fig. 2).

Puffin foraging trips were significantly longer than those of razorbills for both long (LMM, $F_{1,11} = 24.21$, $p < 0.001$) and short trips (LMM, $F_{1,13} = 19.45$, $p < 0.001$; Table 1). In addition to foraging on longer trips, puffins also travelled significantly farther from the colony than razorbills on long (LMM, $F_{1,11} = 17.13$, $p < 0.01$) and short trips (LMM, $F_{1,13} = 18.34$, $p < 0.001$; Table 1). One razorbill made 4 short chick-feeding

trips (0.6 ± 0.3 km), while 4 long chick-feeding trips were recorded from 2 razorbills (35.7 ± 7.5 km). Sample size was too small to statistically test for differences in long and short foraging trips when birds returned to the colony with prey or without. The only confirmed chick-feeding trip for puffins was at 9.9 km from MSI. Reduced chick-feeding rates are attributed to effects of the tags and are described more fully by Symons & Diamond (2019).

3.2. Dive behaviour

On average, puffins foraged in water that was 73.6 ± 20.0 m deeper than razorbills, but there was no difference in mean dive duration between puffins and razorbills (Table 2; LMM: $F_{1,9} = 0.88$, $p = 0.37$; Fig. 1). Approximately 56.8% of razorbill dives were 20–40 s, whereas puffin dive durations extended over a much

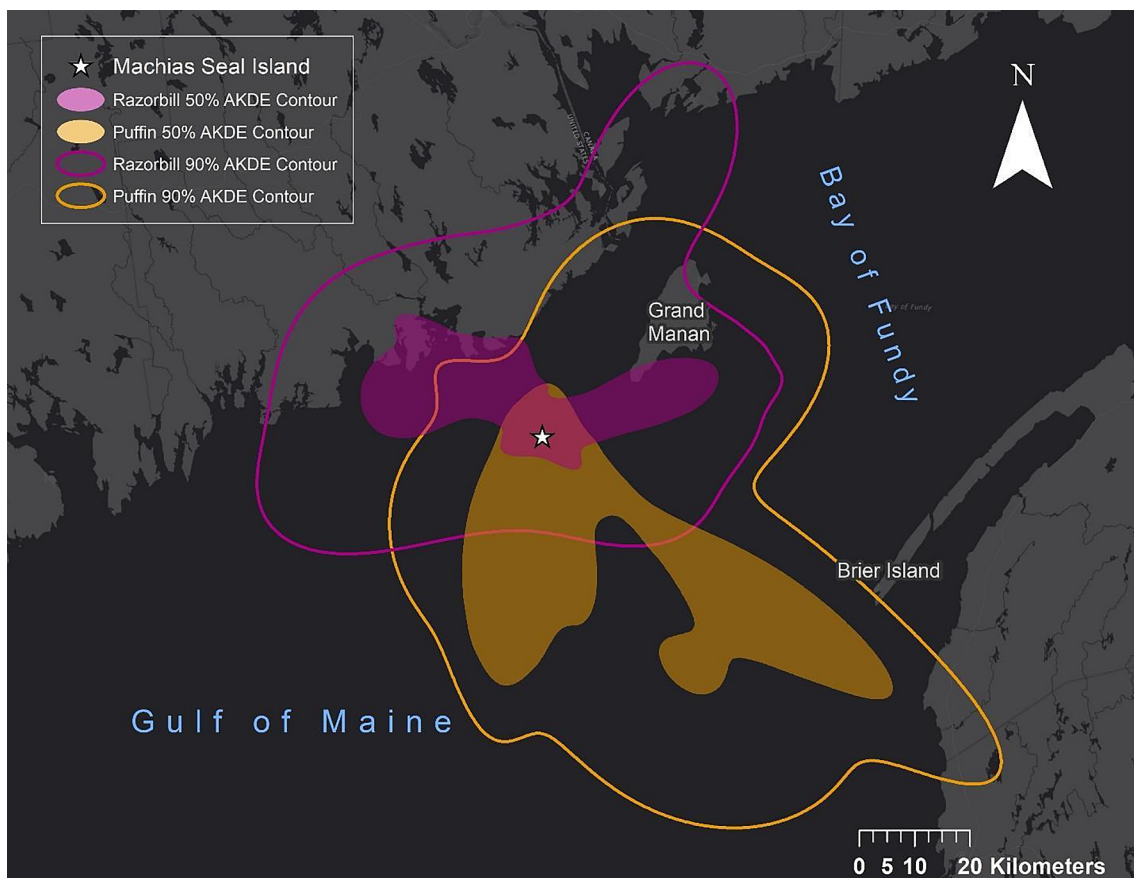


Fig. 2. Autocorrelated kernel density estimates (AKDEs) for Atlantic puffins and razorbills breeding at Machias Seal Island, New Brunswick, in 2014 and 2015. Filled polygons show the core foraging areas (50% AKDE contour), while the 90% AKDE contour shows the total foraging area. Contours are overlaid on a map of the Bay of Fundy and Gulf of Maine, but areas over land are not used as foraging areas. The overlap of the 90% AKDE contour comprised 37.1 and 51.7% of the area of active use by puffins and razorbills, respectively. The overlap of the 50% AKDE contour comprised 8.9 and 18.1% of the core foraging area, respectively. Limited sample size may affect the degree of overlap observed

wider range (15–80 s) with no clear peak (Fig. 3). The depth at diving locations was significantly shallower than available depths for both species (puffins: $t_{1263} = 2.2$, $p = 0.02$; razorbills: $t_{909} = 33.4$, $p < 0.001$; Fig. 4). Puffins performed fewer dives d^{-1} and dove in areas with deeper water, on average (Table 2, Fig. 1). Fewer puffin dives d^{-1} could be attributed to a tag effect.

Razorbills dove longest at dawn (06:00 h Atlantic Daylight Time, up until mid-day [11:00 h]), and had the shortest dives between 00:00 and 03:00 h (Fig. 5a). Puffins dove significantly longer than razorbills controlling for time of day ($F_{1,411} = 26.21$, $p < 0.001$). Dive durations of both species were related to time of day ($F_{23,441} = 4.24$, $p < 0.001$); both species made significantly shorter dives between 00:00 and 04:00 h (i.e. at night) and significantly longer dives between 10:00 and 12:00 h and at 20:00 h (all adjusted p -values < 0.05 ; Fig. 5a). Razorbills made significantly longer dives than puffins between 07:00 and 09:00 h and significantly shorter dives than puffins at 12:00 h and at 20:00 h (all adjusted p -values < 0.05 ; Fig. 5a). Both species showed reduced numbers of dives between 22:00 and 04:00 h (Fig. 5b). The percentage of dives was 2.5 times higher (12.9% for puffins and 16.7% for razorbills) during the 2 h following this lull (Fig. 5b). Subsequently, there was a slow increase in proportion of dives before reaching the highest peak at 17:00 h for puffins and 20:00 h for razorbills (Fig. 5b).

Using the formula from Shoji et al. (2015), a mean dive depth was calculated for each species, weighted to account for multiple records from the same individuals. On average, puffins dove to 17.1 ± 11.5 m and razorbills dove to 11.1 ± 7.1 m. This estimate is biased against shallow dives because the depth/duration relationship has intercept 15 s.

3.3. Diet

In 2014, the prey brought in by puffins at control sites was spread evenly across the main forage fish species (Fig. 6). Razorbills brought mostly herring (35% by mass) and sand lance (37%), followed by hake (23%) and small amounts of haddock. Diet was much less diverse in 2015, consisting mainly of sand lance in both species (puffins: 90%; razorbills: 59%). Razorbills brought in more herring than puffins in both years, consistent with the long-term data since 1995 (Fig. 6); throughout the 21 yr time series of diet studies at MSI, razorbills have brought in a higher proportion of herring than puffins (Diamond 2021).

4. DISCUSSION

We found that puffins and razorbills partitioned food resources on multiple axes. They segregated spatially, using different core foraging areas, and by differences in depth of water and to some extent by time of day of dives. Overall, puffins travelled farther, foraged in deeper water and showed a wider variety of diurnal dive times than did razorbills. Puffins returned to the colony with sand lance more often than razorbills, which returned with more herring. Sample sizes were low, but at least comparable with those of other recent studies in which tracking was only conducted in a single year (Pratte et al. 2017, DeLord et al. 2020, Petalas et al. 2021), whereas we tracked in 2 years. As described by Symons & Diamond (2019), tags interfered with feeding behaviour by reducing (razorbills) or virtually eliminating (puffins) the proportion of foraging trips on which adults brought food for the chick. Although foraging success was clearly reduced by carrying the tag, there is no reason to suggest that the birds sought food in different places than they would normally use, simply that the tag reduced their ability to

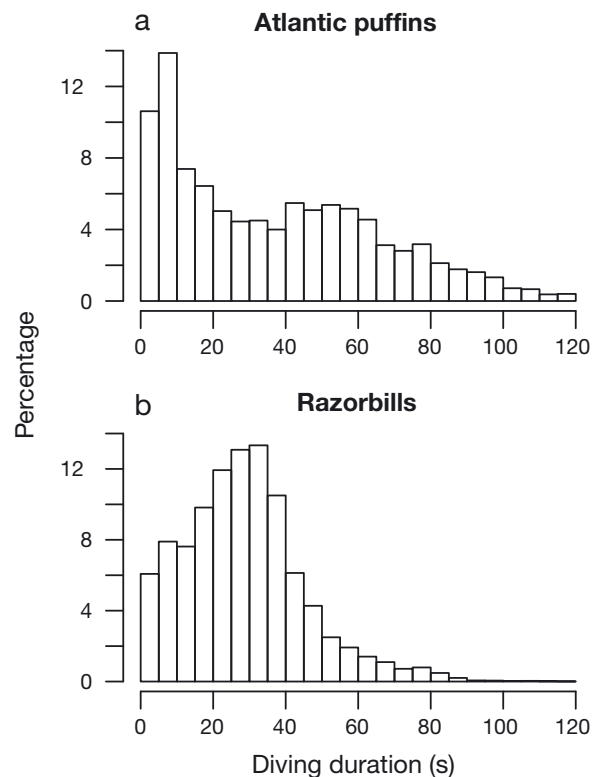


Fig. 3. Percentage of dive durations (s) for (a) puffins and (b) razorbills. Approximately 56.8% of razorbill dives lasted 20–40 s, whereas puffins showed a wider and more even range of dive duration

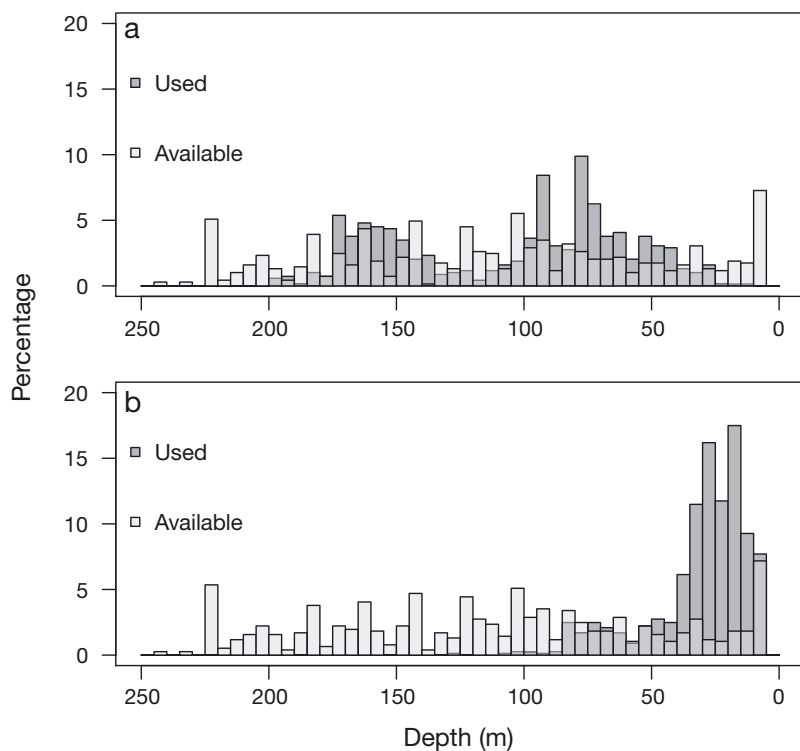


Fig. 4. Subsample of available depths compared with depths at points used by (a) puffins and (b) razorbills diving around Machias Seal Island, New Brunswick. Depths at diving locations were significantly shallower than available depths for both species (puffins: $t_{1263} = 2.2$, $p = 0.02$; razorbills: $t_{909} = 33.4$, $p < 0.001$)

find enough food for themselves and the chick. Thus, our results apply mostly (razorbills) or almost entirely (puffins) to adults foraging for themselves. There were no obvious environmental stressors on auks during this study; breeding success at 71–75% in puffins and 75% in razorbills (Table 2) exceeded the 1995–2015 means of 59 and 54%, respectively.

4.1. Foraging areas

Although the foraging areas of puffins and razorbills overlapped 37.1 and 51.7%, respectively, the core foraging areas (50% AKDE contours) showed only slight overlap, mainly around the colony; outside the 10 km radius around MSI, the core foraging areas overlapped very little. We obtained similar results when looking at differences between long and short foraging trips among puffins and razorbills. Both puffins and razorbills foraged in the areas close to the colony on short trips, while puffins travelled significantly farther from the colony on long foraging trips than razorbills. This dual foraging strategy has been recently observed in puffins at 4 European

colonies (Fayet et al. 2021) but is not the case for all puffin colonies (Harris et al. 2012). This foraging strategy may be indicative of low resource availability close to the colony (Granadeiro et al. 1998).

Video-recorded control and experimental nests showed no significant difference in the number of feedings per day for either species (Symons & Diamond 2019). This result is likely due to small sample sizes, as the mean number of feedings per day of controls was 4 times that of experimental burrows in puffins, and nearly twice in razorbills (see Symons & Diamond 2019 for detailed analysis).

Three puffins travelled over 90 km to the coast of Brier Island, Nova Scotia, where several top predators have been documented taking advantage of intense upwelling and tidal currents (Brown & Gaskin 1988, Johnston & Read 2007, Hunnewell et al. 2016). Razorbills foraged closer to the mainland than puffins, as in Labrador (Pratte et al. 2017) and the Gulf of St. Lawrence (DeLord et al. 2020). Benison et al. (2019) found that puffins (but not razorbills) in Ireland reduced locomotion costs connected to travelling between prey patches by drifting with pelagic tidal movement and diving during drifts. We did not have the data to test whether puffins at MSI were exploiting tidal movement, but several linear patterns of foraging points consistent with this behaviour are apparent in Fig. 1 south and west of Brier Island, and were not seen in razorbill data.

Segregation in foraging areas has been previously observed among sympatric breeding auks (Wanless et al. 1990, Linnebjerg et al. 2013, Barger et al. 2016, Pratte et al. 2017, Gulka et al. 2019) as well as other pursuit-diving seabirds (Frere et al. 2008, Masello et al. 2010, Wilson 2010, Raya Rey et al. 2013, Afán et al. 2014). Fine-scale competition over foraging space has been observed between marbled murrelets *Brachyramphus marmoratus* and common murrelets, where marbled murrelets avoided their larger relatives when breeding sympatrically by foraging farther away from them (Ronconi & Burger 2011). The spatial segregation between puffins and the much larger razorbills may be due partly to such avoidance of a larger competitor by puffins. Puffins are likely

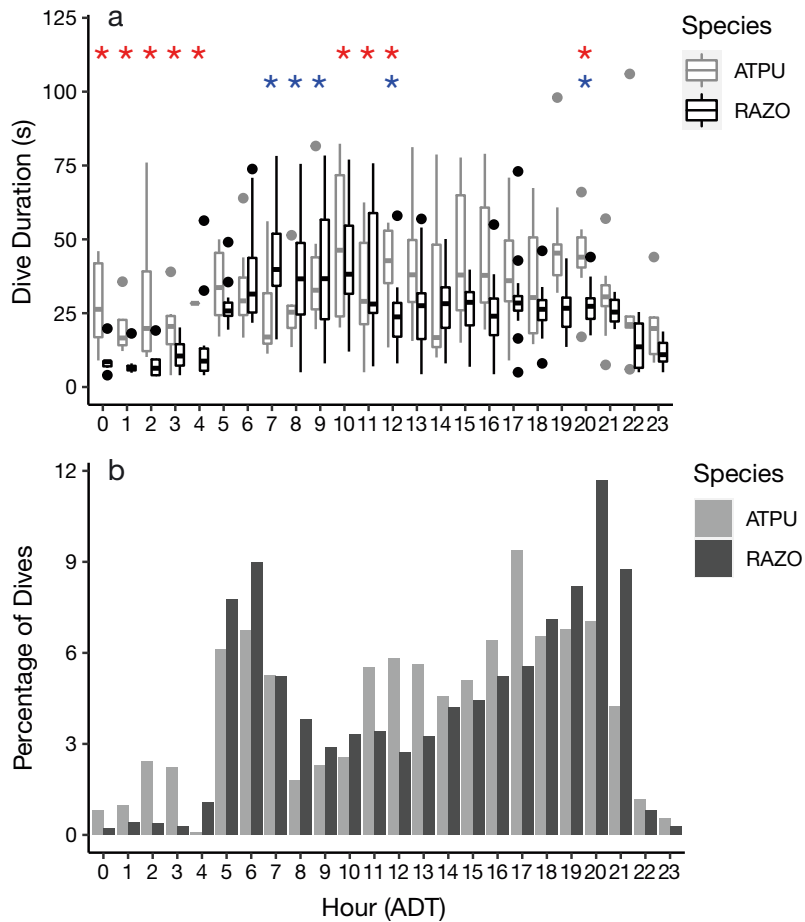


Fig. 5. (a) Dive duration and (b) percentage of dives based on time of day (Atlantic Daylight Time [ADT = UTC - 3 h]) for Atlantic puffins (ATPU) and razorbills (RAZO) in 2014 and 2015 on Machias Seal Island, New Brunswick. Red stars in (a) mark significant differences in length of dives when comparing hours of the day, holding species constant. Blue stars in (a) mark significant differences in dive length between species (boxplots) during that hour. Bar: median; box: interquartile range (IQR); whiskers: max./min. values within 1.5x IQR above/below box; dots: outliers. Local sunrise and sunset during this study ranged from 05:45 to 06:07 h and 21:00 to 21:18 h, respectively

able to support their generally longer foraging trips because of the reduced flight costs incurred by their 20% lower wing-loading compared to razorbills (from data in Kaiser 2007). In both species, foraging range, and perhaps other features of the birds' behaviour, may have been influenced by carrying a tag, as has been demonstrated in several other seabirds (Bodey et al. 2018, Cleasby et al. 2020).

Our study makes an interesting comparison with a recent study of puffin foraging behaviour at 4 well-studied colonies in Europe (Fayet et al. 2021). Compared with the best-performing colony in that study (North Iceland), puffins at MSI had higher breeding success (71–75%, vs. 70% in North Iceland), similar feeding rates (4.5 ± 0.9 vs. 4.2 ± 0.9 d^{-1}), a higher proportion of long trips (65 vs. 30%) and much longer

long trips (116–142 vs. 22 km). The combination at MSI of higher breeding success and feeding frequency with longer foraging trips compared with North Iceland is not consistent with the inverse relationship between breeding success and foraging range suggested by Fayet et al. (2021).

4.2. Dive behaviour

Although dive durations of puffins and razorbills were not significantly different, puffins foraged in deeper water and showed a wider range of dive times when compared to razorbills. If we estimate dive depths from dive duration using the formula from Shoji et al. (2015), razorbills from MSI showed similar diving behaviour to razorbills tracked in the UK and Ireland (Thaxter et al. 2010, Shoji et al. 2015, Chimienti et al. 2017, Wakefield et al. 2017), Iceland (Dall'Antonia et al. 2001), the Baltic Sea (Benvenuti et al. 2001) and the Gannet Islands, Canada (Paredes et al. 2008, Pratte et al. 2017), where the majority of dives were less than 15 m. Similar results were also observed at Matinicus Rock, 161 km southwest of MSI, where most dives occurred during the evening at a mean depth of 13.1 ± 7.8 m (Kauffmann 2012). Puffins from MSI foraged at a similar distance from the colony as puffins at Petit

Manan, 63 km southwest of MSI (Spencer 2012). Spencer (2012) also observed a bimodal distribution of dive frequencies at dawn and dusk, similar to our study, although the mean dive depth estimated at MSI was twice as deep. Overall, differences between razorbill and puffin dive behaviour in our study are similar to those found in other studies where these species coexist; puffins dove in deeper water and farther from the colony than razorbills, overlapping very little in the 3-dimensional space of the ocean.

4.3. Diet

The diving behaviour of puffins in our study may be explained partly by their prey selection. Hake

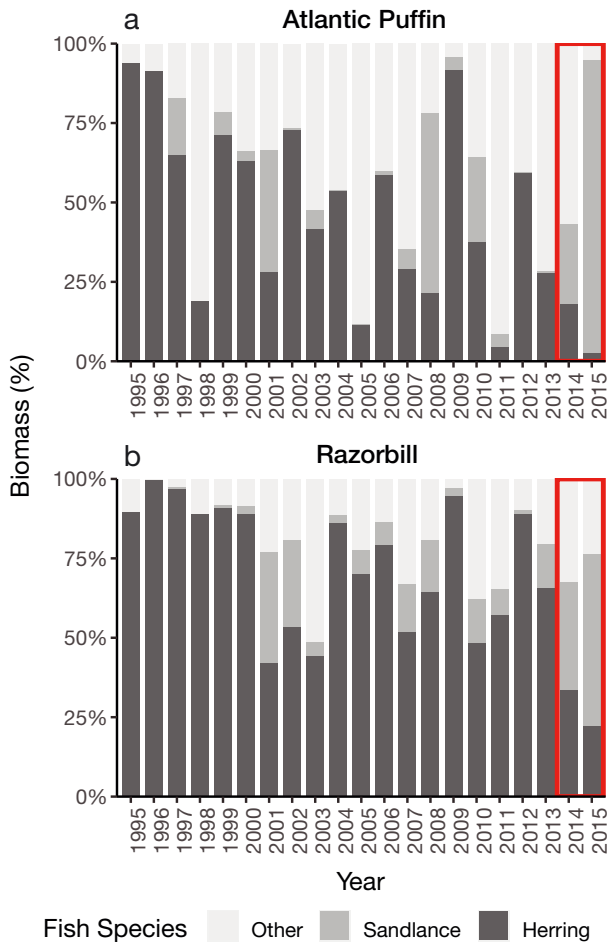


Fig. 6. Percent by mass of prey species brought to (a) puffin and (b) razorbill chicks at Machias Seal Island, New Brunswick, from 1995 to 2015. Over this 21 yr period, razorbills consistently brought in more herring to their chicks than puffins. Herring is declining significantly in the puffin diet (Breton & Diamond 2014). The 'Other' group consists of hake, haddock, krill, butterfish, and larval fish, see also Scopel et al. (2019). Note that diet was variable for both species in 2014, whereas sand lance made up 92.5% of the puffin diet in 2015. In both years when this study took place (red box), razorbills brought in more herring than puffins

(46%), haddock (20%) and sand lance (19%) were the main prey fed to chicks in 2014, and sand lance (93%) in 2015. Sand lance undergo diel vertical migration, burrowing into the substrate at night and moving up the water column in large numbers during the day (Winslade 1974, Meyer et al. 1979, Auster & Stewart 1986). Dawn and dusk are peak feeding times for both puffins and razorbills, when sand lance may be leaving or retreating toward the substrate. Puffin dive length may be related to sand lance availability, whereas the shallow (5–20 m) coastal water where razorbills feed may offer opportunity for searching wider areas. Razorbills may be

taking advantage of known herring spawning areas near the coast of Maine (Overholtz et al. 2004). The greater proportion of herring in razorbill diet in both years has held true at MSI since regular monitoring began in 1995 (Fig. 6).

Breton & Diamond (2014) found a significant reduction over the period 1999–2011 in the proportion of young herring in the puffin chick diet on MSI, and this has continued (Scopel et al. 2019). A change in the dominant fish species from herring to sand lance has already been observed farther south in the Gulf of Maine (Fogarty 1991), and with rapid warming of the Gulf of Maine and Bay of Fundy (Mills et al. 2013), this is reflected in seabird chick diets (Kress et al. 2017, Scopel et al. 2019). The extent to which chick diets may differ from those of adults was addressed by Bowser et al. (2013) using DNA metabarcoding, which found no significant difference between diets of adult puffins and chicks in one year (2009); and by Bond (2006), who found no difference in stable isotopes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between razorbill adults and chicks, and no difference in $\delta^{15}\text{N}$, and a small difference in $\delta^{13}\text{C}$, between puffin adults and chicks.

Dive locations reported here provide insight on important foraging areas for adults, albeit those experiencing the increased stress of carrying a GPS tag. We expect that birds experiencing high stress levels would choose to forage in locations where they can count on finding quality food. Knowledge of these locations may provide first important steps in identifying important conservation plans as sea surface temperatures continue to rise.

5. CONCLUSION

At the largest auk colony in the Gulf of Maine and Bay of Fundy, we identified spatial segregation of foraging locations associated with different habitats/depths, and different proportions of a limited range of prey, contributing to resource partitioning in 2 closely related, sympatrically breeding seabirds in a context of declining food resources.

Although tag effects meant we could not use these data to determine where breeding adults forage specifically for their chicks, especially puffins, we did, for the first time, locate important foraging areas for breeding adults, albeit in birds undergoing demonstrable pressure due to logger attachment. We expect stressed adults to forage in areas with reliable food availability to conserve energy; therefore, the feeding areas we have identified can provide important

guidance for planning marine protected areas. Spatial overlap between the 2 species was limited largely to the area around the colony. Our ability to tie these foraging locations to prey brought to chicks was compromised by the negative effects of the tags, explored more fully by Symons & Diamond (2019). This part of our results highlights important tag effects that need more attention in seabird ecology studies more generally. Further research should use smaller tags, known not to affect chick-feeding behaviour, such as are now available (Fayet et al. 2021), and attempt larger sample sizes in combination with temperature–depth recorders to provide more detailed information on dive behaviour.

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