Spatial variation in isotope values of Hector's dolphins from the north coast of the South Island, New Zealand

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ABSTRACT: The north coast of the South Island, Aotearoa New Zealand, is a region with complex bathymetry and biogeochemistry, where oceanographic variability gives rise to very different local environments at fine scales. This variation also influences the region's isoscape, providing the ability to assess the fine-scale foraging behaviour of top-level marine predators through isotope analyses. Hector's dolphin *Cephalorhynchus hectori hectori*, an endemic coastal dolphin, is resident of the north coast of the South Island, but there is limited information describing its foraging ecology and population dynamics. We analysed carbon and nitrogen stable isotope ratios of skin samples (n = 111) from Golden Bay in the west (n = 14), and Queen Charlotte Sound (n = 41) and Cloudy Bay (n = 56) in the east, to investigate spatial variation in isotope values and niche space, found significant differences between the 2 regions. This is likely driven by a combination of differing prey distributions, underlying oceanographic variability, and varying isotopic baselines that may act as an ecological boundary preventing movement between the 2 regions. The isotopic niche space between the west and east differed, but within the east, Queen Charlotte Sound was a subset of Cloudy Bay. This suggests a common prey source and possible movement of individuals between Queen Charlotte Sound and Cloudy Bay. This research highlights the value of stable isotope analysis to investigate regional-scale variation of top-level marine predators and can provide insight into environmental factors that influence resource use.

KEY WORDS: Stable isotopes · Niche space · *Cephalorhynchus* · Diet

1. INTRODUCTION

Knowledge of foraging ecology is fundamental for understanding the roles of marine species within ecosystems. This knowledge can provide information on the availability and distribution of prey and how species interact with their environment (Bowen 1997, Croll et al. 1998, Kiszka et al. 2015). Physical changes in the environment, such as sea surface temperature, may affect prey distribution and, therefore, foraging success of marine mammals (Croll et al. 1998, Bluhm & Gradinger 2008, Nøttestad et al. 2015). Oceanographic fronts can constitute important boundaries for marine mammals, which often forage at locations with

favourable feeding conditions due to the advection of prey by thermal and water convergence processes (Bost et al. 2009). For example, New Zealand fur seals *Arctocephalus australis forsteri* forage in association with 2 distinct oceanographic features: a seasonal coastal upwelling and a permanent oceanographic front, the Subtropical Front (Baylis et al. 2012); and North Atlantic right whales *Eubalaena glacialis* in Grand Manan Basin feed beneath a thermocline, where copepod density is substantially greater compared to elsewhere in the water column (Baumgartner & Mate 2003, Roman & McCarthy 2010).

Oceanographic variables that influence prey distribution can delineate populations and communi-

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ties of marine mammals. This can be due to prey preferences, such as in North Pacific killer whales *Orcinus orca*: resident ecotypes prey on fish, whereas transient ecotypes predominantly prey on marine mammals (Herman et al. 2005). Sperm whales *Physeter macrocephalus* in the South Pacific exist in sympatric communities, with differing habitat use, movement patterns and feeding success. Communities of sperm whales were found to be differentially affected by environmental conditions that influenced their prey, indicating a fitness consequence for community membership (Whitehead & Rendell 2004).

It is often challenging in the marine environment to determine marine mammal prey availability and consumption, and researchers must rely on physical and chemical cues to elucidate prey distribution and give insight into foraging ecology. Even when trophic interactions of marine mammals are well-documented, spatial and temporal variability is often unknown and likely linked to prey distribution and availability (Young et al. 2015). Foraging activity of cetaceans in particular is difficult to observe directly, and many foraging ecology studies have utilised stomach content analysis (e.g. Santos et al. 2001, Di Beneditto & Siciliano 2007, Meynier et al. 2008, Parra & Jedensjö 2014) and DNA diet approaches (de Vos et al. 2018, Carroll et al. 2019). Taxonomic identification of prey items to species level (e.g. Bowen & Iverson 2013, Parra & Jedensjö 2014) is often possible with these approaches. However, it is not possible to integrate diet over broad temporal scales, and only recently ingested prey can be identified without long-term sampling schemes. There may also be a bias toward less digestible prey types, which can result in overestimating some prey items (Bowen & Iverson 2013, Nielsen et al. 2018).

Stable isotope analysis is a well-established method that overcomes many limitations of other diet assessment approaches. The analysis of carbon and nitrogen isotopes can provide insight into the foraging ecology of marine mammals and identify patterns in spatial and temporal variability (Newsome et al. 2010, Bowen & Iverson 2013, Nielsen et al. 2018). Stable isotope analysis operates on the assumption that a consumer's tissues will reflect the isotopic composition of their prey (DeNiro & Epstein 1978, 1981), enabling researchers to make deductions about the types of prey eaten, the trophic position of the consumer and the origin of prey. Specifically, nitrogen isotopes can indicate trophic position, whereas carbon isotopes are indicators of foraging

location (Peterson & Fry 1987, Newsome et al. 2010, Boecklen et al. 2011, Bowen & Iverson 2013). Carbon isotopes can be used to determine the productivity of marine ecosystems, where more positive values indicate productive, nearshore regions and more negative values indicate offshore regions (Rounick & Winterbourn 1986, Bowen & Iverson 2013). Additionally, they can be used to identify differences between pelagic and benthic foraging locations (Cherel & Hobson 2007).

Depending on target species and tissue type, diet can be integrated over broad timescales ranging from weeks to years (Newsome et al. 2010). Determining diet directly with stable isotope analysis can be challenging due to paucity of prey data, but it remains a popular tool used to identify spatial and temporal patterns in the foraging ecology of cetaceans (e.g. Knoff et al. 2008, Marcoux et al. 2012, Kanaji et al. 2017, van den Berg et al. 2021, Ogilvy et al. 2022). Such patterns can be revealed through the analysis of isotopic niche space, an area in isotope space where the carbon and nitrogen isotope values are used to represent environmental resources (e.g. habitat use) and trophic interactions (e.g. predation), respectively (Newsome et al. 2007, Rossman et al. 2016). This is a powerful way to investigate spatial and temporal patterns of resource use and variability influencing the ecological niche.

Here, we used stable isotope analysis of carbon (δ^{13}C) and nitrogen (δ^{15}N) to investigate the foraging ecology of Hector's dolphins *Cephalorhynchus hectori hectori* from the north coast of Te Waipounamu/ the South Island (hereafter South Island) of Aotearoa New Zealand (hereafter New Zealand). Hector's dolphins are Endangered, coastal dolphins endemic to New Zealand (Reeves et al. 2013) and are often associated with turbid waters including river outflows, estuaries and harbours, which are areas of high productivity (Constantine 2019, Roberts et al. 2019). Individuals typically have small home ranges (approximately 50–60 km) and display high levels of site fidelity (Raymentetal. 2009, Bräger & Bräger 2018, Constantine 2019). Hector's dolphins exhibit seasonal distribution patterns, in which smaller, more dispersed groups of dolphins occur further offshore in winter compared to summer (Bräger et al. 2003, Constantine 2019).

The species is discontinuously distributed around the coast of the South Island (see Fig. 1), where regional subpopulations have been identified along the west, east and south coasts (Hamner et al. 2012, Constantine 2019). Hector's dolphins are generalist consumers that feed throughout the water column and

target juvenile prey (Miller et al. 2013). A region about which little is known of the foraging ecology and population dynamics of Hector's dolphins is the north coast of the South Island (NCSI), with the exception of Te Koko-o-Kupe/Cloudy Bay (Hamner et al. 2017). From west to east, the NCSI includes Mohua/Golden Bay and Te Tai-o-Aorere/Tasman Bay, Tōtaranui/Marlborough Sounds and Cloudy Bay (hereafter Golden Bay, Tasman Bay, Marlborough Sounds and Cloudy Bay, respectively; see Fig. 1).

The NCSI has complex bathymetry and biogeochemistry, with very different local environments present at fine scales. In the west, Golden Bay and Tasman Bay are shallow embayments open to the Tasman Sea, where the average depth is less than 25 m and the seabed is composed of mud, sand and some shell hash (Handley 2006, Chiswell et al. 2021). In contrast, Marlborough Sounds in the east consists of a pair of drowned river valley systems that open into Raukawa Moana/Cook Strait, Pacific Ocean (hereafter, Cook Strait). One of the river valley systems is Queen Charlotte Sound, an area where Hector's dolphins are present year-round (Cross 2019). Queen Charlotte Sound is an enclosed, moderately sheltered subtidal inlet consisting of a series of small bays connected by a convoluted, rugged shoreline (Stevens et al. 2021). Here, water depth increases rapidly from shore and any shallow areas are very narrow (Hayward et al. 1997). Also located in the eastern region of the NCSI is Cloudy Bay, a large, open bay that faces Cook Strait to the north (see Fig. 1). Differing oceanographic processes affect the west and east regions of the NCSI. The shallow waters of the west are susceptible to warming through marine heatwaves affecting the Tasman Sea (Salinger et al. 2019), and circulation is associated with the D'Urville current (Chiswell et al. 2021). The D'Urville current transports nutrient-rich water from a coastal upwelling near Onetahua/Cape Farewell, on the upper west coast of the South Island, northeast to the Cook Strait, although the effect of this upwelling on the western region of the NCSI is not well understood (Chiswell et al. 2016, Chiswell et al. 2021). In the east, the entrance of Queen Charlotte Sound is exposed to swells from Cook Strait (Pacific Ocean) but is sheltered from most winds and has very little freshwater input (Stevens et al. 2021).

The NCSI and the surrounding terrestrial environment have significant economic and recreational importance to New Zealand and, consequently, have been subjected to many anthropogenic and environmental pressures (Chiswell et al. 2021). These pressures differ between the west and east regions of the NCSI; for example, commercial and recreational fishing activities have severely modified the seabed in the west. Shellfish aquaculture farms are prevalent in this region and may influence water flow and nutrient loads (Plew 2011), which has contributed to the decline of mussel *Perna canaliculus*, scallop *Pecten novaezealandiae* and oyster *Crassostrea gigas* populations (Handley 2006). In both west and east NCSI, there are strong linkages between primary production and modified land use in the surrounding area that affect the supply of organic matter to bivalve communities (Schlieman et al. 2022). In eastern NCSI, sustained terrigenous sedimentation, overfishing and physical disturbances to the seabed are ongoing (Handley 2006, Urlich & Handley 2020). Parts of eastern NCSI (e.g. Queen Charlotte Sound) also experience high levels of vessel traffic (Stevens et al. 2021) and are susceptible to high levels of sediment erosion, especially during periods of heavy rain (Fahey & Coker 1992). The contrasting processes between west and east regions of the NCSI are likely to influence the isotopic baseline in each region. The east NCSI is susceptible to runoff associated with anthropogenic land utilisation in the surrounding areas (Fahey & Coker 1992, Urlich & Handley 2020). This can cause baseline $\delta^{15}N$ values to decrease over time due to the use of synthetic fertilisers which are depleted in ^{15}N (Sabadel et al. 2020). Salmon farms in east NCSI may also alter the composition of basal organic matter in the surrounding soft-sediment communities, which can influence the $\delta^{13}C$ baseline, even at fine spatial scales (McMullin et al. 2021). Overall, the west and east NCSI have a variety of natural and anthropogenic impacts that generate a dynamic isoscape in the region.

Here, we aimed to investigate if there are any differences in the foraging ecology of Hector's dolphins between the west and east regions of the NCSI, an area where little research has been conducted on this species. We used $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis from small skin biopsies of live Hector's dolphins to investigate differences in isotopic niche space between west (Golden Bay) and east (Cloudy Bay, Queen Charlotte Sound) regions of the NCSI that could reflect dietary differences and/or environmental differences in underlying isoscapes. Given that samples were collected during surveys to undertake genetic monitoring, most samples have an associated DNA profile that includes genetically identified sex. Therefore, a secondary objective was to determine if there were any sex-related differences in foraging ecology.

2. MATERIALS AND METHODS

2.1. Sample collection and study area

Small skin biopsy samples used in stable isotope analysis were collected from 2011–2022 using a small, lightweight biopsy dart (PaxArms NZ) fired from a modified veterinary capture rifle (Krützen et al. 2002) during boat-based surveys conducted by the Department of Conservation–Te Papa Atawhai (DOC), Oregon State University and the University of Auckland–Waipapa Taumata Rau (Hamner et al. 2012, Baker et al. 2017). Samples were collected from February to June. Calves that were assumed to be less than 1 yr old based on size (less than half the length of an adult and in close association with an adult assumed to their mother; Webster et al. 2010) were excluded from biopsy sampling. All samples were stored in 70–90% ethanol until required for analysis. A summary of samples used in the analysis is given in Table S1 in the Supplement at www.int-res.com/articles/suppl/m711p061_supp.pdf. The samples used here were a combination of new (n_{new}) and previously (n_{prev}) collected samples from Cloudy Bay (Hamner et al. 2012; $n_{prev} = 56$, where n_{prev} were collected in 2011/2012), Golden Bay (Baker et al. 2017; $n_{new} = 6$, $n_{prev} = 8$, where n_{prev} were collected in 2014/2015 and n_{new} were collected in 2021/2022) and Queen Charlotte Sound (Baker et al. 2017; $n_{new} = 30$, $n_{prev} = 11$, where n_{prev} were collected in 2016 and n_{new} were collected in 2022). For previously analysed samples, we drew on existing DNA profile data to uniquely identify individuals. These profiles comprised genetically identified sex, mitochondrial DNA haplotype and multi-locus microsatellite genotype (Hamner et al. 2012, Baker et al. 2017).

In the context of this study, west NCSI refers to the bays west of D'Urville Island and includes Golden and Tasman Bays. The eastern region of NCSI encompasses Marlborough Sounds (including Queen Charlotte Sound) and Cloudy Bay (Fig. 1). As summarised in Section 1, these regions have differing anthropogenic impacts and oceanographic features.

2.2. Sample preparation

Cetacean skin is rich in lipid content. Lipids are depleted in ^{13}C and can confound the interpretation of carbon isotope ratios (^{13}C:^{12}C) measured in lipid-
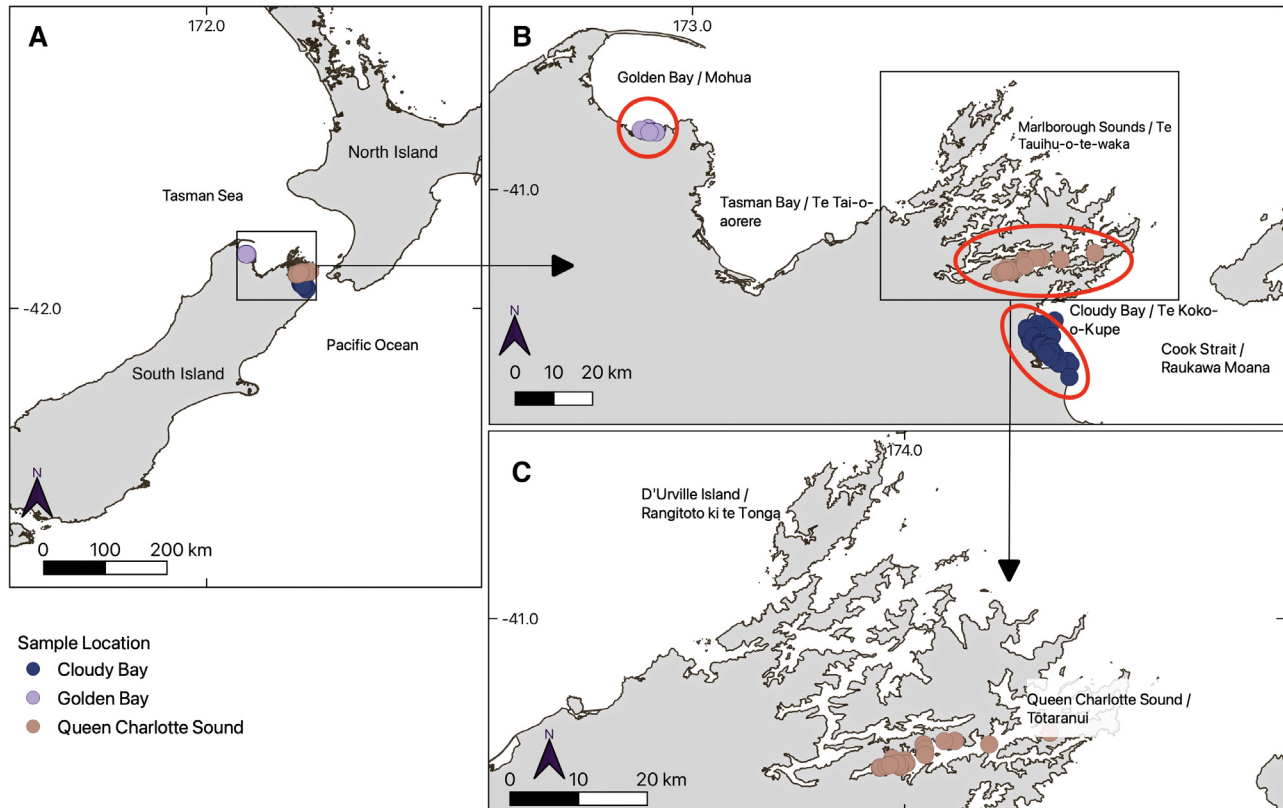

Fig. 1. (A) Outline of New Zealand; magnified views of the (B) north coast of the South Island and (C) Marlborough Sounds area on the north-east coast

rich tissues (Lesage et al. 2010, Yurkowski et al. 2015, Giménez et al. 2016). To mitigate the effect of ^{13}C depletion in lipid-rich tissues, all skin samples were lipid-extracted with a 2:1 solution of chloroform and methanol (Newsome et al. 2018). Lipid extraction was deemed successful if the C:N ratio was between 3.0 and 4.0 (Sweeting et al. 2006, Post et al. 2007, Wilson et al. 2014, Yurkowski et al. 2015). Following lipid extraction, samples were sent to Isotrace NZ (University of Otago) for bulk stable isotope analysis of ^{13}C and ^{15}N.

2.3. Stable isotope analysis

Nitrogen and carbon isotopes were assayed by combustion of the whole material to N_2 and CO_2 gas in a Thermo Flash elemental analyser (Thermo Scientific) linked to a Thermo 'Delta Q' (Thermo Scientific) isotope ratio mass spectrometer in continuous flow mode. Stable isotope ratios are reported in δ-notation:

$$\delta^x = [(R_{sample} / R_{standard}) - 1] \times 1000 \qquad (1)$$

where x is the isotope of interest (^{13}C or ^{15}N) and R is the ratio of heavy to light isotope (e.g. $^{13}C/^{12}C$). Analytical precision for $\delta^{13}C$ was ±0.1‰ and for $\delta^{15}N$ was ±0.2‰. Details of standards and normalisation processes are provided in Text S1.

2.4. Controlling for atmospheric changes to δ^{13}C values

A correction for the oceanic Suess effect (0.011‰ yr^{-1}; Keeling 1979, Gruber et al. 1999, Eide et al. 2017, Ogilvy et al. 2022) was applied to the carbon stable isotope ratios of the skin samples, using the average year between years of sampling (2016) as a reference, to allow the comparison of $\delta^{13}C$ values from different time periods (Vales et al. 2020).

2.5. Tests for heterogeneity of isotope values throughout space, time and by demographic state

The $\delta^{13}C$ and $\delta^{15}N$ values for Hector's dolphin samples were plotted in R v.4.1.2 (R Core Team 2020) to visually inspect the data for any trends. Statistical analyses were carried out in R. To test if $\delta^{13}C$ and $\delta^{15}N$ were normally distributed, we used the Shapiro-Wilk test. To assess differences in $\delta^{13}C$ and $\delta^{15}N$ values for categorical variables, we used 1-way

ANOVA, Kruskal-Wallis and post hoc Dunn's multiple comparison tests. Significance was assessed at the level of α = 0.05.

2.6. Isotopic niche space analysis

To compare the isotopic niche space of Hector's dolphins from different regions, we used the stable isotope Bayesian ellipses (SIBER; v.2.1.6) package in R (Jackson et al. 2011). The isotopic niche space of Hector's dolphins from the west and east regions of the NCSI was estimated with bivariate ellipses of $\delta^{13}C$ and $\delta^{15}N$ values (95% confidence intervals). Bayesian standard ellipse areas (SEA_B) were calculated using SIBER to demonstrate niche overlap and evaluate differences in isotopic niche space between regions. Niche area is reported as ‰^{2}. Estimates of niche area were determined by running 2 Markov chain Monte Carlo chains implemented in 'rjags' (1 00 000 iterations following 100 000 burn-ins; Plummer 2018). Convergence was assessed with a Gelman-Rubin diagnostic test and was indicated when the scale reduction factor was less than 1.1 (Gelman & Rubin 1992).

3. RESULTS

3.1. Stable isotope ratios of Hector's dolphin skin samples

A total of 111 Hector's dolphin skin samples were included in the stable isotope analysis (Table 1). The samples had an overall median (±SD) $\delta^{13}C$ value of −17.1 ± 0.7‰ (range: −18.9 to −14.1‰) and a median $\delta^{15}N$ value of 15.1 ± 0.7‰ (range: 14.3 to 17.7‰; Table 1). The $\delta^{13}C$ and $\delta^{15}N$ distributions of the combined data set were not normally distributed (Shapiro-Wilk W-test: $\delta^{13}C$: n =111, p < 0.05; $\delta^{15}N$: n = 111, p < 0.0005; Fig. 2).

3.2. Spatial variation in isotope values

The $\delta^{13}C$ and $\delta^{15}N$ values of Hector's dolphins were significantly different between the 3 sampling locations ($\delta^{13}C$: Kruskal-Wallis [K-W] χ^2 = 38.4, p < 0.001; $\delta^{15}N$: K-W χ^2 = 27.1, p < 0.001). Post hoc Dunn's multiple comparison tests showed each location was significantly different from every other (p < 0.05; Tables S2 & S3). The $\delta^{13}C$ values in east NCSI were significantly higher than in west NCSI, and in the west NCSI, $\delta^{15}N$

Table 1. Hector's dolphin skin biopsy samples included in stable isotope analysis. Median $\delta^{13}C$ and $\delta^{15}N$ values are provided for each sampling location. Genetically determined sex is provided where available. (−) indicates no data

Location	$\delta^{13}C$ Median ± SD (range)	$\delta^{15}N$ Median ± SD (range)	Year	Males	Females	Total (n)
Cloudy Bay	−16.7 ± 0.7 (−18.0 to −14.1)	15.2 ± 0. (14.3 to 17.7)	2011 2012	15 12	14 15	29 27
Golden Bay	−17.8 ± 0.9 (−18.9 to −15.4)	15.8 ± 0.7 (14.7 to 17.4)	2014 2015 2021 2022	2 2 2 −	2 1 0 −	5[a] 3 2 4
Queen Charlotte Sound	−17.2 ± 0.4 (−17.8 to −16.2)	14.8 ± 0.4 (14.3 to 15.8)	2016 2021 2022	5 − −	6 − −	11 1 29
Overall	−17.1 ± 0.7 (−18.9 to −14.1)	15.1 ± 0.7 (14.3 to 17.7)	Total	38	38	111

[a]Sex could not be determined for one sample

3.3. Variation in isotope values by sex

Of the 111 Hector's dolphin biopsy samples analysed, 76 were associated with a DNA profile including genetically determined sex (Table S1, Table 1). This subset comprised 38 males and 38 females from the 3 sampling locations (Table 2). The subset of data where sex was known (n = 76) was not normally distributed with respect to $\delta^{13}C$ (Shapiro-Wilks test: W = 0.96, p < 0.05) or $\delta^{15}N$ (Shapiro-Wilks test: W = 0.92, p < 0.005). In the overall population, there were no significant differences in $\delta^{15}N$ between sexes (K-W: χ^2 = 2.0, df = 2, p > 0.05), but $\delta^{13}C$ values were significantly different (K-W: χ^2 = 4.7, df = 2, p < 0.05). To investigate further, we tested for significant differences between sexes in $\delta^{13}C$ and $\delta^{15}N$ values for each location; none were found (p > 0.05; Table 2).

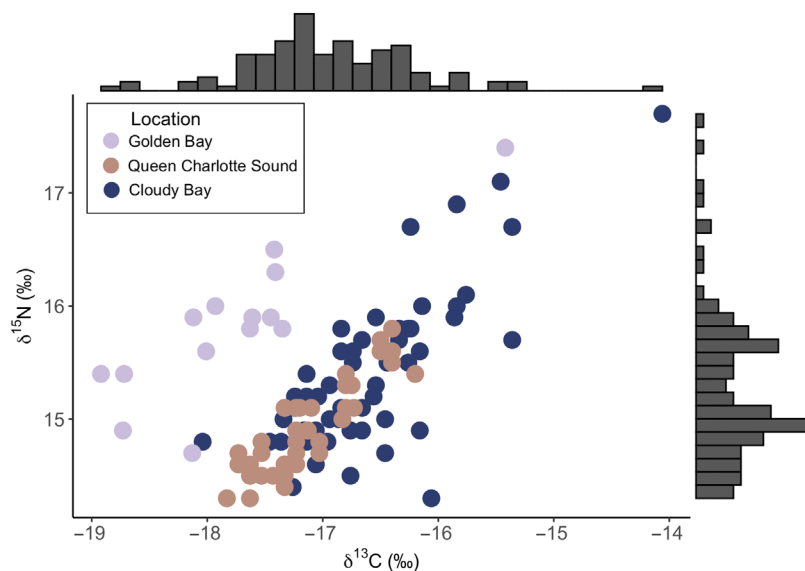Fig. 2. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values of 111 Hector's dolphin skin biopsy samples. Isotope ratios are coloured according to sample location. Frequency distributions of $\delta^{13}C$ and $\delta^{15}N$ are shown as marginal histograms

values were significantly higher than in the east NCSI (Fig. 3).

The SIBER analysis of Hector's dolphin skin samples indicated distinct isotopic niche spaces between west and east regions, with minimal overlap (Fig. 4). Within the east region of the NCSI, the isotopic niche of dolphins from Queen Charlotte Sound overlapped entirely with the isotopic niche of dolphins from Cloudy Bay, and the former was a subset of the latter (Fig. 4A). The largest niche space occurred in west NCSI, whereas the smallest isotopic niche space was observed in the east (Fig. 4B).

4. DISCUSSION

Here, we document $\delta^{13}C$ and $\delta^{15}N$ values in the skin of an endangered coastal dolphin, Hector's dolphin, collected from 3 locations in the west (Golden Bay) and east (Queen Charlotte Sound and Cloudy Bay) of the NCSI of New Zealand (Fig. 1). We identified clear differences in isotope values and minimal
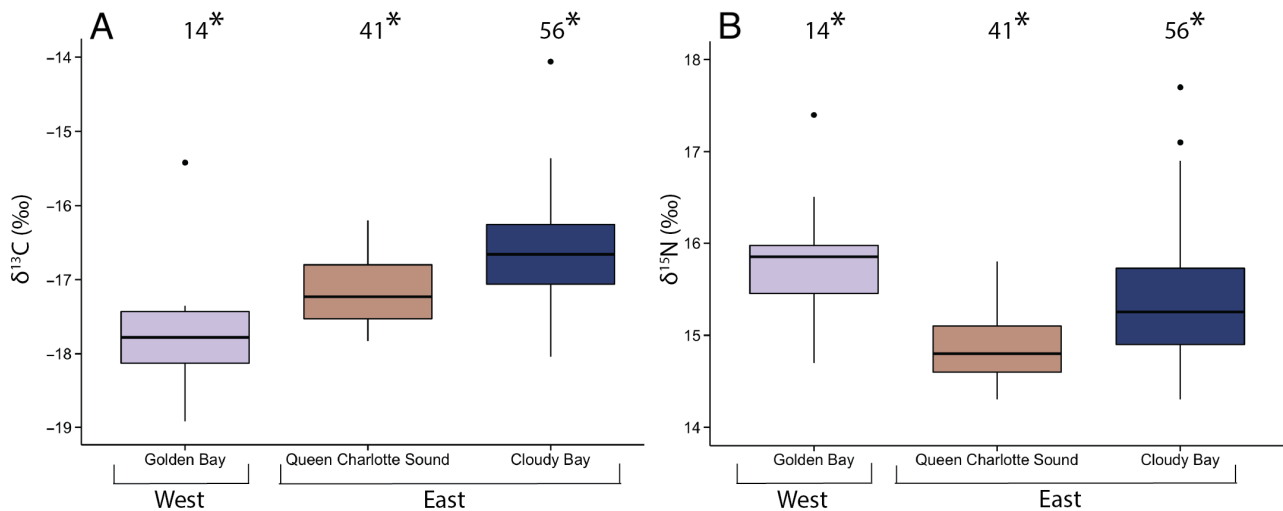
Fig. 3. Median (A) $\delta^{13}C$ and (B) $\delta^{15}N$ values of Hector's dolphin biopsy samples from the west and east regions of the north coast of the South Island. Kruskal-Wallis and post hoc Dunn's multiple comparisons tests were used to assess if sampling locations were significantly different. Black line: median; shaded boxes: interquartile range; whiskers: minimum and maximum isotope values; black dots: outliers. Sample size is shown above each box. Asterisks indicate sample locations which are significantly different (Kruskal-Wallis test, p < 0.001)
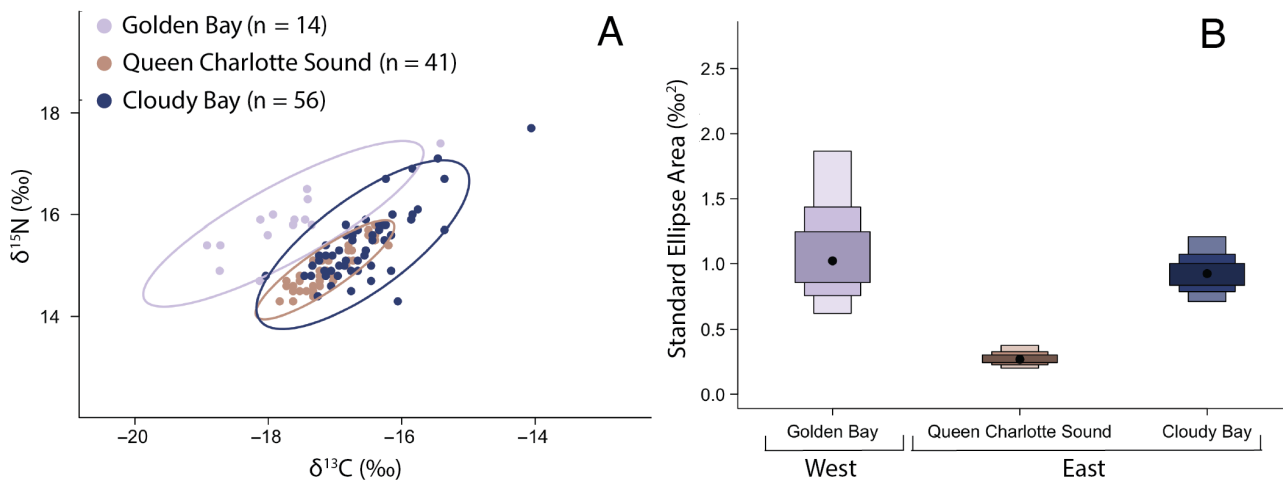

Fig. 4. (A) Isotopic niche space indicated by 95 % CI bivariate ellipses and (B) Bayesian standard ellipse area of isotopic signatures in biopsies of skin samples from Hector's dolphins collected from west (Golden Bay) and east (Cloudy Bay and Queen Charlotte Sound) regions of the north coast of the South Island. Black dots: mode; shaded boxes: 50, 75 and 95 % credible intervals, from dark to light

isotopic niche space overlap between the west and east regions, suggesting there may be differences in prey availability and diet. In contrast, we observed overlap of isotopic niche space within eastern regions, which may reflect a common prey source and/ or the movement of individuals between the 2 areas of Queen Charlotte Sound and Cloudy Bay (Fig. 4A). In the absence of information on the foraging behaviour and prey choice of Hector's dolphins from the NCSI, our study highlights the value of stable iso-

topes in identifying fine-scale patterns in foraging ecology in regions with different bathymetry, biogeochemistry and anthropogenic pressures.

4.1. Potential drivers of spatial variation in isotope values

The relationship between cetaceans and physical oceanographic features is often mediated by the re-

Table 2. Samples and statistical tests used to investigate differences in isotope values between sexes of Hector's dolphins at each sampling location. Data include sample size per sex (F: females; M: males) and total sample size (n). **p < 0.01

Location	F	M	n	Isotope	W (Shapiro-Wilk normality test)	Statistical test	Test statistic
Cloudy Bay	29	27	56	$\delta^{13}C$	0.9**	Kruskal-Wallis	$\chi^2 = 2.1$
				$\delta^{15}N$	0.9**		$\chi^2 = 3.5$
Golden Bay	6	3	9	$\delta^{13}C$	0.86	Student's 2-sample t-test	$t = 0.62$
				$\delta^{15}N$	0.87		$t = 0.86$
Queen Charlotte Sound	5	6	11	$\delta^{13}C$	0.92	Student's 2-sample t-test	$t = 1.6$
				$\delta^{15}N$	0.92		$t = 1.6$

sponses of their prey to such features. For example, foraging behaviours in species that feed on plankton and/or pelagic fish are often associated with biological and physical oceanographic processes that structure the distribution and availability of lower trophic level prey sources (Bertrand et al. 2014, Cox et al. 2018). Habitat features such as fronts, offshore banks, eddies and tidal stream environments may act as prey hotspots and areas of increased foraging success for cetaceans (Bost et al. 2009, Scales et al. 2014, Benjamins et al. 2015). Here, we have shown that there is a statistically significant difference in isotope values of Hector's dolphins from the west and east regions of the NCSI. This likely reflects a difference in foraging ecology that is driven by differing prey distributions and underlying oceanographic variability between the 2 regions. This finding was not unexpected; other cetacean species can exhibit spatial differences in foraging ecology due to occupation of different habitats. For example, sperm whales from the northern Gulf of Mexico and the Gulf of California have significantly different $\delta^{13}C$ and $\delta^{15}N$ values, likely driven by variation in prey availability and geographic variation in biogeochemical cycling (Ruiz-Cooley et al. 2012). Stable isotope values of North Pacific killer whales *Orcinus orca* from different regions are associated with region-specific prey preferences (Herman et al. 2005).

The effect of habitat on foraging ecology is also evident in Hector's dolphins, with significant differences in diet between dolphins on the west and east coasts of the South Island (Miller et al. 2013). Demersal and benthopelagic species such as red cod *Pseudophycis bachus* and ahuru *Auchenoceros punctatus* were the most prevalent species found in the stomach contents of dead Hector's dolphins around the South Island. However, differences between west and east coasts were due to the presence of javelinfish *Lepidorhynchus denticulatus*, a mid- to deepwater species, that was only found in west coast dol-

phin stomachs where deep water can be found closer to shore compared to the east coast (Miller et al. 2013). This highlights how physical oceanographic features such as depth can affect prey distribution and diet composition in Hector's dolphins.

We suggest that a similar pattern occurs for the west and east regions of the NCSI, where the spatial variation in isotope values reflects differing prey distributions and isotopic baselines, which are both mediated by contrasting physical and chemical processes found in each region (Casey & Post 2011). The isotopic baseline of the NCSI, especially between regions, is not well understood, and baseline data were not available for this study. However, given the contrast in environments and oceanographic processes across the NCSI, it is likely there would be notable differences in isotopic baseline (Udy et al. 2019).

Oceanographic processes and physical features can also directly influence the distribution of marine mammals, independent of prey. Environmental variables such as thermoclines can act as ecological boundaries to movement (Au & Perryman 1985, Reilly 1990, Ballance et al. 2006). Oceanographic features such as salinity, temperature and productivity levels have been suggested as barriers to genetic connectivity in several species of dolphins (Fullard et al. 2000, Natoli et al. 2005, Bilgmann et al. 2007, Möller et al. 2011). Ecological boundaries to genetic connectivity between local populations of Hector's dolphins around the South Island may also exist. For example, higher levels of genetic differentiation were reported between Hector's dolphins separated by only ~12 km of coast, including a deep submarine canyon (~60 km long and 1200 m deep; Lewis & Barnes 1999), than between populations separated by 50 km of coastline with no deep water features (Hamner et al. 2016). The deep water of the Cook Strait is also likely to act as a deterrent for movement between Hector's dolphins (which are commonly found in depths of less than 50–60 m; Bräger et al.

2002, Rayment et al. 2009, Bräger & Bräger 2018) and the closely related Māui dolphin *C. h. maui* to the north. However, recent long-range movements of Hector's dolphins from the South Island to the west coast of the North Island have occurred, though it is not known if this movement occurred via the Cook Strait or an offshore corridor of shallower water to the northwest (Hamner et al. 2014). Genetic differentiation has been identified in Hector's dolphins from the west and east coasts of New Zealand (Hamner et al. 2012). Preliminary genetic analysis has revealed genetic similarity between dolphins from the east coast South Island and the east NCSI; the same was true for west coast South Island animals and those from west NCSI (Baker et al. 2017). This needs to be interpreted with caution due to small sample sizes, but the apparent genetic differentiation in Hector's dolphins between west and east coasts suggests there may be an ecological driver of the sub-population boundary that could impact genetic connectivity and movement and contribute to the observed significant differences in isotope values and niche space (Figs. 3 & 4) (Hamner et al. 2016, Bräger & Bräger 2018).

4.2. Potential drivers for spatial variation in isotopic niche space

The concept of the isotopic niche is a powerful approach used to inform questions which were traditionally only considered within ecological niche studies (Newsome et al. 2007). The use of this approach to inform questions on resource use, habitat partitioning and foraging ecology in marine mammals has increased substantially in recent years (e.g. Yurkowski et al. 2016, Ciancio et al. 2021, Drago et al. 2021, Durante et al. 2021, Teixeira et al. 2021, Parra et al. 2022). Particularly, the width or breadth (referred to as width from here on) of the isotopic niche can be estimated using the variance of stable isotope values such as $\delta^{13}C$ and $\delta^{15}N$, and this can reflect changes in prey distribution and availability (Bearhop et al. 2004, Newsome et al. 2012). In many species, large isotopic niche spaces may reflect prey diversity (Bearhop et al. 2004). Conversely, a narrowing of isotopic niche space often reflects changing availability of key prey species. For example, interannual fluctuations of isotopic niche space in little penguins have been associated with fluctuations in the abundance of anchovy *Engraulis australis* and other key prey species (Kowalczyk et al. 2015). Similarly, increasing isotopic niche width in ringed seals *Pusa hispida*, beluga whales *Delphinapterus leucas*

and Māui dolphins have been associated with increased prey diversity and ecological opportunity (Yurkowski et al. 2016, Ogilvy et al. 2022).

Here, we observed 2 distinct niche spaces in Hector's dolphins from the west and east regions of the NCSI (Fig. 4). Within the east, the niche space of Queen Charlotte Sound was a subset of Cloudy Bay, which may suggest a common prey source for both locations in the east. However, it is also possible for different prey types to have similar isotope signatures and, therefore, overlap in isospace (Riccialdelli et al. 2010, Lerner et al. 2018). The width of isotopic niche in Queen Charlotte Sound was very narrow, which is unusual in generalist predators that consume a range of different prey types and often have broad isotopic niches (e.g. Tixier et al. 2019, Cloyed et al. 2021, Jory et al. 2021). Increases in sediment deposition have been associated with decreased isotopic niche width (Burdon et al. 2020), and sediment deposition in Queen Charlotte Sound is extensive (Fahey & Coker 1992, Handley 2006, Urlich & Handley 2020). Isotopic niche width may vary between years, and a similarly narrow isotopic niche has been observed in Māui dolphins sampled in 2021; it was thought this may reflect a climate-mediated shift in prey distribution (Ogilvy et al. 2022). It is possible a combination of both environmental processes and prey distribution may be occurring here and contributing to the decreased isotopic niche width in Queen Charlotte Sound. Similar seasonal variation in isotopic niche width has been observed in little penguins from Queen Charlotte Sound, where smaller niche space is associated with foraging around the mouth of Queen Charlotte Sound versus wider niche space associated with foraging offshore in the Cook Strait (Poupart et al. 2017).

Species with narrow isotopic niches are more vulnerable to sources of anthropogenic disturbance, which can affect their habitat and/or the availability of key prey (Cloyed et al. 2021). It is possible for species that are dietary generalists at the population level to be composed of a group of individuals that use a subset of available resources and exhibit high site fidelity (e.g. Anderson et al. 2008, Woo et al. 2008, Ceia & Ramos 2015). This individual specialisation can be reflected by narrow isotopic niche width. Groups of specialised individuals are more vulnerable to location-specific habitat degradation, and this has been observed in populations of bottlenose dolphins *Tursiops truncatus* (Gonzalvo et al. 2014). However, we do not think the narrow niche width in Queen Charlotte Sound reflects a subset of specialised individuals with high site fidelity, as there is

preliminary genetic evidence to suggest that movement of Hector's dolphins in the east NCSI may occur (Baker et al. 2017, Hamner et al. 2017). Seasonal distribution patterns exist in Hector's dolphins from Queen Charlotte Sound and Cloudy Bay; dolphins are present in greater densities during summer, whereas in winter, density reduces and the dolphins show a preference for offshore waters (MacKenzie & Clement 2014, Cross 2019). The seasonal density patterns, in addition to the genetic similarity between Hector's dolphins in Queen Charlotte Sound and Cloudy Bay (Baker et al. 2017), support the hypothesis that movement between these 2 regions may occur and is a potential explanation for the overlap in niche space (Fig. 4A).

The effects of anomalous, climate-driven oceanographic events such as marine heatwaves have previously had severe effects on the NCSI of New Zealand. The western region faces the Tasman Sea, which is very susceptible to ocean warming and marine heatwave events (de Burgh-Day et al. 2022). Three marine heatwaves have occurred since 2017 and have caused significant ecological impacts on kelp *Macrocystis pyrifera*, shellfish, salmon *Oncorhynchus tshawytscha* and kingfish *Seriola lalandi lalandi* in New Zealand (Oliver et al. 2017, Tait et al. 2021, de Burgh-Day et al. 2022). In the Marlborough Sounds, a severe marine heatwave in 2017–2018 led to an increase in sea surface temperature that coincided with substantial farmed salmon mortality (Eder 2018, Salinger et al. 2019). Some dolphin samples (n = 6) from the western NCSI used in this analysis reflect prey consumption under marine heatwave conditions (Browning et al. 2014, Oliver et al. 2017, Morton 2021, de Burgh-Day et al. 2022). The large niche space observed in western NCSI (Fig. 4B) may suggest either a shift in prey distribution during this time, opportunistic feeding during unfavourable oceanographic conditions (possibly as an effect of climate-mediated events such as marine heatwaves) or a combination of the 2. Interestingly, despite this variation, there was limited overlap with the isotopic niche between west and east. A similar pattern was observed in the isotopic niche space of Māui dolphins in 2015–2016 during a strong El Niño event, where niche space was significantly different and larger than in other years (Ogilvy et al. 2022). Correlations between isotope values, niche space and El Niño conditions are also evident in other species such as Humboldt penguins *Spheniscus humboldti*, Australian gannets *Morus serrator*, Guadalupe fur seals *Arctocephalus philippii townsendi* and California sea lions *Zalophus californianus* (Elorriaga-

Verplancken et al. 2016, Chiu-Werner et al. 2019, Rodríguez-Malagón et al. 2021).

Here, the lowest $\delta^{13}C$ values of the 3 sample locations were in western NCSI (Fig. 3), which could suggest consumption of more offshore prey sources (Cherel & Hobson 2007) compared to dolphins from eastern NCSI. However, the absolute difference in median $\delta^{13}C$ values between western and eastern regions was <1‰. If there were an extensive difference between offshore and inshore feeding, this difference would likely be greater than we see here, as has been observed in other coastal dolphin species (e.g. Gross et al. 2009, Riccialdelli et al. 2010, Gibbs et al. 2011, Mèndez-Fernandez et al. 2012). It is also likely that variation in isotopic baseline between the 2 regions is influenced by terrigenous sedimentation and runoff associated with land utilisation, which may contribute to the observed difference in $\delta^{13}C$ values (McMullin et al. 2021).

The difference in median $\delta^{15}N$ values between west and east regions was <1‰, which is less than the trophic enrichment factor estimated for similar delphinids (Browning et al. 2014, Ogilvy et al. 2022) and suggests Hector's dolphins from both regions occupy a similar trophic level. This was not unexpected; *Cephalorhynchus* species, including Hector's dolphins, are generalist consumers known to feed throughout the water column (Riccialdelli et al. 2010, Miller et al. 2013, Dawson 2018, Ogilvy et al. 2022). This does not necessarily suggest Hector's dolphins from the west and east regions consume similar prey; similarities in isotopic baseline of different habitats can confound the interpretation of prey preferences and trophic level estimation. Similar isotope values have been observed in cetaceans which are known to occupy different habitats and have completely different prey preferences (Riccialdelli et al. 2010). It is likely the $\delta^{15}N$ baseline between west and east regions also influences the $\delta^{15}N$ of Hector's dolphins observed here.

4.3. Sex-related differences in foraging ecology

Sexual dimorphism can often result in sex-related differences in foraging strategies of marine mammals (Shine 1989, Page et al. 2005, Lewis et al. 2006, Beerman et al. 2016). This was not the case for NCSI Hector's dolphins, as Hector's dolphins do not show sexual dimorphism, which suggests they consume similar prey and no sex-dependent foraging strategies are occurring. This was not unexpected, as we see the same in Māui dolphins (Ogilvy et al. 2022) and Com-

merson's dolphins *Cephalorhynchus commersonii commersonii* (Riccialdelli et al. 2013), although sex-segregation among social groups of the *Cephalorhynchus* genus does occur in some larger populations. For example, Hector's dolphins in Te Pātaka-o-Rākaihautū/Banks Peninsula, along the east coast of the South Island, have a high degree of sex-segregation reflected in lower $\delta^{15}N$ values of males compared to females (Miller et al. 2013).

4.4. Caveats

Due to the difficulty in obtaining tissue samples, there is a discrepancy in sample size between western (n = 14) and eastern (n = 97) regions. We have accounted for the difference in sample size between regions when calculating isotopic niche width, as the bivariate ellipses are modelled in a Bayesian framework and are unbiased with respect to sample size (Jackson et al. 2011). We are aware that temporal variation of isotope values can be significant in marine mammals (e.g. Marcoux et al. 2012, Watt & Ferguson 2015, Cardona et al. 2017). However, the comparison of Hector's dolphin isotope values from west and east regions of the NCSI does not account for temporal variation. The data set presented here spans 11 yr, and samples from each region were collected in different years. Most of the samples used here were collected in austral summer/autumn and therefore reflect prey consumption during late spring/early summer. However, several samples were collected outside of this period, during the austral winter (n = 11; Table S1). We checked temporal variation within the east and found that between-year variation in this region sat within the distinct isotopic niche space of the east and had little to no overlap with isotopic niche space in the west (Fig. S1). Furthermore, we acknowledge that the patterns observed here are likely driven by a combination of prey and underlying variation in the isotopic baseline of each region (Barnes et al. 2009, Casey & Post 2011). We are aware of the importance of monitoring the isotopic baseline and are supporting efforts to implement a long-term baseline monitoring programme in this region to enable future trophic studies of Hector's dolphins and other coastal species.

4.5. Summary

Here, we show that there is a significant difference in isotope values of Hector's dolphins from the west

and east regions of the NCSI, suggesting a difference in Hector's dolphin foraging ecology between the 2 regions. This is likely driven by differences in prey distribution, which are possibly mediated by the contrasting physical and chemical oceanographic features of each region that influence both prey and isotopic baselines. We observed distinct isotopic niche spaces between west and east regions, and within the eastern region, there is isotopic niche overlap between Queen Charlotte Sound and Cloudy Bay. The overlap of these 2 areas within the eastern region of the NCSI may reflect a common prey source but is also moderate evidence to support the hypothesis that movement of individuals between these areas may occur. The use of stable isotopes has enabled us to understand potential drivers of population structure and fill a gap in knowledge about the foraging ecology of this endemic coastal species.

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