Vol. 669: 227–240, 2021
https://doi.org/10.3354/meps13755

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published July 8

Dietary plasticity of two coastal dolphin species in the Benguela upwelling ecosystem

Michelle Caputo[1,2,*], Simon Elwen[3], Tess Gridley[3], Sophie A. Kohler[4], Jean-Paul Roux[5], Pierre William Froneman[2], Jeremy J. Kiszka[1]

[1]Institute of Environment, Department of Biological Sciences, Florida International University, 3000 NE 151 St., North Miami, FL 33181, USA

[2]Department of Zoology and Entomology, Rhodes University, PO Box 94, Grahamstown 6140, South Africa

[3]Department of Botany and Zoology, University of Stellenbosch Cape Town, South Africa, c/o Sea Search Research and Conservation NPC, 4 Bath Road, Muizenberg, Cape Town 7945, South Africa

[4]Animal Demography Unit, Department of Biological Sciences, Private Bag X3, University of Cape Town, Rondebosch 7701, South Africa

[5]SEACODE and Namibia Nature Foundation, PO Box 583, Lüderitz 9000, Namibia

ABSTRACT: Defining the trophic relationships of marine predators and their dietary preferences is essential in understanding their role and importance in ecosystems. Here we used stable isotope analysis of skin samples ($\delta^{15}N$ values reflecting trophic level and $\delta^{13}C$ values reflecting foraging habitat) to investigate resource partitioning and spatial differences of the feeding ecology of dusky dolphins *Lagenorhynchus obscurus* and Heaviside's dolphins *Cephalorhynchus heavisidii* from 2 coastal study sites separated by 400 km along the coast of central (Walvis Bay) and southern (Lüderitz) Namibia in the Benguela upwelling ecosystem. Overall, isotopic niches of both predators were significantly different, indicating partitioning of resources and foraging habitats. Despite their smaller body size, Heaviside's dolphins fed at a significantly higher trophic level than dusky dolphins. Stable isotope mixing models revealed that both species fed on high trophic level prey (i.e. large *Merluccius* spp., large *Sufflogobius bibarbatus*, and *Trachurus t. capensis*) at Walvis Bay. The diet of both dolphin species included smaller pelagic fish and squid at Lüderitz. Spatial differences highlight that Heaviside's and dusky dolphins may exhibit dietary plasticity driven by prey availability, and that they likely form distinct population segments. Important prey for both dolphin species, specifically *Merluccius* spp. and *T. t. capensis*, are the main target of trawl fisheries in the Benguela upwelling ecosystem, highlighting potential resource overlap between dolphins and fisheries.

KEY WORDS: Cetaceans · Foraging · Stable isotopes · Trophic ecology · Mixing models · Dusky dolphin · *Lagenorhynchus obscurus* · Heaviside's dolphin · *Cephalorhynchus heavisidii*

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

Understanding the trophic interactions of predators is critical to assess their role and importance in marine ecosystems (Bowen 1997, Estes et al. 2016). Small cetaceans can be locally abundant and have the potential to consume a considerable amount of high-quality prey due to their high metabolic rates (Katona & Whitehead 1988, Bowen 1997, Spitz et al. 2012). As a consequence, they have the potential to strongly affect the structure and dynamics of communities and ecosystems (Bowen 1997, Kiszka et al. 2015, Estes et al. 2016). In addition to their roles as consumers in food webs, small cetaceans can also

*Corresponding author: mcaputo@fiu.edu

© Inter-Research 2021 · www.int-res.com

translocate and contribute to the recycling of nutrients within and across ecosystems (Bowen 1997, Kiszka et al. 2015). Understanding the trophic relationships of marine predators, such as small cetaceans, is thus central to understanding how these consumers can be affected by fisheries, particularly if resources are depleted or under intense exploitation (Read 2008).

Investigating the diet of free-ranging dolphins is challenging. These predators are elusive, and their foraging behavior is rarely observed. Traditionally, stomach content analyses of caught or stranded animals have been employed. Stomach content analyses generate the most qualitative and quantitative information on the diet of marine predators, providing a snapshot of their diet over 1–3 d of feeding behavior (Pierce & Boyle 1991, Polito et al. 2011, Giménez et al. 2017b, Petta et al. 2020). However, samples from either stranded or bycaught animals may not always be available. Additionally, stomach content analyses may be biased due to differential digestion rates of the various prey items (Polito et al. 2011, Petta et al. 2020), and contents may differ between stranded and non-stranded animals (Sekiguchi et al. 1992). Increasingly, analyses of stable isotopes of various elements (most commonly carbon and nitrogen) in the tissues of animals is used to assess the trophic interactions of small cetaceans (e.g. Walker & Macko 1999, Kiszka et al. 2014, Rossman et al. 2015, Loizaga de Castro et al. 2016a,b). The ratios of stable isotopes of elements within the tissues of a consumer reflect both those of its prey and its habitat, providing a useful method of characterizing its feeding ecology. Heavier isotopes are typically retained in tissues while lighter ones are secreted and thus lost in the transition of nutrients between prey and their consumers, creating a predictable increase in the ratios of stable nitrogen isotopes ($\Delta^{15}N$) at each trophic level. The minimal increase in carbon isotope ratios ($\Delta^{13}C$) reflects primary production at the base of the food chain, and is used to identify foraging habitats and sources of primary production (Post 2002, Newsome et al. 2007, 2010). Isotope values in certain tissues (skin, muscle, bone, etc.) have the advantage of being assimilated slowly in comparison to stomach contents, and therefore represent trophic interactions over a much longer time period (Walker & Macko 1999, Newsome et al. 2010).

Stable isotope analysis can be used to examine resource partitioning between sympatric species (e.g. Fernandez et al. 2011, Browning et al. 2014b, Ansmann et al. 2015) and to estimate the relative contributions of prey resources to the diet of a consumer (e.g. Giménez et al. 2017b). Specifically, the size of an animal's niche can be measured from ellipses fitted over the bivariate isotope data which incorporate a set percentage (e.g. 95%) of these data. These ellipses can also be used to measure the degree of overlap between multiple species, indicating an overlap in resource use (Newsome et al. 2007). Further, using the stable isotope values of tissue samples from both prey and predators, mass-balance mixing models estimate the contribution of various prey to the diet of a predator (Parnell et al. 2010, Stock et al. 2018). These mixing models account for the difference in stable isotopes between consumers and prey, known as the diet–tissue discrimination factor or trophic enrichment factor (TEF; Caut et al. 2011, Borrell et al. 2012, Browning et al. 2014c, Giménez et al. 2016, Stock et al. 2018). TEFs vary widely based on a number of factors (e.g. species, tissue type, and age, among others), creating a potential source of error in stable isotope mixing models (Browning et al. 2014c, Kiszka et al. 2014, Giménez et al. 2016). This is especially true given that the best available TEF values for small cetaceans are derived from feeding experiments with limited prey sources (Browning et al. 2014c, Giménez et al. 2016). Despite limitations, these niche investigations and mixing models contribute to improve our understanding of the trophic ecology of small cetaceans (e.g. Fernandez et al. 2011, Kiszka et al. 2014, Giménez, et al. 2017a,b).

Dusky dolphins *Lagenorhynchus obscurus* (hereafter DD) and Heaviside's dolphins *Cephalorhynchus heavisidii* (HD) are 2 relatively abundant sympatric coastal species in the Benguela upwelling marine ecosystem off the coast of Namibia (Martin et al. 2020). In this region, both species occur in nearshore and shelf habitats, although HD have a more inshore distribution than DD (Elwen & Gopal 2018, Alafaro-Shiguieto et al. 2019, De Rock et al. 2019). In Namibian waters, DD occur from shallow waters to the shelf edge (Findlay et al. 1992). HD mostly prefer waters less than 100 m deep, with some evidence that they exhibit diel movements in response to prey movements and behavior (Findlay et al. 1992, Elwen et al. 2006, Leeney et al. 2011, Golaski 2013). DD are larger than HD (190 vs. 175 cm maximum body length; Best 2007), and are considered as generalist feeders throughout their range, feeding on either pelagic schooling fish or demersal prey (Sekiguchi et al. 1992, Best 2007, Van Waerebeek & Würsig 2009, Loizaga De Castro et al. 2016a). Stomach content analysis from stranded, bycaught, and captured individuals of both species from 1966 to 1990 in South African and Namibian waters (Sekiguchi et al. 1992)

indicate that hake (*Merluccius* spp.) and bearded goby (*Sufflogobius bibarbatus*) were the main prey of HD, whereas DD fed on a wider variety of prey, including hake, squids (*Todarodes* spp.), horse mackerel *Trachurus trachurus capensis*, and small pelagic and meso-pelagic fishes.

The Benguela ecosystem is characterized by cold-water upwelling cells that generate areas of high productivity that create a diverse and abundant ecosystem with strong spatial structure (Best 2007, Blamey et al. 2015, De Rock et al. 2019). The coastal waters in southern Namibia have a strong and permanent wind-driven upwelling cell, and constitute the main source of nutrients for the northern Benguela ecosystem (Hutchings et al. 2009, Blamey et al. 2015). Primary production and associated life, including juvenile *Merluccius* spp. and dolphins, are more abundant downstream (i.e. northwards) of the strong upwelling in less turbulent waters (Elwen et al. 2010). Therefore, there are higher concentrations of phytoplankton off the central Namibian coast near Walvis Bay than off the Lüderitz upwelling cell itself (Hutchings et al. 2009). The waters in north-central Namibia surrounding Walvis Bay are characterized by a high productivity which attracts schools of small pelagic fish, particularly *Sardinops sagax, Engraulis japonicus*, and juvenile *T. t. capensis*. Shallow-water Cape hake *M. capensis* are more abundant off central Namibia in summer and south-central Namibia in winter (Burmeister 2001, Mecenero et al. 2006b, Wilhelm et al. 2015). A well-established commercial fishery off Namibia targets a variety of fish species, including *Merluccius* spp. and *T. t. capensis* (Chiripanhura & Teweldemedhin 2016). The Benguela upwelling ecosystem has undergone significant changes due to increased fisheries pressure and global climate change (Watermeyer et al. 2008, Roux et al. 2013), potentially affecting the prey availability for pelagic predators in the region.

Understanding the trophic interactions and feeding ecology of marine top predators along the coast of Namibia is critical to understanding their trophic role in the Benguela upwelling ecosystem, and to predict how these species could potentially be impacted by fisheries and global change through competitive interactions. Long-term research on the diet of Cape fur seals *Arctocephalus pusillus pusillus* has shown that their diet in Namibia has changed dramatically over the past few decades due to changes in prey availability (Mecenero et al. 2006b,c), notably the collapse of the sardine fishery in the 1970s (Utne-Palm et al. 2010, Cedras et al. 2011, van der Bank et al. 2011). This collapse caused an increase in abundance of *S. bibarbatus* and *T. t. capensis* which became more prevalent in the diet of seals (Mecenero et al. 2006c). In addition, the diet of Cape fur seals at colonies in central Namibia differs greatly from those in southern Namibia, which has been correlated with spatial differences in prey availability between those areas (Mecenero et al. 2006b).

In this study, we investigated resource use and partitioning of DD and HD off the Namibian coastline using stable isotope analyses from skin samples collected out of Walvis Bay and Lüderitz, Namibia. We examined the contribution of a variety of prey to the diet of these 2 dolphin species using Bayesian mass-balance stable isotope mixing models, and compared our results with previously published stomach content analyses (Sekiguchi et al. 1992) to investigate changes in dolphin diet over time. Based on trends found for Cape fur seals in the same region, we hypothesized that (1) results from stable isotope analyses would be consistent with previous stomach content results (Sekiguchi et al. 1992), but with increased importance of *S. bibarbatus* and *T. t. capensis* as they have increased in the area, and (2) resource use by DD and HD would differ spatially in relation to prey availability (i.e. Walvis Bay and Lüderitz).

2. MATERIALS AND METHODS

2.1. Data collection

Skin samples of DD and HD were collected during boat-based surveys out of Walvis Bay (22° 55′ S, 14° 30′ E) and Lüderitz (26° 36′ S, 15° 8′ E) between 2009 and 2013, as part of a broader project investigating the abundance and habitat use of these species (Fig. 1). Walvis Bay is a shallow (<15 m deep on average) and sandy-bottomed bay approximately 10 × 10 km. The bay is highly affected by anthropogenic activities, including tourism, shipping, aquaculture, and fishing activities (Griffiths et al. 2004, Elwen et al. 2010). The same human activities occur at Lüderitz, but on a smaller scale, making it less impacted than Walvis Bay (Griffiths et al. 2004, Leeney 2011). The Lüderitz area is a mix of rocky shores with several smaller sandy-bottomed bays. Samples were collected from bow-riding dolphins during calm sea conditions, using a 'Hawaiian sling' fitted with a 20 mm long × 10 mm external diameter stainless-steel corer with internal barbs to retain the sample. Tips were only used once per day and cleaned and disinfected thoroughly between uses to prevent any contamination. Samples were kept on ice until processed.

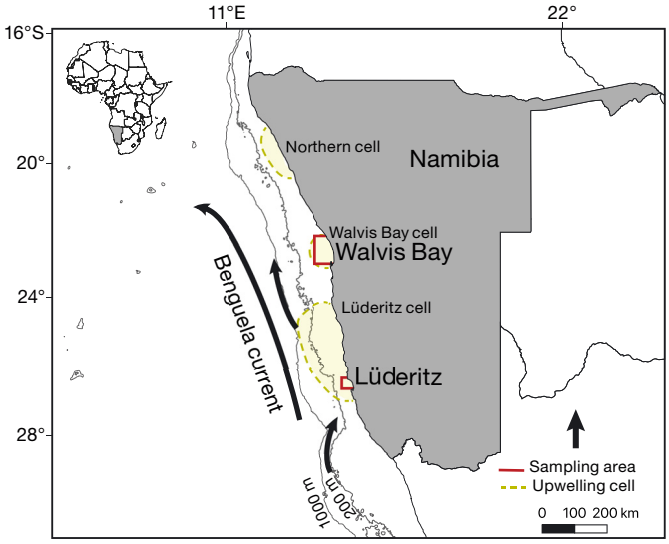

Fig. 1. Sampling locations off the coast of Namibia: Walvis Bay and Lüderitz, including currents (arrows) and areas of wind-driven upwelling (i.e. upwelling cells), where cold water and nutrients rise to the ocean surface. Made using the WGS 84-Pseudo-Mercator coordinate system

2.2. Stable isotope analysis

Blubber was removed from each sample, and only skin was frozen at −20°C until further processing. Skin samples were dried at 50°C for 48 h to remove any water. Samples were ground into a fine powder, and aliquots of approximately 0.6–0.7 mg were weighed into tin capsules. Isotopic analysis was undertaken by IsoEnvironmental (Botany Department, Rhodes University, South Africa) on a Europa Scientific 20-20 isotope ratio mass spectrometer linked to an ANCA SL Prep Unit. All results are referenced to Vienna Pee Dee belemnite for carbon isotope values, and to air for nitrogen isotope values. Results are expressed in delta notation on a per mille scale using the standard equation:

$$\delta X(‰) = [(R_{sample}/R_{standard} - 1] \times 1000 \quad (1)$$

where $X = {}^{15}N$ or ${}^{13}C$ and R represents ${}^{15}N/{}^{14}N$ or ${}^{13}C/{}^{12}C$, respectively. Analytical precision was <0.14‰ for $\delta^{13}C$ and <0.09‰ for $\delta^{15}N$.

The presence of lipids in skin samples can deplete $\delta^{13}C$ values, which is indicated by a C:N ratio >3.5. As all of our samples had C:N ratios >3.5, a correction factor was applied as per Cloyed et al. (2020) to remove any bias as follows:

$$\Delta^{13}C = 6.43 - 20.25/C{:}N_{Bulk} \quad (2)$$

This correction factor was selected as it is specific for correcting the effect of lipids in dolphin skin samples (Cloyed et al. 2020).

2.3. Data analysis

Data were tested for normality and homogeneity using a Shapiro-Wilk test and Levene's test, respectively. A MANOVA followed by post hoc ANOVAs were used to assess the effect of species and study site (Walvis Bay vs. Lüderitz, Fig. 1) on the stable isotope values of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in dolphin skin. Stable isotopes incorporate into tissues based on species and tissue-type-specific turnover rates. Half-life turnover rates (± SD) are 24.2 ± 8.19 d for ${}^{13}C$ and 47.6 ± 19 d for ${}^{15}N$ (Giménez et al. 2016), estimated from bottlenose dolphin *Tursiops truncatus* skin samples. Therefore, isotopes in DD and HD skin are reflective of foraging activities several weeks prior to sample collection. Isotopic niche width and overlap for both dolphin species were calculated using Stable Isotope Bayesian Ellipses in R (SIBER) metrics (Jackson et al. 2011). We calculated the Bayesian standard ellipse area (SEA_B) and the SEA corrected for small sample size (SEAc), which are used to account for any biases caused by differences in sample size and the small (<30) number of DD samples.

Bayesian mass-balance stable isotope mixing models were performed using the 'MixSIAR' package (Stock et al. 2018) to estimate the relative contribution of potential prey to the diet of DD and HD at Walvis Bay and Lüderitz. Isotope values from white muscle tissue of potential prey species were taken from previous studies conducted in Namibia (Table 1; van der Lingen & Miller 2011, Iitembu et al. 2012, Erasmus 2015, Iitembu 2015). Potential prey species were selected based on previous research on the diet of DD and HD using stomach content analyses (Sekiguchi et al. 1992). As many of these potential prey species as possible were taken from one source (i.e. Iitembu 2015), as this sampling was done during a similar time period as dolphin sampling and included numerous potential prey. *Merluccius* spp. were separated into large (>40 cm) and small (<40 cm) size classes. Fish species were grouped using a *k*-means cluster analysis in R (Kaufman & Rousseeuw 1990), which included $\delta^{15}N$ and $\delta^{13}C$, and habitat as grouping variables (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m699p227_supp.pdf). The optimal number of 5 clusters was determined using the 'Silhouette Method' outlined by Kaufman & Rousseeuw (1990), as 5 had the highest average 'silhouette.' Average 'silhouette' is a measure of the quality of clustering based on how well each data point falls within the cluster. Habitat and trophic level for each prey species were obtained from FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org).

Table 1. Prey species used for mixing model analysis of dolphin diet, including the sample size (n), mean ± SD of $\delta^{13}C$ and $\delta^{15}N$, habitat, average trophic level (TL), source, and year of sampling for each group (A–E). Groups were defined based on *k*-means cluster analysis. Habitat and trophic level for each prey were taken from FishBase and SeaLifeBase

Species	n	$\delta^{13}C$	$\delta^{15}N$	TL	Source	Sampling years
Group A: small pelagic prey	211	−16.97 ± 0.59	11.91 ± 0.84			
Sufflogobius bibarbatus (<5.7 cm)	15	−16.6 ± 0.05	11.24 ± 0.05	2.55	van der Bank et al. (2011)	2008
Diaphus meadi	21	−17.24 ± 0.82	11.73 ± 1.19	3.00	Erasmus (2015)	2012–2014
Lampanyctus australis	28	−16.99 ± 0.79	11.8 ± 1.16	3.33	Erasmus (2015)	2012–2014
Etrumeus whiteheadi	127	−16.79 ± 0.59	12.19 ± 1.05	3.40	van der Lingen & Miller (2011)	2009
Lampanyctodes hectoris	20	−17.24 ± 0.72	12.6 ± 0.73	3.16	Erasmus (2015)	2012–2014
Group B: mid-size pelagic prey	127	−16.1 ± 0.22	12.11 ± 0.4			
Sufflogobius bibarbatus (5.8–9.0 cm)	21	−16.1 ± 0.05	11.82 ± 0.11	2.80	van der Bank et al. (2011)	2008
Engraulis japonicus	105	−16.2 ± 0.60	12.1 ± 1.1	3.00	Iitembu et al. (2012)	2008
Histioteuthidae	1	−16 ± 0	12.4 ± 0	4.11	Iitembu et al. (2012)	2008
Group C: small demersal fish	86	−16.62 ± 0.69	13.17 ± 0.63			
Merluccius capensis (<40 cm)	34	−16.62 ± 1.0	12.87 ± 0.82	3.23	Iitembu (2015)	2011
M. paradoxus (<40 cm)	26	−16.65 ± 0.50	13.06 ± 0.64	3.33	Iitembu (2015)	2011
M. paradoxus (>40 cm)	26	−16.58 ± 0.56	13.57 ± 0.42	0.46	Iitembu (2015)	2011
Group D: large pelagic fish	11	−16.5 ± 0.40	13.6 ± 0.40			
Trachurus t. capensis	11	−16.5 ± 0.40	13.6 ± 0.40	0.97	Iitembu et al. (2012)	2008
Group E: large demersal fish	60	−15.63 ± 0.29	13.69 ± 0.44			
M. capensis (>40 cm)	19	−15.76 ± 0.52	13.26 ± 0.74	4.49	Iitembu (2015)	2011
Sufflogobius bibarbatus (>9.0 cm)	41	−15.5 ± 0.05	14.12 ± 0.14	3.05	van der Bank et al. (2011)	2008

No TEFs have been calculated for either DD or HD tissues. Therefore, we used TEFs from the skin of bottlenose dolphins which were based on feeding experiments which took place over 350 d, ensuring that isotopes stabilized in the samples before calculation of TEFs (Giménez et al. 2016). The TEFs (± SD) used here were 1.01 ± 0.37‰ for $\delta^{13}C$ and 1.57 ± 0.52‰ for $\delta^{15}N$. A mixing polygon was constructed (see Smith et al. 2013) to evaluate whether the TEF was appropriate for predators and sources (see Fig. 3b). Mixing models were run using 3 Monte Carlo chains of 300 000 draws and a burn-in rate of 200 000 draws. Convergence was checked using Gelmin-Rubin and Geweke diagnostics. We fitted 4 different models including the covariates of species and area, then compared these models using the leave-one out cross-validation (LOO) and the widely applicable information criterion (WAIC; also known as the Watanabe-Aikaike information criterion) to determine which model was the most appropriate (Table S1 in the Supplement). All statistical analyses were performed in R v.4.0.0.

Table 2. Mean ± SD of $\delta^{13}C$ and $\delta^{15}N$ values of skin samples of dusky dolphin *Lagenorhynchus obscurus* and Heaviside's dolphin *Cephalorhynchus heavisidii* at Walvis Bay and Lüderitz, Namibia. Within columns, different superscript letters indicate significant differences ($p < 0.05$) between paired values, estimated from Tukey's post-hoc testing

	N	$\delta^{13}C$	$\delta^{15}N$
Lüderitz	51		
Dusky	10	-15.09 ± 0.40^{a}	14.28 ± 0.58^{cde}
Heaviside's	41	-14.49 ± 0.43^{ab}	14.97 ± 0.70^{d}
Walvis Bay	39		
Dusky	7	-14.67 ± 0.24^{c}	15.19 ± 0.55^{c}
Heaviside's	32	-15.08 ± 0.45^{bc}	15.26 ± 0.63^{e}

3. RESULTS

3.1. Stable isotope ratios

A total of 90 skin biopsy samples from adult DD (n = 17) and HD (n = 73) were collected from Walvis Bay and Lüderitz, Namibia (Table 2). In the overall dataset with data combined for both locations, HD had significantly higher $\delta^{15}N$ values ($F = 5.1$, df = 1, $p = 0.026$) than DD, but not $\delta^{13}C$ values ($F = 1.9$, df = 1, $p = 0.17$). When species data were pooled, sampling location had a significant effect on $\delta^{15}N$ ($F = 6.30$, df = 1, $p = 0.014$), with higher values at Walvis Bay. There was no significant difference in $\delta^{13}C$ values between sampling locations; however, the interaction between species and sampling location was significant ($F = 18.78$, df = 1, $p < 0.0001$). Pairwise post hoc testing revealed that at Lüderitz, HD were significantly ($p < 0.05$) enriched in $\delta^{13}C$ values compared to DD. Additionally, HD at Lüderitz were also

significantly ($p < 0.05$) enriched in $\delta^{13}C$ values compared to HD from Walvis Bay.

3.2. Isotopic niche partitioning

HD had a wider overall isotopic niche than DD based on SEA_B calculations (1.18‰^{2} [95% CI = 0.91–1.46‰^{2}] vs. 0.59‰^{2} [95% CI = 0.31–0.90‰^{2}]). The DD area overlapped the HD area by 68.9%, with a 30.9% overlap of the HD area with the DD niche (Table 3, Fig. 2). The extent of isotopic niche overlap varied between the 2 sampling locations (Fig. 2), with a higher overlap between the 2 species at Walvis Bay then at Lüderitz (Table 3). HD sampled at Walvis Bay had the widest isotopic niche (0.98‰^{2} [95% CI = 0.65–1.33‰^{2}]; Fig. 2). At Walvis Bay, the range in $\delta^{15}N$ values was 1.75‰ for HD, and 1.5‰ for DD. The range in $\delta^{13}C$ values were larger for HD (2.05‰) than for DD (0.5‰).

3.3. Stable isotope mixing models

In the mixing polygon simulation (Fig. 3b), a number of predators fell outside of the 95% contour, and as such, these were removed from the mixing models (HD = 11, DD = 1). The mixing model using both species and area as fixed effects was the most supported based on LOO and WAIC and was therefore used here (see Stock et al. 2018). All contributions are presented as mean ± SD. At Walvis Bay, large demersal fish (47.9 ± 16.2%) and large pelagic fish (24.5 ± 20.4%) contributed most to DD diet, with smaller contributions from mid-size pelagic prey (13.7 ± 7.8%) and mid-size demersal fish (10.2 ± 12.6%), and high individual variation (as demonstrated by high SD). At Lüderitz, mid-sized pelagic prey (42.3 ± 14.0%) and large demersal fish (39.3 ± 10.4%) were the only 2 major contributors to DD diet (Fig. 4). The diet of HD consisted primarily of 2 prey groups at both study sites (Fig. 4). At Walvis Bay, their diet consisted primarily of large demersal fish (55.5 ± 4.5%) and large pelagic fish (27.1 ± 21.1%). At Lüderitz, HD diet also consisted primarily of large demersal prey (60.8 ± 6.5%), with a 24.9 ± 7.1% contribution of small demersal fish and lower individual variation. No other prey group contributed >10% to HD diet at either location; however, small demersal fish did contribute 9.4 ± 13.1% at Walvis Bay.

Table 3. Percentage of area overlapped of each row by each column, from Bayesian ellipses of dusky dolphin *Lagenorhynchus obscurus* and Heaviside's dolphin *Cephalorhynchus heavisidii* stable isotope samples taken in Walvis Bay and Lüderitz, Namibia

	Dusky – Lüderitz	Heaviside's – Lüderitz	Dusky – Walvis Bay	Heaviside's – Walvis Bay
Dusky – Lüderitz		24.7	11.6	24.4
Heaviside's – Lüderitz	16.8		25.0	18.2
Dusky – Walvis Bay	17.5	52.9		53.0
Heaviside's – Walvis Bay	13.0	13.3	18.3	

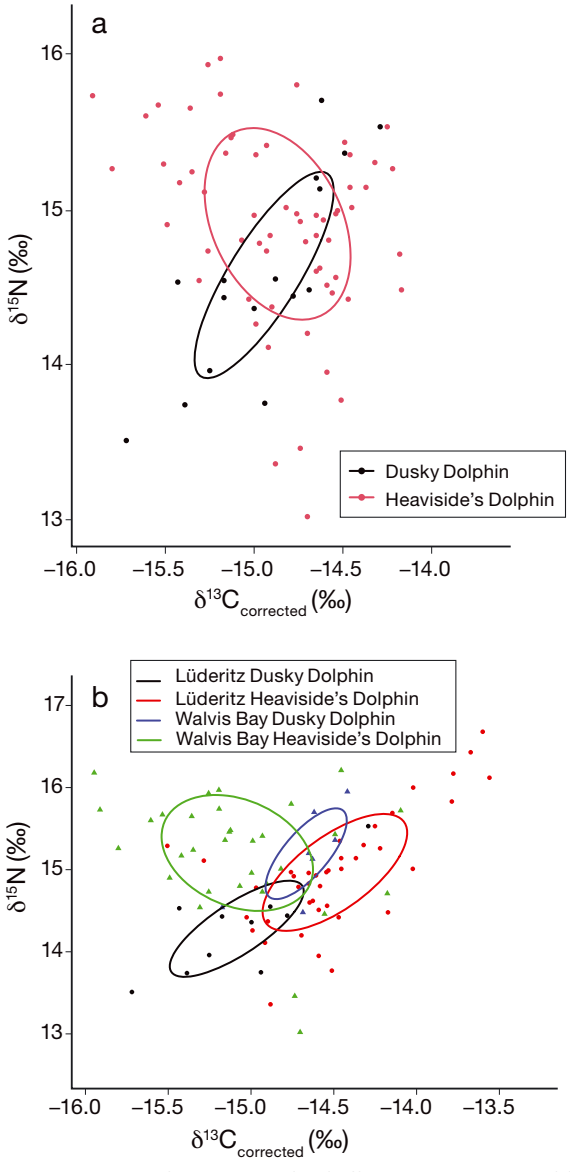

Fig. 2. Isotopic niche (i.e. standard ellipse area corrected for small sample size, SEAc) from (a) dusky dolphins *Lagenorhynchus obscurus* and Heaviside's dolphins *Cephalorhynchus heavisidii* skin samples, as well as (b) from both species separated by the location of collection, i.e. Lüderitz and Walvis Bay, Namibia

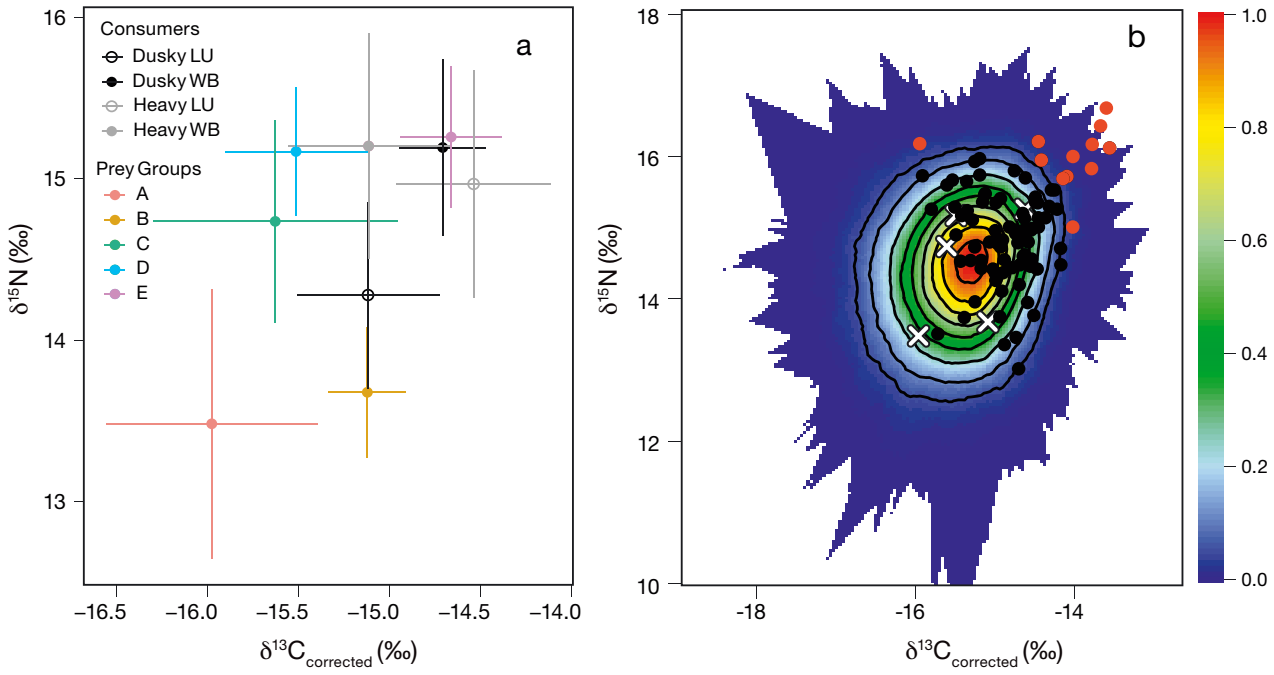

Fig. 3. (a) Average $\delta^{15}N$ and $\delta^{13}C$ values (error bars = SD) of dusky dolphins *Lagenorhynchus obscurus* and Heaviside's dolphins *Cephalorhynchus heavisidii* skin samples and their prey taken from Namibia. All animals were grouped as per Table 1, and the trophic enrichment factor from Giménez et al. (2016) was applied to prey values (1.01 ± 0.37‰ for $\delta^{13}C$ and 1.57 ± 0.52‰ for $\delta^{15}N$). LU: Lüderitz; WB: Walvis Bay. (b) Simulated mixing region for the biplot in (a). The dolphin consumers (black dots) are shown, with the average sources (white crosses). The contours are the probability contours, and the colours represent this probability. The contours are at every 10%, with 5% at the outer contour (i.e. 95% probability contour). All consumers falling outside of the 95% mixing region (red dots) were removed from mixing models

4. DISCUSSION

The results presented here are the first to investigate the trophic interactions and feeding ecology of DD and HD in the Benguela upwelling ecosystem off the coast of Namibia using stable isotope analyses. Isotopic niche analysis and stable isotope mixing models are increasingly being used to better understand the trophic interactions and ecological roles of predators in marine ecosystems (Jackson et al. 2011, Browning et al. 2014c, Stock et al. 2018). Investigations of isotopic niches can provide information on how sympatric animals partition resources and foraging habitats (Schoener 1974, Pinela et al. 2010, Fernandez et al. 2011, Kiszka et al. 2011, 2012, Browning et al. 2014a,b), which is important for understanding community dynamics and potential competitive interactions within predator guilds. Increasing efforts to reduce bias by improving lipid extraction calculations, TEFs, and understanding of tissue turnover rates have improved these models (Post et al. 2007, Caut et al. 2009, Tarroux et al. 2010, Browning et al. 2014c, Giménez et al. 2016, 2017c, Cloyed et al. 2020). The main limitation in our study remains the choice of TEFs employed in the mixing model, as these are the largest potential sources of error in these models (Caut et al. 2011, Borrell et al. 2012, Browning et al. 2014c, Kiszka et al. 2014, Giménez et al. 2016). To minimize this potential error, TEFs from experiments on bottlenose dolphins were used (Giménez et al. 2016), as no specific TEFs have been calculated for HD and DD, and it is generally accepted that TEFs of taxonomically close species will be similar (Giménez et al. 2016, Healy et al. 2018). It should also be noted that biopsy sampling can potentially be biased, as some individuals (males vs. females, adults vs. immatures) can occur closer to the research vessel than others, and can therefore be more accessible for sampling. Published research suggests that sex ratio biases can occur, but infrequently (Bilgmann et al. 2007, Quérouil et al. 2010, Kellar et al. 2013, Loizaga De Castro et al. 2013). Sampling biases are challenging to assess and could not be quantified in the present study.

The dietary overlap of the HD niche with the DD niche was limited (Walvis Bay: 18.3%; Lüderitz: 16.8%), but the DD niche was highly overlapped by that of HD (68.9%). This suggests that although there

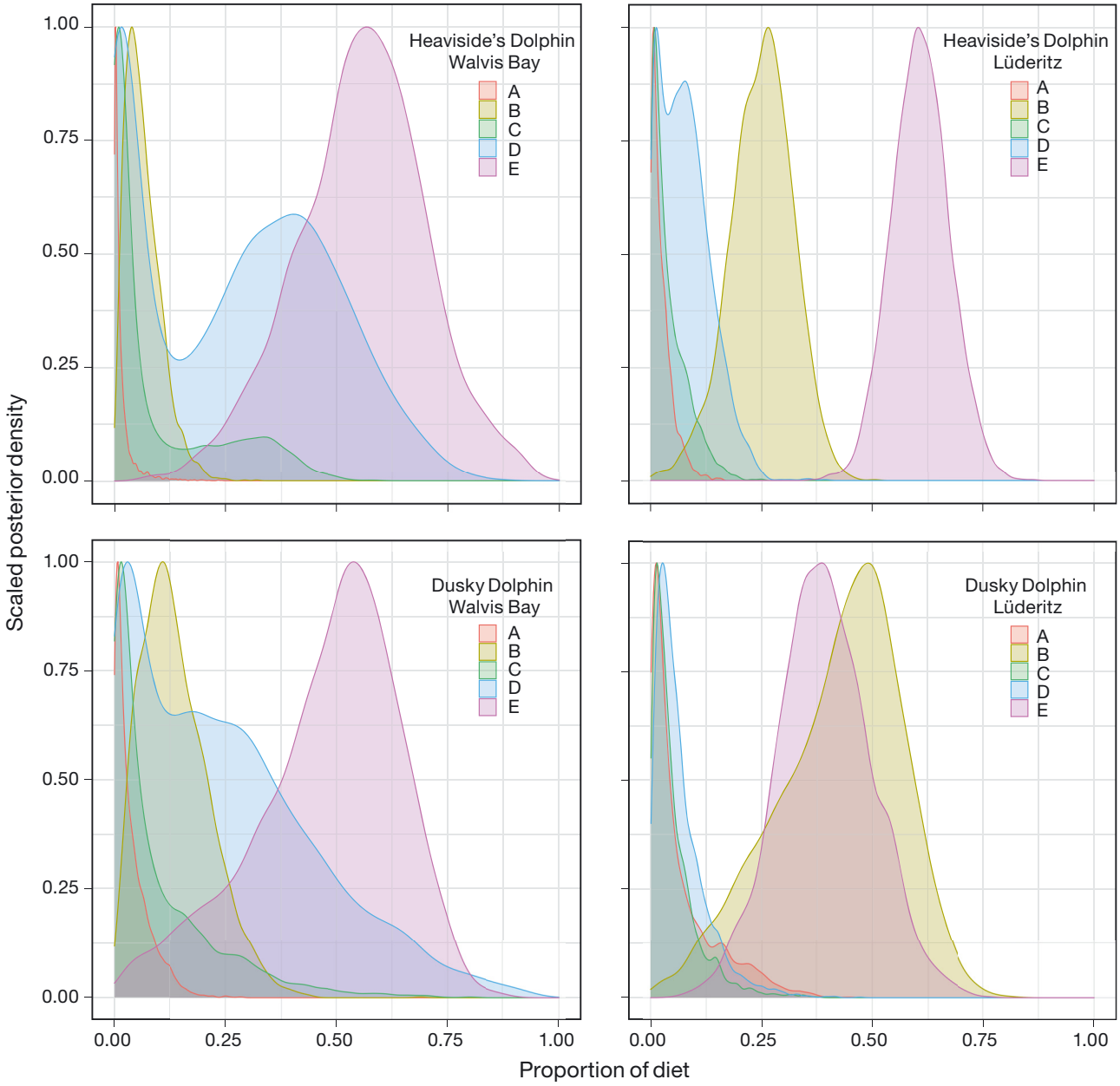

Fig. 4. Results of mixing models showing the proportion of each prey group (as defined in Table 1) in diet of dusky dolphins *Lagenorhynchus obscurus* and Heaviside's dolphins *Cephalorhynchus heavisidii* from Walvis Bay (WB) and Lüderitz (LU), Namibia, using skin stable isotope ratios (i.e. $\delta^{13}C$ and $\delta^{15}N$)

is competition for resources within the isotopic niche of DD, this may have a limited effect on HD, as their isotopic niche is larger. This is further demonstrated in the higher $\delta^{15}N$ values of HD, suggesting that despite their smaller body size, they feed on higher trophic level prey than DD. Mixing model results further support this finding as HD fed primarily on high trophic level prey, including large demersal and pelagic fish, whereas DD were meso-predators feeding on a variety of prey, especially at Walvis Bay. The contribution of small pelagic fish, small demersal fish, and squid to the diet of DD, as well as *Trachurus t. capensis* and large *Merluccius* spp., results in a lower trophic level of prey overall. Stomach content analysis from the region showed similar results, with DD having a more generalized diet (4 prey species >10 % contribution by volume, including 30 % by volume from *T. t. capensis*) than HD, whose stomachs mainly contained *Merluccius* spp. (48.9 % by volume) (Sekiguchi et al. 1992). The difference in isotopic

niche and diet between dolphin species may be driven by spatial and/or temporal partitioning of resources as has been shown for other sympatric small cetaceans (e.g. Gowans & Whitehead 1995, Gross et al. 2009, Giménez et al. 2017a, 2018a, Oviedo et al. 2018). Evidence from distribution studies suggests that DD occur farther from shore than HD (Findlay et al. 1992, Elwen et al. 2009), which may be reflected in the depleted $\delta^{13}C$ values found for DD at Lüderitz. Temporal overlap remains unknown, and further research is needed to elucidate whether there is a temporal component to resource partitioning.

Spatial differences were detected in dolphin foraging ecology between central (Walvis Bay) and southern (Lüderitz) Namibia, highlighting how prey availability could potentially affect the diet of these marine predators. Mixing models suggest that large demersal fish are among the main contributors to the diet of both dolphins at both locations. This prey group is comprised of large *M. capensis* and large *Sufflogobius bibarbatus*, which are high trophic level fish in this region. In Walvis Bay, *T. t. capensis* is the secondary prey for both dolphin species, which is also a relatively high trophic level fish. DD also have smaller pelagic fish and squid and other *Merluccius* spp. contributing to their diet in this region. Approximately 400 km south, at Lüderitz off southern Namibia, *T. t. capensis* is not an important prey source for either species, with mid-sized pelagic prey becoming a main contributor to the diet of both dolphin species. Our interpretation is limited by the prey samples used, as we did not have location-specific prey collected at the same time as dolphin samples. Additionally, baseline isotopes from primary producers can vary spatially, potentially affecting isotope values of consumers. However, known information on fish and other consumers support our results. For example, abundances of *T.t. capensis* north of Walvis Bay are significantly higher than south of Walvis Bay (Krakstad & Kanandjembo 2001, Axelsen et al. 2004), which is reflected in their importance to the diet of DD and HD in Walvis Bay, but not farther south at Lüderitz. *S. bibarbatus* have a patchy distribution in northern Namibia, but the main concentrations occur between Walvis Bay and Lüderitz, where they are fed on by both dolphin species (Cruickshank et al. 1980). A similar spatial difference in diet is also observed in Cape fur seals colonies along the Namibian coastline, which is also attributed to prey availability (Mecenero et al. 2006a). In central Namibia, *T. t. capensis* and *Merluccius* spp. are the most consumed species for Cape fur seals, whereas *S. bibarbatus* and myctophids are the main prey at southern colonies (Mecenero et al. 2006b). The clear spatial differences in dolphin diet presented here may to be driven by differences in prey availability along the coast, which is associated with the strong oceanographic structure within the Benguela upwelling ecosystem (Hutchings et al. 2009).

The difference in diet for both DD and HD over a relatively small spatial scale is indicative of both dietary plasticity and fine-scale population structuring, where at least 2 population segments of both species might be driven by oceanographic and biotic conditions (Fernandez et al. 2011, Giménez et al. 2018b, Brotons et al. 2019). Spatial dietary variation has been shown in a variety of taxa, including fish (e.g. Corrigan et al. 2011, Lawton & Pratchett 2012), birds (e.g. Parrish 2000, Buren et al. 2012, Robinson et al. 2019), and mammals (e.g. Spitz et al. 2006, Gulka et al. 2017). These spatial differences largely occur in response to differences in food availability (Gulka et al. 2017). Some species may also shift diet as they move through various habitats in order to fulfil energy budgets (Parrish 2000). In some delphinid species, spatial differences in the feeding ecology of groups can be so distinct that they distinguish population segments, including within genetically defined populations (e.g. Spitz et al. 2006, Botta et al. 2012, Meissner et al. 2012, Quérouil et al. 2013, Wilson et al. 2013, Browning et al. 2014a, Brotons et al. 2019). For DD and HD off Namibia, it remains unclear whether the same animals move along the coast and shift diet depending on prey availability, or whether distinct population segments of each species occur in central and southern Namibian waters.

Predominant prey for both HD and DD diets highlight the potential overlap between the diet of these 2 predators and commercially important fish species in Namibian waters, particularly *Merluccius* spp. and *T. t. capensis.* These relatively high trophic level species form a major part (>50%) of both dolphin diets, when both study areas are combined. The most recent published catch rates from 2012/2013 were approximately 147 000 t of hake and 287 000 t of horse mackerel from trawling vessels (Chiripanhura & Teweldemedhin 2016). The effect of overfishing and prey depletion on marine predators has been widely documented for a variety of taxa, including seabirds (e.g. Montevecchi 1993, 2002, Cury et al. 2011), marine mammals (e.g. Shaughnessy et al. 2003, Plagányi & Butterworth 2009), and sharks (e.g. Kiszka & van der Elst 2015). In some cases, these declines do coincide with a noticeable shift in predator diet (Marcalo et al. 2018), but may have other secondary consequences, including shifts in the fish community.

In Namibian waters, the collapse of the sardine (*Sardinops* spp.) fishery caused a shift in the fish community, including an increase in *T. t. capensis* and *S. bibarbatus* in the region (Utne-Palm et al. 2010, Cedras et al. 2011, van der Bank et al. 2011), which is reflected in the diet of marine predators. Extensive research on the diet of Cape fur seal in the region showed the effect of this shift, with an increased importance of both *T. t. capensis* and *S. bibarbatus* as prey (Mecenero et al. 2006a,c). Stomach content research on both dolphin species may allow us to detect this shift, although direct comparison of the results presented here to the stomach content study on dolphins is limited, as stomach content research was based on samples from both Namibian and South African dolphins (Sekiguchi et al. 1992). However, the contribution of *T. t. capensis* to the diet of both dolphins is markedly higher in our study (stomach content: 4.2% by volume, Sekiguchi et al. 1992; stable isotopes: 24.5–27.1%, this study). Additionally, only small pelagic *S. bibarbatus* were found in DD stomachs previously (Sekiguchi et al. 1992). In our study, these lower trophic level pelagic prey are less prevalent in the diet of dolphins, with a shift to large demersal *S. bibarbatus* and *Merluccius* spp. for both dolphin species at both of our study areas. This shift might have had individual and population-level consequences on both dolphin species, which are currently unknown. As fishing pressure continues to increase in the Benguela (Chiripanhura & Teweldemedhin 2016), the data presented here will be crucial in monitoring how these top predators adapt to changes in prey availability, especially given the overlap between their diet and the main fisheries in Namibia.

5. CONCLUSIONS

The results presented here provide evidence of resource partitioning between DD and HD in Namibian waters. They also highlight the effects of prey availability on dolphin diet, with distinct differences in prey between central and southern Namibia. There is a clear overlap with commercial fisheries (i.e. *Merluccius* spp. and *Trachurus t. capensis*) and dolphin diet in the region that requires future monitoring, especially as dolphins are highly specialized in central Namibia. Ecological adaptations, including trophic ecology, have often been considered when assigning management units in cetaceans, especially as these can lead to distinct spatial and temporal resource use with no overlap between sub-groupings (Esteban et al. 2016, Giménez et al. 2018b, Méndez-Fernandez et al. 2020). Therefore, future research should also focus on investigating temporal shifts in dolphin diet, including collecting site-specific and temporally variable prey samples to further investigate the spatial variation in isotopes. Additionally, further research is needed on the movement patterns and population ecology of both dolphins in the region. This will give a better understanding of whether animals migrate along the coast and shift diet in response to prey availability (i.e. dietary plasticity), or whether there are distinct sub-populations in the region, which can be used in assigning management units. This information is critical for understanding how these dolphins should be managed along the coastline, and how they will respond to increasing anthropogenic pressure on marine environments.

Acknowledgements. All research within Namibia was conducted with the approval of and in collaboration with the Namibian Ministry of Fisheries and Marine Resources (MFMR), although no specific research permits are issued by the department. M.C. was funded through a Rhodes University Post-Doctoral Research Fellowship. T.G. was funded through a University of Pretoria (UP) Vice Chancellor's Post-Doctoral Fellowship (2013–2015). S.A.K. was funded by a post-doctoral fellowship from the Claude Leon Foundation (2012–2014). S.E. was supported by a series of fellowships over the duration of the work including a UP Post-Doctoral Fellowship (2009), Claude Leon Post-Doctoral Fellowship (2010–2011), and a UP Research Fellowship (2012–2015). Field data collection was funded by a series of grants to S.E. and T.G., including 2 grants from the Nedbank Go Green Fund (2009–2010 and 2011–2014), the Rufford Small Grants Foundation, and a Kate Sanderons Bequest through the IUCN SSC. This is contribution no. 277 from the Coastlines and Oceans Division of the Institute of Environment at Florida International University.

LITERATURE CITED

Alafaro-Shiguieto J, Crespo E, Elwen S, Lundquist D, Mangel J (2019) Dusky dolphin. *Lagenorhynchus obscurus*. The IUCN Red List of Threatened Species 2019. e.T11146A175604493. https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T11146A175604493.en (accessed 21 March 2020)

Ansmann IC, Lanyon JM, Seddon JM, Parra GJ (2015) Habitat and resource partitioning among Indo-Pacific bottlenose dolphins in Moreton Bay, Australia. Mar Mamm Sci 31:211–230

Axelsen B, Krakstad JO, Bauleth-D'Almeida G (2004) Aggregation dynamics and diel vertical migration in Cape horse mackerel (*Trachurus trachurus capensis*) in the Namibian Benguela. Implications for acoustic abundance estimation. In: Sumaila U, Steinshamn S, Skogen M, Boyer D (eds) Ecological, economic and social aspects of Namibian fisheries. Eburon Publishers, Delft, p 135–164

Best PB (2007) Whales and dolphins of the southern African subregion. Cambridge University Press, Cambridge

Bilgmann K, Griffiths OJ, Allen SJ, Möller LM (2007) A biopsy pole system for bow-riding dolphins: sampling success, behavioral responses, and test for sampling bias. Mar Mamm Sci 23:218–225

Blamey LK, Shannon LJ, Bolton JJ, Crawford RJM and others (2015) Ecosystem change in the southern Benguela and the underlying processes. J Mar Syst 144:9–29

Borrell A, Abad-Oliva N, Gõmez-Campos E, Giménez J, Aguilar A (2012) Discrimination of stable isotopes in fin whale tissues and application to diet assessment in cetaceans. Rapid Commun Mass Spectrom 26:1596–1602

Botta S, Hohn AA, MacKo SA, Secchi ER (2012) Isotopic variation in delphinids from the subtropical western South Atlantic. J Mar Biol Assoc UK 92:1689–1698

Bowen WD (1997) Role of marine mammals in aquatic ecosystems. Mar Ecol Prog Ser 158:267–274

Brotons JM, Islas-Villanueva V, Alomar C, Tor A, Fernández R, Deudero S (2019) Genetics and stable isotopes reveal non-obvious population structure of bottlenose dolphins (*Tursiops truncatus*) around the Balearic Islands. Hydrobiologia 842:233–247

Browning N, McCulloch SD, Bossart GD, Worthy GAJ (2014a) Fine-scale population structure of estuarine bottlenose dolphins (*Tursiops truncatus*) assessed using stable isotope ratios and fatty acid signature analyses. Mar Biol 161:1307–1317

Browning NE, Cockcroft VG, Worthy G (2014b) Resource partitioning among South African delphinids. J Exp Mar Biol Ecol 457:15–21

Browning NE, Dold C, I-Fan J, Worthy GAJ (2014c) Isotope turnover rates and diet–tissue discrimination in skin of *ex situ* bottlenose dolphins (*Tursiops truncatus*). J Exp Biol 217:214–221

Buren AD, Koen-Alonso M, Montevecchi WA (2012) Linking predator diet and prey availability: common murres and capelin in the Northwest Atlantic. Mar Ecol Prog Ser 445: 25–35

Burmeister LM (2001) Depth-stratified density estimates and distribution of the Cape hake *Merluccius capensis* and *M. paradoxus* off Namibia deduced from survey data, 1990–1999. S Afr J Mar Sci 23:347–356

Caut S, Angulo E, Courchamp F (2009) Variation in discrimination factors ($\Delta^{15}N$ and $\Delta^{13}C$): the effect of diet isotopic values and applications for diet reconstruction. J Appl Ecol 46:443–453

Caut S, Laran S, Garcia-Hartmann E, Das K (2011) Stable isotopes of captive cetaceans (killer whales and bottlenose dolphins). J Exp Biol 214:538–545

Cedras RB, Salvanes AGV, Gibbons MJ (2011) Investigations into the diet and feeding ecology of the bearded goby *Sufflogobius bibarbatus* off Namibia. Afr J Mar Sci 33:313–320

Chiripanhura B, Teweldemedhin M (2016) An analysis of the fishing industry in Namibia: the structure, performance, challenges, and prospects for growth and diversification. Working Paper. African Growth and Development Policy Modelling Consortium, Windhoek

Cloyed CS, DaCosta KP, Hodanbosi MR, Carmichael RH (2020) The effects of lipid extraction on $\delta^{13}C$ and $\delta^{15}N$ values and use of lipid-correction models across tissues, taxa and trophic groups. Methods Ecol Evol 11:751–762

Corrigan LJ, Winfield IJ, Hoelzel AR, Lucas MC (2011) Dietary plasticity in Arctic charr (*Salvelinus alpinus*) in response to long-term environmental change. Ecol Freshw Fish 20:5–13

Cruickshank RA, Cooper J, Hampton I (1980) Extension to the geographical distribution of pelagic goby *Sufflogobius bibarbatus* off South West Africa and some mensural and energetic information. Fish Bull S Afr 13:77–82

Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T and others (2011) Global seabird response to forage fish depletion — one-third for the birds. Science 334:1703–1706

De Rock P, Elwen SH, Roux JP, Leeney RH and others (2019) Predicting large-scale habitat suitability for cetaceans off Namibia using MinxEnt. Mar Ecol Prog Ser 619:149–167

Elwen S, Gopal K (2018) Heaviside's dolphin. *Cephalorhynchus heavisidii*. The IUCN Red List of Threatened Species 2018. e.T4161A50352086. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T4161A50352086.en (accessed 15 March 2020)

Elwen S, Meÿer MA, Best PB, Kotze PGH, Thornton M, Swanson S (2006) Range and movements of female Heaviside's dolphins (*Cephalorhynchus heavisidii*), as determined by satellite-linked telemetry. J Mammal 87: 866–877

Elwen SH, Best PB, Reeb D, Thornton M (2009) Diurnal movements and behaviour of Heaviside's dolphins, *Cephalorhynchus heavisidii*, with some comparative data for dusky dolphins, *Lagenorhynchus obscurus*. Afr J Wildl Res 39:143–154

Elwen SH, Thornton M, Reeb D, Best PB (2010) Near-shore distribution of Heaviside's (*Cephalorhynchus heavisidii*) and dusky dolphins (*Lagenorhynchus obscurus*) at the southern limit of their range in South Africa. Afr Zool 45: 78–91

Erasmus V (2015) Trophic relations of prey species (*Etrumeus whiteheadi*, Myctophidae, and *Sepia*) and their predators (*Merluccius capensis, Merluccius paradoxus, Lophius vomerinus* and *Trachurus capensis*) off Namibia. MSc thesis, University of Namibia, Windhoek

Esteban R, Verborgh P, Gauffier P, Giménez J and others (2016) Using a multi-disciplinary approach to identify a critically endangered killer whale management unit. Ecol Indic 66:291–300

Estes JA, Heithaus M, McCauley DJ, Rasher DB, Worm B (2016) Megafaunal impacts on structure and function of ocean ecosystems. Annu Rev Environ Resour 41:83–116

Fernandez R, Garcia-Tiscar S, Santos MB, Lopez A, Martinez-Cedeira JA, Newton J, Pierce GJ (2011) Stable isotope analysis in two sympatric populations of bottlenose dolphins *Tursiops truncatus*: evidence of resource partitioning? Mar Biol 158:1043–1055

Findlay KP, Best PB, Ross GJBB, Cockcroft VG (1992) The distribution of small odontocete cetaceans off the coasts of South Africa and Namibia. S Afr J Mar Sci 12:237–270

Giménez J, Ramírez F, Almunia J, Forero MG, de Stephanis RG (2016) From the pool to the sea: applicable isotope turnover rates and diet to skin discrimination factors for bottlenose dolphins (*Tursiops truncatus*). J Exp Mar Biol Ecol 475:54–61

Giménez J, Cañadas A, Ramírez F, Afán I and others (2017a) Intra-and interspecific niche partitioning in striped and common dolphins inhabiting the southwestern Mediterranean Sea. Mar Ecol Prog Ser 567:199–210

Giménez J, Marçalo A, Ramírez F, Verborgh P and others (2017b) Diet of bottlenose dolphins (*Tursiops truncatus*) from the Gulf of Cadiz: insights from stomach content and stable isotope analyses. PLOS ONE 12:e0184673

Giménez J, Ramírez F, Forero MG, Almunia J, de Stephanis R, Navarro J (2017c) Lipid effects on isotopic values in

bottlenose dolphins (*Tursiops truncatus*) and their prey with implications for diet assessment. Mar Biol 164:122
Giménez J, Cañadas A, Ramírez F, Afán I and others (2018a) Living apart together: niche partitioning among Alboran Sea cetaceans. Ecol Indic 95:32–40
Giménez J, Louis M, Barón E, Ramírez F and others (2018b) Towards the identification of ecological management units: a multidisciplinary approach for the effective management of bottlenose dolphins in the southern Iberian Peninsula. Aquat Conserv 28:205–215
Golaski S (2013) Spatial and temporal patterns of habitat use of Heaviside's dolphins in Namibia. MSc thesis, University of Pretoria
Gowans S, Whitehead H (1995) Distribution and habitat partitioning by small odontocetes in the Gully, a submarine canyon on the Scotian Shelf. Can J Zool 73:1599–1608
Griffiths CL, Van Sittert L, Best PB, Brown AC and others (2004) Impacts of human activities on marine animal life in the Benguela: a historical overview. Oceanogr Mar Biol Annu Rev 42:303–392
Gross A, Kiszka J, Van Canneyt O, Richard P, Ridoux V (2009) A preliminary study of habitat and resource partitioning among co-occurring tropical dolphins around Mayotte, southwest Indian Ocean. Estuar Coast Shelf Sci 84:367–374
Gulka J, Carvalho PC, Jenkins E, Johnson K, Maynard L, Davoren GK (2017) Dietary niche shifts of multiple marine predators under varying prey availability on the northeast Newfoundland coast. Front Mar Sci 4:324
Healy K, Guillerme T, Kelly SBA, Inger R, Bearhop S, Jackson AL (2018) SIDER: an R package for predicting trophic discrimination factors of consumers based on their ecology and phylogenetic relatedness. Ecography 41:1393–1400
Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM and others (2009) The Benguela Current: an ecosystem of four components. Prog Oceanogr 83:15–32
Iitembu JA (2015) An attempt at modelling the diets of two sympatric species of hake (*Merluccius capensis* and *Merluccius paradoxus*) off the coast of Namibia: isotope mixing model approach. Int Sci Technol J Namibia 7:14–30
Iitembu JA, Miller TW, Ohmori K, Kanime A, Wells S (2012) Comparison of ontogenetic trophic shift in two hake species, *Merluccius capensis* and *Merluccius paradoxus*, from the Northern Benguela Current ecosystem (Namibia) using stable isotope analysis. Fish Oceanogr 21:215–225
Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER — Stable Isotope Bayesian Ellipses in R. J Anim Ecol 80:595–602
Katona S, Whitehead H (1988) Are Cetacea ecologically important? Oceanogr Mar Biol Annu Rev 26:553–568
Kaufman L, Rousseeuw P (1990) Finding groups in data: an introduction to cluster analysis. Wiley, New York, NY
Kellar NM, Trego ML, Chivers SJ, Archer FI, Minich JJ, Perryman WL (2013) Are there biases in biopsy sampling? Potential drivers of sex ratio in projectile biopsy samples from two small delphinids. Mar Mamm Sci 29:336–389
Kiszka J, van der Elst R (2015) Elasmobranchs (sharks and rays): a review of status, distribution and interaction with fisheries in the southwest Indian Ocean. In: van der Elst R, Everett B (eds) Offshore fisheries of the southwest Indian Ocean: their status and the impact on vulnerable species. Spec Publ 10. Oceanographic Research Institute, Durban, p 367–389
Kiszka J, Simon-Bouhet B, Martinez L, Pusineri C, Richard P, Ridoux V (2011) Ecological niche segregation within a community of sympatric dolphins around a tropical island. Mar Ecol Prog Ser 433:273–288
Kiszka J, Simon-Bouhet B, Gastebois C, Pusineri C, Ridoux V (2012) Habitat partitioning and fine scale population structure among insular bottlenose dolphins (*Tursiops aduncus*) in a tropical lagoon. J Exp Mar Biol Ecol 416-417:176–184
Kiszka JJ, Méndez-Fernandez P, Heithaus MR, Ridoux V (2014) The foraging ecology of coastal bottlenose dolphins based on stable isotope mixing models and behavioural sampling. Mar Biol 161:953–961
Kiszka JJ, Heithaus MR, Wirsing AJ (2015) Behavioural drivers of the ecological roles and importance of marine mammals. Mar Ecol Prog Ser 523:267–281
Krakstad JO, Kanandjembo A (2001) A summary of the fishery and biology of Cape horse mackerel in Namibian waters. In: Krakstad JO, Botes F, Kanandjembo A (eds) The research and management of horse mackerel in Namibian waters. Proceedings of an International Workshop. Ministry of Fisheries and Marine Resources, Swakopmund
Lawton RJ, Pratchett MS (2012) Influence of dietary specialization and resource availability on geographical variation in abundance of butterflyfish. Ecol Evol 2:1347–1361
Leeney RH, Carslake D, Elwen SH (2011) Using static acoustic monitoring to describe echolocation behaviour of Heaviside's dolphins (*Cephalorhynchus heavisidii*) in Namibia. Aquat Mamm 37:151–160
Loizaga De Castro R, Hoelzel AR, Crespo EA (2013) Behavioural responses of Argentine coastal dusky dolphins (*Lagenorhynchus obscurus*) to a biopsy pole system. Anim Welf 22:13–23
Loizaga De Castro R, Saporiti F, Vales DG, García NA, Cardona L, Crespo EA (2016a) Feeding ecology of dusky dolphins *Lagenorhynchus obscurus*: evidence from stable isotopes. J Mammal 97:310–320
Loizaga de Castro RR, Saporiti F, Vales DGDG, García NA, Cardona L, Crespo EA (2016b) What are you eating? A stable isotope insight into the trophic ecology of short-beaked common dolphins in the Southwestern Atlantic Ocean. Mamm Biol 81:571–578
Marcalo A, Nicolau L, Giménez J, Ferreira M and others (2018) Feeding ecology of the common dolphin (*Delphinus delphis*) in Western Iberian waters: Has the decline in sardine (*Sardina pilchardus*) affected dolphin diet? Mar Biol 165:44
Martin MJ, Gridley T, Roux JP, Elwen SH (2020) First abundance estimates of Heaviside's (*Cephalorhynchus heavisidii*) and dusky (*Lagenorhynchus obscurus*) dolphins off Namibia using a novel visual and acoustic line transect survey. Front Mar Sci 7:555659
Mecenero S, Kirkman SP, Roux JP (2006a) A refined fish consumption model for lactating Cape fur seals (*Arctocephalus pusillus pusillus*), based on scat analyses. ICES J Mar Sci 63:1551–1566
Mecenero S, Roux JP, Underhill L, Bester M (2006b) Diet of Cape fur seals *Arctocephalus pusillus pusillus* at three mainland breeding colonies in Namibia. 1. Spatial variation. Afr J Mar Sci 28:57–71
Mecenero S, Roux JP, Underhill LG, Kirkman SP (2006c) Diet of Cape fur seals *Arctocephalus pusillus pusillus* at three mainland breeding colonies in Namibia. 2. Temporal variation. Afr J Mar Sci 28:73–88

Meissner AM, MacLeod CD, Richard P, Ridoux V, Pierce G (2012) Feeding ecology of striped dolphins, *Stenella coeruleoalba*, in the north-western Mediterranean Sea based on stable isotope analyses. J Mar Biol Assoc UK 92:1677–1687

Méndez-Fernandez P, Taniguchi S, Santos MCO, Cascão I and others (2020) Population structure of the Atlantic spotted dolphin (*Stenella frontalis*) inferred through ecological markers. Aquat Ecol 54:21–34

Montevecchi WWA (1993) Birds as indicators of changes in marine prey stocks. In: Furness R, Greenwood J (eds) Birds as monitors of environmental change. Springer, Dordrecht, p 217–266

Montevecchi W (2002) Interactions between fisheries and seabirds. In: Sulzycki J, Lynch N (eds) Biology of marine birds. CRC Press, Boca Raton, FL, p 528–547

Newsome SD, Del Rio CM, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Front Ecol Environ 5:429–436

Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. Mar Mamm Sci 26:509–572

Oviedo L, Fernández M, Herra-Miranda D, Pacheco-Polanco JD, Hernández-Camacho CJ, Aurioles-Gamboa D (2018) Habitat partitioning mediates the coexistence of sympatric dolphins in a tropical fjord-like embayment. J Mammal 99:554–564

Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. PLOS ONE 5:e9672

Parrish JD (2000) Plasticity and conservation during migration. Stud Avian Biol 20:53–70

Petta JC, Shipley ON, Wintner SP, Cliff G, Dicken ML, Hussey NE (2020) Are you really what you eat? Stomach content analysis and stable isotope ratios do not uniformly estimate dietary niche characteristics in three marine predators. Oecologia 192:1111–1126

Pierce G, Boyle P (1991) A review of methods for diet analysis in piscivorous marine mammals. Oceanogr Mar Biol Annu Rev 29:409–486

Pinela AM, Borrell A, Cardona L, Aguilar A (2010) Isotope analysis reveals habitat partitioning among marine mammals off the NW African coast and unique trophic niches for two globally threatened species. Mar Ecol Prog Ser 416:295–306

Plagányi ÉE, Butterworth DS (2009) Competition with fisheries. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals, 2nd edn. Academic Press, Amsterdam, p 269–275

Polito MJ, Trivelpiece WZ, Karnovsky NJ, Ng E, Patterson WP, Emslie SD (2011) Integrating stomach content and stable isotope analyses to quantify the diets of pygoscelid penguins. PLOS ONE 6:e26642

Post D (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703–718

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179–189

Quérouil S, Freitas L, Dinis A, Alves F and others (2010) Sex bias in biopsy samples collected from free-ranging dolphins. Eur J Wildl Res 56:151–158

Quérouil S, Kiszka J, Cordeiro AR, Cascão I and others (2013) Investigating stock structure and trophic relationships among island-associated dolphins in the oceanic waters of the North Atlantic using fatty acid and stable isotope analyses. Mar Biol 160:1325–1337

Read AJ (2008) The looming crisis: interactions between marine mammals and fisheries. J Mammal 89:541–548

Robinson BW, Booms TL, Bechard MJ, Anderson DL (2019) Dietary plasticity in a specialist predator, the gyrfalcon (*Falco rusticolus*): new insights into diet during brood rearing. J Raptor Res 53:115–126

Rossman S, Ostrom PH, Stolen M, Barros NB, Gandhi H, Stricker CA, Wells RS (2015) Individual specialization in the foraging habits of female bottlenose dolphins living in a trophically diverse and habitat rich estuary. Oecologia 178:415–425

Roux JP, van der Lingen C, Gibbons M, Moroff N, Shannon L, Smith A, Cury P (2013) Jellyfication of marine ecosystems: lessons from the Benguela. Bull Mar Sci 89:249–284

Schoener TW (1974) Resource partitioning in ecological communities. Science 185:27–39

Sekiguchi K, Klages NTW, Best PB (1992) Comparative analysis of the diets of smaller odontocete cetaceans along the coast of Southern Africa. S Afr J Mar Sci 12:843–861

Shaughnessy P, Kirkwood R, Cawthorn M, Kemper C, Pemberton D (2003) Pinnipeds, cetaceans and fisheries in Australia: a review of operational interactions. In: Gales NJ, Hindell MA, Kirkwood R (eds) Marine mammals: fisheries, tourism and management issues. CSIRO Publishing, Melbourne, p 124–140

Smith JA, Mazumder D, Suthers IM, Taylor MD (2013) To fit or not to fit: evaluating stable isotope mixing models using simulated mixing polygons. Methods Ecol Evol 4: 612–618

Spitz J, Richard E, Meynier L, Pusineri C, Ridoux V (2006) Dietary plasticity of the oceanic striped dolphin, *Stenella coeruleoalba*, in the neritic waters of the Bay of Biscay. J Sea Res 55:309–320

Spitz J, Trites AW, Becquet V, Brind'Amour A, Cherel Y, Galois R, Ridoux V (2012) Cost of living dictates what whales, dolphins and porpoises eat: the importance of prey quality on predator foraging strategies. PLOS ONE 7:e50096

Stock BC, Jackson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX (2018) Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ 6:e5096

Tarroux A, Ehrich D, Lecomte N, Jardine TD, Bêty J, Berteaux D (2010) Sensitivity of stable isotope mixing models to variation in isotopic ratios: evaluating consequences of lipid extraction. Methods Ecol Evol 1: 231–241

Utne-Palm AC, Salvanes AGV, Currie B, Kaartvedt S and others (2010) Trophic structure and community stability in an overfished ecosystem. Science 329:333–336

van der Bank MG, Utne-Palm AC, Pittman K, Sweetman AK, Richoux NB, Brüchert V, Gibbons MJ (2011) Dietary success of a 'new' key fish in an overfished ecosystem: evidence from fatty acid and stable isotope signatures. Mar Ecol Prog Ser 428:219–233

van der Lingen C, Miller T (2011) Trophic dynamics of pelagic nekton in the southern Benguela Current ecosystem: calibrating trophic models with stable isotope analysis. In: Omori K, Guo X, Yoshi N, Fujii N, Handoh I, Isobe A, Tanabe S (eds) Interdisciplinary studies on environmental chemistry — marine environmental modeling & analysis. TERRAPUB, Tokyo, p 85–94

Van Waerebeek K, Würsig B (2009) Dusky dolphin: *Lageno-*

rhynchus obscurus. In: Perrin W, Würsig B, Thewissen JGW (eds) Encyclopedia of marine mammals, 2nd edn. Academic Press, Amsterdam, p 335–338

Walker J, Macko S (1999) Dietary studies of marine mammals using stable carbon and nitrogen isotopic ratios of teeth. Mar Mamm Sci 15:314–334

Watermeyer K, Shannon L, Roux JP, Griffiths C (2008) Changes in the trophic structure of the northern Benguela before and after the onset of industrial fishing. Afr J Mar Sci 30:383–403

Wilhelm MR, Kirchner CH, Roux JP, Jarre A, Iitembu JA, Kathena JN, Kainge P (2015) Biology and fisheries of the shallow-water hake (*Merluccius capensis*) and the deep-water hake (*Merluccius paradoxus*) in Namibia. In: Arancibia H (ed) Hakes: biology and exploitation. John Wiley & Sons, Ltd., Chichester, p 70–100

Wilson RM, Nelson JA, Balmer BC, Nowacek DP, Chanton JP (2013) Stable isotope variation in the northern Gulf of Mexico constrains bottlenose dolphin (*Tursiops truncatus*) foraging ranges. Mar Biol 160:2967–2980

Editorial responsibility: Keith Hobson, London, Ontario, Canada
Reviewed by: 2 anonymous referees

Submitted: October 9, 2020
Accepted: May 17, 2021
Proofs received from author(s): July 5, 2021