



Resource partitioning among South African delphinids



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ABSTRACT

In order to better understand trophic relationships among four species of coastal delphinids, we compared isotopic composition of skin to attempt to assess potential inter- and intra-specific resource partitioning. Skin samples were collected from Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (n = 132), long-beaked common dolphins (*Delphinus capensis*) (n = 78), humpback dolphins (*Sousa chinensis*) (n = 27), and striped dolphins (*Stenella coeruleoalba*) (n = 3) along the coastline of South Africa. While the latter species tends to be found offshore, the other species have overlapping distributions and feed on similar prey, carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analyses revealed resource partitioning with differences in diet and habitat use. Striped dolphin $\delta^{13}\text{C}$ values ($-16.97 \pm 0.25\%$, SD) were consistent with evidence that they typically forage offshore, while $\delta^{13}\text{C}$ values of humpback dolphins reflected their use of inshore habitats ($-15.16 \pm 0.65\%$). Common and bottlenose dolphins had $\delta^{13}\text{C}$ ($-15.48 \pm 0.66\%$ and $-15.76 \pm 0.71\%$ respectively) values that fell between these two extremes. Mean values for $\delta^{15}\text{N}$ ranged from $11.92 \pm 0.20\%$ for striped dolphins to $15.19 \pm 0.73\%$ for humpback dolphins, suggesting either that these species were feeding at different trophic levels or that they were feeding in different trophic systems. Common and bottlenose dolphins had $\delta^{15}\text{N}$ values of $13.49 \pm 0.50\%$ and $14.40 \pm 0.74\%$ respectively. Male bottlenose dolphins were significantly more enriched in $\delta^{15}\text{N}$ compared to females suggesting dietary differences. No sex related differences were found in other species. Isotopic niche width determinations using corrected standard elliptical area (SEA_c) were calculated. Humpback and bottlenose dolphins had the largest SEA_c reflecting a broader trophic niche, while striped dolphins had the smallest SEA_c reflecting a more specialized niche. Overall, these sympatric species appear to reduce potential competitive pressure through a combination of differing prey selection and habitat utilization.

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1. Introduction

Near-shore delphinids found in South African waters include Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), long-beaked common dolphins (*Delphinus capensis*), humpback dolphins (*Sousa chinensis*), and striped dolphins (*Stenella coeruleoalba*). All of these species, particularly those found inshore, face serious threats such as incidental catch in commercial fisheries (e.g., Cockcroft and Krohn, 1994) and shark nets (e.g., Cockcroft and Ross, 1990a, 1990b; Meyer et al., 2011; Peddemors et al., 1990), habitat loss, coastal pollution (e.g., Cockcroft et al., 1991) and overfishing of prey species (e.g., Roy et al., 2007; Sekiguchi et al., 1992).

Relatively little is known about the ecology of these four species and all are considered to be at some degree of risk. Indo-Pacific bottlenose dolphins, designated as “data deficient” throughout southern African waters (IUCN, 2013), are relatively common along the KwaZulu-Natal coast where there are approximately 900 residents with an average group size of 67 individuals (Cockcroft and Ross, 1990a, 1990b). This

species is frequently observed in mixed groups with other delphinid species, both nearshore and in waters up to 30 m in depth (Cockcroft, unpubl. data, Saayman et al., 1972). Common dolphins are also listed as “data deficient” (IUCN, 2013) due to a lack of information on how incidental and direct takes have affected their local populations. Members of this species frequently travel in large groups averaging 250 individuals, but can reach numbers in the thousands (Findlay et al., 1992). Common dolphins inhabit both nearshore and deeper waters in this region and are known to associate with bottlenose dolphins. Striped dolphins are listed as being of “least concern” (IUCN, 2013) due to a relatively large population size, whereas humpback dolphins have been designated as “near threatened” (IUCN, 2013). Being a coastal species, humpback dolphins suffer from both habitat destruction and incidental/direct takes in fisheries (e.g., Karczmarski, 2000) and the entire South African population has been estimated to be comprised of fewer than 1000 individuals (Karczmarski, 1996). Humpback dolphins are typically found nearshore in groups of less than ten individuals (Karczmarski, 1996) where coastal pollution is a significant threat (Cockcroft et al., 1991). Estimates of abundance for the KwaZulu-Natal humpback dolphin population suggest that there are approximately 160 individuals (Atkins et al., 2004) with an average group size of 7

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animals (Karczmarski, 1996). South African humpback dolphins have significantly higher levels of chlorinated hydrocarbons (PCBs, DDT and dieldrin) compared to other marine mammals along the KwaZulu-Natal coast (Cockcroft et al., 1991).

With the exception of striped dolphins, three of these four species are frequently observed in the same geographic area, and in some cases occurring in mixed-species aggregations, suggesting that there is either interspecific competition for resources, or that these sympatric dolphins are partitioning their resources. Stomach content analyses suggest that common dolphins prey primarily on neritic species, although seasonally they take advantage of nearshore species, whereas bottlenose and humpback dolphins feed mostly on inshore species. Pilchard (*Sardinops ocellatus*), chub mackerel (*Scomber japonicus*), elf (*Pomatomus saltatrix*), flying fish (*Cheilopogon* sp.), sardine (*Sardinops sagax*), lanternfish (*Gymnoscopelus bolini*), maasbanker (*Trachurus delagoa*), squid (*Loligo* spp.) and strepie (*Sarpa salpa*), have been noted to be important prey for common dolphins (Ambrose et al., 2013; Sekiguchi et al., 1992; Young and Cockcroft, 1994). Principal prey of bottlenose dolphins include benthic piggies (*Pomadasy olivaceum*), cuttlefish (*Sepia* spp.), chokka squid (*Loligo reynaudii*), and mullet (*Mugil* sp.), as well as some offshore species such as horse mackerel (*Trachurus capensis*) (e.g., Sekiguchi et al., 1992). Humpback dolphins prefer to consume glassnoses (*Thrissa vitrirostris*), striped grunter (*Pomadasy striatum*), and cuttlefish (e.g., Sekiguchi et al., 1992). Glassnoses and striped grunters are found primarily in estuaries and bays along shallow, rocky coasts (van der Elst, 1993). Striped dolphins are unlikely to be seen inshore, though frequent strandings occur and they appear to prey primarily on deeper water species, such as young chokka squid and hake (*Merluccius* sp.), with stomach content analyses revealed that at least 80% of prey had luminous organs indicating a deep water habitat (Ross, 1984; Sekiguchi et al., 1992). In some instances, sex differences in feeding habits have been noted. Male and female common dolphins have been shown to exhibit differences in foraging habits (e.g., Chou et al., 1995; Young and Cockcroft, 1994) with cephalopods comprising a larger fraction of diet for mature females compared to mature males (Silva, 1999). Alternatively, while some stomach content analyses of male and female Indo-Pacific bottlenose dolphins indicated no significant differences in prey preferences (Amir et al., 2005; Walton et al. 2007), others have found sex-specific differences in prey choice (Cockcroft and Ross, 1990a, 1990b).

Historically, research into the feeding ecology of marine mammals has been approached in a variety of ways, including anecdotal observations (e.g., Shane, 1990), fecal analysis of hard remains (e.g., Sinclair and Zeppelin, 2002), DNA analysis of feces (e.g., Dunshea et al., 2013; Meekan et al., 2009), examination of stomach contents of dead stranded animals (e.g., Barros and Wells, 1998; Barros et al., 2000; Dunshea et al., 2013), and stomach lavage (Antonelis et al., 1987; Dunshea et al., 2013; Gibbs et al., 2011). While all are useful techniques, each has limitations. Collection of fecal matter and identifying the source animal presents challenges given the aquatic environment and the reality that animals are often submerged. Collecting stomach contents from live animals (lavage) is invasive and identification of stomach contents either from live or dead animals may be difficult due to erosion of hard parts. Stomach contents may also represent only part of the diet since prey lacking hard parts will not be retained in the gut of the predator and some hard parts (such as squid beaks) may be retained in the stomach and therefore skew interpretation of relative importance of various prey species. Dead animals may have been unhealthy and therefore, not be representative of the population at large as far as stomach contents are concerned. In addition, stomach content analysis typically will only reveal information about the last meal or two, rather than representing long-term feeding history. In recent years, indirect assessments of feeding habits using stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) has become common (e.g., Alves-Stanley et al., 2010; Ambrose et al., 2013; Botta et al., 2011; Das et al., 2000; Fernandez et al., 2013; Gibbs et al., 2011; Gross et al., 2009; Marcoux et al., 2012; Mèndez-Fernandez

et al., 2012; Newsome et al., 2010; Owen et al., 2011; Quérouil et al., 2013; Ruiz-Cooley et al., 2004; Witteveen et al., 2009). With the refinement of isotope methodologies, resource partitioning has been demonstrated in several cetacean species (e.g., Botta et al., 2011; Browning et al., 2014b; Gibbs et al., 2011; Marcoux et al., 2012; Mèndez-Fernandez et al., 2012; Owen et al., 2011).

More recently, metrics have been developed for calculating isotopic niche width and population-level metrics of trophic structure using SIBER (Stable Isotope Bayesian Ellipses in R) (A.L. Jackson et al., 2011; M.C. Jackson et al., 2011; Jackson et al., 2012). The SIBER approach allows for prediction of trophic diversity, with a larger niche width indicating greater trophic diversity (more of a generalist consumer) and a smaller niche width indicating a lower trophic diversity, indicating more of a specialist consumer (A.L. Jackson et al., 2011; M.C. Jackson et al., 2011). These new developments allow for inter- and intra-specific comparisons of trophic levels, niche width and habitat utilization and ultimately an assessment of potential resource partitioning (e.g., Ambrose et al., 2013; Browning et al., 2014b; Fernandez et al., 2013; Gibbs et al., 2011; Quérouil et al., 2013).

There is an indication that, despite significant temporal and spatial overlap in distribution, these delphinid species exploit their habitat differentially suggesting niche differentiation. Resources may be partitioned through variations in habitat use patterns, temporal activity, and/or dietary preferences with the result that coexistence is possible and competition is reduced (Baird and Whitehead, 2000; Gibbs et al., 2011; Parra, 2006; Saayman and Taylor, 1973; Spitz et al., 2011; Wang et al., 2012). Of these, feeding habits are believed to be the largest driving force in niche differentiation (Wang et al., 2012), thus an understanding of species-specific habitat utilization and inter-specific trophic relationships is fundamental to making appropriate conservation and management decisions.

Stable isotope ratios of carbon primarily reflect the source of primary productivity and therefore can lend information about the habitat in which the predator has been foraging (e.g., Kelly, 2000). In aquatic ecosystems, carbon isotope ratios reflect differences between freshwater and marine sources as well as offshore/pelagic habitats versus inshore/benthic sources with values tending to become more enriched between offshore and inshore locations (Kelly, 2000). The coastline of southern Africa is dominated by the influence of the oligotrophic Agulhas Current which moves warm water from the Moçambique Channel along the southern coast as far west as Cape Agulhas (Hill and McQuaid, 2008). Large-scale isotopic signatures of the southern coast of South Africa are influenced by this current and the general positioning of trophic groups are comparable across along a 1400-km stretch of South African coastline (Hill and McQuaid, 2008).

In order to better understand trophic relationships among and within these four species, we examined differences in stable isotopic composition both inter- and intra-specifically. Knowledge of the ecological niche width of individual species can ultimately be used to assess the degree of interactions between different taxa and the goal of the present study was to compare isotopic composition to ultimately assess potential inter- and intra-specific resource partitioning among these four delphinid species. We hypothesized that (1) individuals within each species would have similar isotopic values but that sexes would differ isotopically; (2) that offshore striped dolphins would be distinctly different from nearshore species; and that (3) nearshore species would have distinct trophic niches that would be reflected by different stable isotopic composition.

2. Methods

2.1. Sample collection

Skin samples were collected opportunistically between 1995 and 2005 from Indo-Pacific bottlenose ($n = 119$), humpback ($n = 27$) and common ($n = 78$) dolphins that had become entangled in shark

nets deployed off the coast of KwaZulu-Natal (KZN), South Africa (29.8697° S, 31.0236° E) in order to protect swimming beaches (for a description see Weller et al., 1997). Additionally, three samples were collected from striped dolphins stranded off KZN. During necropsies, sex was determined, morphometrics obtained, and skin samples collected. Frozen skin samples were stored at -20°C until analyzed.

Additional skin samples ($n = 13$) were collected in 2008 from live adult free-ranging bottlenose dolphins in Plettenberg Bay, South Africa (34.0500° S, 23.3667° E) using biopsy darts (see Cockcroft and Krohn, 1994). Samples were removed from the dart, using sterilized forceps, placed into a vial, and stored on ice until returned to shore. Additional information gathered at each event included sampling location, sea conditions, whether the target individual was traveling alone or in a group, estimated body length, and pre- and post-darting behavior. Photographs of dorsal fins were also taken as part of a separate, on-going photo identification study and served to confirm that all samples were from different individuals. Onshore, skin was separated from the underlying blubber layer and kept frozen at -20°C until further processing.

2.2. Sample preparation and stable isotope analysis

Skin samples were oven dried at 60°C for 24 h to remove water. Since lipids are depleted in ^{13}C relative to lean tissue, all samples were lipid-extracted using petroleum ether prior to isotope analysis (Post et al., 2007; Schlechtriem et al., 2003). Lipid-extracted samples were again placed in a drying oven at 60°C for 24 h to remove residual solvent. Dried, lipid-extracted samples were then ground, using a Wig-L-Bug grinder (Dentsply, model MSD), into a homogeneous powder. Aliquots (0.9–1.5 mg) were sealed into 5 mm by 9 mm tin capsules and analyzed at the Stable Isotope Laboratory, Institute of Ecology, University of Georgia, using a Finnigan MAT Delta Plus XL isotope ratio mass spectrometer (IRMS). Data were reported in parts per thousand (‰) using delta notation (δ):

$$\delta X(\text{‰}) = \left(\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right) \times 1000$$

where X is ^{15}N or ^{13}C and R is the corresponding ratio of $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$. Standard reference materials were atmospheric nitrogen gas and carbon from PeeDee Belemnite. To assure quality control in sample analysis of stable isotope ratios, a known standard sample (bovine tissue) was run after every 12 unknown samples. Analytical errors for the standard samples ($n = 20$) were $\pm 0.01\text{‰}$ (SD) for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

Trophic relationships were described using Stable Isotope Bayesian Ellipses in R (SIBER) (A.L. Jackson et al., 2011; M.C. Jackson et al., 2011; Jackson et al., 2012). The Layman metric of convex hull area (TA) (Layman et al., 2007) can be converted directly to a measure of population niche area but it is highly sensitive to sample size and as a result its value increases with increasing sample sizes. In contrast the standard ellipse area (SEA) asymptotes with sample sizes of 30 (Syväranta et al., 2013) and while convex hulls increase as more samples are added, a standard ellipse contains 40% of the data regardless of sample size. The corrected standard ellipse area (SEA_c) provides a highly satisfactory estimate for all sample sizes (A.L. Jackson et al., 2011; M.C. Jackson et al., 2011; Jackson et al., 2012; Syväranta et al., 2013) and therefore we used SEA_c as a measure of the mean core population isotopic niche. Overlap in SEA_c between species was calculated using the overlap function in SIAR with a step function of 1.

Other metrics include NR (nitrogen range) providing information on the trophic length of the community and CR (carbon range) giving an estimate of the diversity of basal resources. Total area of the convex hull and mean distance to centroid (CD) were used to indicate niche width and diversity of diet or population trophic diversity respectively. Mean nearest neighbor distance (MNND), measuring the density and clustering of species in the community, and standard deviation of

nearest neighbor distance (SDNND), measuring the spread of individuals within isotopic space or population trophic evenness were also employed (A.L. Jackson et al., 2011; M.C. Jackson et al., 2011). All metrics were bootstrapped ($n = 10,000$) indicated by subscript b.

2.3. Statistical analyses

Data were tested for normality using Shapiro–Wilks (if sample size < 50) and Kolmogorov–Smirnov (K–S) tests (if sample size > 50), and tested for homogeneity of variance using Levene's test. Differences among species, sex, location and season were explored separately for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ using general linear model (GLM) univariate analysis. Three sex classes were defined: male, female, and unknown, the latter accounted for biopsy darting of live animals where sex was undetermined. Tukey's HSD post hoc tests were performed to determine homogeneous subsets. Raw data were analyzed in general linear models because: transformations failed to improve the few non-normal data; visual inspection of normal Q–Q plots and histograms indicated normality; and general linear models are considered robust to deviations from normality (Field, 2005). Statistical analyses were conducted using SPSS 20.0 with a critical value of $\alpha = 0.05$. Values reported are mean \pm SD.

3. Results

There were no significant differences found between bottlenose dolphins sampled in KwaZulu-Natal or those biopsied in Plettenberg Bay for either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ ($F_{1,130} = 0.903$, $p = 0.344$ and $F_{1,130} = 1.493$, $p = 0.224$ respectively), therefore these individuals were grouped together for further analyses. Overall, mean values for $\delta^{15}\text{N}$ ranged from $11.92 \pm 0.20\text{‰}$ (striped dolphins, $n = 3$) to $15.19 \pm 0.73\text{‰}$ (humpback dolphins, $n = 27$) (Table 1, Fig. 1) and mean $\delta^{13}\text{C}$ values ranged from $-16.97 \pm 0.25\text{‰}$ (striped dolphins) to $-15.16 \pm 0.65\text{‰}$ (humpback dolphins) (Table 1, Fig. 1).

Species showed significant differences in $\delta^{15}\text{N}$ values ($F_{3,239} = 64.092$, $p < 0.0001$), although time of year did not show a significant difference ($F_{1,239} = 1.852$, $p = 0.175$). Post hoc testing indicated that humpback ($15.19 \pm 0.73\text{‰}$), bottlenose ($14.40 \pm 0.74\text{‰}$), common ($13.49 \pm 0.50\text{‰}$) and striped ($11.92 \pm 0.20\text{‰}$) dolphins were all significantly different from each other in $\delta^{15}\text{N}$ (Fig. 1). Bottlenose dolphins of unknown sex ($14.40 \pm 0.45\text{‰}$, $n = 13$) were not significantly different from other males ($14.8 \pm 0.25\text{‰}$, $n = 68$) ($p < 0.001$) and were therefore included with males in intra-species analysis. When examining post hoc test results among categories of sex for $\delta^{15}\text{N}$ values, male/unknown sex and female ($13.8 \pm 0.44\text{‰}$, $n = 64$) bottlenose dolphins were significantly different ($p < 0.001$) from one another.

There were significant inter-specific differences for $\delta^{13}\text{C}$ ($F_{3,239} = 10.852$, $p < 0.0001$), but neither sex ($F_{2,228} = 1.641$, $p = 0.196$) nor time of year ($F_{1,228} = 3.158$, $p = 0.077$) were significantly different. Values for $\delta^{13}\text{C}$ were significantly lower for striped dolphins ($-16.97 \pm 0.25\text{‰}$), but bottlenose ($-15.76 \pm 0.71\text{‰}$), common ($-15.49 \pm 0.50\text{‰}$), and humpback ($-15.16 \pm 0.65\text{‰}$) dolphins were not significantly different from each other (Fig. 1). Unlike for $\delta^{15}\text{N}$, post-hoc tests indicated no significant differences for $\delta^{13}\text{C}$ for male ($-15.71 \pm 0.68\text{‰}$), female ($-15.85 \pm 0.60\text{‰}$) or unknown sex ($-15.51 \pm 1.17\text{‰}$) bottlenose dolphins.

There was no overlap in SEA_c between striped dolphins and any other species or between humpbacked dolphins and common dolphins, but a 40% overlap between *Tursiops* and humpbacked dolphins and a 9% overlap between *Tursiops* and common dolphins (Fig. 2, Table 2). Due to small sample size ($n = 3$), SEA_c for striped dolphins is only descriptive. Common dolphins had the smallest range of NR_b values (2.0%) whereas bottlenose dolphins had the widest (3.5%) (Table 2). Similarly CR_b values showed the greatest range in bottlenose dolphins (4.5%), while humpback dolphins had a much narrower range (2.6%) (Table 2). CD_b values ranged from 0.71‰ in common dolphins to 0.90‰ in bottlenose dolphins (Table 2). Humpback dolphins had a

Table 1
Mean values (\pm SD) of $\delta^{15}\text{N}$ (‰) and $\delta^{13}\text{C}$ (‰) by species.

| Species | Sample size (n) | $\delta^{15}\text{N}$ (‰) | $\delta^{13}\text{C}$ (‰) | C:N |
|---|-----------------|---------------------------|---------------------------|-----------------|
| Humpback dolphin (<i>Sousa chinensis</i>) | 27 | 15.19 \pm 0.73 | -15.16 \pm 0.65 | 3.39 \pm 0.11 |
| Indo-Pacific bottlenose dolphin (<i>Tursiops aduncus</i>) | 132 | 14.40 \pm 0.74 | -15.76 \pm 0.71 | 3.55 \pm 0.21 |
| Common dolphin (<i>Delphinus capensis</i>) | 78 | 13.49 \pm 0.50 | -15.48 \pm 0.66 | 3.54 \pm 0.19 |
| Striped dolphin (<i>Stenella coeruleoalba</i>) | 3 | 11.92 \pm 0.20 | -16.97 \pm 0.25 | 3.27 \pm 0.06 |

greater MNND_b (0.25‰), than either common dolphins (0.15‰) or bottlenose dolphins (0.14‰) (Table 2).

4. Discussion

In the present study, humpback and common dolphins had the most enriched $\delta^{13}\text{C}$ values consistent with nearshore foraging. Striped dolphin $\delta^{13}\text{C}$ values were most depleted, differing significantly from the other three species, consistent with evidence that they typically forage further offshore (>500 m depth; Findlay et al., 1992; Ross, 1984; Saayman et al., 1972). Carbon isotopes values for bottlenose dolphins fell between those of common and striped dolphins.

Inter-specific differences in $\delta^{15}\text{N}$ are consistent with some degree of resource partitioning occurring. Humpback dolphins were most enriched in $\delta^{15}\text{N}$, averaging 3‰ greater than striped dolphins; the most ^{15}N depleted of the four species. Diet-tissue discrimination values for $\delta^{15}\text{N}$ ranges from 1.7 to 3.0‰ in cetaceans (Browning et al., 2014a) and therefore this inter-specific difference could suggest that humpback dolphins were foraging approximately one trophic level above striped dolphins in this ecosystem (Browning et al., 2014a; Rau et al., 1983). Alternatively, it could be a result of feeding in a different trophic system (i.e., inshore vs. offshore) which has a different isotopic base as is suggested by the $\delta^{13}\text{C}$ values of the cetacean species analyzed. Bottlenose and common dolphins were intermediate in $\delta^{15}\text{N}$, but closer to humpbacks than to striped dolphins, consistent with reported analyses of stomach contents (e.g., Ittembu et al., 2012; Nam et al., 2011; Ross, 1984; Sekiguchi et al., 1992; van der Elst, 1993; Young and Cockcroft, 1994). Examining the natural history of potential prey species supports our findings of differences in both carbon and nitrogen composition of dolphin consumers. The $\delta^{15}\text{N}$ findings in the present study are also consistent with previous suggestions, based on stomach content analysis, where these delphinids were feeding on either completely different prey, or different proportions of prey.

Groups of common dolphins are typically found offshore in deeper waters, and stomach content analyses indicate prey of pelagic origin

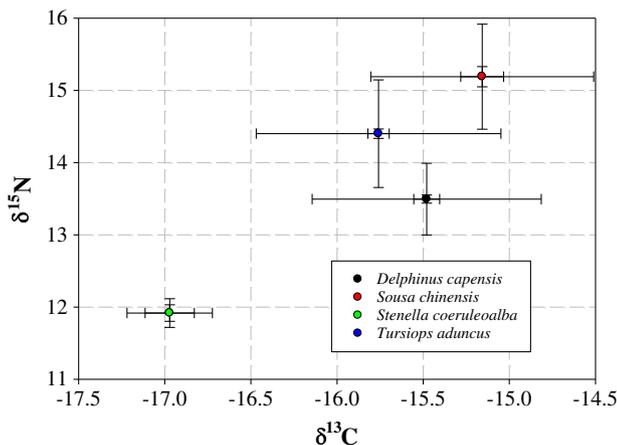


Fig. 1. Stable isotope bi-plot showing inter-specific differences in isotope values (mean \pm SE and SD) of skin for four species of South African delphinids. All species showed significant differences in $\delta^{15}\text{N}$ ($F_{3,239} = 64.092$, $p < 0.0001$) but only *Stenella coeruleoalba* was significantly different for $\delta^{13}\text{C}$.

(Young and Cockcroft, 1994), however, individuals off the KwaZulu-Natal coast move nearshore in response to movements of sardines moving along the coast in the 200 m isobath (Peddemors, 1999; Young and Cockcroft, 1994) and these dolphins presumably would be the animals that become entangled in the shark nets. Stomach content analyses of stranded and shark-net entangled dolphins reveal that near-shore sardines and chub mackerel constitute the bulk of their diet (Ambrose et al., 2013; Sekiguchi et al., 1992; Young and Cockcroft, 1994) and therefore it would be expected that the $\delta^{13}\text{C}$ composition of these dolphins would reflect the carbon-enriched inshore habitat (Barquette et al., 2013; van der Lingen and Miller, 2011). Ambrose et al. (2013) reported similar isotope values for South African common dolphins from analyses of teeth collected between 1980 and 2008. Based on recent assessments of isotopic turnover rates in the skin of captive bottlenose dolphins (Browning et al., 2014a), animals would only need to be feeding in these habitats for three weeks to have their isotopic composition reflect an inshore derived diet.

An observational study by Saayman et al. (1972) documented that South African humpback dolphins remained near shore (within 250 m), foraging on reefs in turbid waters along rocky coastlines. The observation of demersal inshore fish species in the stomach contents of humpback dolphins is consistent with their use of shallow, inshore waters including estuaries and the mouths of rivers and enclosed bays (Barros and Cockcroft, 1991; Karczmarski, 1996). Saayman et al. (1972) also observed bottlenose dolphins following similar inshore routes as humpback dolphins and on occasion being seen in mixed species groups with them. Bottlenose dolphins along the KwaZulu-Natal coast seem to be generalist feeders with diets comprised of over 72 species, although 6 species accounted for approximately 60% of the diet by mass (Cockcroft and Ross, 1990b).

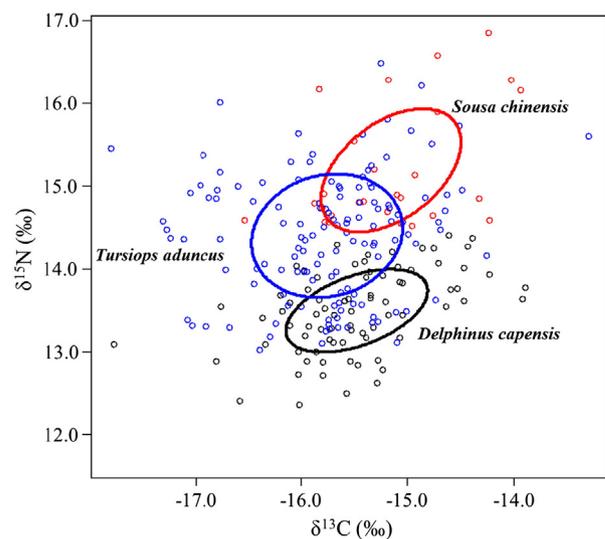


Fig. 2. Stable isotope bi-plot illustrating isotopic niche space of three species of South African delphinids. Lines enclose the standard ellipse area (SEA_c) for each species as calculated using SIBER (A.L. Jackson et al., 2011; M.C. Jackson et al., 2011). There is no overlap in SEA_c between humpbacked dolphins and common dolphins but there is a 40% overlap between bottlenose and humpback dolphins and a 9% overlap between bottlenose and common dolphins.

Table 2Population-level metrics of trophic structure for three coastal species of delphinids. Data for striped dolphins are not included due to small sample size ($n = 3$).

| Species | Sample size (n) | NR _b (‰) | CR _b (‰) | CD _b (‰) | MNND _b (‰) | SDNND _b (‰) | SEA _c (‰ ²) |
|---|-----------------|---------------------|---------------------|---------------------|-----------------------|------------------------|------------------------------------|
| Humpback dolphin (<i>Sousa chinensis</i>) | 27 | 2.32 | 2.60 | 0.85 | 0.25 | 0.22 | 1.37 |
| Indo-Pacific bottlenose dolphin (<i>Tursiops aduncus</i>) | 132 | 3.46 | 4.50 | 0.90 | 0.14 | 0.15 | 1.66 |
| Common dolphin (<i>Delphinus capensis</i>) | 78 | 2.04 | 3.88 | 0.71 | 0.15 | 0.14 | 0.92 |

NR_b = $\delta^{15}\text{N}$ range; CR_b = $\delta^{13}\text{C}$ range; CD_b = mean distance to centroid, MNND_b = mean nearest neighbor distance; SDNND_b = standard deviation of MNND_b; SEA_c = standard ellipse area.

Isotopic values in the present study indicate that these two species (humpback and bottlenose dolphins) are selecting different prey, or different proportions of the same prey, even though they are feeding in the same areas. Saayman et al. (1972) also noted that bottlenose dolphins spent similar amounts of time in deeper waters as they did in shallow inshore waters and this observation is consistent with $\delta^{13}\text{C}$ values that are an average of these two habitats. Given the rapid turnover time of these isotopes in cetacean skin of about 3 weeks (Browning et al., 2014a), the melding of nearshore and offshore isotopic signatures is quite probable.

Overall, these findings suggest some degree of spatial separation in foraging and prey preferences, despite overlapping ranges. The lack of overlap in SEA_c between humpback dolphins and common dolphins, is consistent with their spatial separation. The 40% overlap between *Tursiops* and humpbacked dolphins and a 9% overlap between *Tursiops* and common dolphins is consistent with observed spatial distribution of these species.

Isotopic niche width has been compared to traditional measures of niches used by ecologists. Because stable isotope measurements are influenced directly by what an animal consumes and its habitat, they are indicators of isotopic niche (Newsome et al., 2010). In the present study, humpback and bottlenose dolphins had the largest SEA_c, striped dolphins had the smallest SEA_c, and the SEA_c for common dolphins was intermediate. Larger SEA_c values reflect a broader trophic diversity, while smaller SEA_c values reflect a narrower trophic niche width or a more specialized niche. Excluding striped dolphins, common dolphins had the smallest range of nitrogen values and bottlenose dolphins had the widest. Similarly carbon values showed the greatest range in bottlenose dolphins, with a much narrower range in humpback dolphins. In general, delphinids are thought to be generalist consumers, although, some studies indicate that some species may be more selective in their prey choices and either minimize acquisition costs by targeting soniferous fishes (Gannon et al., 2005) or maximize energy gain by selecting on the basis of prey quality (i.e., Meynier et al., 2008; Spitz et al., 2012). The niche width of striped dolphins was considerably lower than the other three dolphin species indicating a lower trophic diversity. In addition, there was no overlap in SEA_c between striped dolphin and any other species or between humpbacked dolphins and common dolphin, but a 40% overlap between *Tursiops* and humpbacked dolphins and a 9% overlap between *Tursiops* and common dolphin. Previous stomach content analysis of striped dolphins revealed a heavier dependence on cephalopods over fish and striped dolphins had a lower measure of dietary diversity (measured by the Shannon–Wiener Information Measure) when compared to bottlenose and common dolphins (Sekiguchi et al., 1992).

Groups of dolphins can vary dramatically in size, from a few to thousands of individuals, and can range from being extremely fluid with individuals coming and going constantly, to a much more rigid structure (Moeller, 2012). When considering the composition of social groupings of most large delphinid groups, they include mature males and females as well as immature individuals and therefore it is not surprising that there would be some overlap in prey species taken. However, most of these groups retain a fission–fusion nature with an open social network where individuals move in and out due to the low energetic cost of locomotion (Randic et al., 2012). In mammals, female lifetime reproductive success is tied to access to resources such as food, while in males

it is limited to access to receptive mates (Moeller, 2012). This can result in males moving over larger areas than that of female dolphins, hence giving males access to differing prey items. Mature females may also be restricted in range and diving depths because of accompanying nursing calves and/or immature animals that are limited in their distribution (Ringelstein et al., 2006). These factors may lend an explanation for the significant differences in $\delta^{15}\text{N}$ between sexes seen in bottlenose dolphins in the present study and consistent with previous stomach content analyses (Cockcroft and Ross, 1990b).

Male/unknown sex bottlenose dolphins were significantly more enriched in $\delta^{15}\text{N}$ than females, suggesting possible differences in prey selection between male and female bottlenose dolphins, as has previously been suggested using fatty acid analysis of blubber (e.g., Browning et al., 2014b; Samuel and Worthy, 2004). Cockcroft and Ross (1990b) examined gut contents of bottlenose dolphins off the coast of Natal, South Africa and found significant differences in male and female diets. Differences in foraging habits between male and female common dolphins have also been documented where mature females had a significantly higher proportion of cephalopods in their stomachs compared to mature males (Chou et al., 1995; Silva, 1999; Young and Cockcroft, 1994) but no such difference was observed in the present study. Others have found no significant differences in diet between male and female dolphins either when examining stomach contents (e.g., Indo-Pacific bottlenose dolphins – Amir et al., 2005) or isotopic composition (e.g., Commerson's dolphins, *Cephalorhynchus commersonii* – Riccialdelli et al., 2013).

In summary, this study supports evidence for resource partitioning in four sympatric South African delphinid species. It also shows indications of resource partitioning between bottlenose dolphin sexes. Striped dolphins were most different from the other three species (common, bottlenose, and humpback), though more striped dolphin individuals need to be sampled in subsequent work to confirm this pattern. Carbon isotope values indicated differences in habitat utilization among the four species. Sympatric species are able to coexist by reducing competitive pressures through resource partitioning in three primary ways: temporal variation, diet composition, and habitat utilization (Friedlaender et al., 2009; Wang et al., 2012). The present study was the first of its kind to document that South African common, bottlenose, humpback, and striped dolphins are partitioning their foraging space and diet.

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