



Inter- and intra-specific trophic interactions of coastal delphinids off the eastern coast of South Africa inferred from stable isotope analysis

Michelle Caputo^{a,b,*}, Thibaut Bouveroux^c, Megan van der Bank^{d,e}, Jeremy Cliff^f,
Jeremy J. Kiszka^b, Pierre William Froneman^{a,1}, Stephanie Plön^{g,h,1}

^a SARCHI Chair in Marine Ecology, Department of Zoology and Entomology, Rhodes University, P.O. Box 94, Grahamstown, 6140, South Africa

^b Institute of Environment, Department of Biological Sciences, Florida International University, 3000 NE 151 St, North Miami, FL, 33181, USA

^c Dauphin Island Sea Lab, 101 Bienville Blvd., Dauphin Island, 36528, USA

^d Eastern Cape Parks and Tourism Agency, East London, P.O. Box 11235, Southernwood, East London, 5213, South Africa

^e South African National Biodiversity Institute, Private Bag X7, Claremont, Cape Town, 7735, South Africa

^f KwaZulu-Natal Sharks Board, Umhlanga Rocks, 4320 and School of Life Sciences, University of KwaZulu-Natal, Durban, South Africa

^g Department of Pathology, Stellenbosch University, South Africa

^h Bayworld Centre for Research and Education (BCRE), Gqeberha, South Africa

ARTICLE INFO

Keywords:

Tursiops aduncus

Delphinus delphis

Dietary niche analysis

Sardine run

SIBER

South Africa

ABSTRACT

Dietary tracers, such as bulk stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes, can be used to investigate the trophic interactions of marine predators, which is useful to assess their ecological roles within communities. These tracers have also been used to elucidate population structure and substructure, which is critical for the better identification of management units for these species affected by a range of threats, particularly bycatch in fishing gears. Off eastern South Africa, large populations of Indo-Pacific bottlenose (*Tursiops aduncus*) and common dolphins (*Delphinus delphis*) co-occur and are thought to follow the pulses of shoaling sardines (*Sardinops sagax*) heading north-east in the austral winter. Here we used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to investigate the trophic interactions and define ecological units of these two species along a ≈ 800 km stretch of the east coast of South Africa, from Algoa Bay to the coast of KwaZulu-Natal. Common and bottlenose dolphin dietary niche overlapped by 39.7% overall in our study area, with the highest overlap occurring off the Wild Coast (40.7% at Hluleka). Both stable isotopes were significantly enriched in bottlenose dolphins sampled in the western part of our study area (i.e., Algoa Bay and Amathole) compared to eastern animals (i.e., from Hluleka, Pondoland, and KZN). In areas where genetic information is not available or is insufficient, food web tracers (such as stable isotopes) can be used to group individuals based on trophic ecology, which can provide ecological units for management of populations. The distinct isotope signatures found here for bottlenose dolphins can, therefore, be used as management units for conservation efforts in the future.

1. Introduction

In marine ecosystems, predator species can exhibit varying levels of habitat and foraging specialization, both at the individual and/or at the scale of groups or communities (Giménez et al., 2018; Hoelzel et al., 2007; Rossman et al., 2015; Vaudo and Heithaus, 2011). Even within relatively small geographic areas, populations of small cetaceans can exhibit differentiation in their use of habitats and resources, allowing researchers to identify substructure within populations (Barros et al.,

2010; Bisi et al., 2013; Borrell et al., 2013; Browning et al., 2014b; Burton and Koch, 1999; Kiszka et al., 2011; Wilson et al., 2013). This can be particularly useful for the identification of population segments, which have distinct foraging behaviors and habitat use patterns (Browning et al., 2014b; Kiszka et al., 2012). Ultimately, the differential resource/habitat use may lead to genetic differences (Ansmann et al., 2015; Hoelzel et al., 2007), although this is difficult to detect in wild populations. More importantly, the ability to identify ecological units is critical to the management of these species since these groupings may be

* Corresponding author. SARCHI Chair in Marine Ecology, Department of Zoology and Entomology, Rhodes University, P.O. Box 94, Grahamstown, 6140, South Africa.

E-mail address: mcaputo@fiu.edu (M. Caputo).

¹ Pierre William Froneman and Stephanie Plön joint last author

<https://doi.org/10.1016/j.marenvres.2022.105784>

Received 5 April 2022; Received in revised form 4 October 2022; Accepted 17 October 2022

Available online 21 October 2022

0141-1136/© 2022 Elsevier Ltd. All rights reserved.

subject to and respond differently to stressors and disturbances (Barros et al., 2010; Browning et al., 2014b; Giménez et al., 2018; Méndez-Fernandez et al., 2020).

Traditionally, information on the diet of marine predators, such as small cetaceans, has been collected from stomach content analysis of bycaught or stranded animals (Ambrose et al., 2013; di Benedetto and Monteiro, 2015; Kaiser, 2012; Rossman et al., 2015). However, this method only provides short-term insights into their feeding ecology and may be biased due to differential digestion rates of different prey (Pierce and Boyle, 1991), especially as fish otoliths and squid beaks digest or pass through the digestive system relatively slowly (Bowen and Iverson, 2012). Given these limitations, stable isotope analysis has been increasingly employed to assess the trophic ecology of a variety of marine mammals in both inshore and offshore marine ecosystems (Borrell et al., 2013; Burton and Koch, 1999). Predator stable isotope composition, specifically carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios, reflects those of their prey, providing a powerful method of characterizing predator feeding habitats and relative trophic position (Newsome et al., 2007, 2010; Post, 2002). A major limitation in using stable isotope analysis is that it does not provide as detailed a description of a consumer's diet as stomach content analysis. Bayesian mixing models help to resolve this issue by estimating the contribution of prey to a consumer's diet (Stock et al., 2018); however, these require tissue samples of all potential prey, which are often not available. Despite these limitations, isotope values from tissues have the advantage of being assimilated slowly in comparison to stomach contents, and so represent a consumer's trophic interaction over a much longer time period (Newsome et al., 2010; Walker and Macko, 1999). Stable isotope analysis has therefore become increasingly common in cetacean research to understand resource use and partitioning between sympatric species (Browning et al., 2014a; Kiszka et al., 2010; Méndez-Fernandez et al., 2013; Oviedo et al., 2018; Pinela and Borrell, 2010).

Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) and common dolphins (*Delphinus delphis*), hereafter referred to as bottlenose and common dolphins, respectively, are the most abundant small cetaceans in coastal and continental shelf waters off South Africa (Bouveroux et al., 2018; Caputo et al., 2021, 2020, 2017; Cockcroft and Peddemors, 1990; Natoli et al., 2006). These species can occur in large groups, especially when feeding (Bouveroux et al., 2018; Caputo et al., 2021, 2020, 2017; Cockcroft et al., 1991; O'Donoghue et al., 2010; Ross et al., 1987). Past studies indicate that common dolphins are typically found further offshore (water depth 15–60m) than bottlenose dolphins (water depth 8–20m; Best, 2007; Melly et al., 2017). In the coastal province of KwaZulu-Natal (KZN), limited isotopic niche overlap has been found, suggesting these two species occupy two distinct foraging niches in this region (Browning et al., 2014a). However, off the Wild Coast, immediately to the south of KZN, narrowing of the continental shelf and the occurrence of sardines (*Sardinops sagax*) during the austral winter concentrates both dolphin species inshore, leading to increased foraging niche overlap during this particular food pulse (Ambrose et al., 2013; Bouveroux et al., 2018; Browning et al., 2014a; Melly et al., 2017; Natoli et al., 2004; Reisinger and Karczmarski, 2010; Ross et al., 1989; Young and Cockcroft, 1994). The presence of shoaling sardines off the east coast of South Africa is also thought to attract a genetically distinct migratory stock of bottlenose dolphins to the region (Cockcroft et al., 2016; Natoli et al., 2008). In addition, two genetically distinct populations have been described: the Agulhas ecoregion stock and the Natal ecoregion stock (Fig. 1; Vargas-Fonseca, 2018). The link between the migratory stock following the sardine run and these two remains unknown (Cockcroft et al., 2016; Vargas-Fonseca, 2018); however, the oceanography of these two areas differs, as the continental shelf narrows northeasterly, in the Wild Coast and KZN areas. Here we use stable isotopes analysis to investigate whether the trophic ecology of delphinids in the area could be used to identify sub-groupings or ecological

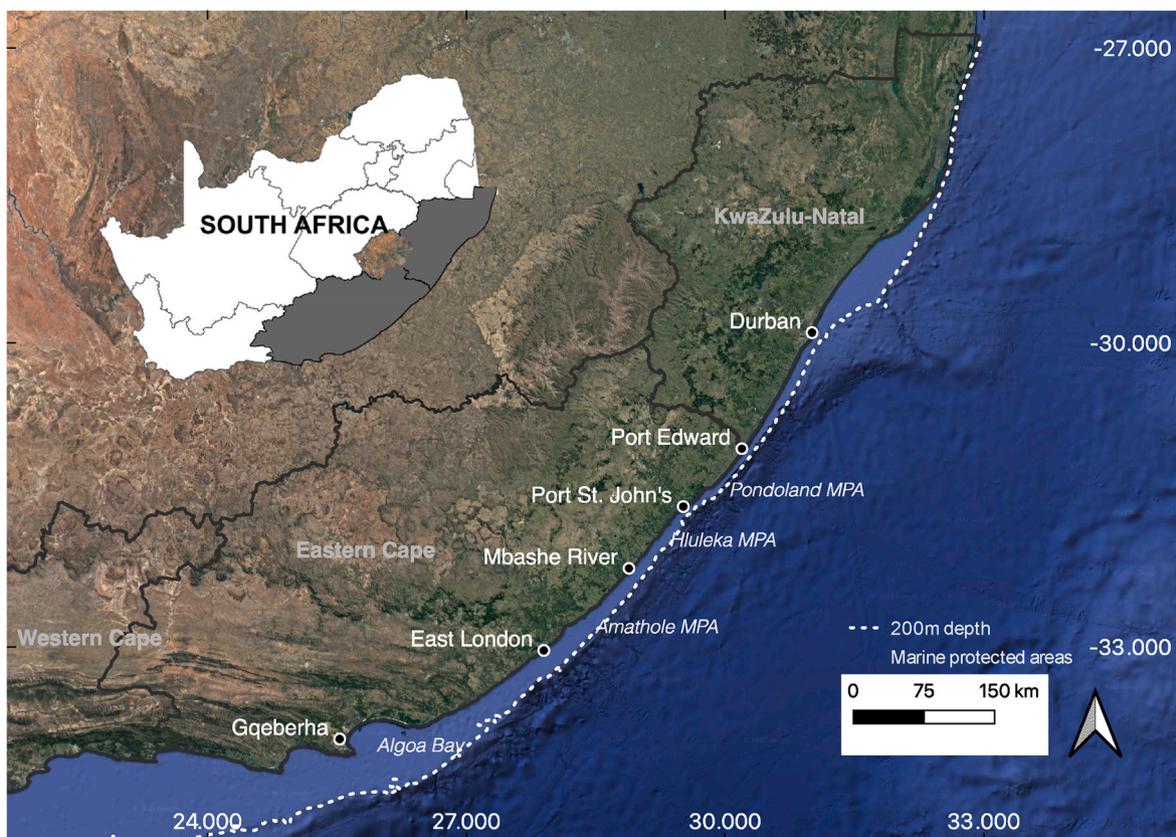


Fig. 1. Map of biopsy sampling (i.e., Algoa Bay and the Wild Coast: i.e. Amathole, Hluleka and Pondoland) and bycatch sites (KwaZulu-Natal) off the eastern coast of South Africa, for Indo-Pacific bottlenose dolphins (BND) and common dolphins (CD). The 200m depth contour is indicated by the dotted line.

units in both bottlenose dolphins and common dolphins, predicting that EC animals would be distinct from KZN. We also examine the intra- and inter-species variations in stable carbon and nitrogen values of bottlenose and common dolphins off the south-eastern coast of South Africa to determine the trophic relationships between these two species, and to explore the short-term spatial and temporal patterns in their feeding ecology, especially as it relates to the sardine run.

2. Methods

2.1. Study area

This study was conducted along the east coast of South Africa in three main focal areas: Algoa Bay, the Wild Coast, and KZN (Fig. 1). Algoa Bay is a relatively shallow bay (<70 m depth), with water temperatures ranging from approximately 17–21 °C, with periodic upwelling events reducing temperatures to below 13 °C (Goschen and Schumann, 2011). Approximately 200 km north-east of Algoa Bay lies the region known as the Wild Coast, which is 330 km long and stretches from East London to Port Edward, the southernmost town in KZN (Fig. 1). This region is predominantly affected by the Agulhas Current, flowing in a south-westerly direction along the continental shelf edge, with average surface velocity exceeding 2.5 m/s (Roberts et al., 2010). The continental shelf narrows in this region, defined largely by the 50m depth contour (Roberts et al., 2010). Important seasonal sardine concentrations in these coastal waters attract a diversity of marine predators, including predatory fish, seabirds, sharks, and cetaceans (Caputo et al., 2017; Lutjeharms et al., 2000; O'Donoghue et al., 2010b; Roberts et al., 2010). Further north along the KZN coastline (Fig. 1), oceanography differs from south-west to north-east, largely reflecting the northward narrowing of the continental shelf. The southernmost and central sections of the south coast of KZN are similar to the Wild Coast in that the continental shelf is narrow, bringing the fast-flowing, warm Agulhas Current waters inshore, within 5 km of the coastline (O'Donoghue et al., 2010a; Roberts et al., 2010). In the northernmost section of the south coast, a large semi-permanent eddy called the Durban Eddy strongly influences the oceanography, occasionally shifting the current northward (O'Donoghue et al., 2010b; Roberts et al., 2010). This region is considered a transition zone between the southern and northern sections of the KZN coast. In the north, currents are dominated primarily by wind, and not by the Agulhas Current, due to the widening of the continental shelf in this area (O'Donoghue et al., 2010b; Roberts et al., 2010).

2.2. Sampling

Biopsy sampling was conducted during surveys in Algoa Bay and off the Wild Coast (Fig. 1). Biopsy samples were taken from adult bottlenose and common dolphins using a modified 0.22 air-fired rifle for veterinary purposes with an adjustable pressure valve (Krützen et al., 2002). In Algoa Bay, boat-based surveys were conducted once a month from July 2015 to July 2016 along the 10m depth contour. Off the Wild Coast, boat-based surveys were conducted out of three Eastern Cape Parks and Tourism Agency (ECPTA) reserves between June 2014 and July 2016 in three different sampling areas: Amathole, Hluleka, and Pondoland, each located within marine protected areas (MPAs; Fig. 1). The surveys took place over three weeks, in June (winter), November/December (summer), and February/March (summer) each year. Only one study area (i. e., Amathole, Hluleka or Pondoland) was sampled per three-week trip, rotating the areas with each new trip. During these trips, surveys were conducted along the 15m and the 30m depth contours, northeast or southwest of the launch site on each alternate trip. Samples were kept frozen (−80 °C) until analysis. All samples were divided into austral winter (May–September) and austral summer (November–March) seasons (Table 1). There were no samples from April or October. This study was conducted with ethical clearance from Rhodes University and

Table 1

Mean (±SD) seasonal (summer and winter) stable isotope carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) values for bottlenose dolphins (*Tursiops aduncus*) and common dolphins (*Delphinus delphis*) from Algoa Bay, the Wild Coast (Amathole, Hluleka and Pondoland), and KwaZulu-Natal (KZN) of South Africa.

	Summer			Winter		
	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Bottlenose dolphins</i>						
Algoa Bay	14	−14.83 ± 0.76	13.99 ± 0.79	8	−14.85 ± 0.33	13.86 ± 0.59
Amathole	4	−14.77 ± 0.34	12.92 ± 0.39	5	−15.03 ± 0.48	12.79 ± 0.47
Hluleka	35	−15.65 ± 0.32	12.39 ± 0.55	30	−15.75 ± 0.33	12.24 ± 0.81
Pondoland	26	−15.95 ± 0.43	12.36 ± 0.53	28	−15.96 ± 0.49	12.06 ± 0.78
KZN	9	−16.46 ± 0.59	12.05 ± 0.35	5	−16.12 ± 0.46	11.97 ± 0.4
<i>Common dolphins</i>						
Algoa Bay	1	−15.80	12.83			
Amathole	12	−15.6 ± 0.21	11.71 ± 0.37	16	−15.14 ± 0.4	12.58 ± 0.46
Hluleka	42	−16.08 ± 0.47	12.05 ± 0.61	38	−15.53 ± 0.45	11.99 ± 0.7
Pondoland	5	−15.85 ± 1.33	12.49 ± 1.19	15	−15.92 ± 0.43	11.67 ± 0.61
KZN	1	−16.20	11.86	6	−15.61 ± 0.61	12.23 ± 0.77

Nelson Mandela University under permit A15-SC-ZOO-012.

Skin samples from south and central KZN waters (Fig. 1) were obtained from animals incidentally caught in bather protection nets (BPN) administered by KZN Sharks Board (Cliff and Dudley, 1992, 2011). North-eastern KZN samples were not available and “KZN” refers only to sampling locations in Fig. 1. Animals were immediately frozen upon collection from nets, which are checked daily except for weekends. No animals retrieved on a Monday were included in this study to ensure the quality of the tissue samples, as these may have been in the net all weekend (Lane et al., 2014). Skin samples were collected from the dorsal region, in the same area as biopsy samples were taken to ensure consistency and kept frozen at −80 °C until analysis. Complete turnover rate of stable isotopes of skin samples of common bottlenose dolphin (*Tursiops truncatus*) is 104.40 ± 35 days for $\delta^{13}\text{C}$ and 205.8 ± 84.49 for $\delta^{15}\text{N}$ (Giménez et al., 2016), which may limit the interpretation of seasonal dietary fluctuations. Thus, seasons reported here reflect only time of sample collection.

2.3. Stable isotope analysis

Biopsy samples were separated into blubber and skin, with only the skin being analysed for stable isotopes (Newsome et al., 2010). Skin samples were oven dried at 60 °C for 48h to remove any water. The samples were then lipid extracted using a modified Bligh and Dyer (1959) method. Individual samples were placed in test tubes and covered with a 2:1 methanol:chloroform solution (Bligh and Dyer, 1959) 1.2 ml per sample), agitated for 20 s using a benchtop mixer (IKA MS3 basic) and then left to stand overnight at room temperature. The methanol:chloroform solution was removed the following day using a pipette. The samples were then dried in an oven at 70 °C for 24 h to remove any remaining solvent and ground into a fine powder (Bligh and Dyer, 1959). Aliquots of approximately 0.6–0.7 mg (tissues) were weighed into tin capsules that were pre-cleaned in toluene.

Isotopic analysis was undertaken on a Flash EA 1112 Series elemental analyser coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system (all equipment supplied by Thermo Fischer, Bremen, Germany), housed at the Stable Isotope Laboratory, Mammal Research Institute, University of Pretoria.

A laboratory running standard (Merck Gel: $\delta^{13}\text{C} = -20.57\text{‰}$, $\delta^{15}\text{N} =$

6.8‰, C% = 43.83, N% = 14.64) and blank sample were run after every 12 samples. 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:

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

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

2.4. Statistical analysis

Data were tested for normality using inspection of Q-Q plots and histograms, and Shapiro–Wilks tests, and for homogeneity of variance using Levene’s test. Differences among species, location, and season were explored for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ separately using a general linear model (GLM). Tukey’s HSD *post hoc* tests were performed to investigate pairwise comparisons. ANOVAs were used to investigate the effect of location and season on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ within each species. Reciprocal transformation of $\delta^{15}\text{N}$ was performed to satisfy the normality assumption. Q-Q plots and histograms appeared normal for $\delta^{13}\text{C}$ and the reciprocal of $\delta^{15}\text{N}$. Statistical analyses were performed in R (v. 3.2.2; R Core Team, 2017). All values are presented as mean \pm SD.

Isotopic niche width was then calculated for each species, each location, and each time-period using SIBER (Stable Isotope Bayesian Ellipses in R) metrics in R (v. 3.2.2; Jackson et al., 2011). Bayesian

ellipses were drawn using 10^5 repetitions to ensure accuracy (Jackson et al., 2011). The standard ellipse area (SEA) was then calculated based on the covariance of the x and y data and corrected for small sample size (SEA_c), which applies a two-dimensional correction to eliminate any bias associated with sample size (Jackson et al., 2011). The overlap in SEA_c between locations was calculated for each species separately using the maximum likelihood fitted ellipses (Jackson et al., 2011). Additionally, the total overlap between the two species within each location and season was calculated. We also calculated the probability that the posterior distributions for each ellipse plotted above was smaller or larger than another. This is achieved by comparing each pair of posterior draws for both groups and determining which is smaller in magnitude. We then find the proportion of draws that are smaller, and this is a direct proxy for the probability that one group’s posterior distribution (of ellipse size in this case) is smaller than the other (Jackson et al., 2011). Due to a paucity of common dolphin samples from Algoa Bay (N = 1), this animal was not included in seasonal or SIBER analyses.

3. Results

A total of 300 samples were collected in the study area, including bottlenose (n = 164; 14 bycaught and 150 biopsied individuals) and common dolphin samples (n = 136; 7 bycaught and 129 biopsied individuals; Table 1).

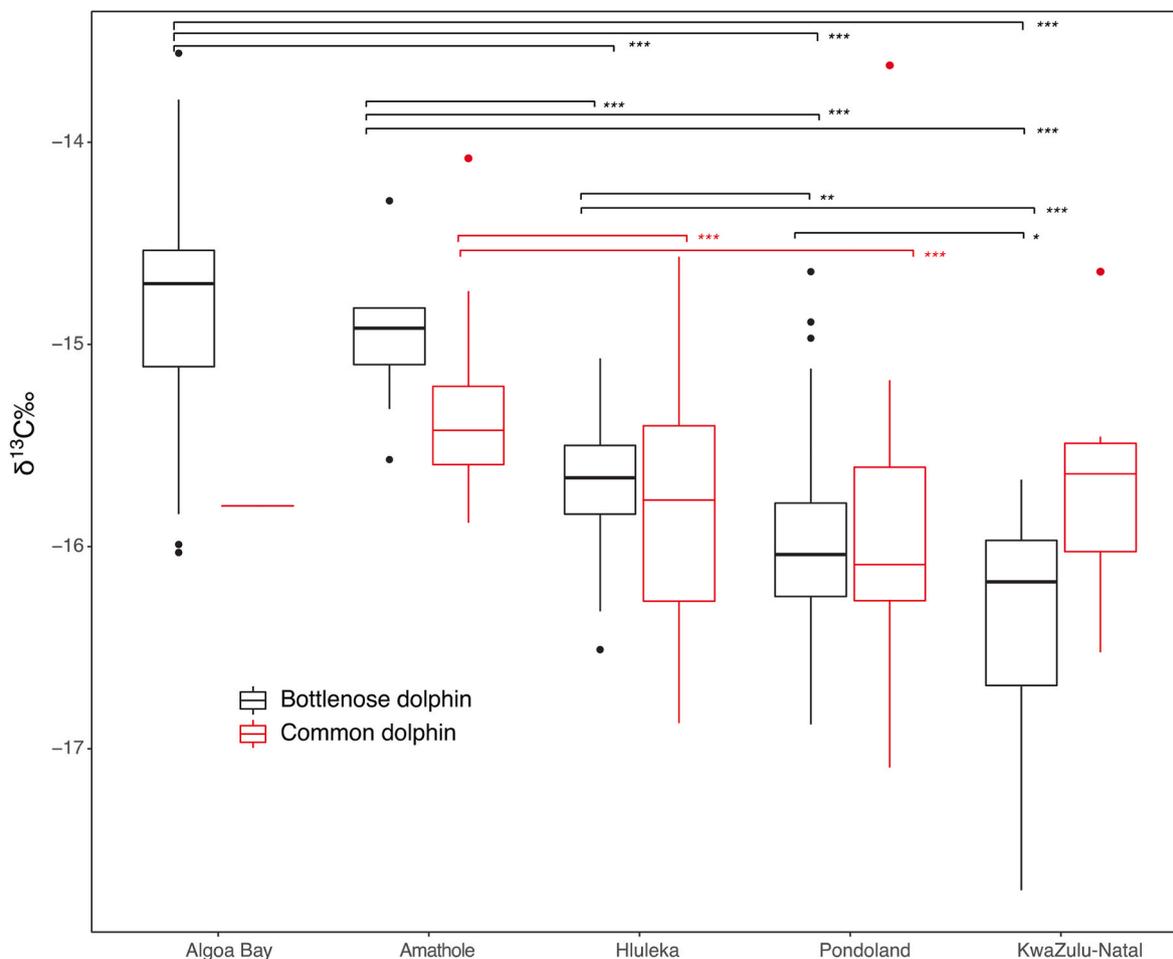


Fig. 2. Boxplot of $\delta^{13}\text{C}$ values from skin samples of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) and common dolphins (*Delphinus delphis*) collected at five different locations off south-eastern South Africa (Algoa Bay, Amathole, Hluleka, Pondoland, and KwaZulu-Natal). *Post-hoc* Tukey’s pairwise comparisons of intraspecific differences are represented as * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$. No horizontal line means no significant difference ($p > 0.05$).

3.1. Inter-species variation

Overall, mean values of $\delta^{13}\text{C}$ were $-15.69 \pm 0.61\text{‰}$ (range = -16.07‰ to -14.29‰) for bottlenose dolphins and $-15.74 \pm 0.58\text{‰}$ (range = -17.09‰ to -13.62‰) for common dolphins (Table 1). GLMs revealed that $\delta^{13}\text{C}$ values did not differ between bottlenose and common dolphins ($F = 0.75$, $p = 0.39$), but winter samples were significantly enriched compared to the summer samples ($F = 8.49$, $p = 0.003$) and $\delta^{13}\text{C}$ varied significantly with location for both species, decreasing along a west-east gradient ($F = 38.07$, $p < 0.0001$; Fig. 2). Post-hoc tests revealed that when both species are pooled, samples from the southernmost (Algoa Bay and Amathole) were significantly higher than northernmost (Hluleka, Pondoland, and KZN) locations were ($p < 0.05$). In addition, Algoa Bay and Amathole were also significantly different ($p < 0.05$), and the difference at each location was investigated separately. At Amathole bottlenose dolphins had significantly enriched $\delta^{13}\text{C}$ values ($F = 7.36$, $p = 0.010$), and at KZN common dolphins were enriched ($F = 6.03$, $p = 0.024$). At Hluleka, bottlenose dolphins were also enriched in $\delta^{13}\text{C}$, but not significantly ($F = 2.76$, $p = 0.099$).

Bottlenose dolphin samples had significantly higher $\delta^{15}\text{N}$ values ($F = 34.30$, $p < 0.001$) than common dolphins. Mean of $\delta^{15}\text{N}$ values were $12.50 \pm 0.87\text{‰}$ (range = 10.90‰ – 14.11‰) for bottlenose dolphins and $12.05 \pm 0.67\text{‰}$ (range = 10.08‰ – 14.05‰) for common dolphins. Season had no significant effect on the $\delta^{15}\text{N}$ values of pooled samples from both species ($F = 3.15$, $p = 0.08$, summer = $12.38 \pm 0.81\text{‰}$, winter = $12.22 \pm 0.82\text{‰}$). For both species, samples pooled from the different

locations were also significantly different $\delta^{15}\text{N}$ values ($F = 27.82$, $p < 0.0001$), and, as a result, the difference at each location was investigated separately. At all three Wild Coast locations, bottlenose dolphins were enriched in $\delta^{15}\text{N}$ values, and significantly so at Amathole and Hluleka (Amathole: $F = 8.68$, $p = 0.0057$; Hluleka: $F = 7.23$, $p = 0.0080$; Pondoland: $F = 3.71$, $p = 0.058$).

Bottlenose and common dolphin dietary niche area overlapped by 39.7% (Fig. 4). The overlap was greatest at Hluleka (47.0%) and Pondoland (32.8%), and lowest at Amathole (15.7%; KZN = 16.8%). The niche area of bottlenose dolphins was larger than that of common dolphins in 81.6% of posterior draws. Seasonally, the isotopic niche of these two species overlapped mainly in summer (34.5% vs. 27.0% in winter, Fig. 4), with both having a wider niche during this season (bottlenose: summer = 1.35‰^2 , winter = 1.01‰^2 , with 80.2% probability of larger ellipses in summer; common: summer = 1.16‰^2 , winter = 0.75‰^2 , 65.6% probability of larger ellipses in summer).

3.2. Intra-species variations

For bottlenose dolphins, $\delta^{13}\text{C}$ values differed between location ($F = 38.41$, $p < 0.0001$; Fig. 2). Tukey's *post-hoc* pairwise comparisons revealed that all locations were significantly different, except Algoa Bay and Amathole ($p < 0.05$). These tests revealed that $\delta^{13}\text{C}$ decreased along a west-east gradient. Bottlenose dolphin $\delta^{13}\text{C}$ values did not differ between season ($F = 0.79$, $p = 0.38$). For $\delta^{15}\text{N}$ isotopes, bottlenose dolphins differed significantly by both location ($F = 7.24$, $p = 0.0079$) and

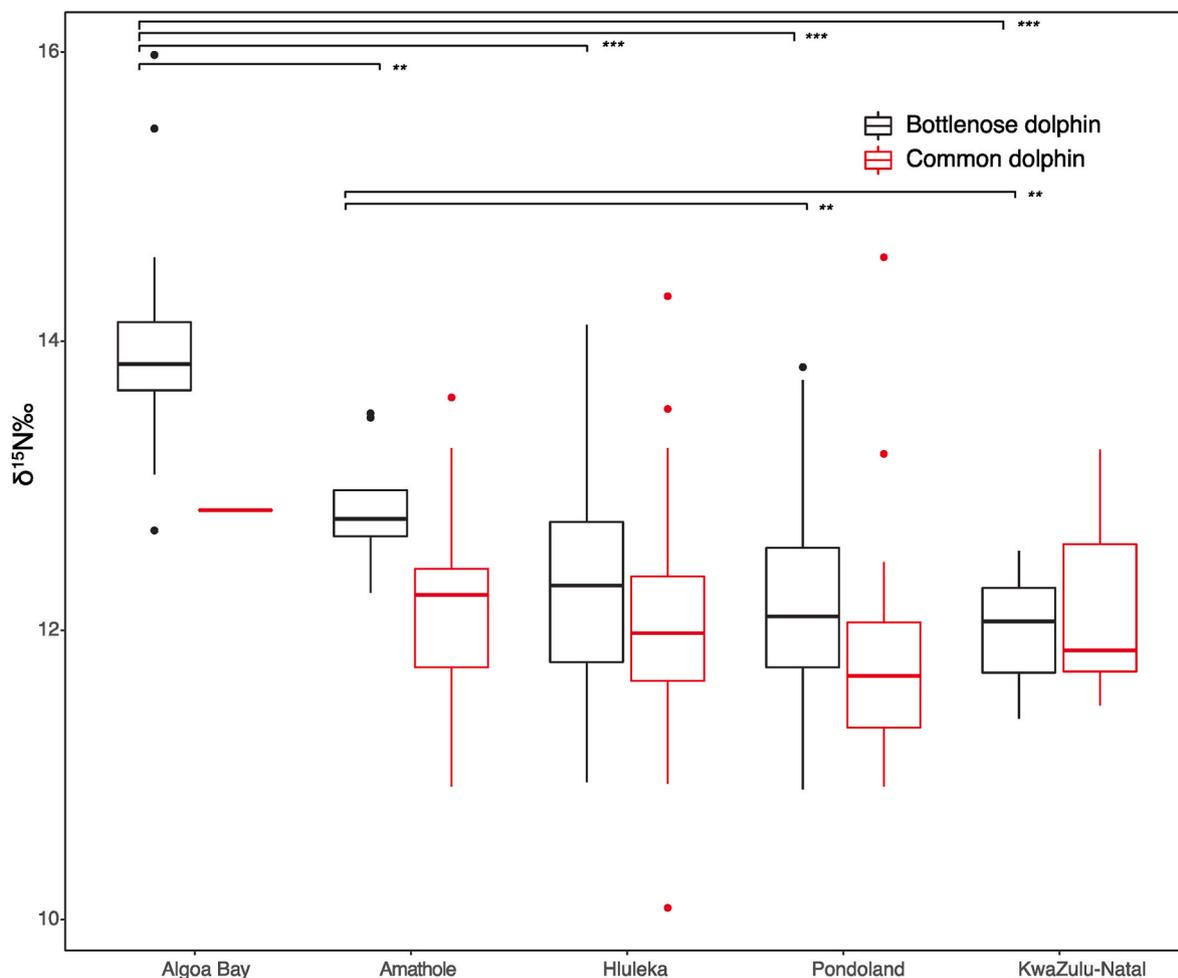


Fig. 3. Boxplot of $\delta^{15}\text{N}$ values from skin samples from Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) and common dolphins (*Delphinus delphis*) collected at five different locations off south-eastern South Africa (Algoa Bay, Amathole, Hluleka, Pondoland, and KwaZulu-Natal). *Post-hoc* Tukey's pairwise comparisons of intraspecific differences are represented as * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$. No horizontal line means no significant difference ($p > 0.05$).

season, with winter values being significantly enriched compared to summer values ($F = 28.20$, $p < 0.0001$). Tukey's post-hoc pairwise comparisons revealed that samples from Algoa Bay were significantly enriched ($p < 0.05$) relative to all other locations and at Amathole, relative to Pondoland and KZN (Fig. 3).

For common dolphins, $\delta^{13}\text{C}$ values were significantly higher for Wild Coast animals sampled in winter ($F = 25.30$, $p < 0.0001$). Common dolphins had significantly different $\delta^{13}\text{C}$ values based on location ($F = 6.02$, $p = 0.0002$); however, only Amathole and Hluleka, and Amathole and Pondoland animals were significantly different ($p < 0.05$) from each other, based on Tukey's post-hoc tests ($p > 0.05$ for all other pairwise comparisons; Fig. 2). For common dolphins, no differences in $\delta^{15}\text{N}$ values were found between locations ($F = 1.50$, $p = 0.21$) or summer and winter ($F = 0.072$, $p = 0.79$; Fig. 3). However, the interaction between season and location was significant ($F = 6.26$, $p < 0.001$), with common dolphins at Amathole having significantly enriched $\delta^{15}\text{N}$ values in summer compared to winter ($p < 0.05$).

For bottlenose dolphins, Algoa Bay animals had the largest isotopic niche area ($\text{SEA}_C = 1.20\text{‰}^2$, probability that ellipses were larger = 70.8–99.4%) when compared to all other locations (Amathole $\text{SEA}_C = 0.50\text{‰}^2$, Hluleka $\text{SEA}_C = 0.68\text{‰}^2$, Pondoland $\text{SEA}_C = 0.81\text{‰}^2$, KZN $\text{SEA}_C = 0.67\text{‰}^2$; Fig. 5). The dietary niche of both Algoa Bay and Amathole bottlenose dolphins did not overlap with any other site (0%). The dietary niche of Hluleka and Pondoland bottlenose dolphins overlapped the most (40.4%), but Pondoland and KZN animals also overlapped greatly (32.4%). The dietary niche of bottlenose dolphins in Hluleka and KZN overlapped by only 8.9%.

Common dolphins from Pondoland had a larger isotopic niche ($\text{SEA}_C = 1.19\text{‰}^2$) than those from Amathole ($\text{SEA}_C = 0.52\text{‰}^2$, probability that ellipses are larger = 98.8%) and Hluleka ($\text{SEA}_C = 0.97\text{‰}^2$, probability that ellipses are larger = 95.9%; Fig. 6). KZN common dolphin samples had larger SEA_C than both Amathole (probability that ellipses are larger = 97.2%) and Hluleka ($\text{SEA}_C = 1.24\text{‰}^2$, probability that ellipses are larger = 91.0%). The dietary niche of common dolphins from Hluleka, Pondoland, and KZN were highly overlapped (>59%), with a 20.0%, 19.7%, and 29.3% overlap with common dolphins from Amathole, respectively.

4. Discussion

This study is the first to examine the trophic ecology of bottlenose and common dolphins off the eastern coast of South Africa. This region is an important transition zone between the Agulhas and Natal ecoregions and the location where sardines extend their range eastward annually during the austral winter. The seasonal differences in stable isotope carbon and nitrogen values in both species investigated highlight the potential importance of the sardine run for dolphins in the region. Common dolphins sampled during winter had enriched $\delta^{13}\text{C}$ values. Common dolphins sampled during winter had enriched $\delta^{13}\text{C}$ values. Due to the isotopic turn-over rates, this reflects $\delta^{13}\text{C}$ enrichment in April/May. Inshore benthic habitats are enriched in $\delta^{13}\text{C}$, compared to offshore/shelf habitats, suggesting that common dolphins are feeding in enriched inshore habitats, possibly on sardines or other predatory fish that move inshore at the start of the sardine run (Ambrose et al., 2013;

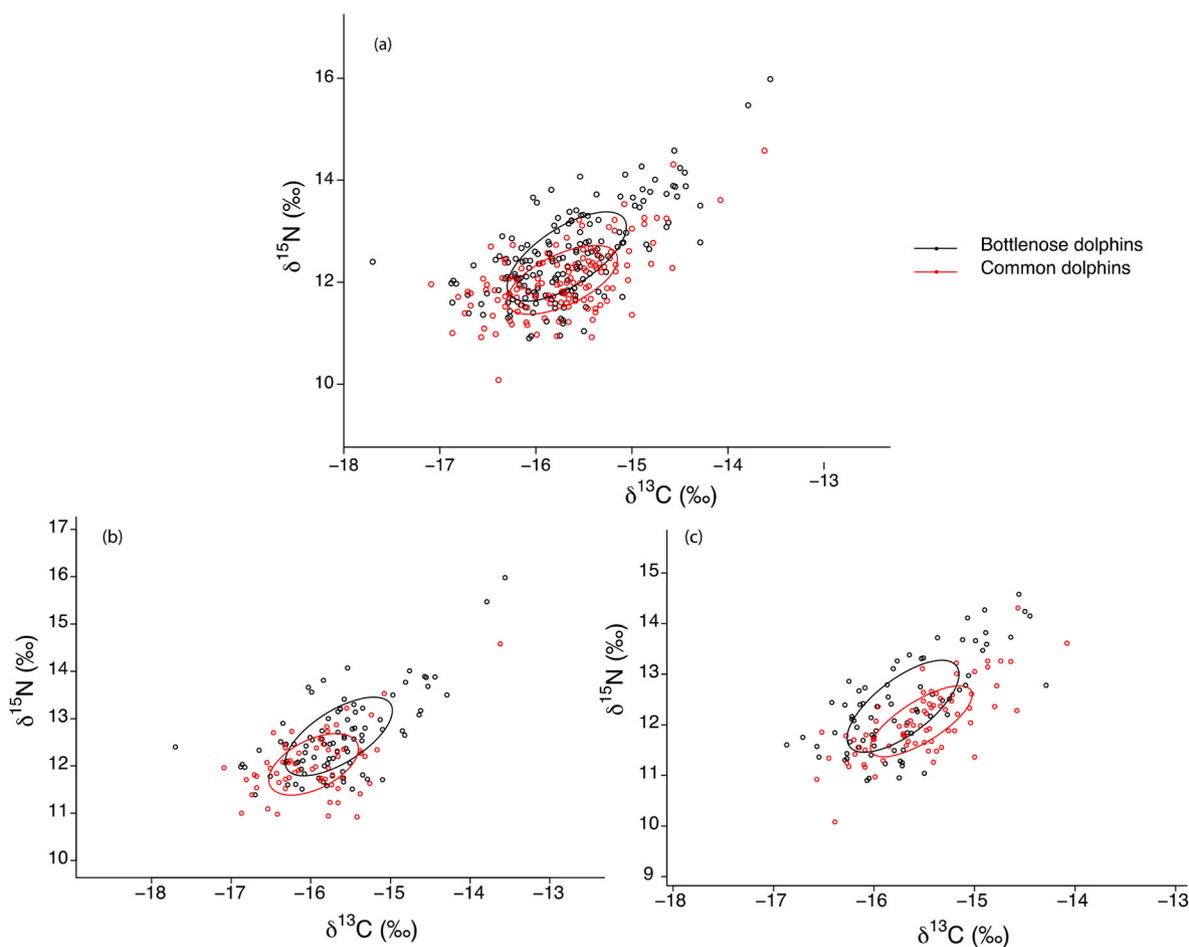


Fig. 4. Isotopic niche area, represented as stable isotope Bayesian ellipses, for skin samples of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) and common dolphins (*Delphinus delphis*) from the Wild Coast of South Africa (Amathole, Hluleka and Pondoland) (a) overall, (b) in summer (May–September), and (c) in winter (November–March).

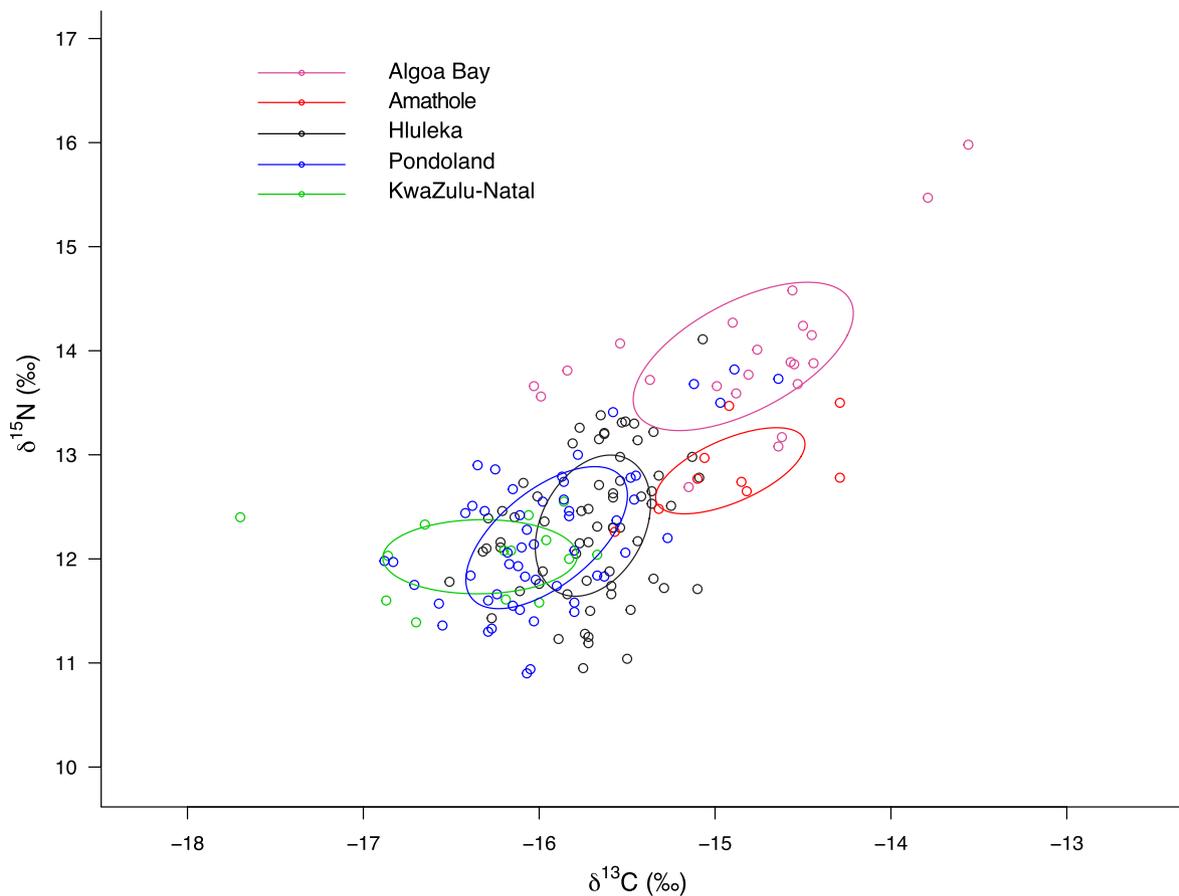


Fig. 5. Isotopic niche ellipses for stable isotope samples taken from the skin of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) off the Wild Coast of South Africa (Amathole, Hluleka and Pondoland), and from Algoa Bay and KwaZulu-Natal.

Cockcroft and Peddemors, 1990; O'Donoghue et al., 2010b, 2010c; Young and Cockcroft, 1994). It is important to note that common dolphin occurrence in inshore waters did not show significant variation with season off the Wild Coast in previous research (Caputo et al., 2020), but as they are known to make daily movements (including inshore/offshore) to feed (Ambrose et al., 2013; Neumann, 2001) it is likely that lower $\delta^{13}\text{C}$ values for animals sampled in summer months reflects foraging in shelf/offshore habitats. Conversely, bottlenose dolphins did not differ in their $\delta^{13}\text{C}$ values between seasons, but were significantly enriched in $\delta^{15}\text{N}$ values during the winter, suggesting that they might feed on higher trophic level prey. This may be indirectly related to the sardine run as it attracts predatory fish also preying upon sardines (Young and Cockcroft, 1994), but more research on their diet is needed to improve predictions of the drivers of enriched $\delta^{15}\text{N}$ values. Our interpretation is limited by the number of samples for each season and location combination, as there was only one common dolphin sample from KZN in summer, one from Algoa Bay, and low numbers of bottlenose dolphin samples at Amathole for both seasons (summer = 4, winter = 5). In addition, due to the isotope turn-over rate for dolphin skin samples, our samples from winter more likely reflect the conditions during April/May, which may be before the sardine run begins.

Our results also show a high percentage of isotopic niche overlap between bottlenose dolphins and common dolphins (up to 47.0%) off the Wild Coast, which contrasts with the low (9%) overlap recorded from stable isotope analyses in KZN animals (Ambrose et al., 2013; Browning et al., 2014a), suggesting that these two species are feeding on similar prey trophically and in similar habitats in the region. This is especially true in Hluleka and Pondoland, where the overlap was greater than 40%. Overlap was high in both seasons, but interestingly their isotopic niches overlapped more in summer than in winter. The presence

of common dolphins off the Wild Coast outside of the sardine run has also been shown in another study that forms part of a broad research project off south-eastern South Africa (Caputo et al., 2020). Despite the high overlap, bottlenose dolphins had a higher mean $\delta^{15}\text{N}$ than common dolphins, suggesting that bottlenose dolphins may be feeding on a wider variety of prey, including higher trophic level species (Kaiser, 2012). This is not surprising as bottlenose dolphins have been shown to feed on higher trophic level prey in other regions where these two species co-occur (e.g. Borrell et al., 2021; Kanaji et al., 2017). Here, common dolphins may specialize their diet on smaller shoaling fishes (Ambrose et al., 2013), as has been shown in previous studies (Borrell et al., 2013; Méndez-Fernández et al., 2013; Pinela and Borrell, 2010).

Intra-specific variation found in bottlenose dolphins provide important insight into their populations in the region. In areas where genetic information is not available or lacks the ability to identify differences in genetic population structure is lacking, ecological tracers, such as stable isotopes have been used to infer fine-scale population structure (Bisi et al., 2013; Borrell et al., 2013; Brotons et al., 2019; Iverson et al., 1997; Lowther and Goldsworthy, 2011; Quérouil et al., 2010; Segura-García et al., 2018). Here, south-western (Algoa Bay and Amathole) bottlenose dolphins were differentiated from north-eastern animals (Hluleka, Pondoland, and KZN) with no overlap in isotopic niche between these groups. This delineation is consistent with most recent genetic research using double digest Restriction Site Associated DNA sequencing (Vargas-Fonseca, 2018). This research suggested two genetically distinct ecoregions: populations that have been named based on their location: the Agulhas ecoregion, and the Natal ecoregion and separated at the Mbashe River; however, samples were only collected from the Plettenberg Bay area (approximately 200 km west of Algoa Bay), and the KZN coast, with no sampling in Algoa Bay, or the Wild

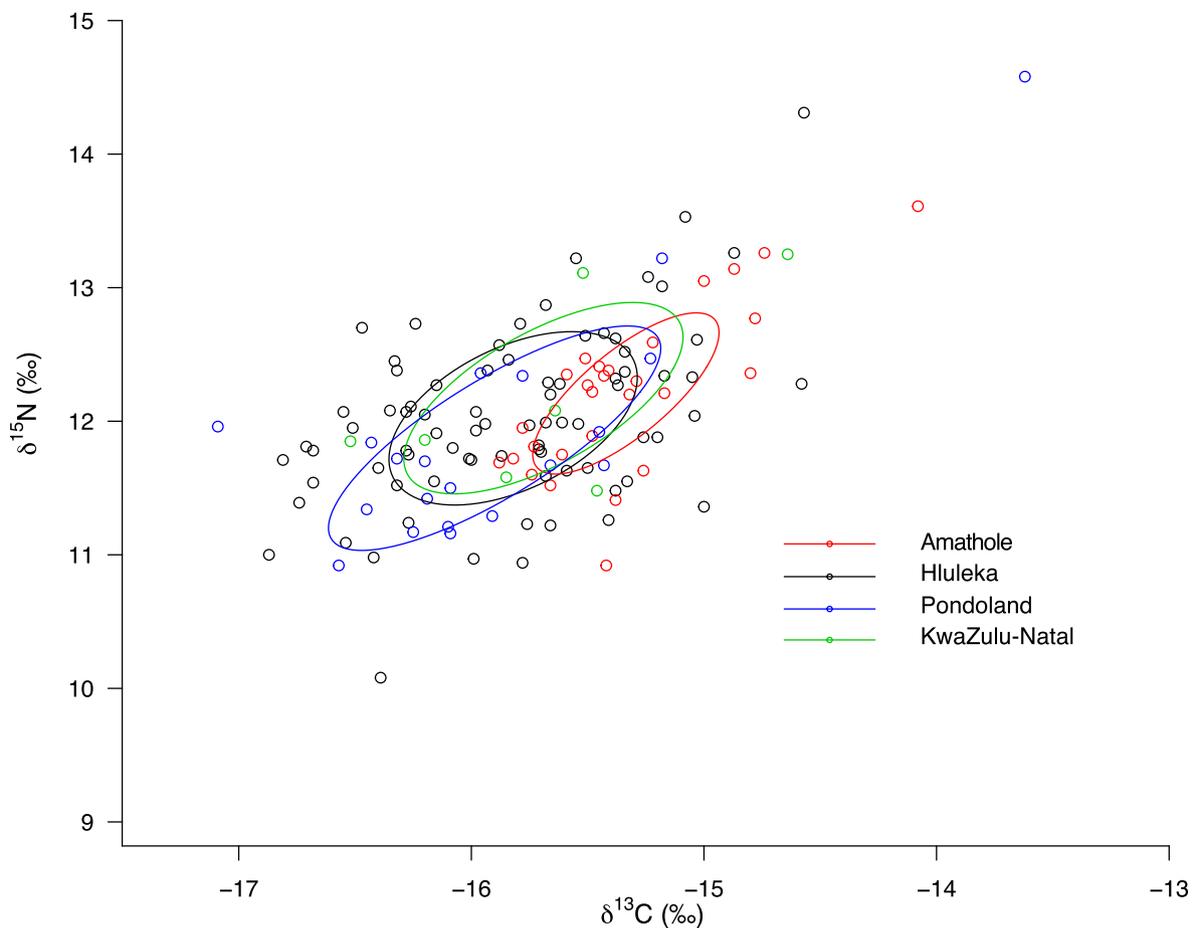


Fig. 6. Isotopic niche ellipses for stable isotope samples taken from the skin of common dolphins (*Delphinus delphis*) off the Wild Coast of South Africa (Amathole, Hluleka and Pondoland), plus limited samples from KwaZulu-Natal.

Coast. The significant isotopic differences, specifically for $\delta^{13}\text{C}$, reoccurring along a west-east gradient suggest the existence of population segments within the two panmictic populations, as found by [Vargas-Fonseca \(2018\)](#) using genetic markers. These segments or management units include: Algoa Bay, Amathole, and north Wild Coast/KZN, as these three areas three had no isotopic niche overlap. In KZN waters, previous studies based on microsatellite and mitochondrial DNA also showed genetic separation of bottlenose dolphins between north and south coast populations ([Goodwin et al., 1996](#); [Hammond et al., 2012](#); [Natoli et al., 2008](#)), providing evidence that there is further fine-scale population structuring occurring in KZN as well, despite relatively close proximity of putative groups and lack of obvious barriers to movement. The spatial variation in $\delta^{13}\text{C}$ values demonstrated for bottlenose dolphins was not present for common dolphins, with a relatively high overlap in isotopic niche for common dolphins between all study sites. Given the generally large groups of common dolphins observed in South African waters and the highly mobile nature of this species ([Cockcroft and Peddemors, 1990](#); [Evans, 1994](#)), defining population segments (or ecological units) is more challenging, and our data do not provide evidence of population substructure along the east coast of South Africa.

Defining management units is essential for conservation and management, particularly as common and bottlenose dolphins are impacted by incidental captures in bather protection nets along the east coast of South Africa ([Ashe et al., 2021](#); [Giménez et al., 2018](#)). Isotope analysis suggests that additional ecological units may exist in bottlenose dolphins in Eastern Cape waters, despite evidence of panmictic populations of bottlenose dolphins in the Agulhas and Natal ecoregions. Less distinct differences were found for common dolphins, suggesting that they do

not form these distinct population segments. These results could have implications for future management decisions, especially in the event of outbreaks of zoonotic diseases or with increasing impacts from oil and gas exploration. Eastern Cape animals should be included in genetic research to provide additional evidence of distinct units for management purposes.. In addition, further information on dietary sources from the Wild Coast would help us understand how common and bottlenose dolphins partition resources in this area and allow us to better understand the role of the sardine run in their trophic ecology.

Author statement

Michelle Caputo: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – Original draft, Writing – Review and editing; **Thibaut Bouveroux:** Methodology, Investigation, Writing – Review and editing; **Megan van der Bank:** Conceptualization, Investigation, Writing – Review and editing; **Jeremy Cliff:** Resources, Writing – Review and editing; **Jeremy J. Kiszka:** Validation, Writing – Review and editing; **Pierre William Froneman:** Conceptualization, Methodology, Resources, Writing – Review and editing, Supervision, Project Administration, Funding Acquisition; **Stephanie Plön:** Conceptualization, Methodology, Resources, Investigation, Writing – Review and editing, Supervision, Project Administration, Funding Acquisition.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Stephanie Plon reports equipment, drugs, or supplies was provided by Dr. Leszek Karczmarski. Stephanie Plon reports financial support and equipment, drugs, or supplies were provided by Eastern Cape Parks and Tourism Authority. Stephanie Plon reports financial support was provided by Petroleum Oil and Gas Corporation of South Africa Ltd.

Data availability

Data will be made available on request.

Acknowledgements

We first thank the numerous volunteers who helped in the data collection during fieldwork. Thank you to Dr. Leszek Karczmarski for the loan of his biopsy gun, without which the project would not have been possible. Thanks to Dr. Grant Hall and the Stable Isotope Laboratory of the Mammal Research Institute, University of Pretoria for sample analysis. Thanks to Dr. Greg Hofmeyr and to Bayworld/Port Elizabeth Museum for assistance and samples. Thanks to the Operations staff at the KwaZulu-Natal Sharks Board for providing the animals sampled. We are also grateful to M. Maclean, A. Opperman J. Greeff and, L. Machane for skippering the research vessels that were used during this study and to the Eastern Cape Parks and Tourism Agency for providing the research vessel and accommodation during field trips along the Wild Coast.

This research was conducted under research permits # RES 2013/35, RES 2014/56, RES 2015/14, RES 2016/57 issued by the Department of Environmental Affairs (South Africa) and # 002/16 issued by South African National Parks (SANParks) and Eastern Cape Parks and Tourism Agency (ECPTA) to SP. Ethical clearance was provided by Rhodes University and Nelson Mandela University under permit A15-SC-ZOO-012. Funding for this study was provided by PetroSA (Contract No: LEG/2013/045) and Rhodes University Council Research Grants to SP. Eastern Cape Parks and Tourism Agency (ECPTA) provided contributions-in-kind under research agreement RA 0183 to SP. This is contribution #1500 from the Institute of Environment at Florida International University.

References

- Ambrose, S., Froneman, P., Smale, M., Cliff, G., Plön, S., 2013. Winter diet shift of long-beaked common dolphins (*Delphinus capensis*) feeding in the sardine run off KwaZulu-Natal, South Africa. *Mar. Biol.* 160, 1543–1561. <https://doi.org/10.1007/s00227-013-2208-6>.
- Ansmann, I.C., Lanyon, J.M., Seddon, J.M., Parra, G.J., 2015. Habitat and resource partitioning among Indo-Pacific bottlenose dolphins in Moreton Bay, Australia. *Mar. Mamm. Sci.* 31, 211–230. <https://doi.org/10.1111/mms.12153>.
- Ashe, E., Williams, R., Clark, C., Erbe, C., Gerber, L.R., Hall, A.J., Hammond, P.S., Lacy, R.C., Reeves, R., Vollmer, N.L., 2021. Minding the data-gap trap: exploring dynamics of abundant dolphin populations under uncertainty. *Front. Mar. Sci.* 8, 1–10. <https://doi.org/10.3389/fmars.2021.606932>.
- Barros, N.B., Ostrom, P.H., Stricker, C.A., Wells, R.S., 2010. Stable isotopes differentiate bottlenose dolphins off west-central Florida. *Mar. Mamm. Sci.* 26, 324–336. <https://doi.org/10.1111/j.1748-7692.2009.00315.x>.
- Best, P.B., 2007. Whales and Dolphins of the Southern African Subregion. Cambridge. Cape Town.
- Bisi, T.L., Dorneles, P.R., Lailson-Brito, J., Lepoint, G., Azevedo, A.D.F., Flach, L., Malm, O., Das, K., 2013. Trophic relationships and habitat preferences of dolphins from the southeastern Brazilian coast determined by carbon and nitrogen stable isotope composition. *PLoS One* 8, 8–15. <https://doi.org/10.1371/journal.pone.0082205>.
- Bligh, E.G., Dyer, W.J., 1959. A rapid method of total lipid extraction and purification. *Can. J. Biochem. Physiol.* 37, 911–917.
- Borrell, A., Gazo, M., Aguilar, A., Raga, J.A., Degollada, E., Gosalbes, P., Garc a-Vernet, R., 2021. Niche partitioning amongst northwestern Mediterranean cetaceans using stable isotopes. *Prog. Oceanogr.* 193, 102559.
- Borrell, A., Velasquez Vacca, A., Pinela, A.M., Kinze, C., Lockyear, C.H., Vinghi, M., Aguilar, A., 2013. Stable isotopes provide insight into population structure and segregation in eastern north Atlantic sperm whale. *PLoS One* 8, e82398.
- Bouveroux, T., Caputo, M., Froneman, P., Plön, S., 2018. Largest reported groups for the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) found in Algoa Bay, South Africa: trends and potential drivers. *Mar. Mamm. Sci.* 34, 645–665.
- Bowen, W.D., Iverson, S.J., 2012. Methods of estimating marine mammal diets: a review of validation experiments and sources of bias and uncertainty. *Mar. Mamm. Sci.* 29, 719–754. <https://doi.org/10.1111/j.1748-7692.2012.00604.x>.
- Brotons, J.M., 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. <https://doi.org/10.1007/s10750-019-04038-7>.
- Browning, N.E., Cockcroft, V.G., Worthy, G., 2014a. Resource partitioning among South African delphinids. *J. Exp. Mar. Biol. Ecol.* 457, 15–21. <https://doi.org/10.1016/j.jembe.2014.03.016>.
- Browning, N.E., McCulloch, S.D., Bossart, G.D., Worthy, G.A.J., 2014b. Fine-scale population structure of estuarine bottlenose dolphins (*Tursiops truncatus*) assessed using stable isotope ratios and fatty acid signature analyses. *Mar. Biol.* 1307–1317. <https://doi.org/10.1007/s00227-014-2420-z>.
- Burton, R., Koch, P., 1999. Isotopic tracking of foraging and long-distance migration in northeastern Pacific pinnipeds. *Oecologia* 119, 578–585.
- Caputo, M., Bouveroux, T., Froneman, P.W., Shaanika, T., Plön, S., 2021. Occurrence of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) off the Wild Coast of South Africa using photographic identification. *Mar. Mamm. Sci.* 37, 220–234. <https://doi.org/10.1111/mms.12740>.
- Caputo, M., Froneman, P.W., Plön, S., 2020. Common dolphin *Delphinus delphis* occurrence off the wild coast of South Africa. *Afr. J. Mar. Sci.* 42, 439–448. <https://doi.org/10.2989/1814232X.2020.1841676>.
- Caputo, M., Froneman, P.W., Preez, D., Thompson, G., Plön, S., 2017. Long-term trends in cetacean occurrence during the annual sardine run off the Wild Coast, South Africa. *Afr. J. Mar. Sci.* 39, 83–94. <https://doi.org/10.2989/1814232X.2017.1304451>.
- Cliff, G., Dudley, S.F.J., 2011. Reducing the environmental impact of shark-control programs: a case study from KwaZulu-Natal, South Africa. *Mar. Freshw. Res.* 62, 700–709.
- Cliff, G., Dudley, S.F.J., 1992. Protection against shark attack in South Africa, 1952–90. *Aust. J. Mar. Freshw. Res.* 43, 263–272.
- Cockcroft, V., Peddemors, V., 1990. Seasonal distribution and density of common dolphins *Delphinus delphis* off the south-east coast of southern Africa. *S. Afr. J. Mar. Sci.* 9, 371–377. <https://doi.org/10.2989/025776190784378853>.
- Cockcroft, V., Natoli, A., Reisinger, R., Elwen, S., Hoelzel, R., Atkins, S., Plön, S., 2016. A conservation assessment of. In: Child, M., Roxburgh, L., do Linh San, E., Raimond, D., Davies-Mostert, H. (Eds.), *Tursiops aduncus*. <https://doi.org/10.1016/B978-0-12-373553-9.00141-3>. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African Biodiversity Institute and Endangered Wildlife Trust.
- Cockcroft, V., Ross, G.J.B., Peddemors, V.M., 1991. Distribution and status of bottlenose dolphin *Tursiops truncatus* on the south coast of Natal, South Africa. *S. Afr. J. Mar. Sci.* 11, 203–209. <https://doi.org/10.2989/025776191784287538>.
- di Benedetto, A.P.M., Monteiro, L.R., 2015. Isotopic niche of two coastal dolphins in a tropical marine area: specific and age class comparisons. *J. Mar. Biol. Assoc. U. K.* 96, 1–6. <https://doi.org/10.1017/S0025315415001095>.
- Evans, W., 1994. Common dolphin, white-bellied porpoise *Delphinus delphis* Linnaeus. In: Ridgeway, S., Harrison, R. (Eds.), *Handbook of Marine Mammals*. Academic Press, San Diego, pp. 191–224. San Diego.
- Giménez, J., Louis, M., Barón, E., Ramírez, F., Verborgh, P., Gauffier, P., Esteban, R., Eljarrat, E., Barceló, D., Forero, G.M., de Stephanis, R., 2018. 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. <https://doi.org/10.1002/aqc.2814>.
- Giménez, J., Ramírez, F., Almunia, J., Forero, M.G., de Stephanis, R., Forero, G.M., de Stephanis, R., 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. <https://doi.org/10.1016/j.jembe.2015.11.001>.
- Goodwin, J., Durham, B., Peddemors, V., Cockcroft, V., 1996. Genetic variation in the bottlenose dolphin *Tursiops truncatus* along the Kwazulu/Natal coast, South Africa. *Afr. J. Mar. Sci.* 17, 225–232.
- Goschen, W., Schumann, E., 2011. *The Physical Oceanographic Processes of Algoa Bay, with Emphasis on the Western Coastal Region*.
- Hammond, P., Bearzi, G., Bjørge, A., Forney, K., Karczmarski, L., Kasuya, T., Perrin, W., Scott, M., Wang, J., Wells, R., Wilson, B., 2012. *Tursiops aduncus* [WWW Document]. The IUCN Red List of Threatened Species. <https://doi.org/10.2305/IUCN.UK.2012.RLTS.T41714A17600466.en>.
- Hoelzel, R., Hey, J., Dahlheim, M., Nicholson, C., Burkanov, V., Black, N., 2007. Evolution of population structure in a highly social top predator, the killer whale. *Mol. Biol. Evol.* 24, 1407–1415. <https://doi.org/10.1093/molbev/msm063>.
- Iverson, S.J., Frost, K.J., Lloyd, F., 1997. Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. *Marine Ecological Progress Series* 151, 255–271.
- Jackson, A., Inger, R., Parnell, A., Bearhop, S., Parnell, A., Inger, R., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER – stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.* 80, 595–602.
- Kaiser, S., 2012. Feeding Ecology and Dietary Patterns of the Indo-Pacific Bottlenose Dolphin (*Tursiops Aduncus*) off KwaZulu-Natal. Nelson Mandela Metropolitan University, South Africa.
- Kanaji, Y., Yoshida, H., Okazaki, M., 2017. Spatiotemporal variations in habitat utilization patterns of four Delphinidae species in the western North Pacific, inferred from carbon and nitrogen stable isotope ratios. *Mar. Biol.* 164, 1–10. <https://doi.org/10.1007/S00227-017-3107-Z/FIGURES/6>.
- Kiszka, J., Oremus, M., Richard, P., Poole, M., Ridoux, V., 2010. The use of stable isotope analyses from skin biopsy samples to assess trophic relationships of sympatric delphinids off Moorea (French Polynesia). *J. Exp. Mar. Biol. Ecol.* 395, 48–54. <https://doi.org/10.1016/j.jembe.2010.08.010>.
- 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. <https://doi.org/10.1016/j.jembe.2012.03.001>.
- 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. <https://doi.org/10.3354/meps09165>.
- Krützen, M., Barre, L.M., Möller, M., Heithaus, M.R., Simms, C., Sherwin, W., 2002. A biopsy system for small cetaceans: darting success and wound healing. *Mar. Mamm. Sci.* 18, 863–878.
- Lane, E.P.E., de Wet, M., Thompson, P., Siebert, U., Wohlsein, P., Plon, S., Thompson, P., Plön, S., 2014. A systematic health assessment of Indian Ocean bottlenose (*Tursiops aduncus*) and Indo-Pacific humpback (*Sousa plumbea*) dolphins, incidentally caught in the shark nets off the KwaZulu-Natal coast, South Africa. *PLoS One* 9, e107038. <https://doi.org/10.1371/journal.pone.0107038>.
- Lowther, A.D., Goldsworthy, S.D., 2011. Detecting alternate foraging ecotypes in Australian sea lion (*Neophoca cinerea*) colonies using stable isotope analysis. *Mar. Mamm. Sci.* 27, 567–586. <https://doi.org/10.1111/j.1748-7692.2010.00425.x>.
- Lutjeharms, J.R.E., Valentine, H.R., Ballegooyen, R.C. Van, 2000. The hydrography and water masses of the Natal Bight, South Africa. *Contin. Shelf Res.* 20, 1907–1939.
- Melly, B., McGregor, G., Hofmeyr, G., Plön, S., 2017. Spatio-temporal distribution and habitat preferences of cetaceans in Algoa Bay, South Africa. *J. Mar. Biol. Assoc. U. K.* 1–15.
- Méndez-Fernandez, P., Pierce, G.J., Bustamante, P., Chouvelon, T., Ferreira, M., González, A.F., López, A., Read, F.L., Santos, M.B., Spitz, J., Vingada, J.V., Caurant, F., 2013. Ecological niche segregation among five toothed whale species off the NW Iberian Peninsula using ecological tracers as multi-approach. *Mar. Biol.* 160, 2825–2840. <https://doi.org/10.1007/s00227-013-2274-9>.
- Méndez-Fernandez, P., Taniguchi, S., Santos, M.C.O., Cascão, I., Quérouil, S., Martín, V., Tejedor, M., Carrillo, M., Rinaldi, C., Rinaldi, R., Barragán-Barrera, D.C., Fariás-Curtidor, N., Caballero, S., Montone, R.C., 2020. Population structure of the Atlantic spotted dolphin (*Stenella frontalis*) inferred through ecological markers. *Aquat. Ecol.* 54, 21–34. <https://doi.org/10.1007/s10452-019-09722-3>.
- Natoli, A., Cañadas, A., Peddemors, V.M., Aguilar, A., Vaquero, C., Fernández-Piqueras, P., Hoelzel, A., 2006. Phylogeography and alpha taxonomy of the common dolphin (*Delphinus* sp.). *J. Evol. Biol.* 19, 943–954. <https://doi.org/10.1111/j.1420-9101.2005.01033.x>.
- Natoli, A., Peddemors, V., Hoelzel, A., 2004. Population structure and speciation in the genus *Tursiops* based on microsatellite and mitochondrial DNA analyses. *J. Evol. Biol.* 17, 363–375. <https://doi.org/10.1046/j.1420-9101.2003.00672.x>.
- Natoli, A., Peddemors, V.M., Hoelzel, A.R., 2008. Population structure of bottlenose dolphins (*Tursiops aduncus*) impacted by bycatch along the east coast of South Africa. *Conserv. Genet.* 9, 627–636. <https://doi.org/10.1007/s10592-007-9379-y>.
- Neumann, D., 2001. Activity budget of free-ranging common dolphins (*Delphinus delphis*) in the northwestern Bay of Plenty, New Zealand. *Aquat. Mamm.* 27, 121–136.
- Newsome, S.D., Clementz, M.T., Koch, P.L., 2010. Using stable isotope biogeochemistry to study marine mammal ecology. *Mar. Mamm. Sci.* 26, 509–572. <https://doi.org/10.1111/j.1748-7692.2009.00354.x>.
- Newsome, S.D., Del Rio, C.M., Bearhop, S., Phillips, D.L., 2007. A niche for isotopic ecology. *Front. Ecol. Environ.* 5, 429–436. [https://doi.org/10.1890/1540-9295\(2007\)5\[429:ANFIE\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[429:ANFIE]2.0.CO;2).
- O'Donoghue, S.H., Drapeau, L., Dudley, S.F., Peddemors, V.M., 2010a. The KwaZulu-Natal sardine run: shoal distribution in relation to nearshore environmental conditions, 1997–2007. *Afr. J. Mar. Sci.* 32, 293–307. <https://doi.org/10.2989/1814232X.2010.501587>.
- O'Donoghue, S.H., Drapeau, L., Peddemors, V.M., 2010b. Broad-scale distribution patterns of sardine and their predators in relation to remotely sensed environmental conditions during the KwaZulu-Natal sardine run. *Afr. J. Mar. Sci.* 32, 279–291. <https://doi.org/10.2989/1814232X.2010.501584>.
- O'Donoghue, S.H., Whittington, P. a, Dyer, B.M., Peddemors, V.M., 2010c. Abundance and distribution of avian and marine mammal predators of sardine observed during the 2005 KwaZulu-Natal sardine run survey. *Afr. J. Mar. Sci.* 32, 361–374. <https://doi.org/10.2989/1814232X.2010.502640>.
- Oviedo, L., Fernández, M., Herra-Miranda, D., Pacheco-Polanco, J.D., Hernández-Camacho, C.J., Auriol-Gamboa, D., 2018. Habitat partitioning mediates the coexistence of sympatric dolphins in a tropical fjord-like embayment. *J. Mammal.* 99, 554–564. <https://doi.org/10.1093/jmammal/gy021>.
- 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, A., Borrell, 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. <https://doi.org/10.3354/meps08790>.
- Post, D., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83, 703–718.
- Quérouil, S., Freitas, L., Cascão, I., Alves, F., Dinis, A., Almeida, J.R., Prieto, R., Borrás, S., Matos, J.a., Mendonça, D., Santos, R.S., 2010. Molecular insight into the population structure of common and spotted dolphins inhabiting the pelagic waters of the Northeast Atlantic. *Mar. Biol.* 157, 2567–2580. <https://doi.org/10.1007/s00227-010-1519-0>.
- R Core Team, 2017. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.
- Reisinger, R.R., Karczmarski, L., 2010. Population size estimate of Indo-Pacific bottlenose dolphins in the Algoa Bay region, South Africa. *Mar. Mamm. Sci.* 26, 86–97. <https://doi.org/10.1111/j.1748-7692.2009.00324.x>.
- Roberts, M.J., van der Lingen, C.D., Whittle, C., van den Berg, M., 2010. Shelf currents, lee-trapped and transient eddies on the inshore boundary of the Agulhas Current, South Africa: their relevance to the KwaZulu-Natal sardine run. *Afr. J. Mar. Sci.* 32, 423–447. <https://doi.org/10.2989/1814232X.2010.512655>.
- Ross, G.J.B., Cockcroft, V.G., Butterworth, D.S., 1987. Offshore distribution of bottlenose dolphins in Natal coastal waters and Algoa Bay, eastern Cape. *S. Afr. J. Zool.* 22, 50–56.
- Ross, G.J.B., Cockcroft, V.G., Melton, D.a., Butterworth, D.S., 1989. Population estimates for bottlenose dolphins *Tursiops truncatus* in Natal and Transkei waters. *S. Afr. J. Mar. Sci.* 8, 119–129. <https://doi.org/10.2989/02577618909504555>.
- Rossmann, S., Berens McCabe, E., Barros, N.B., Gandhi, H., Ostrom, P.H., Stricker, C.A., Wells, R.S., 2015. Foraging habits in a generalist predator: sex and age influence habitat selection and resource use among bottlenose dolphins (*Tursiops truncatus*). *Mar. Mamm. Sci.* 31, 155–168. <https://doi.org/10.1111/mms.12143>.
- Segura-García, I., Rojo-Arreola, L., Rocha-Olivares, A., Heckel, G., Juan, , Gallo-Reynoso, P., Hoelzel, R., 2018. Eco-evolutionary processes generating diversity among bottlenose dolphin, *Tursiops truncatus*, populations off Baja California. *Mexico* 45, 223–236. <https://doi.org/10.1007/s11692-018-9445-z>.
- Stock, B.C., Jackson, A.L., Ward, E.J., Parnell, A.C., Phillips, D.L., Semmens, B.X., 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ* 1–27. <https://doi.org/10.7717/peerj.5096>, 2018.
- Vargas-Fonseca, O.A., 2018. Population Ecology of Indo-Pacific Bottlenose Dolphins along the South-East Coast of South Africa. PhD. Nelson Mandela University.
- Vaudo, J.J., Heithaus, M.R., 2011. Dietary niche overlap in a nearshore elasmobranch mesopredator community. *Mar. Ecol. Prog. Ser.* 425, 247–260. <https://doi.org/10.3354/meps08988>.
- 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.
- Wilson, R.M., Nelson, J.A., Balmer, B.C., Nowacek, D.P., Chanton, J.P., 2013. Stable isotope variation in the northern Gulf of Mexico constrains bottlenose dolphin (*Tursiops truncatus*) foraging ranges. *Mar. Biol.* 160, 2967–2980. <https://doi.org/10.1007/s00227-013-2287-4>.
- Young, D., Cockcroft, V., 1994. Diet of common dolphins (*Delphinus delphis*) off the south-east coast of southern Africa: opportunism or specialization? *J. Zool.* 234, 41–53.