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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 ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analyses revealed resource partitioning with differences in diet and habitat use. Striped dolphin $\delta^{13}C$ values (-16.97 ± 0.25‰, SD) were consistent with evidence that they typically forage offshore, while $\delta^{13}C$ values of humpback dolphins reflected their use of inshore habitats (-15.16 ± 0.65‰). Common and bottlenose dolphins had $\delta^{13}C$ (-15.48 ± 0.66‰ and -15.76 ± 0.71‰ respectively) values that fell between these two extremes. Mean values for $\delta^{15}N$ ranged from 11.92 ± 0.20‰ for striped dolphins to 15.19 ± 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 $\delta^{15}N$ values of 13.49 ± 0.50‰ and 14.40 ± 0.74‰ respectively. Male bottlenose dolphins were significantly more enriched in $\delta^{15}N$ 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.

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 (*Pomadasys 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 (*Pomadasys 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 ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) 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