*Winter diet shift of long-beaked common dolphins (*Delphinus capensis*) feeding in the sardine run off KwaZulu-Natal, South Africa*

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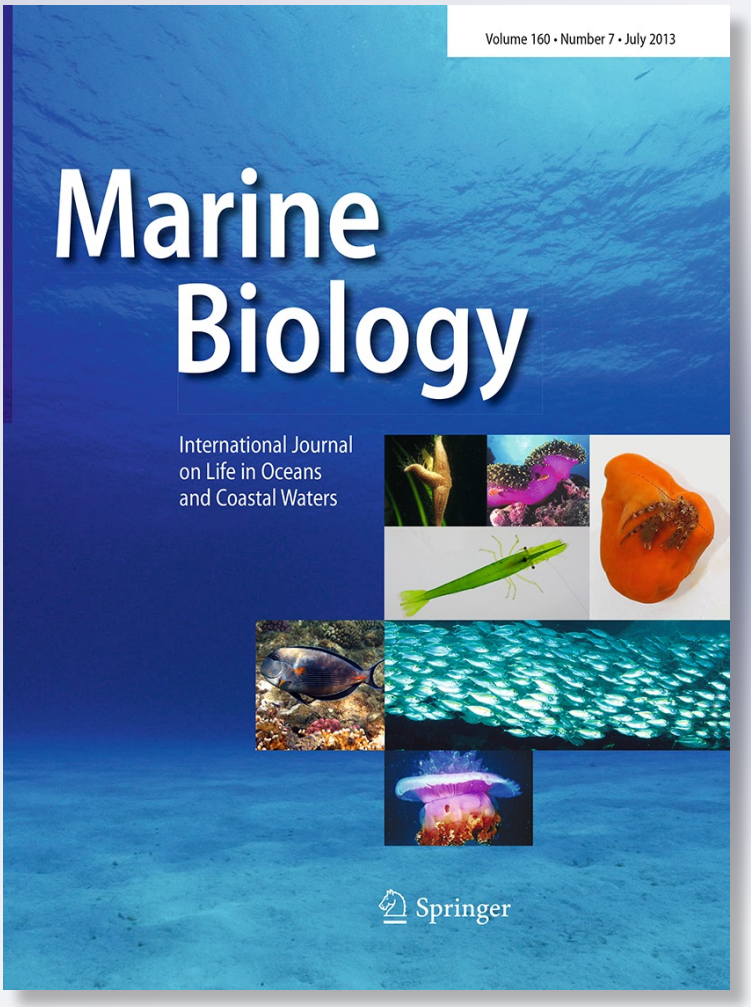

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ORIGINAL PAPER

Winter diet shift of long-beaked common dolphins (*Delphinus capensis*) feeding in the sardine run off KwaZulu-Natal, South Africa

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Abstract Unpredictable inter-annual variations in the timing, spatial extent and intensity of the sardine run (*Sardinops sagax*) have been documented in recent years along the coastline of KwaZulu-Natal, South Africa. This study aimed to determine whether variations in the availability of sardine were reflected in the diet and condition of common dolphins (*Delphinus capensis)* over the past three decades. Stomach contents from 95 common dolphins incidentally caught between 2000 and 2009 were analysed and compared to historical data collected between 1972 and 1992. A shift in the principal prey species consumed by the dolphins was observed over the past 30 years. Prior to 1992, sardine comprised up to 49 % of the total stomach contents by mass, whilst chub mackerel (*Scomber japonicus*) was the dominant prey recorded in the stomach contents between 2000 and 2009 (66 %). As common dolphins prey on locally abundant fish species, this dietary shift may indicate changes in the availability of the most abundant fish prey. Stable isotope analyses of tooth tissue revealed no significant changes in the $\delta^{15}N$ and $\delta^{13}C$ isotopic ratios over the past three decades ($P = 0.283$ for N and $P = 0.922$ for C). Blubber thickness as a percentage of body length and blubber weight as a percentage of total body weight were assessed as indicators of animal condition. No significant changes in proportional blubber weight or blubber thickness were seen over the last 40 years (1970–2009) for all age cohorts. This species appears to be well adapted to cope with changes in prey species availability, without impacting on body condition.

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Introduction

As large predators, cetaceans play a vital role in marine ecosystems and are consumers of production at almost all trophic levels (Bowen 1997; Pauly et al. 1998). Due to their links to lower levels in the trophic pyramid, as well as a strong dependence on environmental quality, they are likely to experience the most acute effects of changes in the marine environment, such as increasing sea-surface temperatures (SST), changes in the abundance and distribution of their prey stocks, and the impacts of overfishing (Sekiguchi et al. 1992; Bowen 1997; Bearzi et al. 2003).

Common dolphins are small cetaceans with a particularly wide tropical and temperate geographical range, being found both in coastal and in offshore waters between 60°N and 50°S, in water temperatures ranging from 10 to 28 °C (Cockcroft and Peddemors 1990; Klinowska 1991; Findlay

et al. 1992; Heyning and Perrin 1994). Research on common dolphins off the South African coast has focused on the distribution of the species (Cockcroft and Peddemors 1990; Findlay et al. 1992), their reproductive biology (Mendolia 1989), diet (Sekiguchi et al. 1992; Young 1993; Young and Cockcroft 1994; Young and Cockcroft 1995), ecotoxicology (Cockcroft 1990) and their incidental capture in shark nets (Cockcroft 1990). At present, it is thought that two species of common dolphin inhabit South African waters: the long-beaked common dolphin (*Delphinus capensis*) with a coastal distribution and the short-beaked common dolphin (*Delphinus delphis*) with a more offshore distribution (Best 2007). However, the morphological characteristics used to distinguish the two species in this area vary in other parts of the world, and genetic evidence has so far not provided support for the separation of morphotypes along the southern African coastline (Samaai et al. 2005). Consequently, some uncertainty still exists as to the present species classifications within the genus *Delphinus* (Natoli et al. 2006). Based on morphometric analyses, Samaai et al. (2005) concluded that all of the common dolphins incidentally caught in the shark nets off KwaZulu-Natal, South Africa, were of the long-beaked variety. For this reason, all of the animals examined in this study were treated as belonging to *D. capensis*. The species is abundant in South African waters from 31°S on the West Coast (St. Helena Bay) to 28°S on the East Coast (Richard's Bay) (Sekiguchi et al. 1992; Samaai et al. 2005). Cockcroft and Peddemors (1990) used aerial surveys over the period 1988–1989 to estimate that the South African long-beaked common dolphin population stood between 15,000 and 20,000 individuals. No recent population estimate is available.

The year-round distribution of *D. capensis* in the coastal waters of South Africa is not well documented; however, the animals appear to occupy the cooler waters along the south-east coast of the continent during austral summer, in the region south of 33° latitude (Young and Cockcroft 1994). A lengthy northwards migration towards the warmer waters of the tropics during winter has been observed in some of these common dolphins—a journey which seems to be undertaken in response to the sardine run. The sardine run is an annual migration of vast shoals of South African sardine (*Sardinops sagax*), which are known to be an important food source for many predators (Cockcroft and Peddemors 1990; Young and Cockcroft 1994). The parent stock of sardine is thought to be primarily resident on the south and west coasts (from Namibia south and eastwards to Port Elizabeth), concentrated around the region of the Agulhas Bank for 10–11 months of the year (Crawford 1981; O'Donoghue et al. 2010a). A subsection of this population then moves north-east along the coastline with the onset of winter, reaching the waters off KwaZulu-Natal around June/July (Crawford 1981; O'Donoghue et al. 2010a). *D. capensis* is one of the main predators feeding in the annual sardine run and has been credited with the ability to control much of the bait ball feeding activity (O'Donoghue et al. 2010b). The diet of the long-beaked common dolphins feeding in KwaZulu-Natal demonstrates strong inter-annual variability, which is likely to be a reflection of changes in the intensity and duration of the annual sardine run (Young 1993). Hence, dietary data from this species may be useful in obtaining information on the occurrence and abundance of small pelagics (Sekiguchi et al. 1992). However, the diet of the long-beaked common dolphin from South Africa has not been studied since the early 1990s (Sekiguchi et al. 1992; Young 1993; Young and Cockcroft 1994). The spatial and temporal distribution and intensity of the sardine run appear to have changed considerably in recent years, with evidence indicating a decrease in the intensity of the sardine run between 2002 and 2006, both in terms of sardine presence (O'Donoghue et al. 2010a) and sardine egg abundance on the KwaZulu-Natal south coast during winter (Connell 2010a). This phenomenon may represent a significant change in the winter food resources of the common dolphin in southern African waters (O'Donoghue et al. 2010a).

The feeding habits of marine mammals are particularly difficult to observe directly, and detailed data on long-term trends are rare in these animals (Walker and Macko 1999). A conventional tool for studying diet in marine mammals is stomach content analysis, but this usually only provides a snapshot of the animals' diet, unless long-term data sets are available (Sekiguchi et al. 1992; Kaschner et al. 2006). Other biases inherent in stomach content analyses include difficulties in identifying dismembered prey, the overestimation of cephalopod contribution to the diet (their hard beaks are resistant to digestion and accumulate in the stomach), and the introduction of secondary prey (smaller species ingested by fish prey, not directly by the dolphin) (Santos et al. 2004; Zeppelin et al. 2004). The prey remains found in any cetacean stomach may therefore not all originate from the same single meal due to the different rates of digestion of structures such as fish otoliths and squid beaks (Sekiguchi et al. 1992). However, it is worth noting that Ross (1979) estimated the gut passage time of captive bottlenose dolphins (*Tursiops aduncus*) to be around 48 h, suggesting that the prey items recorded in their guts are unlikely to be derived from several meals. Furthermore, small fish otoliths were completely digested within this time period. Additionally, more than two-thirds of the ingested cephalopod beaks had been egested within 22 h after feeding (Ross 1979). The rapid digestion rate of otoliths (comprised of calcium carbonate) suggests that the otoliths found in good condition in the stomach likely originate from the most recent meal (Ross 1979). Thus,

despite its limitations, stomach content analysis is still widely employed as a valuable technique enabling the study of cetacean diets and predator–prey relationships in marine systems (Fitch and Brownell 1968; Ross 1984; Sekiguchi et al. 1992; Smale et al. 1995).

The advent of stable isotope analysis has provided a means to study the both long- and short-term feeding history of marine mammals and is particularly useful in determining the nutrients assimilated by the animal, as opposed to merely identifying those ingested (Walker and Macko 1999). Due to the differential turnover times of body tissues, the isotopic ratios of certain body parts may differ, and so give both a short-term reflection of diet in tissues with a high turnover rate (such as skin), and a long-term feeding history in those with slower turnover times (such as teeth) (Walker and Macko 1999; Newsome et al. 2010). The organic portions of teeth preserve well, making them an ideal tissue type for use in historical, archaeological and palaeoecological studies (Walker and Macko 1999; Newsome et al. 2010). Whilst tooth enamel is formed early in the animal's life, the dentin is deposited within the root and crown of the tooth for a number of decades (Newsome et al. 2010). Using the isotopic signal of the entire tooth gives a long-term measure of diet, trophic position, and habitat use (Niño-Torres et al. 2006; Knoff et al. 2008; Newsome et al. 2010), whilst micro-sampling of individual growth layer groups (annuli) can provide a detailed ontogenetic record of dietary changes from suckling to adulthood (Hobson and Sease 1998; Newsome et al. 2010).

Studying long-term diet through stomach content and isotope analyses can be complemented by assessing the general body condition of the animals. Blubber is one of the most specialized tissues in the body of a marine mammal, and its thickness as well as overall contribution to body weight, can be measured as an indicator of body condition (Ognetov 1990). It provides a long-term energy store, allowing the animal to stock up fat reserves during plentiful feeding seasons, creating an energy reserve for pregnancy or periods of prey scarcity (Ognetov 1990; Caon et al. 2007; Koopman 2007; Konishi et al. 2008).

The aim of this study was to assess the long-term feeding ecology of the long-beaked common dolphins incidentally caught in the shark nets along the KwaZulu-Natal coastline (Cliff and Dudley 1992) using a multi-pronged approach of stomach content analysis, stable isotope analysis, and examination of condition using blubber thickness data over the last four decades. Global climate change and expanding fisheries are likely to result in future changes in the distribution and abundance of fish species around the South African coastline (Coetzee et al. 2008). Assessing the diet of one of their predators, such as the common dolphin, may be one way to gain insight into the changes which occur in these fish stocks. In the event that the sardine run and other shoal characteristics of pelagic prey species change, it is important to understand how the common dolphin population may respond, and how likely (and feasible) prey-switching behaviour may be (Sekiguchi et al. 1992). Long-term studies are particularly applicable in this context, as secondary effects in top predators may only become apparent over longer time frames.

Materials and methods

All samples and data analysed during this study were obtained from dolphins incidentally caught in the shark nets maintained by the KwaZulu-Natal Sharks Board (KZNSB) at popular bathing beaches along the KwaZulu-Natal coastline (Fig. 1), which provide protection against shark attack. The nets are examined on approximately 20 days each month (weather permitting), and any catches are recorded and frozen whole, pending dissection at a later date. The data and a variety of tissues were subsequently accessioned to the Graham Ross Marine Mammal Collection at the Port Elizabeth Museum (PEM) (Plön et al. 2012). Data collected during the present study were compared to the results of the similar study conducted by Young and Cockcroft (1994) covering the period 1974–1992. Additionally, the $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios from teeth of *D. capensis* caught in the shark nets off KwaZulu-Natal over the last 40 years were analysed. These teeth were used to assess whether long-term changes

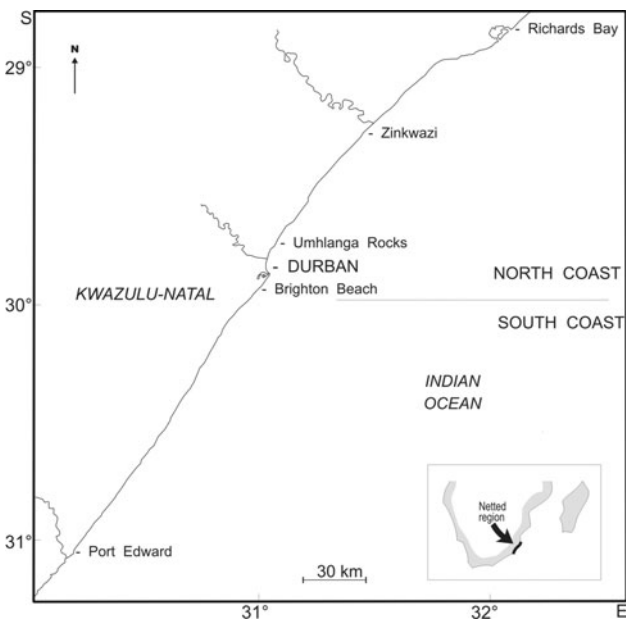

Fig. 1 Location of shark nets along the KwaZulu-Natal coastline (KZN Sharks Board 2012). Netted beaches are found between Richards Bay in the north and Port Edward in the South

Table 1 Sample sizes and time periods of all samples analysed in this study

Sample type	Period	Sample size (*N*)	Males	Females
Dolphin stomach contents	2000–2009	95	40	55
Teeth	1980–2008	16	7	9
Blubber thickness	1970–2009	73	36	37
Blubber total weight	1974–1995	154	80	74

in feeding were reflected in the isotopic signatures of the dentine in teeth. Analysis was also made of the long-term trends in blubber thickness and blubber total weight records for common dolphins incidentally caught in the KwaZulu-Natal shark nets dating back to 1970, which were available from the PEM. These blubber measurements were used to assess trends in body condition of net-caught long-beaked common dolphins over the last 40 years. Table 1 outlines the sample sizes of dolphin stomach contents, teeth, blubber thickness and blubber total weight measurements which were analysed in this study, as well as the time periods from which the samples originate. Ninety-five dolphin stomachs spanning a period of nine years were analysed, along with 16 teeth spanning a range of 28 years (1980–2008), 73 blubber thickness measurements spanning 39 years (1970–2009), and 154 total blubber weight measurements spanning 21 years (1974–1995).

Stomach content analysis

The entire stomach was removed whole from each animal, after cutting and tying the oesophagus anterior to the forestomach, and the duodenum posterior to the pylorus. Stomachs were stored in sealed, labelled plastic bags, which were frozen until examination. Stomachs from 95 common dolphins (55 females, 40 males) caught between 2000 and 2009 were examined for prey items. Stomach dissections took place in accordance with procedures used by Young and Cockcroft (1994). Prey items were removed, measured, weighed, photographed and identified to species level if possible using fish otoliths and cephalopod beaks. Otoliths and cephalopod beaks were identified using the PEM reference collection and published guides (Clarke 1986; Smale et al. 1995). The number of each fish species in the stomach was estimated by counting the maximum number of either left or right otoliths, added to half of the otoliths for which side was not determinable. The number of cephalopods in each stomach was estimated by counting the maximum number of upper or lower beaks (Young 1993). All otoliths were measured to the nearest 0.1 mm using a Zeiss binocular microscope fitted with an eyepiece graticule. The lower rostral length was measured for cephalopod beaks using digital callipers, except in the case of octopods and sepiids, for which lower crest length was measured. Original prey dimensions and weights were back-calculated from otolith and cephalopod beak dimensions using established regressions (Clarke 1986; Smale et al. 1995). Reconstituted weights of all fish and cephalopod remains from each stomach were summed to obtain a reconstituted meal weight for that stomach. In order to avoid inaccuracy associated with size reduction due to digestion, only undamaged otoliths and beaks were used in regressions to calculate the body size and weight of prey items. The majority of fish species were identified to species level. Where otoliths and cephalopod beak identification to species level was ambiguous, as in the case of the unresolved *Loligo* species complex, identification was made to genus level. Regressions were not available for all species, and for prey species lacking suitable regressions, body weights and lengths were estimated from the PEM reference collection material for that species in the nearest size range.

An Index of Relative Importance (IRI) was calculated to assess the relative contributions and importance of each prey species to the diet (Pinkas et al. 1971). The following equation was used for calculating the IRI value for each prey species (Ferry and Cailliet 1996; Young and Cockcroft 1994):

$$\mathrm{IRI} = (\%\ \text{number} + \%\ \text{reconstituted mass}) \times \%\ \text{frequency of occurrence}$$

where % number was calculated as the number of prey items of each species relative to the total number of prey individuals collected in all stomachs, % reconstituted mass was calculated as the reconstituted mass (based on otolith or squid beak dimensions) of each prey species relative to the reconstituted mass of all prey in the stomach contents, and % frequency of occurrence was calculated as the number of stomachs in which a prey species occurred relative to the total number of predator stomachs processed (Ferry and Cailliet 1996; Young and Cockcroft 1994).

Dolphins were allocated to age categories based on the standard length and weight specifications of Young and Cockcroft (1994): calves (<175 cm body length, 18–75 kg body mass), juveniles (males between 75 and 100 kg, females between 75 and 90 kg body mass) and adults (males >110 kg and females >90 kg body mass). The sample for this study consisted of 20 calves (eight males and 12 females), nine juveniles (two males and seven females), and 66 adults (30 males and 36 females). The number of dolphin stomachs available for examination varied from year to year, depending on the incidental catches from the shark nets.

In order to determine whether there have been any changes in the diet of the common dolphins in the waters of KwaZulu-Natal, the data obtained during this study were compared to historical data collected between 1974 and

1992 and analysed by Young (1993). One problem to overcome was the change in the management of the shark nets, which altered over time: historical data were collected when shark nets were in the water almost year round, whilst recent data were collected when shark nets were regularly lifted from the water during peak sardine run activity to avoid excessive mortalities of sharks and dolphins. Once an apparent shift in diet had been observed between the 'historical' and 'recent' data sets, it became necessary to account for sampling bias between the two studies. Between 1974 and 1992, high numbers of common dolphins were caught both during the peak of the sardine run (June and July) and in the following three months, whilst between 2000 and 2009, the majority of incidental catches took place in the months directly after the sardine run (August and September). Therefore, it was necessary to re-sample a subset of the historical data collected by Young (1993) in order to determine that the shift in diet was legitimate and not a product of a later annual incidental catch of common dolphins in recent years. Hence, the original otoliths and cephalopod beaks from the 'historical' study (1974–1992) were re-sampled, using a smaller subset (41 individuals) of the original animals due to time constraints. Animals were selected from periods representing incidental catches during the peak of the sardine run (June and July), directly after the peak of the sardine run (August, September and October), and at other times of the year (any month outside of June to October), with an as even as possible spread across the years and between sexes. This sub-sample consisted of

- During the sardine run (June and July): 16 individuals (six males, 10 females)
- Directly after the sardine run (August, September and October): 19 individuals (six males, 13 females)
- Other times of the year: six individuals (two males, 4 females)

This sub-sample was used to compare the diet between 'historical' (1974–1992) and 'recent' (2000–2009) common dolphin incidental catches, and between the periods inside and outside of the sardine run. As only a single common dolphin was caught outside of the sardine run period (i.e. other times of the year) between 2000 and 2009, no comparison was made between 'historical' and 'recent' dolphin diets for this period. Having found a seasonal diet shift between the two time periods, we aimed to explore whether this would also have implications for annual or long-term dietary changes. To do this, we analysed both isotopic signatures and blubber measurement data.

Data on fish abundance

In order to relate the changes documented in the diet of the long-beaked common dolphins to relevant data on fish abundance, attempts were made to obtain data on the pelagic stocks of sardine and mackerel in KwaZulu-Natal waters over the corresponding time period. However, due to the lack of data on fish abundance for KwaZulu-Natal, egg density data were used as a proxy for spawner biomass in the area during the period of the sardine run. Data on sardine and chub mackerel egg densities sampled from the water column over the inshore shelf off Park Rynie, KwaZulu-Natal, every winter between 1987 and 2009 were made available by Connell (2010b). Although egg density data are not a direct measure of the abundance of these two fish species, it does provide an indication that the two fish species had moved into the area to spawn, over the same period that the incidental dolphin catches occurred. It is, however, important to note that using egg density data as a proxy for sardine abundance can be problematic as they form high-density schools with very patchy distributions (Barange and Hampton 1997). For this reason, spatially limited water column sampling might be inadequate for detecting the presence and abundance of sardine and their eggs (Barange and Hampton 1997). The patchy distribution of sardine shoals appears to be density independent (Barange et al. 2005), and hence, limited sampling of sardine eggs from the water column may hit or miss high-density shoals, leading to a high degree of variability in the egg density data. Nonetheless, in the absence of stock density data along the east coast of South Africa, we use egg density data here as a rough guideline for fish presence, noting its inherent biases. IRI (Index of Relative Importance) values calculated for sardine and mackerel in the diet of the common dolphins over the period of this study (2000–2009), as well as those presented by Young (1993) for the period 1974–1992, were compared to egg density data for these two species in KwaZulu-Natal over the corresponding years in an attempt to relate the biomass of sardine and mackerel in those waters in winter to the importance of these two species as prey items for the long-beaked common dolphin.

Stable isotope analysis

Stable isotope analysis was employed to investigate whether the long-term trends in the feeding ecology of long-beaked common dolphins as observed during the stomach content analysis would be reflected in long-term isotopic signatures. To obtain sufficient material for isotope analysis, two or three teeth needed to be used per animal (Newsome et al. 2010). Only teeth from sexually mature animals were selected; these were males >220 cm in total body length and females >210 cm in total body length (Mendolia 1989). The samples used for this analysis were all from the dentine portion of the tooth, which is deposited over the course of the dolphin's life until the pulp cavity

becomes filled in adulthood (Walker and Macko 1999). The neonatal line could be determined macroscopically in sectioned teeth in this study. The growth layer groups (GLGs) formed during the neonatal phase and during suckling were excluded from the sample, because $\delta^{15}N$ values for calves are significantly enriched compared to those of their mothers (Niño-Torres et al. 2006) as suckling calves essentially feed at a higher trophic level (off their mothers) during this time. In order to avoid any GLGs laid down during the pre-weaning period when the dolphin was suckling, only tooth matter from around the third GLG inwards (post-natal dentine) was drilled out, as much care as possible was taken to only drill the latest 10–12 GLGs in each tooth.

A total of 16 adult animals were selected (seven males, nine females), eight of which represented the 'historical' animals (caught between 1980 and 1992), and eight of which represented the 'recent' animals (caught between 2000 and 2008; Table 1). These two categories were selected to coincide with data from the stomach content analysis and to ascertain whether a shift in trophic level feeding had occurred over the last three decades. Macerated teeth which had been stored dry were rinsed in distilled water and dried with paper towel prior to mounting on a small glass slide in a horizontal plane using PEG (polyethylene glycol 4000—Merck) in crystalline form. Teeth were sectioned longitudinally using a Buehler Isomet low-speed saw. Each sectioned tooth was freed from the mounting material and cleaned, and the latest 10–12 GLGs of the tooth were carefully drilled out using an electric dental technicians drill (Volvere GX, Model NE22L), with care being taken to avoid the cementum, neonatal and pre-weaning layers. The resulting tooth powder was collected in foil cups and decalcified using 1 ml of 1 M HCl in closed Eppendorf tubes, shaken for 1 min, and then left open for 2 h whilst effervescence took place. After 2 h, the tubes were closed, shaken again and then centrifuged at 12,000 rpm for 2 min to ensure that decalcified tooth material formed a pellet. Excess HCl was pipetted off, and the pellets were rinsed by washing with distilled water and shaking to re-suspend decalcified material. After rinsing, tubes were centrifuged at 12,000 rpm for a further 2 min. The excess distilled water was then removed from each tube, after which they were dried in an oven at 40 °C for 2 days to form a dry pellet of decalcified material. These samples underwent stable light isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) at the IsoEnvironmental cc facility at Rhodes University. Samples were analysed using a double collector Europa Scientific 20–20 CF-IRMS linked to an Elemental Analysis Preparation system. In-house standards (ammonium sulphate and beet sugar) and a certified protein standard were calibrated against IAEA (International Atomic Energy Agency) standards IAEA-CH-6 and IAEA-N-1. Based on replicate analyses of samples and standards, the precision levels for $\delta^{13}C$ and $\delta^{1}5$ N for this instrument are 0.10 and 0.16 ‰, respectively. Tooth samples were analysed in duplicate, and the resulting values averaged for each animal.

No ontogenetic shift in the diet of *D. capensis* was detected (Ambrose, unpublished data), thus dentine from all age groups could be used equally. However, given that the sampled tooth dentin represents the latest 12-year maximum of the animal's life, some material used for stable isotope analysis may have resulted in overlapping time periods without a clear distinction between 'historical' and 'recent' time periods used in this study, depending on the age of the animal at the time of capture. To improve the rigorousness of the study, we selected a smaller subset of animals, for whom tooth material drilled showed no overlap in feeding period between the 'historical' and 'recent' delineations, and analysed this subset separately, to substantiate the results obtained from the larger dataset. This subset included only sexually mature animals (over 12 years of age in males and nine years of age in females) following Mendolia (1989). Body lengths for these dolphins were known, and their ages at death were estimated from the growth curve produced by Mendolia (1989). Using the known date of death, it was possible to back-calculate the 10–12 year time span for which GLG's were drilled in the teeth. Using these dates, we removed any dolphins from the dataset for which tooth matter could have been drilled from years overlapping the 'historical' and 'recent' periods in this study. Mendolia (1989) provides a growth curve for female animals only, so all of the seven dolphins selected for this subsample were female. This smaller subset of seven of the original 16 dolphins included three dolphins from the 'historical' period (1974–1992) and four dolphins from the 'recent' period (2000–2009).

Blubber records

Following PEM dissection protocol, blubber thickness for three regions (mid-dorsal, mid-lateral and mid-ventral) was measured to the nearest 1 mm using vernier callipers for all common dolphins incidentally caught in the shark nets. Total blubber mass was also recorded for many of these dolphins during the dissection process. Blubber thickness measurements for 78 dolphins (37 females and 36 males) dating from 1970 to 2009, and blubber total weight measurements for 154 dolphins (74 females and 80 males) dating from 1974 to 1995, were obtained from the PEM Graham Ross Marine Mammal Collection and used to assess body condition over the last 40 years (Table 1). As cetacean blubber allocation was found to vary with age cohort and reproductive state (Young 1998; McLellan et al. 2002; Koopman 2007), we split the data into age cohorts (calf, juvenile, adult male, adult resting female, pregnant

female and lactating female). Blubber thickness and blubber weight measurements were used to assess body condition as blubber represents the stored energy reserves of the animal, and its thickness decreases in times of illness, pregnancy, lactation, or starvation and also changes according to age, sex and season (Ognetov 1990; Caon et al. 2007; Konishi et al. 2008). We used blubber thickness as a percentage of total body length and blubber weight as a percentage of total body weight to account for size in all our calculations.

Statistical analyses

Dietary data

Temporal patterns in the diet of male and female dolphins were assessed employing the software package PRIMER v. 6.0 (Clarke 1993), STATISTICA v. 9.0 (StatSoft Inc. 2009), CANOCO v. 4.5 (ter Braak and Šmilauer 2002), and Microsoft Excel 2007. As very little resource partitioning was found between sex and size groups of dolphins in this study (Ambrose 2010), and for comparative purposes with Young (1993), all age groups were pooled to assess the diet of the population as a whole. Using a species accumulation curve in Primer v.6, the predicted maximum number of species in the diet was calculated, to ensure adequate representation of the complete diet within the sample size used in this study. A canonical correspondence analysis (CCA) was conducted in CANOCO v. 4.5 using the stomach content raw data from the 95 dolphins analysed in this study (caught between 2000 and 2009), and the subsample of 41 dolphins re-analysed from the study of Young (1993) (caught between 1974 and 1992) to investigate any possible trends in the feeding ecology of the dolphins. This analysis was performed to determine whether the diets of the dolphins from the two time periods differed. CCA is a multivariate method used to elucidate relationships between assemblages of species and their environment. It makes use of abundance data for species, and corresponding environmental variables or class variables, and extracts synthetic environmental gradients which are used to create ordination plots (ter Braak 1986). Sites or species (in this case individual dolphins) are represented by points and data classes (age cohort, sex, capture year and sardine run period) by triangles. The data points (here representing the individual dolphins in terms of their diet composition) are plotted in two-dimensional space on the basis of similarity. The data points are clustered around the class variable which most strongly determines their distribution. Therefore, the distance between two data points shows how similar they are (in this case how similar individual dolphin diets were), and the distance between a data point and a triangle denoting a class indicates which class most strongly determines the placement of that data point within the two-dimensional ordination. In this analysis, the stomach content data (% mass for each species in the diet) for dolphins from the two time periods were entered, along with the nominal environmental (class) variables which were considered to have possible roles in determining diet composition: sex, age class, capture year and sardine run period (during, directly after or at other times of the year) (ter Braak and Šmilauer 2002). The SIMPER function in PRIMER v. 6.0 was used to determine the species contributing to the within-group similarity between the diets of all 'historical' and all 'recent' dolphins (Clarke 1993).

Fish egg density data

A Pearson's product–moment correlation coefficient was calculated in Microsoft Excel 2007 to assess the relationship between the egg densities of the two dominant prey species (*Scomber japonicus* and *Sardinops sagax*) and the relative IRI of these two prey species in the diet of the long-beaked common dolphins in KwaZulu-Natal waters. Sample sizes varied slightly for these tests depending on the availability of fish egg density data, and due to the fact that not all of the dolphins examined consumed both sardine and chub mackerel.

Isotope data

T-tests were performed using STATISTICA v. 9.0 (StatSoft Inc.) on the stable isotope signatures of dolphin tooth material obtained from the larger dataset of 16 animals, as well as the smaller subset of seven female animals with no overlap between 'historical' and 'recent' periods, in order to determine whether there were any significant differences in isotopic signals between 'historical' and 'recent' data sets, as well as between the male and female dolphins.

Blubber thickness data

Linear regressions were performed on blubber thickness and proportional blubber weight data for each age cohort in order to determine any significant trends over time.

Results

Stomach content analysis

Only one calf stomach was found to be completely empty, whilst five of the 20 calf stomachs contained only milk. A total of 23 teleost species and five cephalopod species were identified from the stomach contents of the 89 dolphins in which hard remains were found (Table 2). The maximum predicted number of species in the diet was calculated as

Table 2 Fish and cephalopod prey of all *D. capensis* incidentally caught in shark nets off KwaZulu-Natal between 2000 and 2009, and their calculated Index of Relative Importance (IRI) values

Prey species	Common name	Number	% Number	Mass (g)	% Mass (g)	Frequency of Occurrence (FO)	% FO	IRI	IRI Rank
Fish									
Ambassis natalensis	Slender glassy	2	0.18	9.00	0.006	1	1.053	0.195	23
Apogon sp.	Cardinalfish	1	0.09	2.00	0.001	1	1.053	0.096	27
Bregmaceros sp.	Codlet	10	0.90	26.15	0.017	2	2.105	1.928	18
Decapterus macarellus	Mackerel scad	20	1.80	1442.80	0.951	7	7.368	20.248	13
Diaphus sp.	Lanternfish	166	14.92	289.31	0.191	13	13.684	206.705	5
Diplodus sargus	White seabream	1	0.09	90.95	0.060	1	1.053	0.158	24
Engraulis japonicus	Japanese anchovy	56	5.03	880.02	0.580	5	5.263	29.534	10
Etrumeus whiteheadi	Whitehead's round herring	7	0.63	263.73	0.174	1	1.053	0.845	21
Exocoetidae sp. *(Cheilopogon* sp.*)*	Flying fish	29	2.61	9074.00	5.981	10	10.526	90.387	7
Gymnoscopelus cf. bolini	Lanternfish	83	7.46	6328.00	4.171	5	5.263	61.203	8
Katsuwonus pelamis	Skipjack tuna	1	0.09	500.00	0.330	1	1.053	0.442	22
Myctophidae sp.	Lanternfish	1	0.09	1.49	0.001	1	1.053	0.096	27
Pagellus bellottii natalensis	Natal pandora	30	2.70	933.38	0.615	13	13.684	45.304	9
Pomatomus saltatrix	Elf/bluefish	28	2.51	8565.23	5.646	12	12.632	103.094	6
Rastrelliger kanagurta	Indian mackerel	10	0.90	1007.00	0.664	1	1.053	1.644	19
Sardinops sagax	Sardine/pilchard	154	13.84	9860.76	6.500	22	23.158	470.946	2
Sarpa salpa	Salema porgy	11	0.99	1203.31	0.793	2	2.105	3.751	16
Scomber japonicus	Chub mackerel	233	20.93	94784.89	62.479	46	48.421	4038.945	1
Scombridae sp. *(cf. Euthynnus affinis)*	Mackerel tuna/ kawakawa	15	1.35	3360.26	2.215	6	6.316	22.501	12
Sparidae sp.	Sea bream	1	0.09	31.78	0.021	1	1.053	0.117	26
Sphyraena sp. *(cf. acutipinnis)*	Guinean barracuda	10	0.90	407.59	0.269	4	4.211	4.914	15
Trachurus delagoa	African scad	130	11.68	5702.31	3.759	18	18.947	292.526	3
Valamugil cf. seheli	Bluespot mullet	2	0.18	367.00	0.242	2	2.105	0.888	20
Cephalopods									
Enoploteuthis sp.	Enope (squid)	1	0.09	12.00	0.008	1	1.053	0.103	25
Loligo spp.	Inshore squid	48	4.31	4970.65	3.276	26	27.368	207.702	4
Lycoteuthis diadema	Crowned firefly (squid)	42	3.77	1400.47	0.923	5	5.263	24.720	11
Ommastrephes sp.	Red flying squid	9	0.81	37.45	0.025	3	3.158	2.632	17
Sepia sp.	Cuttlefish	12	1.08	156.33	0.103	5	5.263	6.217	14

$N = 89$

29.88 (Primer v.6), just one species more than that observed in the stomach contents. This suggests that the sample size was sufficiently large enough to adequately encompass the variability within the diet of *D. capensis*. Nine prey species were found to be dominant (constituting >1 % by mass) in the diet of common dolphins between 2000 and 2009 (Fig. 2b). These were flying fish (*Cheilopogon* sp.), lanternfish (*Gymnoscopelus cf. bolini*), elf (*Pomatomus saltatrix*), sardine (*Sardinops sagax*), chub mackerel (*Scomber japonicus*) and maasbanker (*Trachurus delagoa*), as well as a Scombroid species resembling mackerel tuna (*Euthynnus affinis)*, and two cephalopod species: *Loligo* and *Lycoteuthis diadema*. The possibility that the lanternfish may have been ingested as secondary prey was discounted due to their intact and well-preserved nature in the stomach contents.

The overall winter diet of common dolphins caught in recent years shows a marked difference to the diet of those

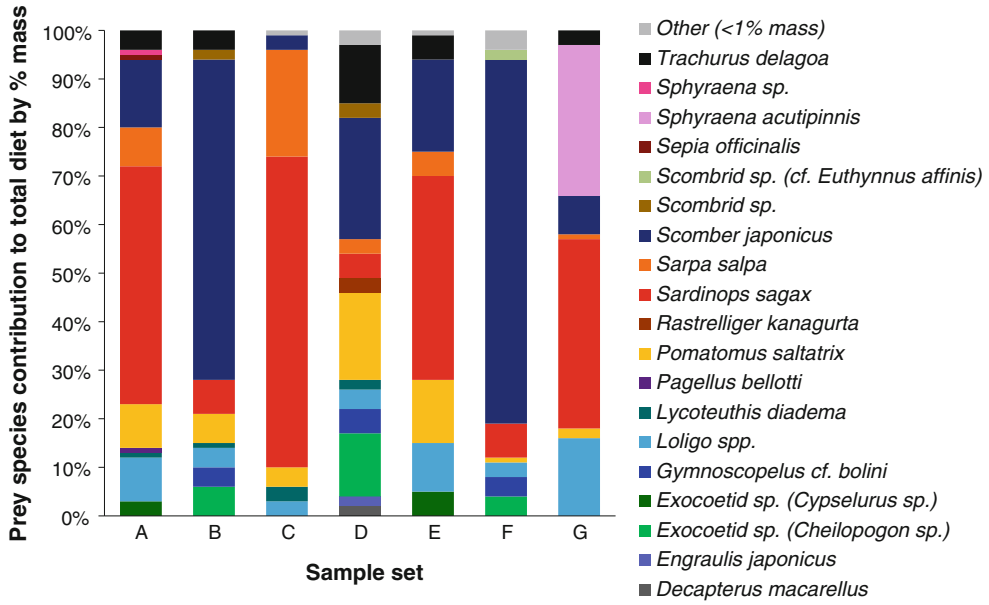

Fig. 2 Dietary composition of *D. capensis* incidentally caught in shark nets off the coast of KwaZulu-Natal for the periods; **a** 1974–1992 (Young 1993, $N = 297$), **b** 2000 to 2009 ($N = 89$), **c** during the sardine run (June and July) between 1974 and 1992 ($N = 16$), **d** during the sardine run (June and July) between 2000 and 2009 ($N = 28$), **e** directly after the sardine run (August, September and October) between 1974 and 1992 ($N = 19$), **f** directly after the sardine run (August, September and October) between 2000 and 2009 ($N = 56$), **g** outside of the influence of the sardine run (November to May) between 1974 and 1992 ($N = 6$). Only dominant prey species (>1 % of diet by mass) are shown

caught between 1974 and 1992 (Fig. 2a). The species composition of the diet within the two time periods is very similar, with flying fish (*Cheilopogon* sp.), elf (*Pomatomus saltatrix)* and maasbanker (*Trachurus delagoa)*, as well as *Loligo* and *Lycoteuthis* cephalopod species being present in the diet over both time periods. However, the proportional contributions of sardine and chub mackerel are very different between the two data sets. There is a significantly higher proportion of sardine relative to mackerel in the diet between 1974 and 1992 by mass ($P < 0.005$) and significantly more chub mackerel than sardine in the diet between 2000 and 2009 ($P < 0.001$). Strepie (*Sarpa salpa*) abundance also fell from 8 % of the diet by mass between 1974 and 1992 to 0.8 % over the last decade.

Comparing historical and recent diets

With few exceptions, the canonical correspondence analysis (CCA) illustrated a clear separation between the historic and recent dietary composition for the long-beaked common dolphins off the coast of KwaZulu-Natal (Fig. 3). The separation of the two groups was largely due to the variations in the contribution of sardine and mackerel in the diet of the dolphins during the two periods. The partial overlap in diet of the dolphins recorded periodically reflected the wide suite of prey species consumed by the common dolphin between the two time periods. None of the four chosen class variables (sex, capture year, sardine run period, or age class) explained a significant portion of the variability in the data or was particularly dominant in separating the groups (all fell close to the origin).

The diet of common dolphins caught during the sardine run (June and July) was largely comprised of five prey species (chub mackerel, maasbanker, chokka squid, elf, and flying fish), which collectively contributed 92 % of the similarity within the grouping (Table 3). Directly after the sardine run, the similarity between individual dolphin diets was attributed to only two dominant species: chub mackerel and sardine (Table 3). The SIMPER analysis revealed that in recent years (2000–2009), common dolphins in KwaZulu-Natal fed on a wider range of prey species during the annual sardine run and targeted only two main prey items (chub mackerel and sardine) outside of this winter feeding bout (Table 3). Collectively, these six dominant species accounted for >90 % of all the prey identified in the stomachs of the dolphins during and after the sardine run (Table 3).

To confirm that the diet shift detected between the 'historical' and 'recent' dietary analyses was not a product of biased sampling periods, the diet during the two time frames was broken down into dolphins caught during the sardine run, and those caught directly after the sardine run. These results illustrate differences in the pattern of changing diet diversity during and after the sardine run between the two time frames (Fig. 2c–f). Between 1974 and 1992, the diversity of the diet was low during the

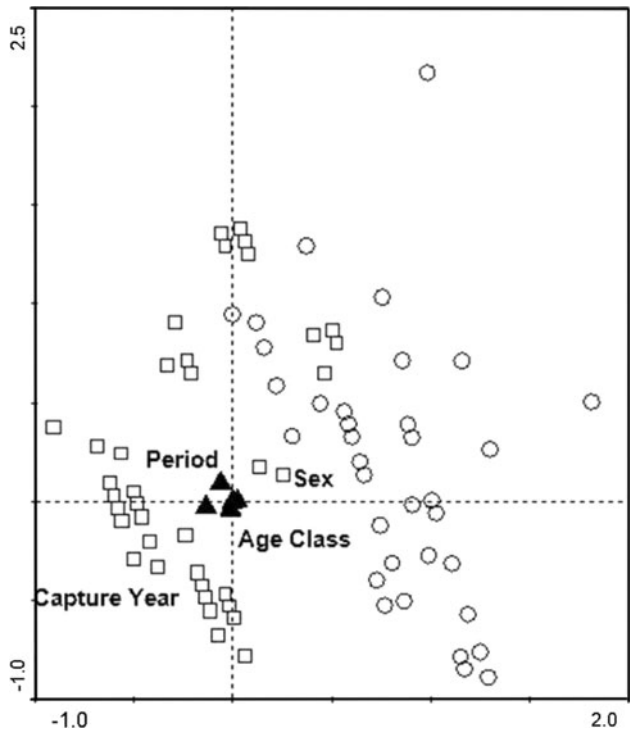

Fig. 3 Canonical correspondence ordination of 'historical' and 'recent' dietary data for *D. capensis* incidentally caught in shark nets along the coastline of KwaZulu-Natal. Historic data from 1974 to 1992 (shown as *circles*) and recent data from 2000 to 2009 (shown as *squares*) are plotted in terms of their dietary similarity, alongside environmental variables which may affect their distribution: sex, age class, capture year and sardine run period (shown as *black triangles*)

Table 3 Average Bray–Curtis similarity between the diets of long-beaked common dolphins during and directly after the sardine run between 2000 and 2009 (SIMPER Analysis—Primer v.6)

Prey species	Common name	% Contribution	Cumulative %
During the Sardine run (June and July)			
Scomber japonicus	Chub mackerel	33.19	33.19
Trachurus delagoa	Maasbanker	31.13	64.32
Loligo spp.	Chokka squid	13.33	77.66
Pomatomus saltatrix	Elf/bluefish	8.60	86.25
Exocoetidae sp.	Flying fish	6.05	92.30
Directly after the Sardine run (Aug, Sept and Oct)			
Scomber japonicus	Chub mackerel	78.13	78.13
Sardinops sagax	Sardine	13.78	91.92

sardine run (dominated by sardine, which accounted for 64 % of the total diet) and increased after the sardine run, with a range of other fish species increasing in their importance in the diet, most notably, a decline in sardine, and increase in chub mackerel and elf in the diet. The opposite trend is seen over the last decade. Between 2000 and 2009, prey diversity was highest during the sardine run (with similar contributions of mackerel, elf, flying fish and maasbanker) and falls after the peak sardine run period (with chub mackerel dominating the diet by 75 % by mass). There is also a wider suite of prey species forming small contributions to the diet during the sardine run over the last decade than there was between 1974 and 1992. This is interesting to note, as the periods 'during' and 'directly after' corresponded to exactly the same months in both data sets.

A historical sample of long-beaked common dolphins incidentally caught outside of the influence of the sardine run between 1974 and 1992 (Fig. 2g) displayed a diet that was largely comprised of sardines (39 % by mass), indicating that some sardine were available in KwaZulu-Natal year round during this period. Sharpfin barracuda (*Sphyraena acutipinnis*) plays an important role in the diet outside of the sardine run. Inshore squid were also more abundant in the diet outside of the influence of the sardine run (16 % by mass) than they were during and just after the sardine run. Chub mackerel (*Scomber japonicus*) reached its highest abundance in the diet directly after the sardine run between 1974 and 1992 (19 % by mass) (Fig. 2e), but once again forms a much smaller component of the diet in months outside of the influence of the sardine run (8 % by mass) (Fig. 2g).

Long-term variation in IRI values

When long-term trends in the importance of each prey species to the diet are considered (Fig. 4), it becomes apparent that the diet of the common dolphin is extremely variable between years, with a suite of seven dominant prey species showing large inter-annual variations in their proportional contributions to dietary make-up. Whilst sardine (*Sardinops sagax*) exhibited high IRI values during the early 1980 and 1990, its contribution to the diet over the last decade has decreased. The opposite trend is seen in the contribution of chub mackerel (*Scomber japonicus*) to the diet, with IRI values lower than those of sardine prior to the year 2000 and higher than those of sardine over the last decade (with the exception of the three dolphins caught in 2009, which had no mackerel in their stomachs). Strepie (*Sarpa salpa*) was absent from the diet of the common dolphins over the period 2006–2009.

Relationship between dolphin prey species and long-term trends in fish egg density

The estimates of sardine egg density in the waters of KwaZulu-Natal were generally equal to or higher than mackerel egg density during the 1980s and 1990s (Fig. 5a). However, from 2001 onwards, a general decline in sardine

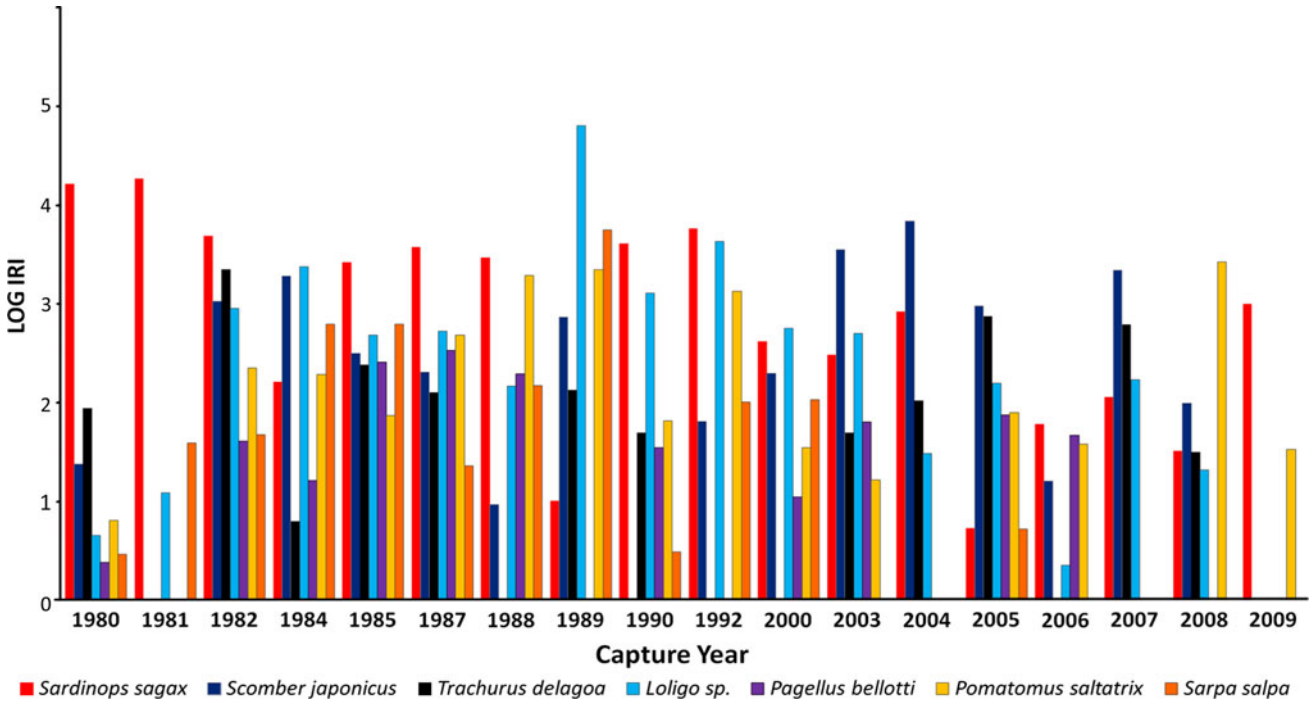

Fig. 4 Annual variation in LOG IRI (Index of Relative Importance) values for dominant prey species in the diet of *D. capensis* (all age cohorts combined) over the period 1980–2009 (including dolphins caught both inside and outside of the sardine run). Only species contributing >5 % of the diet by mass are shown

egg density was observed, and a corresponding increase in mackerel egg density was seen (Fig. 5a). During the period 2005–2008, sardine egg density in the waters off KwaZulu-Natal appears to have declined dramatically. Mackerel egg density also declined over the same period (notably in 2006 and 2008), but to a much lesser extent. After 2005, the density of mackerel eggs far exceeds that of sardine. In some years, the relative egg densities of sardine and mackerel parallel the trends in the importance of these prey species in the diet of the common dolphins, but this was not consistently the case (Fig. 5b). Between 1980 and 1992, sardine was the more important prey in the diet, with the exception of the years 1984 and 1989, in which mackerel was more abundant. However, after 2000, mackerel becomes relatively more important in the diet than sardine in all years, with the exception of 2006 and 2009. There was a positive correlation between sardine (*Sardinops sagax*) egg densities in KwaZulu-Natal waters and the IRI of sardine in the diet of the long-beaked common dolphins ($r = 0.69$, $N = 13$, $P < 0.01$). However, no significant correlation was found between chub mackerel (*Scomber japonicus*) egg densities and the relative importance of this prey species in the diet of the long-beaked common dolphin over the same period ($r = 0.18$, $N = 11$, $P > 0.05$). There was also no statistical support for a correlation between sardine egg density (used as a proxy for sardine abundance) and the consumption of chub mackerel (*Scomber japonicus* IRI) by the long-beaked common dolphins in KwaZulu-Natal ($r = -0.43$, $N = 10$, $P > 0.05$).

Stable isotope analyses

No significant changes were observed in trophic level signature of the common dolphins from KwaZulu-Natal waters over the period 1980 to 2008. The average $\delta^{15}N$ signature for 'historical' tooth dentine was 13.43 ± 0.7 ‰, whilst that for 'recent' teeth was 13.15 ± 0.3 ‰. The average $\delta^{13}C$ signature for 'historical' tooth dentine was −13.34 ± 0.6 ‰, whilst for 'recent' teeth it was −13.31 ± 0.8 ‰. The average values for all 16 common dolphins in this sample were 13.29 ± 0.5 ‰ for $\delta^{15}N$ and −13.32 ± 0.6 ‰ for $\delta^{13}C$. No significant difference was found between the $\delta^{15}N$ and $\delta^{13}C$ isotopic ratios of historical versus recent teeth ($P = 0.283$ for N and $P = 0.922$ for C), with $\delta^{15}N$ signatures ranging from 12.59 to 14.57 ‰ and $\delta^{13}C$ signatures ranging from −14.51 to −12.09 ‰. Likewise, there was no significant difference in either $\delta^{15}N$ or $\delta^{13}C$ isotopic signals between the male and female common dolphins for which dentine was analysed ($P > 0.05$). The *t*-test carried out on the smaller subset of seven dolphins whose feeding periods did not overlap between 'historical' and 'recent' periods corroborated this result, with no significant differences being detected

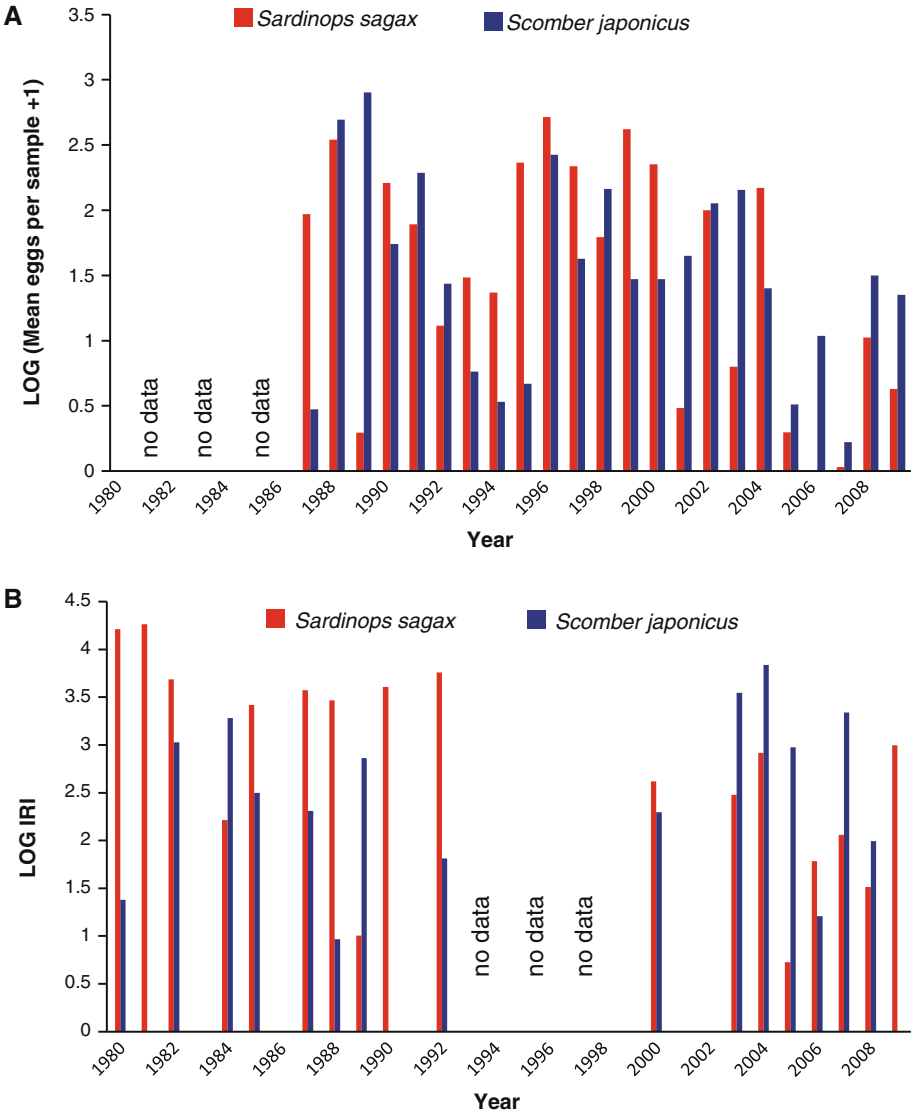

Fig. 5 Estimates of *Sardinops sagax* (sardine) and *Scomber japonicus* (chub mackerel) egg densities sampled from the water column offshore of Park Rynie, KwaZulu-Natal in mid-winter each year between 1987 and 2009 (Connel 2010b) (**a**), and annual variation in IRI (Index of Relative Importance) values for these two dominant prey species in the diet of *D. capensis* over the periods 1974–1992 (Young 1993) and 2000–2009 (**b**)

between the two time periods for either $\delta^{15}N$ or $\delta^{13}C$ ($P = 0.192$ for N and $P = 0.868$ for C).

Blubber thickness and blubber weight records

Due to the different sampling protocols for blubber over the last 40 years employed by PEM staff, the sample sizes for blubber thickness data and blubber total weight data varied slightly. For blubber thickness data: calf ($N = 18$), juvenile ($N = 0$), adult male ($N = 21$), adult resting female ($N = 4$), pregnant female ($N = 6$) and lactating female ($N = 14$). For blubber total weight data: calf ($N = 53$), juvenile ($N = 19$), adult male ($N = 42$), adult resting female ($N = 9$), pregnant female ($N = 7$) and lactating female ($N = 23$). Blubber thickness as a percentage of body length showed no significant change over the last four decades for any of the age cohorts at mid-dorsal, mid-lateral and mid-ventral sites (R^2 values ranged from 0.001 to 0.25). Similarly, blubber total weight as a percentage of body weight also showed no significant change over the last 40 years for any of the age cohorts: calf ($R^2 = 0.013$), juvenile ($R^2 = 0.003$), adult resting female ($R^2 = 0.031$), adult male ($R^2 = 0.073$), pregnant female ($R^2 = 0.411$) and lactating female ($R^2 = 0.107$).

Discussion

The diet of *Delphinus capensis* off the KwaZulu-Natal coast of southern Africa is representative of the pelagic habitat of the species and its group feeding dynamics. The bulk of its diet consists of pelagic and epipelagic shoaling fish species which can be herded into bait balls by cooperative foraging. Most of the prey species in the diet of *D. capensis* off KwaZulu-Natal are fish species which migrate along the coastline in high numbers during winter

and are found in water depths shallower than 250 m (with the exception of *Trachurus delagoa* which is found down to 400 m, and *Sarpa salpa*, which is an inshore schooling herbivore) (van der Elst 1995; Heemstra and Heemstra 2004). Long-beaked common dolphin pod movement, particularly during these winter months, is closely linked to that of their preferred prey species (Selzer and Payne 1988; Cockcroft and Peddemors 1990; Brophy et al. 2009).

When discussing the ecological role and foraging strategy of the common dolphin, it is necessary to define whether this species is a generalist (opportunistic) or specialist in terms of its prey selection. Elucidating specific types of prey selection has always been difficult for marine mammals, primarily because most studies must rely on stomach content results, without the ability to also quantify prey availability in the foraging habitat of the cetacean (Berens McCabe et al. 2010). Prey abundance is an important influencing factor for the development of foraging strategy in animals—if the prey suite available is narrow, their diet should be more generalized to minimize the time taken to find food, whilst if the prey suite available to the animal is particularly large, the animal can afford to be more selective, taking time to select prey of higher nutritional value (MacArthur and Pianka 1966). A generalist (opportunistic) species is able to occupy and exploit a wide range of habitats and show a high degree of dietary plasticity (Ruffino et al. 2011). According to optimal foraging theory, generalist (opportunistic) species prey on the most readily available, high quality food resources in order to maximize their net energy intake rate and can rapidly switch when other resources become more abundant on a seasonal basis (MacArthur and Pianka 1966; Pyke et al. 1977). Conversely, a specialist species exhibits a much more restricted and less diverse diet, preferring to focus on a limited suite of potential prey items (MacArthur and Pianka 1966).

The results of this study support the classification of the common dolphin as a specialist in its feeding strategy. Although the overall diet shows a wide suite of 28 prey species, the vast majority of the diet (over 94 %) comprises only nine prey species. The other 19 prey species all constituted less than 1 % of the total diet in terms of mass. This adaptation to feeding on the locally most abundant prey is a common feature of the feeding strategy of common dolphins worldwide. For example, Romero et al. (2012) demonstrated that the diet of short-beaked common dolphins (*D. delphis*) in the south-west Atlantic was dominated by one prey species: the Argentine anchovy (*Engraulis anchoita*), which made up over 80 % of their prey intake by number and 62 % of their prey intake by weight. Silva (1999) found that although the short-beaked common dolphins off the Portuguese coast took a wide variety of prey items, over 75 % of their diet was made up of only four fish and two cephalopod species. Meynier et al. (2008a) identified only three dominant species in the diet of the common dolphins (*Delphinus* sp.) off New Zealand, despite the overall diet appearing quite diverse (31 fish and seven cephalopod species). Similar evidence was shown by Berens McCabe et al. (2010) for the common bottlenose dolphin (*Tursiops truncatus*) being a specialist feeder within resident populations. Their results show positive selection by the dolphins for a small number of prey species and negative selection against the wider array of potential prey species (i.e. the dolphins were consuming prey species in different proportions to their availability in the local environment). Worldwide, *T. truncatus*, like *D. capensis*, shows divergent feeding specializations when different regional localities are compared. However, there is clear evidence to show that within a given habitat, each population has specialized its diet to a smaller subset of the prey suite available to it (Berens McCabe et al. 2010).

Previous research demonstrated that the common dolphin diet in KwaZulu-Natal waters comprised mainly sardine (*Sardinops sagax* 48.1 % by mass), chub mackerel (*Scomber japonicus* 13.5 %), elf (*Pomatomus saltatrix* 8.7 %), squid (*Loligo spp*. 8.4 %) and strepie (*Sarpa salpa* 8.1 %) (Young and Cockcroft 1994). The relative contribution of the different species to the diet of the common dolphin, however, demonstrated a high degree of inter-annual variability, probably reflecting changes in prey availability during the sardine run (Young and Cockcroft 1994). Several studies have documented seasonal variation in the diets of common dolphins (Collet 1981; Desportes 1985; Young 1993; Santos et al. 2004; Brophy et al. 2009), but the annual sardine run phenomenon in South Africa is likely to be one of the most outstanding examples of marked seasonal changes in common dolphin diet, due to the mass movement of both predator and prey species. Several species of predatory fish, such as chub mackerel (*Scomber japonicus*), elf (*Pomatomus saltatrix*) and strepie (*Sarpa salpa*), also migrate into KwaZulu-Natal during winter, a behaviour that is either a result of the occurrence of favourable spawning conditions or the increased food availability resulting from the high abundance of sardine prey (van der Elst 1995; Heemstra and Heemstra 2004; Fennessy et al. 2010). Thus, a wider suite of prey species is available to the dolphins during this annual migration, and their diet is reflective of this wider prey spectrum (Young 1993). The increased diversity in the diet of common dolphins during the sardine run found in our study reflects the increased incidence of predatory fish moving into KwaZulu-Natal during winter. This increased dietary diversity was not evident for the sardine run period between 1974 and 1992. This could be due to two reasons: our smaller subset of this data was not large enough to

encompass the same degree of diversity, or some level of prey switching has occurred in recent years, meaning that the common dolphins are supplementing their diet with higher proportions of other species when sardine are less abundant. Seasonal variation in the contributions of different prey to the diet of common dolphins is a common occurrence throughout their range (Young and Cockcroft 1994; Meynier et al. 2008b; Brophy et al. 2009). Current data pertaining to the abundance and duration of availability of sardine on the east of South Africa would be necessary to help support the argument for prey switching.

After the sardine run, the bulk of the diet (75 % by mass) of the long-beaked common dolphin still comprised chub mackerel, with sardine forming a small component (7 % by mass). The dolphins may gain energetic benefits from consuming larger fish such as chub mackerel, as they occur in relatively high densities during this time and have a higher calorific content than sardine (10.1 kJ g^{-1} for mackerel and 8.6 kJ g^{-1} for sardine) (Young 1993). The vast majority of the winter diet in all years consists of energy-rich fish (chub mackerel and sardine), a factor which is likely to make this annual long-distance migration into KwaZulu-Natal energetically rewarding. The cooperative hunting tactics employed by common dolphins, whereby some members of the group constantly herd fish into a bait ball, whilst other members feed on them, are likely to be energetically expensive, and hence more viable if calorie-rich prey are targeted (Meynier et al. 2008b). According to optimal foraging theory (MacArthur and Pianka 1966; Charnov 1976; Pyke et al. 1977), focusing their attention on high-energy, shoaling fish species is advantageous, as the dolphins are able to maximize their energy intake rate. Due to the spatial heterogeneity of food resources in the offshore environment, common dolphins migrate both daily and seasonally in search of prey and may spend up to 54.8 % of their time travelling, and 17 % feeding (Neumann 2001), and only an energy-rich diet would be able to support this highly mobile lifestyle. Young (1998) also demonstrated that the mean dietary intake of common dolphins was found to contain more than double the energy value of the prey consumed by bottlenose dolphins feeding in the same area of KwaZulu-Natal, South Africa. Having found some correlations between dietary intake, water temperature, and blubber thickness, Young (1998) attributed this difference to the increased energetic demands of faster swimming in colder offshore waters for the common dolphin population.

In contrast to the earlier study by Young (1993), the diversity of the diet of the common dolphin over the period 2000–2009 attained the highest levels during the sardine run. Young (1993) hypothesized that the increased relative contribution of elf and mackerel during the winter months was either due to the dolphins moving into deeper, offshore waters to feed once the sardine shoals had dispersed, or as a result of the larger predatory fish moving inshore to feed on sardines during this period. Young (1993) also documented increased incidental catches of common dolphins in the shark nets late in the year (October) in 1964 and 1982, when the sardine run was particularly strong and lengthy. Hence, it seems that the return movement of the common dolphins back towards the south coast is controlled largely by the presence of sardine, and possibly mackerel shoals, in KwaZulu-Natal. As was the case in 1992, there is still little information today on the diet of common dolphins outside of the winter sardine run period, although the occurrence of sardine in the stomachs of stranded dolphins from the Eastern Cape coast suggests that sardine may occur along the south and east coasts throughout the year, providing a continued prey source for the common dolphin at other times of the year (Young 1993; Young and Cockcroft 1995). With the eastwards shift of the majority of the sardine spawning stock in recent years (Coetzee et al. 2008; Crawford et al. 2008), the contribution of sardine to the diets of south and east coast common dolphins may be expected to increase.

During the period 2000–2009, the species composition of the diet of common dolphins changed very little from that observed by Young and Cockcroft (1994) for the period 1974–1992, despite inter-annual and seasonal fluctuations in the proportion of each species to the diet. It was thought that the temporal bias in dolphin incidental catches between the two studies (due to a reduction in nets off beaches (Dudley and Cliff 2010)) could be affecting the overall abundance of mackerel and sardine in the diet when results are pooled for the whole catch period and compared to the results of Young (1993). However, when broken into two periods, 'during' and 'directly after' the sardine run, it becomes apparent that even after the peak of the sardine run, substantially more sardine were being consumed by common dolphins between 1974 and 1992 than over the last decade. This verifies that the shift over the last decade towards a mackerel-dominated diet is a genuine result and not a sampling bias.

Long-term comparisons between fluctuations in local fish stocks and the prey suite consumed by common dolphins aid in determining how the diet of the dolphins reflects prey species abundance (Meynier et al. 2008b). There is a strong spatial bias in the collection of data on fish abundance from South Africa, with an almost complete absence of relevant data on fish abundance from the East coast (O'Donoghue et al. 2010a). As a consequence, we have employed fish egg density as a proxy for prey availability. O'Donoghue et al. (2010a) report significantly lower sardine presence on the East coast in the years 2003, 2006 and 2007, and increased variability in sardine presence over the last decade. Young (1993) also reported an

increase in the diversity of the diet during the sardine run period, with an increase in the mackerel component; however, in most years between 1974 and 1992 (with the exception of 1984 and 1989), sardine were still the dominant prey item. It is clear that although the suite of prey species in the diet is very similar between the present study and that of Young (1993), the proportions of these prey species differ widely over the last four decades.

A similar trend to that found in the present study has also been observed in the diet of sharks caught in the shark nets in KwaZulu-Natal during the annual sardine run. Dudley and Cliff (2010) analysed the occurrence of sardine in the stomachs of net-caught sharks between 1979 and 2005 and also found a decline in the abundance of sardine in their diets over this period. More than 70 % of the stomachs sampled between 1978 and 1984 contained sardine prey, whilst only 9.5 % of the shark stomachs sampled between 1999 and 2005 contained sardine (Dudley and Cliff 2010). Although both shark and common dolphin diet analysis seems to suggest a decline in the abundance of sardine in KwaZulu-Natal during winter over the last decade, beach seine netting sometimes reveals contradictory evidence. For example, particularly high catches of sardine in beach seine nets were recorded in 2005, indicating that the shoals were still highly abundant in nearshore waters (van der Lingen et al. 2010). This prompts the question, that if sardine are still abundant and being netted inshore, why are the large predators not feeding on them to the same degree as they used to in previous decades?

The South African sardine stock shows inherently high variability in recruitment strength (possibly a result of environmental forcing) and is characterized by decadal-scale fluctuations in population size (Hutchings et al. 2009). Acoustic surveys carried out in South African waters also fail to provide accurate biomass estimates for chub mackerel, as these fast-swimming fish appear to evade capture by the small pelagic trawl used for sampling, leading to a paucity of data on their abundance and location (Hutchings et al. 2012; J. Coetzee pers comm.). Egg density measurements would appear to give the impression that chub mackerel stocks have been more stable over the last decade than that of sardine, but these data do not give a reliable proxy for spawner biomass. Hence, it is impossible to give an accurate account of chub mackerel population dynamics in South African waters at present. The decline in strepie (*Sarpa salpa*) in the diet is also unexplained, as no recent stock size estimate is available for this species in KwaZulu-Natal waters. However, van der Walt and Govender (1996) determined that the fishing pressure on strepie was sustainable, and that, even if it increased, the stock would be unlikely to be over-exploited along this stretch of coastline.

The changes observed in the diet of the common dolphins over time appear to be somewhat linked to the abundance of their two most important teleost prey species in KwaZulu-Natal waters. However, other factors such as the patchy shoal distribution of sardine, as well as prey selection by the dolphins, may also play a key role in creating the fluctuation in IRI of prey species seen in the diet. The differences in spatial dynamics between the two dominant prey species may contribute to the lack of correspondence between egg density data and fluctuations of IRI seen in the diet of the dolphins. The density-independent patchiness of sardine shoals means that certain areas may have very high sardine density, whilst neighbouring areas show very low to no sardine presence (Barange and Hampton 1997). Water column sampling in a limited area may simply miss patches of high sardine density and hence not correlate well with the IRI for this prey species in the diet of the dolphins.

The correlation between sardine egg density data and sardine IRI in the diet, but lack of correlation between chub mackerel egg density data and mackerel IRI, suggests that the common dolphin may prey selectively on sardine, but in times of low sardine abundance will eat a higher proportion of chub mackerel. Given this seemingly selective predation on sardine, the high IRI of chub mackerel in the diet over the last decade could indicate changes in the shoaling characteristics of the most abundant fish prey. If mackerel occur in very high densities relative to sardine (thus making them equally easy to catch), it would make energetic sense to prey on these larger fish (the average reconstituted total length for chub mackerel was 34.78 cm, as opposed to 19.27 cm for sardine). Additionally, because mackerel have a higher calorific value (approximately 10.1 kJ g^{-1} compared to 7–8.6 kJ g^{-1} for sardine) (Young 1993; Pichegru et al. 2010), the dolphins may gain energetic benefits from targeting larger mackerel if their occurrence in high numbers makes predation on the species easier. When long-term trends in the IRI of each prey species to the diet are considered, it is apparent that the proportions of its preferred prey species are quite variable between years. As the common dolphin is able to make use of whichever prey species are locally abundant at the time, this inter-annual variability in the contribution of different prey to the dietary make-up is a key feature of their feeding ecology (Young and Cockcroft 1994). These findings make it possible to hypothesize that in most years, the long-beaked common dolphin preys predominantly on sardine in winter, because of their seasonal abundance in KwaZulu-Natal waters. However, in poor sardine run years, their intake of sardines, as well as the abundance of sardine eggs in the water column, declines. The absence of a correlation between chub mackerel egg abundance and the consumption of chub mackerel by the dolphins is likely to be due to the fact that the long-beaked common dolphins will only consume large amounts of chub mackerel in years when

sardine are numerically much less abundant, and hence, the consumption of chub mackerel is not related to their abundance. The long-term analysis of IRI of prey species indicates that although there have been inter-annual shifts in the principal prey species consumed, the same suite of prey species has always been available to the common dolphins.

No long-term changes in feeding or body condition were detected by the stable isotope and blubber measurement analyses, despite the stomach content results showing a significant shift in the winter diet of the common dolphins in KwaZulu-Natal. The sardine run feeding bout represents only two to three months of their annual diet and hence is unlikely to be detected in the assimilated signal incorporated in teeth. Since blubber thickness and weight are used as proxies for animal condition (Ognetov 1990; Konishi et al. 2008), it can be argued that the general body condition of the animals has not declined over the corresponding period. This result improves our understanding of the common dolphin as an adaptable, but specialist feeder. The dolphins will aim to maintain body condition, and hence, if the abundance of a preferred prey species declines in the local environment, the dolphins will adapt to include higher proportions of less favoured prey, but those which are of similar energetic quality, into their diets in order to maintain condition. However, more detailed data on blubber weights, particularly since 1995, would have been favourable for the present analysis. This highlights the need to revise the current sampling protocol by the PEM and re-introduce detailed sampling of blubber data, particularly blubber weights, from by-caught animals in an attempt to get a more detailed insight into long-term changes of this character.

Prey distribution is known to be one of the main factors in controlling the distribution of cetacean species (Gambaiani et al. 2008). The abundance and distribution of the prey species consumed by cetaceans are largely driven by temperature regimes, riverine nutrient fluxes, hydrographic features (e.g. fronts) controlled by wind-driven mixing and plankton productivity (Lafuente et al. 2002; Sabatés et al. 2006; Gambaiani et al. 2008). Cetaceans, as large predators, are likely to experience the effects of global warming on an acute level, due to the culmination of different climatic changes affecting the availability of their food sources. Cetacean prey species including sardine and cephalopods are sensitive to changes in water temperature and pH (Gambaiani et al. 2008). For example, the extent of the sardine run in South Africa is limited to water temperatures below 20–21 °C (Coetzee et al. 2010). Examples are already emerging of changes in cetacean populations as a result of climatic shifts. Bearzi et al. (2003) have documented changes in the distribution of the prey species of the short-beaked common dolphin in the Adriatic Sea, which are likely the result of prey depletion, habitat degradation, and climate change. There is also evidence that demersal fish species in the North Sea have changed their depth and latitudinal ranges over the last 25 years (Perry et al. 2005), and that cetacean species are already responding to changes in sea temperature. MacLeod et al. (2005) documented a range reduction in white-beaked dolphins (*Lagenorhynchus albirostris*) and range expansion in short-beaked common dolphins in north-west Scotland. Marine mammals are highly mobile species and are generally credited with the ability to adapt to changes in prey distribution and diversity both by migration and by prey-switching behaviour (Simmonds and Isaac 2007). The extent of their adaptability to these changes is, however, as yet unknown and difficult to predict (Simmonds and Isaac 2007).

The most recent research on the sardine run indicates that this phenomenon is primarily a spawning migration, made possible by the cooling of inshore waters and the extension of a habitat suitable for sardine occupancy (Fréon et al. 2010). In addition, the movement of sardine shoals into the Durban area is also reliant on the existence of inshore countercurrents and the sporadic occurrence of the cyclonic Durban eddy (Roberts et al. 2010). These factors are necessary for the sardine shoals to migrate against the flow of the warm Agulhas current (Roberts et al. 2010). Since strong sardine movement only occurs when low sea-surface temperatures (<20 °C) and the presence of these enabling oceanographic features coincide, it appears that oceanographic conditions provide the mechanisms which both enable, and limit, the movement of the sardine shoals up the east coast (O'Donoghue et al. 2010a). Currently, we have very little understanding of how sardine run dynamics may possibly be changing in response to global climate change. Despite growing evidence that the sardine run has, over the past decade, demonstrated a high degree of unpredictability (O'Donoghue et al. 2010a), long-beaked common dolphins have been able to adjust to these fluctuations by altering the proportions of their preferred prey species in their diet (i.e. decreased sardine intake and increased chub mackerel intake). These data confirm the status of the common dolphin both locally and internationally as being highly adaptable to local conditions and local prey species (Sekiguchi et al. 1992; Young and Cockcroft 1994; Silva 1999; Das et al. 2000; Meynier et al. 2008a; Lauriano et al. 2009; Romero et al. 2012). Results of both stable isotope and blubber data analyses indicate that the trophic position and general condition of the long-beaked common dolphins along the east coast of South Africa have remained stable over the past four decades. Providing sufficient alternative pelagic fish species are abundant in the region when sardine runs are poor, it would appear the long-beaked common dolphin is well adapted to respond to variations in the timing and intensity of the

winter sardine run. Future research focusing on the link between sardine run intensity and the diet of the common dolphin in South Africa may yield interesting information regarding how important this natural phenomenon is in the species' feeding ecology.

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