FEEDING ECOLOGY AND DIET SHIFT OF LONG-BEAKED COMMON DOLPHINS *DELPHINUS CAPENSIS (GRAY 1828*) INCIDENTALLY CAUGHT IN ANTI-SHARK NETS OFF KWAZULU-NATAL, SOUTH AFRICA

by

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Abstract

The long-beaked common dolphin, *Delphinus capensis* (Gray 1828), is one of the most enigmatic predators feeding in the annual sardine run (*Sardinops sagax*) off the coast of KwaZulu-Natal (KZN), South Africa. In recent years, unpredictable inter-annual variations in the timing, spatial extent and intensity of the sardine run have been documented, possibly resulting in changes in the suite of prey available to the common dolphin during winter. Although the diets of a number of predators during the sardine run have been studied in detail (e.g. sharks and flying seabirds), little is known about the diet of long-beaked common dolphins during this period. Each year, a low number of common dolphins are incidentally caught in the anti-shark nets in the waters of KwaZulu-Natal. These captures provide a valuable source of data on selected aspects of the ecology of the long-beaked common dolphins along the KwaZulu-Natal coastline. The objective of this study was to provide new dietary data for the common dolphins feeding in the waters of KwaZulu-Natal during winter over the period 2000 to 2009, as well as to determine if any dietary changes had taken place since the common dolphin diet was last assessed, over 15 years ago. Stomach contents from 95 common dolphins (55 females, 40 males) caught between 2000 and 2009 were analysed and compared to historical data from dolphins caught between 1974 and 1992. Mesopelagic fish and squid dominated the diet, with 23 fish and 5 squid species represented in adult dolphins. Multidimensional Scaling (MDS) indicated that there was no resource partitioning between adult male and female dolphins. Numerical analyses indicated that there was a shift in the principal prey species consumed by the dolphins over the past decade, particularly during the winter. Prior to 1992, sardine comprised up to 49% of the total stomach contents, while chub mackerel (*Scomber japonicus*) was the dominant prey item (66% by mass) recorded in the stomach contents over the period 2000 to 2009. The shift in the relative contributions of sardine and mackerel in the diets of the dolphin appeared to correspond to fluctuations in the availability of the two principal prey species. Between 2000 and 2009, the diversity of the dolphins' diets was highest during the sardine run, reflecting the presence of a wide suite of predatory teleosts in the waters of KwaZulu-Natal during the annual sardine run. Conversely, prior to 2000, the diet was dominated by sardine during the peak of the sardine run, whilst diet diversity increased after this period. Apart from sardine and chub mackerel, elf (*Pomatomus saltatrix*), maasbanker (*Trachurus delagoa*), strepie (*Sarpa salpa*) and flying fish (*Exocoetid* sp.) also formed important components of the diet both prior to 1992, and over the last decade. Blubber thickness was assessed as an indicator of animal condition. No significant change in blubber total weight ($R^2 = 0.0016$, $N = 185$), nor dorsal, lateral or ventral blubber thickness ($R^2 = 0.3146$, $R^2 = 0.0003$, and $R^2 = 0.0003$ respectively, $N = 78$) was seen over the last 30 years (1970 to 2009). Results of stable isotope analyses conducted on tissue derived from the teeth of *D. capensis* indicated that there has been no significant shift in the trophic position ($\delta^{15}N$) and potential prey consumed ($\delta^{13}C$) over the corresponding period. These data would suggest that the long-beaked common dolphins along the KwaZulu-Natal coastline can be considered as opportunistic predators generally consuming the most abundant prey species available locally. As common dolphins feed opportunistically, this dietary shift appears to indicate changes in the shoaling characteristics of the most abundant fish prey in KwaZulu-Natal during winter. Given the "Data Deficient" status of the long-beaked common dolphin on the IUCN Red Data List, and the strong climatic forcing of the sardine run, such dietary data have important implications for their conservation in the light of expanding fisheries and climate change.

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Chapter 1

General Introduction

Role of marine mammals in aquatic ecosystems

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 e.g. increasing sea-surface temperatures (SST), changes in the abundance and distribution of their prey stocks, and the impacts of over-fishing (Sekiguchi *et al*. 1992, Bowen 1997). This high sensitivity not only makes them more vulnerable to environmental perturbations, but also makes them good indicator species or barometers of environmental change (Sekiguchi *et al*. 1992, Bowen 1997). Due to their large body size and abundance, marine mammals are believed to have important impacts on the populations of their prey species (Trites *et al.* 1997). The smaller cetacean species have, however, rarely been implicated in having an effect on commercially valuable fish stocks (Sekiguchi *et al*. 1992). The impact of human harvesting of the fish species which make up the diet of cetaceans, as well as incidental captures of cetaceans in commercial fishing gear, however, negatively impacts cetacean populations (Sekiguchi *et al*. 1992, Bowen 1997). Kaschner *et al.* (2006) found that the consumption of small pelagic fishes by marine mammals and seabirds did not compromise human harvesting for commercial purposes, but that a human-induced reduction in the availability of small prey species is a likely problem for piscivorous predators. As dolphins may consume prey of a similar size to that targeted in fisheries off the South African west and south coasts, there is the risk of overlap between dolphins and fisheries in their exploitation of small pelagic fishes in this area (Kaschner *et al.* 2006, Young 1993). The conflict between the feeding activities of marine mammals and the catch of small pelagic fisheries is expected to be mitigated by the high mobility of cetaceans, although marine mammal population declines have been documented in areas of intense competition (Bearzi *et al.* 2003, Bearzi *et al.* 2006, Bearzi *et al.* 2008). For example, short-beaked common dolphin (*Delphinus delphis*) populations in the Mediterranean and Ionian Seas have been dramatically reduced due to the massive commercial exploitation of small pelagic fishes in the area for booming local seafood markets, as well as for use in the farming of Bluefin tuna (Kaschner *et al.* 2006). In order to assess the potential impact of human fishing activities and global climate change on the populations of cetaceans, it is essential that their feeding ecology and trophic functioning is understood (Bowen 1997).

Long-beaked common dolphin (*Delphinus capensis*)

Taxonomic status

The long-beaked common dolphin is classified as belonging to the Order Cetacea, Suborder Odontoceti, Family Delphinidae, Genus *Delphinus* and Species *Delphinus capensis* (Gray 1828). Common dolphins are small cetaceans with a particularly wide tropical and temperate geographical range, being found both in coastal and offshore waters between 60˚N and 50˚S in water temperatures ranging from 10˚C to 28˚C (Klinowska 1991, Heyning & Perrin 1994). They exhibit a range of colouration (Stockin & Visser 2005) and some variability in skeletal characteristics, which have led to considerable taxonomic confusion (Samaai *et al.* 2005).

Until recently, it was assumed that only one species of common dolphin existed, with an almost global distribution range in temperate waters. Heyning & Perrin (1994) subsequently identified two distinct species: the short-beaked common dolphin (*Delphinus delphis*) and the long-beaked common dolphin (*Delphinus capensis*). The short-beaked common dolphin, *Delphinus delphis,* is a pelagic cetacean species which has a wide distribution range, occurring in all tropical, subtropical and temperate seas (Evans 1976). The long-beaked *D. capensis* species is found in disjunct populations in the coastal waters off Japan, Taiwan, Korea, South and West Africa, California, Mexico, Peru, Venezuela and Argentina (Heyning & Perrin 1994, Best 2007). Common dolphins may also occur off Mozambique and Kenya, as well as Namibia, although these populations have yet to be identified to the species level (Findlay *et al.* 1992). Since the short-beaked and long-beaked forms were only recognized as separate species in 1994, their distribution ranges may need to be revised (Heyning & Perrin 1994, Hammond *et al*. 2008).

The existence of two species of common dolphin was established using both morphological (colouration, body and rostral lengths) and mitochondrial DNA differences – the short-beaked common dolphin (*D. delphis*), and the long-beaked common dolphin (*D. capensis*), with the addition of a sub-species of the long-beaked variety; the Indo-Pacific common dolphin (*D.capensis tropicalis*) which appears to be distributed in the Arabian Sea as far as the west coast of Pakistan (van Bree 1971, Heyning & Perrin 1994, Rosel *et al.* 1994, Jefferson & Van Waerebeek 2002, Best 2007). Heyning & Perrin (1994) documented two forms of common dolphin in the eastern North Pacific (based on colouration, rostral length and total body length), but stomach content analyses revealed no distinct feeding differences between the two forms. Heyning and Perrin (1994) also separated the long-beaked and short-beaked species using morphological data from Californian populations living in sympatry. They found significant differences between the two forms based on colouration, total body length, rostral length, vertebral and tooth counts. In general, Heyning & Perrin (1994) found that the long-beaked form inhabited shallower waters over the continental shelf, while the short-beaked form demonstrated a more oceanic distribution. This geographic separation corresponds to that given by Best (2007) for the southern African Subregion, with *D. capensis* being found along the coastline, and *D. delphis* in more isolated oceanic populations.

Genetic evidence (using mitochondrial and nuclear DNA markers) supports the morphological delineation into the two sympatric species in the eastern North Pacific (Kingston & Rosel 2004). However, the morphological characteristics used to distinguish the two species in this area have been found to vary in other parts of the world, and genetic evidence does not support 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.* 2005). Natoli *et al*. (2005) hypothesize that the lack of congruence between morphometric and genetic species delimitations in southern Africa suggests that these morphotypes are a result of local adaptation rather than genetic differentiation into distinct lineages. Natoli *et al*. (2005) suggest that the evolution of long-beaked forms of both the common dolphin and bottlenose dolphin in nearshore environments may simply be evidence of convergence in similar environments, a hypothesis which remains to be tested. Kingston & Rosel (2004) reiterate the difficulty of conducting genetic analyses to delineate delphinid species, as they are typified by remarkably high levels of intraspecific variation, and extremely low levels of interspecific variation.

The long-beaked common dolphin exhibits high genetic variation and a lack of monophyly (Natoli *et al.* 2005). This suggested that the species may have evolved independently several times in different coastal regions from founder events, arising from the panmictic parent stock of oceanic common dolphins (i.e. it is likely to be polyphyletic) (Natoli *et al.* 2005, Best 2007). Morphological convergence in response to habitat selection and similar feeding modes may account for the similar morphology of these separated populations (Natoli *et al.* 2005). Pinela *et al.* (2008) studied common dolphins off Mauritania (NW Africa), and concluded that both long-beaked and short-beaked forms co-exist in Mauritanian waters, with beak-length being more indicative of foraging habitat than of taxonomic separation. It is clear that the common dolphin exhibits a range of morphological variants throughout its global distribution range, and that to date, genetic analyses have not been able to make clear species delimitations within the genus *Delphinus*. It is worth noting that Natoli *et al.* (2005) found that the South African common dolphins showed the highest levels of genetic differentiation, and consequently South Africa is given as the type locality for the long-beaked form, *D. capensis* (Gray 1828).

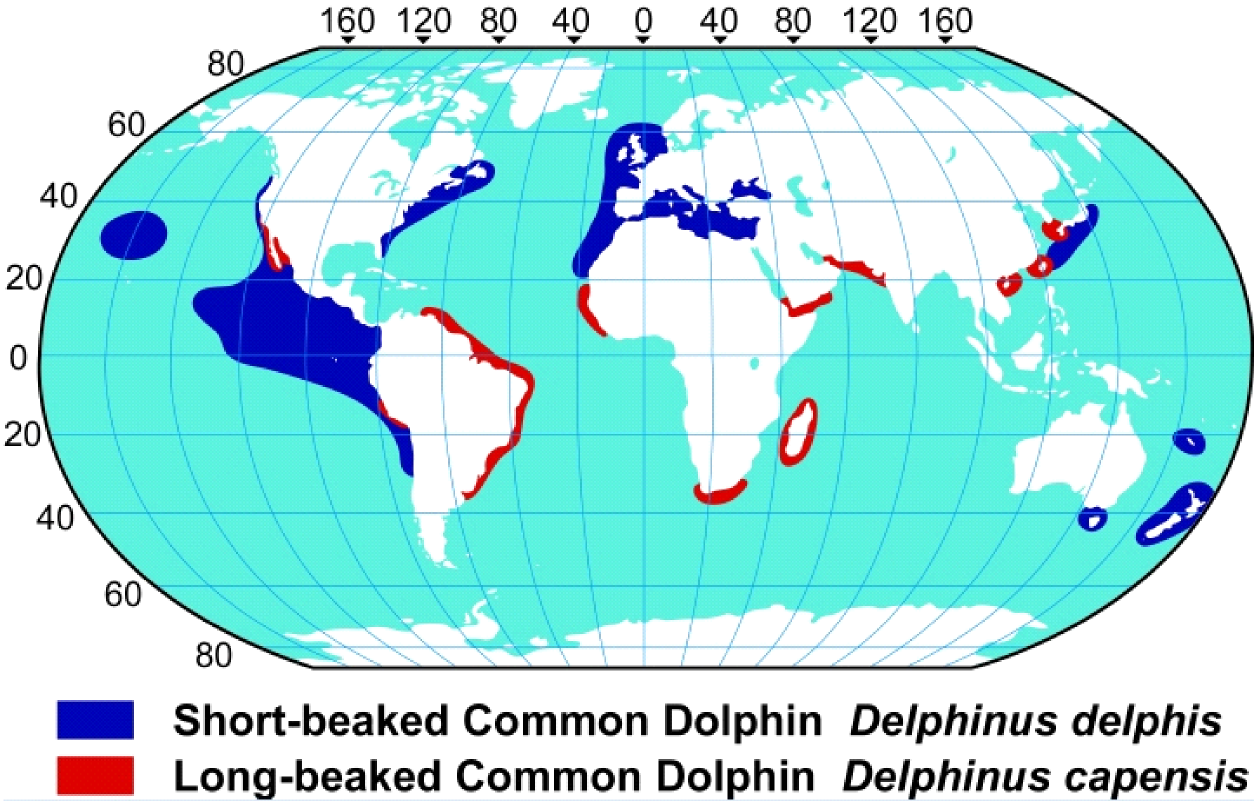

Figure 3.1 Global distribution ranges of the short-beaked (*Delphinus delphis*) and long-beaked common dolphin (*Delphinus capensis*) (after Gorter 2003)

Jefferson and Van Waerebeek (2002) concluded (from an analysis based on skull morphometrics) that the South African specimens were indeed representative of the long-beaked form *D. capensis*. However, they also add that occasional strandings recorded off the Western Cape were more similar to the short-beaked form, and could not rule out the possibility of *D. delphis* occurring off the South African coastline. Although some uncertainty still exists, Best (2007) indicates that offshore populations of the short-beaked form do occur in offshore waters around South Africa. The next nearest population of short-beaked common dolphins reported by Jefferson and van Waerebeek (2002) was that off Western Australia.

Samaai *et al.* (2005) found no statistically significant differences between any of the 72 adult common dolphin specimens they examined from South Africa using a principal component analysis based on skull characteristics. However, plotting zygomatic width against rostral length identified three individuals falling outside the normal range for *D. capensis* (two of them falling within the range for *D. delphis* from the North Pacific) (Heyning & Perrin 1994, Samaai *et al.* 2005). These three individuals were smaller, had shorter beaks and longer flippers, with wider flukes and larger dorsal fins than other specimens, and their tooth counts fell within, but closer to the upper end of, the range for *D. delphis*. Interestingly, vertebral counts for all South African specimens examined by Samaai *et al.* (2005) and Heyning & Perrin (1994) were well below those of both long and short-beaked common dolphins off California. Samaai *et al.* (2005) also found a marked difference in the diets of the three short-beaked individuals, with these animals having taken a diet predominantly consisting of myctophids (mesopelagic fish), whilst the long-beaked form had targeted anchovy and round herring (epipelagic shoaling fish). According to Samaai *et al.* (2005), the short-beaked common dolphin may also occur off South Africa, but given the very small sample size of individuals thought to represent this species, and their imperfect correspondence with morphometrics of *D. delphis* or *D. capensis* from the North Pacific, a large amount of uncertainty still occurs in their precise identification. It seems likely that the short-beaked common dolphin may exist in isolated populations around southern Africa, such as near Tristan da Cunha (Best *et al.* 2009), but inhabiting waters much further offshore than its long-beaked counterpart, and hence yielding very few strandings and accidental captures (Samaai *et al.* 2005). The long-beaked common dolphin occurs in disjunct populations in the nearshore waters off South Africa, West Africa (Gabon, Congo-Brazzaville and Angola), California, Mexico, Peru, Venezuela, Argentina, Korea, Japan and Taiwan (Heyning & Perrin 1994, Findlay *et al*. 1992, Best 2007). No estimates are available of the global abundances of long-beaked common dolphins, but some local estimates have been cited in the published literature:

California : 11 000 to 49 000 individuals (averaging 22 000) (Hammond *et al*. 2008)

Gulf of California : 69 000 individuals (Gerrodette & Palacios 1996)

Mexican EEZ : 55 000 individuals (Gerrodette & Palacios 1996)

South Africa : 15 000 to 20 000 individuals (Cockcroft & Peddemors 1990)

In 2009, the International Whaling Commission (IWC) sub-committee on small cetaceans agreed that the global distribution of mitochondrial lineages did not lend support to the current taxonomy for the existence of two species of common dolphin. Their report states that a new paradigm is needed to describe the common dolphin, in which “common dolphins represent a single, widely distributed ‘super-species’, with numerous partially isolated populations, some of which exhibit a high degree of local adaptation and may be in the process of speciation (i.e. incipient species).” Character development appears to exhibit a high degree of plasticity in common dolphins, with features such as beak-length now appearing to be the result of convergent evolution in different areas (e.g. the long-beaked morphotypes in South Africa and the eastern North Pacific are clearly from different lineages) (IWC Annex L 2009). It is now clear that the taxonomy of the common dolphin is highly uncertain and a more detailed phylogeographical and genetic analysis will be needed to consolidate the species delineations. All of the animals involved in this study were morphologically similar to *D. capensis*, and because this species has a more coastal distribution range, it is assumed that all the animals caught in anti-shark nets off KwaZulu-Natal are of the long-beaked variety. 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). As all the animals examined in this study are considered to be representatives of the long-beaked form, the terms ‘long-beaked common dolphin’ and simply ‘common dolphin’ will be used interchangeably in the discussion of this species hereafter.

Life History

Common dolphins are easily identified by the characteristic criss-cross or hour-glass marking on their sides, with a distinctive yellow/buff patch meeting a grey patch mid-way up the flank (Best 2007). The short-beaked form (*D. delphis*) exhibits a more distinct colour pattern, with the yellow thoracic patch being much brighter than in the long-beaked variety (*D. capensis*), and showing a greater contrast between the grey and yellow patches on the flanks (Heyning & Perrin 1994, Murphy & Rogan 2006, Best 2007). Males are slightly larger than females, with an average adult length of 2.54m for males and 2.22m for females (Best 2007). Both sexes of the long-beaked common dolphin are significantly larger than individuals of the short-beaked species (Heyning & Perrin 1994). The average age at which sexual maturity is reached for common dolphins in southern Africa is ≈10 -12 growth layer groups (GLGs) in the teeth or 220cm body length for males and 9 GLGs or 213cm body length for females (each growth layer group is thought to represent one year (Klinowska 1991)).

Figure 1.4 Long-beaked common dolphin (*Delphinus capensis*) from the south-east coast of South Africa (Algoa Bay). Photograph: S. Plön

Calving is thought to occur throughout the year, but always peaks in summer, with most births recorded during February and March (Ross 1984). The gestation period is estimated at 11 months, with most conceptions taking place in March and April (Mendolia 1989). Lactation takes place for at least 6 months or until the calf is approximately 1.75m long, and may continue even once the female has fallen pregnant again (Mendolia 1989, Young & Cockcroft 1994). The average calving interval has been estimated at 3 years, but may be longer in older females (Mendolia 1989). Ross (1984) documented that common dolphins off the south-east coast of southern Africa calve in summer, with the young being approximately 100cm in length at birth, and nurse until a body length of around 1.5m is attained.

Long-beaked common dolphin pods normally consist of a few hundred individuals, and the formation of mixed aggregations with other delphinid species is rare (Best 2007). The precise age and sex composition of long-beaked common dolphin schools in South African waters has not been studied in detail, however, strandings in the Eastern Cape seem to be dominated by mature females (many of which were pregnant), with a lower number of mature males, and few juveniles, which may give some insight into the school structure

(Young & Cockcroft 1995). Large schools are very vocal and appear to communicate and coordinate movements whilst travelling using synchronous whistles and squeaks, which may be timed with the porpoising of each group (Best 2007).

Seasonal foraging range in South African waters

Long-beaked common dolphins are predominantly found in waters above the continental shelf, in depths between 100 to 200m, and not further than 180km from the coastline (Best 2007). It has been suggested that long-beaked common dolphins frequent areas exhibiting elevated benthic topography (Evans 1976, Findlay *et al.* 1992, Jefferson and van Waerebeek 2002, Best 2007). The distribution of long-beaked common dolphins in southern African waters appears to be strongly linked to the annual occurrence of the sardine run. Long-beaked common dolphins are found in the cooler waters along the south-east coast of the continent during austral summer, in the region south of 33° latitude, and mostly offshore (Young & Cockcroft 1994). A lengthy northward migration has been documented in some of these dolphins, towards the warmer inshore waters of the east coast during winter – a migration which seems to be undertaken in response to the 'sardine run'(Cockcroft & Peddemors 1990, Peddemors 1999). The 'sardine run' is an annual migration of vast shoals of South African sardine (*Sardinops sagax*) (Jenyns 1842), which are known to be an important food source for many predators (Cockcroft & Peddemors 1990, Young & Cockcroft 1994). The 'sardine run' is not restricted to the mass movement of sardine alone; anchovy (*Engraulis encrasicolus*), red-eye or West-Coast round herring (*Etrumeus whiteheadi*) are common clupeiform species that also partake in the annual movement up the east coast at this time of year (O'Donoghue *et al.* 2010 (a), van der Lingen *et al.* 2010).

The parent stock of sardines are believed to be primarily resident on the south and west coasts of southern Africa (from Namibia south and eastwards to Port Elizabeth), concentrated around the region of the Agulhas Bank for 10 to 11 months of the year. A subsection of this population migrates north-east along the coastline with the onset of winter, reaching the waters of the Eastern Cape and KwaZulu-Natal (KZN) around June/July (Crawford 1981, Peschak 2005, O'Donoghue 2009). This northward migration is thought to reflect a range expansion in response to the spreading of a plume of cold water up the East Coast every year during winter, usually between June and August (Armstrong *et al.* 1991, Peschak 2005, van der Lingen *et al.* 2010). Sardines prefer water temperatures of between 14 and 20˚C, and their distribution is largely controlled by water temperature and temperature fronts (O'Donoghue 2009). Every year, sardine movement extends as far north as an area of the Transkei coastline called Waterfall Bluff – a natural inlet which has a concentrating effect on the sardine shoals (Peschak 2005, O'Donoghue *et al.* 2010 (c)). It is thought necessary for the prevailing currents to weaken and allow cold, upwelled water to reach the surface, to allow the sardine run to proceed northwards of Waterfall Bluff, eventually reaching the beaches of Durban, where the fish are harvested in huge numbers by the local community (Peschak 2005). The sardine shoals usually reach the lower Wild Coast in May each year, and move into KZN waters by June (O'Donoghue 2009). After reaching the vicinity of Durban the sardine run appears to cease, with the remaining fish moving southwards again, possibly now in deeper waters, with the flow of the Agulhas Current (Connel 2001, van der Lingen *et al.* 2010). Egg collections from the water column off Park Rynie each year indicate that the sardines move back through this area between October and December (Connel 2001). Sardines are known to spawn in the waters of KwaZulu-Natal every winter, with a peak around the time of the sardine run (usually in June or July) (Connel 2001). The most recent research on the sardine run appears to indicate that this migration may actually be the result of the "seasonal spawning migration of a genetically distinct subpopulation of sardine responding to a strong instinct of natal homing" (Fréon *et al.* 2010 pg 476).

It seems likely that some sardine are also present in the waters of the south coast year-round as they have been recorded in the diet of Cape gannets in Algoa Bay (Batchelor & Ross 1984). Long-beaked common dolphins are regularly seen in low numbers in coastal waters between East London and Port Elizabeth in most months of the year, and sardine have been recorded in the stomachs of stranded dolphins in this region (Cockcroft & Peddemors 1990). Long-beaked common dolphins appear to follow the shoals of sardine north along the coastline and onto the narrow continental shelf within the Agulhas Current boundary north of East London and upwards towards Richards Bay (Cockcroft & Peddemors 1990). The densities of long-beaked common dolphin seen off the KwaZulu-Natal coast during the winter months are much higher than those observed off the south coast, where they are believed to be resident during the rest of the year (Cockcroft & Peddemors 1990, Peschak 2005). The increased abundances of long-beaked common dolphins in the waters off the KwaZulu-Natal coastline in winter are thought to be due to their concentration in response to the sardine run (Peschak 2005). Alternatively, the elevated densities may be a product of the much narrower continental shelf along the east coast, which may cause sardine shoals to become trapped in a narrow strip of water, thereby causing their predators to concentrate in a similarly small area (Cockcroft & Peddemors 1990). Cockcroft & Peddemors (1990), using aerial surveys, estimated the common dolphin population off the south-east coast to be between 15 000 and 20 000 individuals, with approximately 9 000 to 12 000 of these moving into the waters off KwaZulu-Natal during winter. There is, however, a lack of information available on the current status of the long-beaked common dolphin population within the region (Cockcroft & Peddemors 1990, Hammond *et al*. 2008). The long-beaked common dolphin is credited with being able to control much of the sardine run activity due to its occurrence in superpods of up to 5 000 animals (Peschak 2005), and active herding of fish into baitballs near the surface. These activities also make the shoal accessible to other predators including gannets and sharks (O'Donoghue 2009). Long-beaked common dolphins are often documented in feeding associations with seabirds, sharks, fur seals and Bryde's whales in nearshore waters, most noticeably during the annual sardine run moving up the east coast during winter (Best 2007). Long-beaked common dolphins have been observed to demonstrate a cooperative feeding strategy; using bubble clouds to herd prey shoals into dense balls and force them to the surface, thereby also making them easily accessible to other predators such as seabirds (Peschak 2005).

Whilst the occurrence of long-beaked common dolphins in the water of KZN corresponds with sardine presence, their diet has not always reflected a dependence on sardine during winter (Young & Cockcroft 1994). Long-beaked common dolphins may prey on other species during periods of low sardine activity/availability (O'Donoghue 2009). The presence of common dolphins is however, recognised as the key indicator for incoming sardine shoals, and is used as an alert by the KwaZulu-Natal Sharks Board of the need to lift the anti-shark nets from the water ahead of intense feeding activity close to shore (Dudley & Cliff 2010).

Feeding ecology of common dolphins

The bulk of the common dolphin diet consists primarily of cephalopods and small epipelagic shoaling fish species found above 200m depth, although myctophids also commonly occur in the diet, showing that foraging down to the deep scattering layer also takes place (Silva 1999, Overholtz & Waring 1991, Meynier *et al.* 2008 (a), Brophy *et al.* 2009). Since prey availability varies both spatially and temporally in any given region (Meynier *et al*. 2008 (a)), and because common dolphins feed opportunistically, there is also a large amount of variation in the most common prey species found in the diet of common dolphins between different regions (Silva 1999, Young & Cockcroft 1994, Meynier *et al.* 2008 (a), Brophy *et al.* 2009).

Considerable dietary variation has been documented in common dolphins in accordance with seasonal fluctuations in prey availability and distribution, and the movement patterns of delphinids appear to be linked to those of their principal prey (Selzer & Payne 1988, Young & Cockcroft 1994). Stomach content analyses of common dolphins off southern California included the expected epipelagic fish such as sardines, and some myctophids and northern anchovy (*Engraulis mordax*) which are deep-sea species. This provides an indication that common dolphins may feed as low as the deep-sea scattering layer (Fitch & Brownell 1968). The diet of short-beaked common dolphins (*Delphinus delphis*) off the Portuguese coast was found to contain a diverse mixture of prey species, but consisted predominantly of four fish and two cephalopod species (Silva 1999). The most abundant prey species were sardine, blue whiting, snipefish, and loliginids. As sardine is one of the most abundant pelagic species in this area, the results of Silva (1999) support the idea that common dolphins feed opportunistically on the most locally available prey species. Silva (1999) also found that prey size was related to dolphin size. Furthermore, Silva (1999) postulated that juveniles prey on the same fish species, but choose smaller prey individuals due to differences in their physical features or foraging prowess. The improved diving ability of mature dolphins allows them to forage at greater depths, theoretically allowing for some mitigation of feeding competition between the ontogenetic stages within the school (Silva 1999). In the Bay of Biscay, common dolphins (*D. delphis*) were also found to target common shoaling species such as anchovy, sprat, sardine and horse mackerel (Meynier *et al.* 2008 (a)). Similarly, in the eastern Ionian Sea, common dolphins primarily fed on sardine and anchovy (Agazzi *et al*. 2004), while in New Zealand, common dolphins (*Delphinus* sp.) fed primarily on arrow squid, jack mackerel and anchovy (Meynier *et al*. 2008 (b)). In South African waters, the common dolphin (*D. capensis*) feeds mainly on small pelagic shoaling fish species such as sardine (*Sardinops sagax*), anchovy (*Engraulis encrasicolus*), and round herring (*Etrumeus whiteheadi*), as well as chokka squid (*Loligo* spp.) (Sekiguchi *et al.* 1992, Young & Cockcroft 1994).

Dolphins feeding off KwaZulu-Natal, South Africa have a diet dominated by sardine (*Sardinops occelatus* 48.1% by mass), mackerel (*Scomber japonicus* 13.5%), elf (*Pomatomus saltatrix* 8.7%), squid (*Loligo spp*. 8.4%) and strepie (*Sarpa salpa* 8.1%) (Young & Cockcroft 1994). Sekiguchi *et al.* (1992) found that the diet of the common dolphins in the Western Cape was similar to those feeding in Eastern Cape, comprising 42.7% chokka squid, 17% anchovy, 9.8% hake, 8.8% sardine, 8.2% horse mackerel and 6.9% round herring. Differences in the diet of common dolphins between KwaZulu-Natal and Eastern Cape waters are likely to reflect seasonal changes in prey availability (Young & Cockcroft 1994).

Young and Cockcroft (1994) analysed stomach contents from 297 common dolphins caught in the shark nets off the KwaZulu-Natal coast. They found that 38 different prey species (34 fish species and 4 cephalopod species) had been consumed by the common dolphins and suggested that although the diet during the northward migration is largely made up of sardine (*Sardinops sagax*), other pelagic fish species are also likely to take part due to their inclusion in the diet. The appearance of migrating sardine shoals off KwaZulu-Natal is erratic, with large inter-annual variations in timing and intensity (O'Donoghue 2009). The distribution and migration patterns of the common dolphin appear to be influenced accordingly (Young and Cockcroft 1994). Common dolphins generally consume the most readily available and easily captured prey, with changes in the abundance of sardine in the diet reflecting local changes in sardine density and the abundance of other prey species (Young and Cockcroft 1994). Seasonal and inter-annual variations in the diet are marked not by changes in prey species composition, but rather by changes in the proportion of the diet made up by a particular species (Young and Cockcroft 1994). Despite the variety of prey species taken, only five species dominated the diet in terms of abundance in the waters of KwaZulu-Natal.

Different sex and size classes also feed on different proportions of the same suite of prey species with males targeting only sardine (probably the most plentiful or easily caught) and mature females having a more diverse range of prey (perhaps being more selective for certain species, or maximising their energy intake by consuming a range of prey species) (Young and Cockcroft 1994). Lactating females also consumed a larger proportion of large, fast swimming species such as mackerel. Pregnant and lactating females took significantly more squid (Young and Cockcroft 1994). It seems likely that reproductive state influences prey selection. Catching fewer, larger prey may prove more efficient in terms of meeting the elevated energetic costs of a pregnant female (Young and Cockcroft 1994). Young and

Cockcroft (1994) state that although squid are of low calorific value, they have a very high water content, a characteristic which may make them a valuable component of the diet during milk production. Females also seem to select alternative prey species during pregnancy and lactation. Young and Cockcroft (1994) recorded that pregnant and lactating females were the only dolphins to feed on flying fish (*Cypselurus* sp.). In contrast to data collected for bottlenose dolphins, Young and Cockcroft (1994) found that common dolphin calves do not consume a diet most similar to that of lactating females, but rather more similar to the diet of non-lactating females and other juveniles.

Some degree of resource partitioning between male and female juveniles and adolescents is evident, with young males taking a larger proportion of sardine than their female counterparts (Young & Cockcroft 1994). This pattern may be a reflection of their earlier induction into adult feeding groups, whilst females and weaning calves make up “nursery groups” (Young and Cockcroft 1994). The dietary composition of the different ontogenetic stages and sexes within common dolphin schools may reflect both their relative energetic costs, as well as their social structure (Young and Cockcroft 1994). Calves may be separated from the main feeding group during intense feeding activity due to their vulnerability, which may explain why there is a poor connection between the diets of calves and lactating females (Young 1993). Pregnant and lactating females would be compelled to leave their calves and join the main feeding group in order to replenish energetic reserves (Young 1993). Resource partitioning appears to occur in common dolphins off the KwaZulu-Natal coastline, which is likely to be a result of the intense nature of feeding during the sardine run, where enormous shoals of sardine and other fish species are, for a limited time frame, highly concentrated by the narrow continental shelf off Durban (Young 1993). In the Eastern Cape, the diet of females and calves is similar, with little resource partitioning evident. This is possibly due to the less aggressive feeding behaviour in this region, which may allow mother and calf pairs to stay together, and feed with the rest of the school (Young 1993).

In general, the diet of common dolphins off the south-east coast of southern Africa reflects the local availability of prey species, with dolphins off KwaZulu-Natal feeding predominantly on sardine, whilst those off the Eastern Cape take a higher proportion of *Loligo* spp. (Young 1993). Common dolphin density is also closely tied to prey concentrations, with dolphin densities being highest along the south-east coast in summer – this high density moves northwards to KwaZulu-Natal during the winter sardine run, which is accompanied by a change in the most abundant prey species from squid to sardine (Young 1993). The main difference between the dietary composition of common dolphins from KwaZulu-Natal and the Eastern Cape is the higher proportion of cephalopod prey in the Eastern Cape (45.8% cephalopod, 54.2% fish), where a cooler coastal upwelling regime favours a predominance of squid prey (Young 1993). The warmer waters off KwaZulu-Natal are not favourable for squid spawning, and here the diet is comprised of 88.8% fish and only 11.2% cephalopod (Young 1993). Calving occurs off the south-east coast, where squid prey are abundant as a food resource for lactating females, and the annual arrival of the sardine run may present an opportunity to wean calves once they are old enough to transition onto fish prey, and strong enough to undertake a substantial migration along the coast (Young 1993). In general, it seems common dolphins off KwaZulu-Natal are opportunistic feeders, feeding on at least four shoaling pelagic fish species within the upper 200m of the water column, each in different proportions dependent on their abundance (Young 1993). Hence this species may be used as an indicator species, useful in obtaining information on the occurrence and abundance of small pelagic fishes (Sekiguchi *et al.* 1992).

Global climate change

There is growing evidence from a variety of research areas that anthropogenic carbon emissions are beginning to have disruptive effects in many ecosystems at a global scale (Learmonth *et al*. 2006, Gambaiani *et al*. 2008). The IPCC (Intergovernmental Panel on Climate Change) predicts that the planet will warm by 1.8 to 4˚C by the year 2100 (IPCC 2007). Additionally, the Southern Ocean is becoming less efficient at sequestering carbon from the atmosphere (Le Quéré *et al.* 2007), and ocean acidification is likely to drastically affect the species composition of the phytoplankton, with subsequent shifts in food web structure being predicted (Feely *et al.* 2004, Learmonth *et al*. 2006, Gambaiani *et al*. 2008).

Climate change is now regarded as the foremost threat to biodiversity, and if CO_2 emissions and global temperatures continue to rise at their current rate, many species will be facing global extinction within the next few decades (Thomas *et al.* 2004, Simmonds & Isaac 2007). Continued sea-level rise and more frequent El Niño conditions are expected with continued climatic changes, which will in turn affect precipitation, river discharge rates and nutrient inputs into the marine environment (Timmermann *et al.* 1999). Climatic triggers also have the potential to disrupt wind circulation patterns, change upwelling regimes and current patterns, and consequently change species distribution ranges as their thermal or chemical tolerances are gradually exceeded, or their dispersal patterns and distances undergo changes (Walther *et al*. 2002, Gambaiani *et al*. 2008). The distribution of species such as plankton which support the base of the trophic pyramid, are highly dependent on oceanographic conditions, and are hence likely to be strongly impacted by climate change (Turley 1999). Changes in current patterns may also change cetacean migration routes and the location of calving grounds (Gambaiani *et al*. 2008).

Prey distribution is known to be the main factor in controlling the distribution of cetacean species (Gambaiani *et al*. 2008). The abundance and distribution of the prey species consumed by cetaceans are often strongly 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 (Simmonds & Isaac 2007). Cetacean prey species including sardines and cephalopods are sensitive to changes in water temperature and pH. Bearzi *et al.* (2003) have already documented changes in the distribution of the prey species of the short-beaked common dolphin in the Adriatic Sea which are likely to have been the result of climate change (Gambaiani *et al*. 2008).

Sabatés *et al*. (2006) found a positive relationship between annual temperature anomalies in the western Mediterranean and the annual fishery landings (CPUE) of round sardinella (*Sardinella aurita*) between 1950 and 2003. Increased landings of sardinella were recorded following positive temperature anomalies, with the warmer SST in April of the years preceding high catches possibly stimulating gonad maturation in adult fish, and consequently enhancing their reproductive capacities (Sabatés *et al*. 2006). In addition to increased sardinella abundances, they found that the distribution range of sardinella stocks also shifted northwards over the course of a few decades. This pattern appears to be in response to the warming trend in sea-surface temperatures in the region. A temperature threshold of 18˚C was found to control the distribution of this species, and its northernmost distribution limit has shifted by approximately 200km within the last 50 years (Sabatés *et al*. 2006). The authors caution that although the northward shift of sardinella is largely attributed to warming of the surface waters, the concomitant decline in stocks of anchovy and sardine over the past 15 years may also have favoured its expansion. This should serve as a reminder of the possibility of exacerbated cumulative effects when climate change and over-fishing combine as drivers of ecosystem change. Climate change could also bring cetacean species into increased competition with fishermen for fish stocks, raising the chances of their incidental, and intentional capture (Bearzi 2002, Gambaiani *et al*. 2008).

It is thought that the grouping behaviour of sympatric delphinids populations is a function of their feeding behaviour, but attempts to relate these patterns to climatic variability are made difficult by the interaction of multiple nonlinear relationships in natural systems (Lusseau *et al*. 2004). Lusseau *et al*. (2004) used a mean-field model to relate the grouping behaviour of Atlantic bottlenose dolphins and Pacific killer whales to climatic fluctuations. They demonstrated that climatic variation indirectly affects the size of salmon populations, which in turn directly influences the grouping behaviour of dolphins and killer whales. Their results showed that both salmon catches, and bottlenose dolphin critical group sizes were significantly related to the winter North-Atlantic Oscillation, with a 2-year lag phase. This study adds to the growing body of evidence that climatic fluctuations alter marine productivity on large spatial scales, and impacts on cetacean social behaviour. It is useful in illustrating the lag-phase phenomenon, whereby these impacts are only seen after a number of years, as they affect large predators indirectly, as well as highlighting the bottom-up effects that climate change can have in marine systems (Lusseau *et al*. 2004).

It seems inevitable that cetaceans will be forced to adapt to these ongoing changes by shifting their feeding localities and even changing feeding strategies and switching prey species. Such changes could have negative effects on reproductive potential, and ultimately the survival of cetacean populations (Bearzi 2002, Simmonds & Isaac 2007, Gambaiani *et al*. 2008). Ill-health and malnutrition in dolphins of the Ionian Sea has been linked to reduced prey availability, habitat degradation, and longer foraging times (Politi *et al.* 2000).

Increasingly high temperatures may encourage coastal cetaceans to move offshore, further changing their foraging grounds. Changes in sea-surface temperature and ocean current patterns may make navigation increasingly difficult for cetaceans (Simmonds & Isaac 2007). Most importantly, the predicted future rate of change in climate may well fall outside the rates of change ever experienced by cetacean populations, and it is unclear whether they will be able to evolve rapidly enough to be able to deal with these perturbations (Simmonds & Isaac 2007). It has been suggested that rising temperatures may increase the likelihood of pathogens and viruses spreading, as well as making conditions favourable for epizootic outbreaks such as the dolphin morbillivirus (Raga *et al*. 2008, Gambaiani *et al*. 2008). Mobilization of pollutants stored in blubber in response to starvation may also hinder normal immune system functioning, potentially reducing the survival chances of dolphins already pushed to their physical limits by prey scarcity (Aguilar *et al.* 1999). Climatically-driven changes in food web dynamics and prey distribution may bring cetacean predators into new foraging grounds, and into competition with each other for scarcer food resources (Bearzi *et al.* 2003).

Climate change is likely to be the largest long-term threat facing cetacean populations, as they are unlikely to be able to adapt rapidly enough to cope with fluctuating environmental conditions and alterations in prey availability, although their behavioural plasticity may enable them to maintain smaller populations in the immediate future by shifting foraging ranges and prey species (Learmonth *et al.* 2006, Simmonds & Isaac 2007, Gambaiani *et al*. 2008). Cetaceans are long-lived species with relatively slow reproduction, and hence are more at risk of becoming endangered due to the inability of small populations to recover rapidly from reduction by disease or starvation (Dhermain *et al*. 2002). In essence, climate change is likely to dramatically alter ecosystem functioning, reducing resilience and stability, and causing changes in food web and trophic linkages on a global scale (Gambaiani *et al*. 2008). Therefore it is imperative that the impacts of climate change on the survival of cetacean species are thoroughly understood and monitored, and all efforts taken to mitigate their negative effects.

Conservation status

Between 1988 and 1989 the population size of common dolphins off the south-east coast of South Africa (Port Elizabeth to Richards Bay) was estimated at between 15 000 and 20 000 individuals (Cockcroft & Peddemors 1990). A total of 1 023 common dolphins were incidentally killed in the anti-shark nets off the KwaZulu-Natal coastline between 1980 and 2005, with an annual average of 39 deaths (Best 2007). This number has declined dramatically in recent years, with an average of 12 common dolphins being caught per year between 2005 and 2009. In addition to these mortalities, some common dolphins are regularly caught as by-catch in the purse-seine and long-line fisheries off the Western Cape

(Best 2007). Given their large population size, these annual mortalities are likely to be sustainable for the common dolphin population in South African waters. The IUCN rates long-beaked common dolphins as 'Data Deficient' due to incidental and directed takes of unknown proportions globally (Hammond *et al.* 2008). Common dolphins in general are listed as Lower Risk: Least Concern, and in the South African Red Data Book, long-beaked common dolphins are rated as of Least Concern (Best 2007). *D. capensis* appears in Appendix II of CITES.

In the Mediterranean Sea, the short-beaked common dolphin (*D. delphis*) which was once abundant in the region, has been in decline since the 1960's (Bearzi *et al*. 2008). Since 2003 it has been classified as Endangered on the IUCN Red List of Threatened Species due to a dramatic decline in population size and deterioration of its habitat (Bearzi *et al.* 2003, Bearzi *et al*. 2008). It is now usually only observed in the Sardinian Sea, the Sicily Channel and the Ionian Sea (Notarbartolo di Sciara *et al.* 1993). *D. delphis* is listed in Appendix II of CITES (which allows controlled trade), and Appendix II of the Bern Convention, as well as Annex IV of the EC Habitats Directive (under which its disturbance, capture, killing, keeping, sale or exchange are prohibited) (Brereton *et al*. 2004). The common dolphin is also theoretically given global protection under the United Nations Convention on the Law of the Sea which encourages signatories to cooperate in efforts to conserve cetaceans, but enables states and international bodies to surpass the legislation of the Convention to control the exploitation of marine mammals (Brereton *et al*. 2004).

Some concern has recently been raised over the number of long-beaked common dolphins killed as bycatch in purse-seine and gill net fisheries off the coast of southern California and from direct harpooning in north-eastern Taiwan and eastern Venezuela (Margarita Island). The trawl and net fisheries off India and China, and numerous kills for human consumption or shark bait in Peru also represent significant sources of mortality for long-beaked dolphins (Hammond *et al.* 2008). To date the only conservation initiatives actively pursued are vessel quotas for the incidental take of *Delphinus sp*. in the eastern tropical Pacific which are issued and monitored by the IATTC (Inter-American Tropical Tuna Commission) (Hammond *et al.* 2008).

Why is it necessary to monitor common dolphin diet?

Studying the stomach contents of marine predators makes valuable information available relevant to both predator and prey distribution patterns, prey stock abundance, distribution and seasonality, predator diving ability and foraging strategy, as well as competitive interactions with other species, trophic links, and perturbations in ecosystem structure and functioning (Santos *et al.* 2001). Bearing in mind the likely impacts of global climate change and expanding fisheries, and its implications for the distribution and abundance of fish species around the South African coastline, it seems imperative to monitor the changes which may already have started to occur using one of their main predators – the common dolphin. 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 knock-on effects in large predators may only become apparent over longer time frames. Research on common dolphins off the South African coast has focused on the distribution of the species (Cockcroft & Peddemors 1990, Findlay *et al*. 1992), their reproductive biology (Mendolia 1989), diet (Sekiguchi *et al.* 1992, Young 1993, Young & Cockcroft 1994, Young & Cockcroft 1995), ecotoxicology (Cockcroft *et al*. 1990) and their incidental capture in shark nets (Cockcroft 1990).

Focus of this study

The common dolphin is one of the main (most numerically abundant) cetacean species feeding on the large shoals of South African sardine (*Sardinops sagax)* that migrate annually northwards along the Eastern Cape and southern KwaZulu-Natal coastline. Recent studies indicate a decrease in the intensity of the sardine run between 2002 and 2006, both in terms of sardine presence (O'Donoghue 2009) and sardine egg abundance on the KwaZulu-Natal South Coast during winter (Connell 2010). The decrease in the availability of sardine may have resulted in a change in the diet of common dolphins and alterations in their migration patterns.

The aim of this study is to determine whether changes in the diet and feeding ecology of common dolphins (*Delphinus capensis*) off south-eastern South Africa have occurred over the last few decades in response to the variability in the intensity of the sardine run. Stomach contents from common dolphins incidentally caught in the anti-shark nets off KwaZulu-Natal between 2000 and 2009 will be used to describe the diet of this species in the waters of the East Coast during winter over the last decade. These data will then be compared to the results of a previous study conducted by Young & Cockcroft (1994) who analysed stomach contents from net-caught common dolphins over the period 1974 to 1992, to identify long-term trends in the diet of common dolphins in the coastal waters off KwaZulu-Natal. Identification of stomach contents, stable isotope analysis of dentine from common dolphin teeth, and assessments of blubber thickness records will be used to determine sex-based and ontogenetic differences in diet, as well as seasonal and long-term shifts in the feeding ecology.

Chapter 2

Diet and feeding biology of long-beaked common dolphins (*Delphinus capensis)* off KwaZulu-Natal over the period 2000 to 2009

Introduction

Dolphin catches in the KwaZulu-Natal shark nets

Gill nets (110m long and 10m deep) have been deployed off the east coast of South Africa since 1952 in an effort to reduce the possible interaction of sharks with swimmers along the most popular beaches in this area (Cockcroft 1990). These nets are made from black multifilament polyethylene braid (Dudley & Cliff 2010) and are set in a fixed position, at staggered intervals approximately 400 – 500m offshore, in 10 to 14m of water. The nets are examined daily by KwaZulu-Natal Sharks Board staff to remove all incidental captures (Cockcroft 1990). The gillnet installation along the KZN coastline was at its maximum extent in the 1990's, with a total of 44km of netting protecting beaches along this stretch of coastline (Dudley & Cliff 2010). Long-beaked common dolphins (*Delphinus capensis*), Indo-Pacific humpback dolphins (*Sousa chinensis*) and Indian Ocean bottlenose dolphins (*Tursiops aduncus*) are regularly found as incidental captures in the nets. Concerns that these catches could lead to population declines of both bottlenose and humpback dolphins led to the initiation of various by-catch reduction measures (Cockcroft 1990). In order to reduce the number of incidental dolphin captures in the shark nets, acoustic deterrents called 'pingers' and sonar-reflecting floats have been installed in the nets. In general, these measures appear to have been successful in reducing the number of dolphins caught in the nets annually (Peddemors 2006). However, only the nets at Durban and Umhlanga beaches are fitted with dolphin-deterrent pingers (Geremy Cliff, pers. comm.). Currently, a total length of 23.4km of nets protects popular swimming beaches along a 320km stretch of coastline (KZN Sharks

Board 2002). The anti-shark nets are currently removed during the peak of the annual sardine run in order to reduce bycatch during this intense feeding period (Peddemors 2006). Significant reductions in cetacean by-catch have also been effected by the total removal of nets at the less popular beaches, a reduction in the total length of netting, and replacing some nets with drumlines (cables containing baited hooks, which target sharks and not cetaceans) (KZN Sharks Board 2002). These measures had led to a reduction in the length of net installations from a total of 44km to 27.3km of netting by the end of 2005 (Dudley & Cliff 2010).

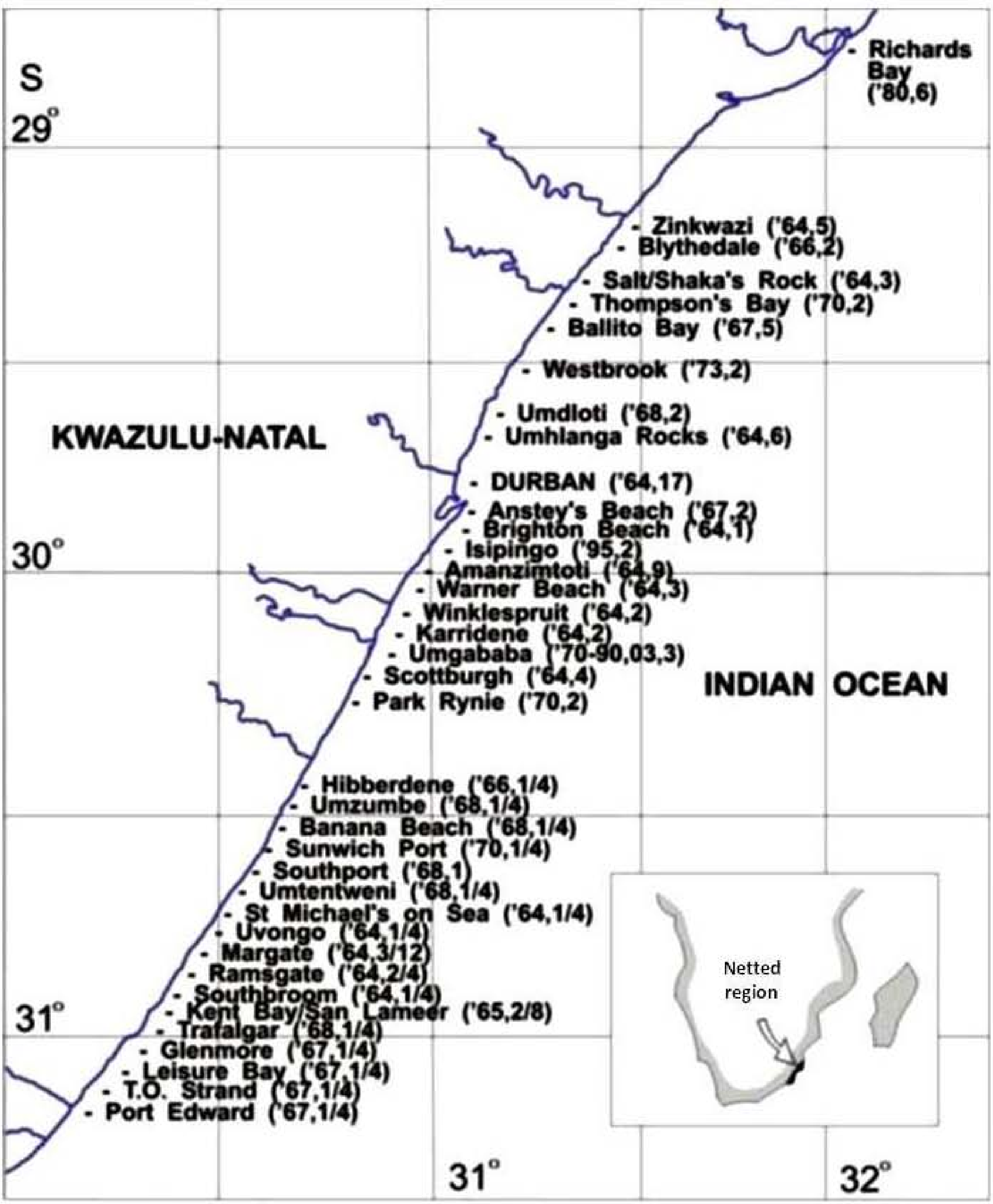

Figure 2.1 Location of anti-shark nets along the KwaZulu-Natal coastline. In parentheses, the first number indicates the year of installation, and the second the number of nets/drumlines deployed (KZN Sharks Board 2002)

The number of common dolphins caught in the anti-shark nets demonstrates significant inter-annual variation, with a marked seasonality, which is likely to be related to an increase in prey availability in nearshore waters (Cockcroft 1990). On average, 12 common dolphins were caught per year between 2005 and 2009. Each year, most dolphins are caught in winter and spring i.e. between June and October (Cockcroft 1990, Young 1993). Significantly more female common dolphins are caught in the nets than males in most years (Young 1993). Common dolphin captures are much higher in winter and spring, reflecting the seasonal migration of this species into KwaZulu-Natal waters in response to the annual pilchard migration or 'sardine run' between April and July (Cockcroft 1990). The catch-rate of common dolphins appears to increase whenever conditions favour the inshore movement of pilchard shoals, suggesting that common dolphin movement patterns are strongly coupled to those of their prey (Cockcroft 1990).

The sex ratio and size composition of common dolphin schools in South African waters is unknown. However, the substantially greater incidence of capture of mature females than males, combined with the fact that predominantly weaned calves were captured, suggests that the females may be moving inshore to make use of the abundant food resource to wean their calves and replenish body fat reserves after their summer calving period (Cockcroft 1990). With estimates of common dolphin numbers off south-eastern Africa being in the range of 15 000 to 20 000 individuals, these incidental captures in the anti-shark nets represent a mortality of less than 1% of the total population, and hence are not considered a threat to the survival of the species (Cockcroft 1990). The low incidental capture of dolphins in the anti-shark nets off KwaZulu-Natal currently provides the only source of stomach content samples from healthy, wild populations along the coastline.

Stomach content analysis

Due to the immense difficulty of monitoring cetacean diets in the wild, most feeding studies rely on stomach content analyses (Sekiguchi *et al.* 1992, Lahaye *et al*. 2005). By identifying the hard parts of the prey which remain in the stomach, such as otoliths and squid beaks, researchers have made considerable progress in documenting and understanding the diets of a number of odontocete species, including spotted dolphins (*Stenella attenuata*) (Bernard & Hohn 1989), bottlenose dolphins (Cockcroft & Ross 1990), humpback dolphins

(*Sousa chinensis*) (Barros & Cockcroft 1991) and common dolphins (Pascoe 1986, Overholtz & Waring 1991), as well as pilot whales (*Globicephala* spp.) (Gales *et al.* 1992). Quantitative assessments of dietary composition can be made by calculating the size of prey species from relevant measurements of otoliths and squid beaks found in the stomach (Wijnsma *et al.* 1999). There are, however, a number of potential drawbacks in employing stomach content analyses to assess the diets of cetaceans and other large predators in marine systems. Sekiguchi *et al.* (1992) caution that dolphins caught and killed incidentally in nets may provide biased results in terms of stomach content analysis as these animals are usually caught whilst feeding on the particular fish species targeted in the fishery. As a consequence, their stomach contents give an over-estimation of the normal proportion of that prey species in the diet. This effect is likely to be more intense in active fisheries (e.g. dolphins caught in purse-seine nets) than for inactive nets (e.g. anti-shark nets). The dolphins used for stomach content analysis in this study will be those incidentally captured in the anti-shark nets off the KwaZulu-Natal coastline, which do not target any particular fish species, and hence would presumably not bias results in any significant way. However, during the annual sardine run, some bias may occur in these incidental captures as most of the dolphins feeding in the area are presumably attracted by the shoal of sardines moving northwards along the coast. Furthermore, it has also been demonstrated that dolphins subject to stress may regurgitate their stomach contents (Tomlin 1967). Dolphins captured in the anti-shark nets may regurgitate part of their last meal, giving a less accurate estimation of meal size and prey consumed (Young 1993).

Studies of cetacean diet composition have traditionally been plagued by the problem of obtaining sufficient sample sizes. Also, there is the tendency to overestimate the contribution of cephalopods to the total prey consumed as their hard beaks are resistant to digestion and accumulate in their stomachs (Santos *et al.* 2001, 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). This aside, it is unlikely that hard parts in the stomach contents represent the remains from several meals, as Ross (1979) estimated the gut passage time of captive bottlenose dolphins to be around 48 hours. Furthermore, he found that small fish otoliths would be completely digested within this time period. Additionally, more than two thirds of the ingested cephalopod beaks had been egested within 22 hours after feeding. 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. The detailed structure of fish otoliths is a species-specific trait, and hence a useful tool in the identification of prey species from the gut contents of piscivorous predators (Ross 1984, Smale *et al*. 1995). Otoliths are protected by the skull of the fish, making them one of the last species-specific features of fishes to undergo digestive degradation within the stomachs of marine predators (Smale *et al*. 1995). Since the 1960's, otoliths have been collected, catalogued and used in the identification of prey species; a technique which has greatly advanced the study of trophic ecology and predator-prey relationships of predators in marine systems (Fitch & Brownell 1968, Ross 1984, Sekiguchi *et al.* 1992, Smale *et al*. 1995).

Finally, the condition of the cetacean prior to death may also introduce bias into the analysis of its stomach contents. Stranded animals are often sick or weak prior to death, and cease to feed, or move inshore where they may feed on a range of prey species which are uncharacteristic of their normal diet. Hence the diets of stranded dolphins tend to be over-representative of coastal prey species (Sekiguchi *et al.* 1992, Kaschner *et al.* 2006). Stomach samples ultimately provide only brief snapshots of the highly-variable dietary composition of most marine mammals, and do not incorporate geographic and inter- and intra-annual variation in feeding (Kaschner *et al.* 2006).

Previous research on the diet of the common dolphin

Assessing the diet of any species is a fundamental component in understanding its ecology (Hooker *et al*. 2001, Samuel & Worthy 2004). There have been numerous studies of the diet of common dolphins in other regions of the world's oceans including southern California (Norris & Prescott 1961, Fitch & Brownell 1968, Evans 1976), in the Mid-Atlantic Bight (Overholtz & Waring 1991), in the north-east Atlantic (Brophy *et al.* 2009), off Plymouth in the UK (Pascoe 1986), in the English Channel (De Pierrepont *et al.* 2005), in the Mediterranean (Silva 1999, Santos *et al.* 2004) and Black Sea (Tomlin 1957), in the Bay of Biscay (Lahaye *et al*. 2005, Meynier *et al.* 2008 (a)), in the western North Pacific (Ohizumi *et al*. 1998) and in New Zealand (Stockin 2008). All of these previous studies, with the exception of that of Ohizumi *et al*. (1998), have dealt exclusively with the short-beaked form, *Delphinus delphis*. Much less dietary information is available for the long-beaked common dolphin, *Delphinus capensis*, despite the two forms co-occurring within the waters off

Mauritania (Pinela *et al*. 2008), in the western North Pacific (Ohizumi *et al*. 1998, Samaai *et al.* 2005) and in South Africa (Best 2007). This lack of information on the long-beaked variety is due to the fact that the two species were only recognized as distinct in 1994 (Heyning & Perrin 1994). It is for this reason that all previous publications on the diet of common dolphins in South Africa have referred to the species as *Delphinus delphis,* the short-beaked form. Although populations of *D. delphis* are now known to occur in southern African waters, they are found far offshore, with only very occasional strandings of this species being recorded along the South African coastline.

Our current understanding of the movements and feeding ecology of the long-beaked common dolphin in South African waters is limited. Ross (1984) first published dietary data for common dolphins from the east coast of South Africa. Young & Cockcroft (1994, 1995) continued work on net-caught and stranded dolphins from the east coast, providing dietary data for a much larger sample (N = 297). Sekiguchi *et al.* (1992) described the diet of this species on the west coast (N = 53) using both stranded animals and incidental captures in trawl fishing operations over the period 1966 to 1990. All of these previously-studied South African specimens are now believed to be *D. capensis*, the long-beaked form.

Aim of this study

The diet of the long-beaked common dolphin (*Delphinus capensis*) (Gray 1828) from South Africa has not been studied since the early 1990’s (Sekiguchi *et al.* 1992, Young 1993, Young & Cockcroft 1994). Given its opportunistic feeding strategy, the common dolphin may be used as an indicator species to obtaining information on the occurrence and abundance of small pelagic fish species (Sekiguchi *et al.* 1992). Recent evidence suggests that the spatial and temporal range, as well as the intensity of the sardine run have exhibited marked fluctuations over the last decade (O’Donoghue 2009). This annual migration of sardine (*Sardinops sagax*), and other small pelagic species such as anchovy (*Engraulis encrasicolus*) and round herring (*Etrumeus whiteheadi*) represents a valuable food source for the common dolphin population on the south and east coasts of southern Africa (Young & Cockcroft 1994). Changes in the timing and intensity of the sardine run could represent significant changes in the suite of prey available to the common dolphins in this region during winter. This study aimed to provide new data on the diet of the common dolphin in the waters of KwaZulu-Natal over the period 2000 to 2009.

Materials & Methods

Stomach content analysis

All samples and data analysed in this study were obtained from dolphins incidentally caught and drowned in the anti-shark nets off the KwaZulu-Natal coast (Figure 2.1). Dolphins caught in the anti-shark nets were removed within 24 hours of capture as the nets are maintained daily by the KwaZulu-Natal Sharks Board. All catches are retrieved and frozen whole pending dissection at a later date. Prior to dissection, dolphins were thawed and weighed, and their total length measured, as well as a variety of morphometric measurements recorded according to the Port Elizabeth Museum dissection protocol. Notes are made on the overall condition of the animal and relevant pathology. Thereafter, 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 re-frozen until examination. The stomachs of 95 common dolphins (*D. capensis*) incidentally caught in the anti-shark nets between 2000 and 2009 were examined for prey items. Stomach dissections took place in accordance with procedures described by Young & Cockcroft (1994) and Silva (1999).

Whole stomachs were thawed and weighed to the nearest gram to obtain a weight of the full stomach. Stomachs were then cut open down the oesophagus, opening the fore-stomach, main and pyloric chambers entirely, and then washed under running water at least three times, so that all contents were rinsed into a plastic basin. Empty, thoroughly washed stomachs were then weighed to obtain the weight of the empty stomach (allowing calculation of meal mass), and then disposed of. Intact prey were removed, measured, weighed, photographed and identified to the species level if possible. Otoliths were then removed from intact fish skulls, and squid beaks from buccal masses to aid further identification of prey items consumed. Semi-intact prey (most of vertebral column present) were measured, photographed, and weighed. Loose heads of eels and fish were also removed from stomach contents, and where possible, otoliths were extracted. Stomach contents were then repeatedly rinsed within the plastic basin. Contents were agitated, allowing suspended loose tissue and other soft material to be drained off. With progressive rinses, all visible otoliths, squid beaks and other characteristic hard parts were removed using fine forceps. Otoliths were cleaned in distilled water by brushing with a fine paintbrush and dissecting needle. Otoliths were dried and stored in gelatine pill capsules while the cephalopod beaks were stored in 70% ethanol for further identification using the Port Elizabeth Museum reference collection and a published guide (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 the side was not determinable (Young & Cockcroft 1994). The number of cephalopods in each stomach was estimated by counting the maximum number of upper or lower beaks. 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. All otoliths were measured to the nearest 0.02mm using a Zeiss binocular microscope fitted with an eyepiece graticule. Both otolith full length and anti-rostral length were measured. For fragile otoliths (such as those of sardine) where the tip of the otolith was often found broken, the anti-rostral length was measured and the full length estimated by comparing the anti-rostral length with the same measurement for unbroken otoliths. Otoliths which were too damaged or digested to identify and measure with certainty were excluded from the analysis (Silva 1999, Young & Cockcroft 1994).

Original prey dimensions and weights were back-calculated from otolith and cephalopod beak dimensions using established regressions (Cooper 1979, Clarke 1986, Smale *et al*. 1995). The direct relationship that exists between otolith length and fish length for all species, allows fish length to be estimated from otoliths retrieved from cetacean stomachs (Fitch & Brownell 1968). Digestion in stomach acid causes erosion of the edges of the otolith, making subsequent under-estimation of prey length likely (Smale *et al*. 1995, Wijnsma *et al*. 1999). The rate of digestion of otoliths depends on the temperature at which the stomach is kept (Wijnsma *et al.* 1999). Freezing of all specimens used in this study as soon after removal from shark nets as possible will dramatically slow the rate of digestion, but subsequent thawing (during dissection and sample transport) may once again have increased digestion rate for a short period of time prior to dissection of the stomach. The majority of fish species were identified to the 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. In the present study, beaks resembling both *Loligo duvaucelii* and *Loligo vulgaris reynaudii* were removed from stomach contents. Due to the taxonomic uncertainties involved with identification of Loliginid species in South Africa (Roeleveld 1998), all Loliginid prey items have been grouped and referred to as *Loligo spp*.

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 (determined by examination under a dissecting microscope) were used in the regressions to calculate body size and weight of prey items. For prey species lacking suitable regressions, body weights and lengths were estimated from Port Elizabeth Museum 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 of the common dolphin, according to Pinkas *et al.* (1971). The following equation was used for calculating the IRI value for each prey species:

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

where % number was calculated as the number of prey items of each species relative to the total number of prey individuals collected, % 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 & Cailliet 1996, Young & Cockcroft 1994).

Statistical analyses

Stomach contents from 95 common dolphins (55 females, 40 males) caught between 2000 and 2009 were analysed as follows. Dolphins were allocated to age categories based on the standard length and weight specifications of Young and Cockcroft (1994); calves (<180cm body length, 18 to 75kg body mass), juveniles (males between 75 and 100kg, females between 75 and 90kg body mass) and adults (males >110kg and females >90kg body mass). The sample for this study consisted of 20 calves (8 males and 12 females), 9 juveniles (2 males and 7 females) and 66 adults (30 males and 36 females). Diet composition was analysed in Microsoft Excel 2007, and temporal patterns in the diet of male and female dolphins were assessed employing the software package PRIMER v. 6.0 (Clarke 1993). Stomach content data expressed as the mass (g) of each prey species were square-root transformed before the analyses (Multi-dimensional Scaling, SIMPER and ANOSIM in PRIMER v. 6.0) were conducted. A square-root transformation was used to convert mass (g) of each prey species in the diet into percentage mass before analyses were performed. A species accumulation plot was calculated in order to determine whether the sample size used in this study adequately represented the diet of *D. capensis*. The species accumulation curve shows the rate at which new species are found in the diet, and can be extrapolated to provide an estimate of overall species richness of the diet. The species accumulation curve plotted in PRIMER v.6.0 plotted the cumulative number of species recorded as a function of sampling effort (number of individual stomachs examined). A SIMPER analysis was carried out on stomach content data, where groups of dolphins were predefined as being caught during (June and July), or directly after the sardine run (August, September and October). The SIMPER analysis assesses the role of different species to contributing to the within-group similarity of dolphins caught either during, or after the sardine run. An ANOSIM was carried out on stomach content data to compare similarity of diet between males and females, as well as adults, juveniles and calves. These groups were pre-defined in the analyses. T-tests were carried out in STATISTICA v. 9.0 (StatSoft Inc. 2009) to determine if there were significant differences in the size of prey eaten by adult male and female common dolphins.

Results

The number of dolphin stomachs available for examination varied from year to year, depending on the catches from the anti-shark nets (Figure 2.2). Particularly high catches of common dolphins were recorded in 2004 and 2005, with 30 and 28 common dolphins caught in each year, respectively. From 2006 onwards, common dolphin catches were <6 individuals per year. No common dolphins were caught in 2001 and 2002.

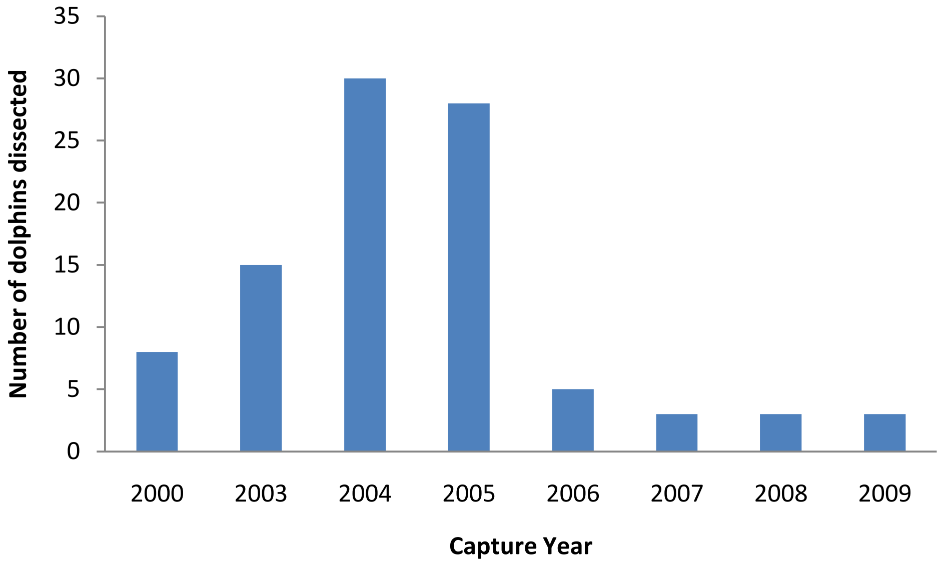

Figure 2.2 Number of *D. capensis* individuals dissected for each sample year of study. No data are presented for 2001 and 2002 as no common dolphins were incidentally caught in the anti-shark nets during these years.

Overall diet composition

Only one calf stomach was found to be completely empty, with an additional five of the calf stomachs containing only milk remains. A total of 23 fish species and 5 cephalopod species were identified from stomach contents (Table 1). Nine prey species were found to be dominant (constituting >1% by mass) in the diet of common dolphins between 2000 and 2009. 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 Scombrid species resembling mackerel tuna (*Euthynnus affinis)*, and two cephalopod species; *Loligo* and *Lycoteuthis diadema* (Figure 2.3, Table 2.1). Collectively, these species constituted 94% of the prey consumed by the common dolphin over the study period.

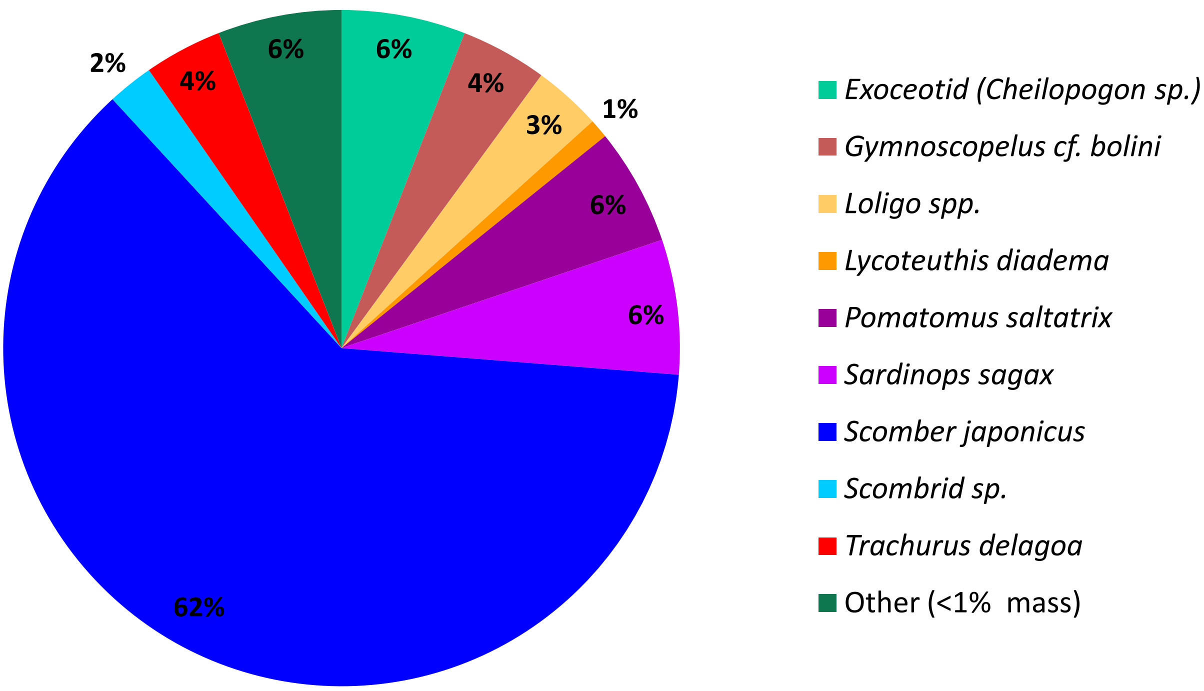

Figure 2.3 Diet composition by percentage mass of each prey species for all age cohorts of *D. capensis* incidentally caught in anti-shark nets along the KwaZulu-Natal coastline between 2000 and 2009. Values presented are the mean of 95 individuals.

Although the diet of the common dolphin showed inter-annual variation over the period 2000 to 2009, in general it was comprised predominantly of chub mackerel (*Scomber japonicus*) by mass (62 %). Sardine (*Sardinops sagax*), flying fish (*Exoceotid* sp.) and elf (*Pomatomus saltatrix*) form smaller components (6 % each), with all cephalopod species forming a combined total of only 4 % of the total diet. Those species which individually formed <1% of the total mass of prey species, collectively make up 6% of the diet.

Table 2.1 Fish and cephalopod prey of all *D. capensis* incidentally caught in anti-shark nets off KwaZulu-Natal between 2000 and 2009, and their calculated Index of Relative Importance (IRI) values. N = 95

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

Table 2.2 Average total length of common prey species recorded in the diet of *D. capensis* adult dolphins. N = 66 (30 males, 36 females)

Prey species	Average Total Length (cm)
Fish	
Bregmaceros sp.	3.07
Decapterus macarellus	16.99
Diaphus sp.	4.89
Engraulis japonicus	13.32
Etrumeus whiteheadi	17.23
Exocoetid sp.	34.35
Gymnoscopelus cf. bolini	19.10
Pagellus bellotti natalensis	12.60
Pomatomus saltatrix	31.26
Rastrelliger kanagurta	19.95
Sardinops sagax	19.27
Sarpa salpa	19.02
Scomber japonicus	34.78
Scombrid sp. *(cf. Euthynnus affinis)*	29.72
Sphyraena acutipinnis	20.40
Trachurus delagoa	15.57
Cephalopods	
Loligo spp.	14.77
Lycoteuthis diadema	8.85
Sepia sp.	5.93
Mean total length of all prey:	17.95

The long-beaked common dolphin targeted a wide range of prey sizes, with the fish and cephalopod species found in the diet ranging from ±3cm (*Diaphus sp.*) to >34cm (*Scomber japonicus/*chub mackerel and *Exocoetid sp.*/flying fish) in total length.

A species accumulation curve plotted in PRIMER (v.6) was used to establish whether the sample size used in this study was large enough to encompass the variation in the diet of the long-beaked common dolphin (Figure 2.4).

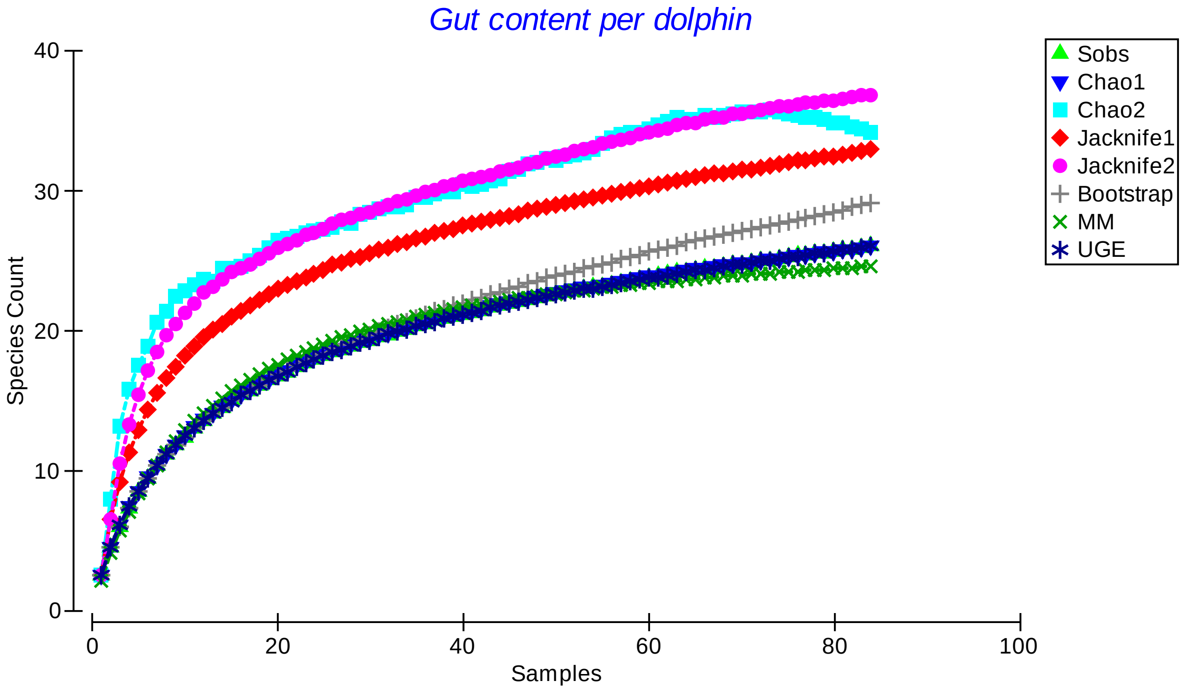

Figure 2.4 Species accumulation curve for the prey species in the diet of *D. capensis* from KwaZulu-Natal caught between 2000 and 2009 (Smax = 29.88)

All curves appear to be nearing an asymptote, with the Chao 2 curve beginning to decline. The maximum predicted number of species was calculated as 29.88, just one species higher than that observed in the stomach contents during this study. This suggests that the sample size analysed during this investigation was sufficient to encompass the variability within the diet of *D. capensis*.

Comparison of diet between sexes

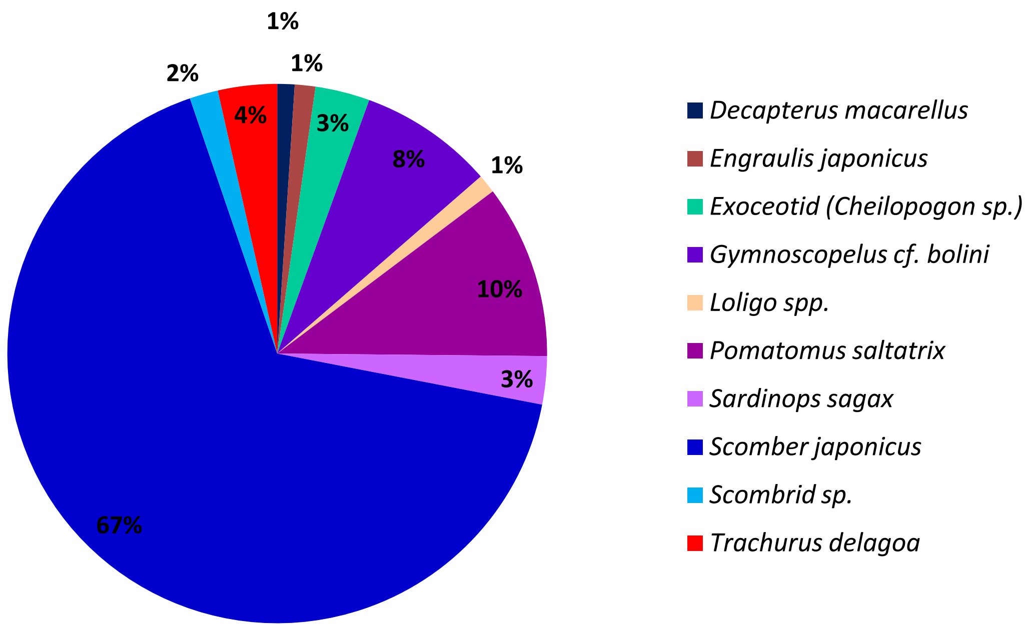

Figure 2.5 Dominant prey species (>1 % mass) in the diet of male *D. capensis* incidentally caught in anti-shark nets off the KwaZulu-Natal coastline between 2000 and 2009

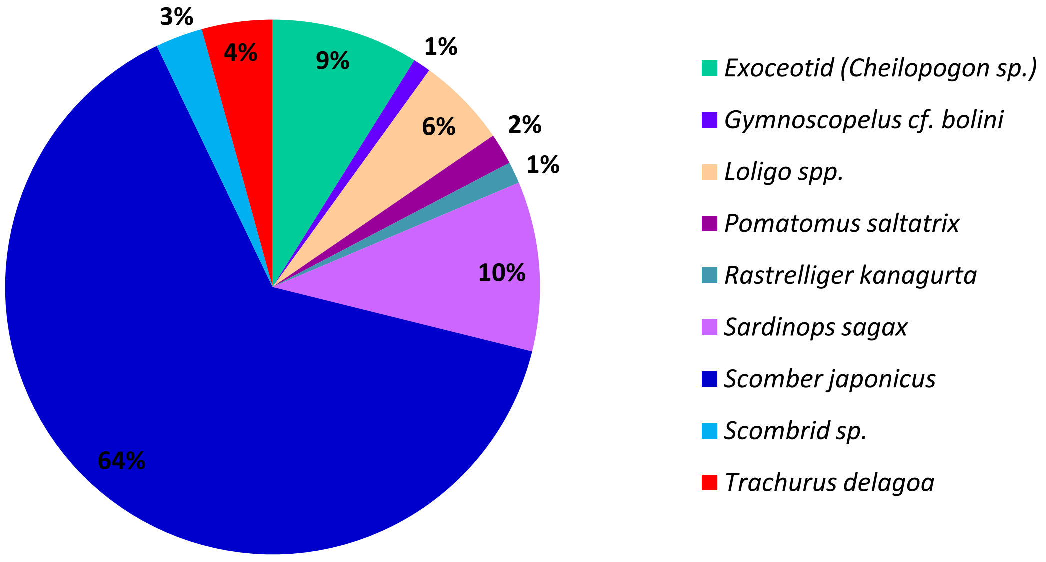

Figure 2.6 Dominant prey species (>1 % mass) in the diet of female *D. capensis* incidentally caught in anti-shark nets off the KwaZulu-Natal coastline between 2000 and 2009

The diets of male and female common dolphins during the investigation were very similar (Figures 2.5 and 2.6). Multidimensional scaling (MDS) indicated that there was a high degree of overlap in the prey consumed between male and female long-beaked common dolphins, suggesting little or no resource partitioning between the two sexes (Figure 2.7). Indeed, an ANOSIM revealed no significant differences in the diet of male and female common dolphins during the study period (Sample statistic/Global R = 0.025, significance of sample statistic = 10.8%). Mackerel comprised nearly two thirds of the total dietary intake in terms of percentage mass, with the remaining third consisting of a mixture of other pelagic fish and squid species. Female common dolphins appeared to prey slightly less on elf than their male counterparts (2% of diet in females and 10% in males), and slightly more on sardine (10% of diet in females and 3% in males). Females also consumed more squid than males (6% of diet in females and 1% in males).

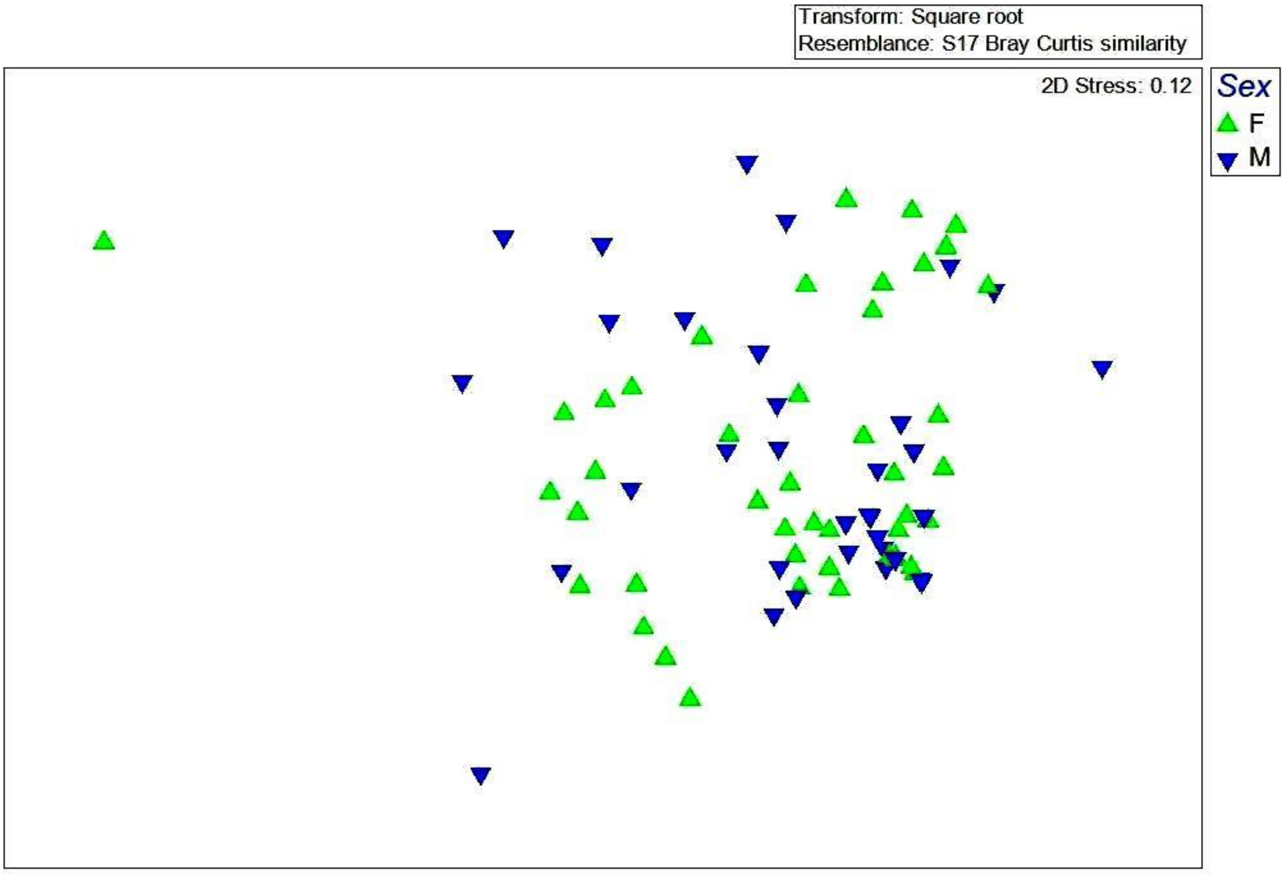

Figure 2.7 MDS ordination for the diet composition of male (blue) and female (green) *D. capensis* incidentally caught in anti-shark nets along the KwaZulu-Natal coastline between 2000 and 2009.

Despite a high degree of overlap between the diets of male and female common dolphins, the SIMPER analysis revealed that female common dolphins consume a wider variety of prey than their male counterparts (the similarity between female diets being a product of 4 dominant prey species) than males (whose diets consisted primarily of only 2 dominant species) (Table 2.3).

Table 2.3 Average Bray-Curtis similarity between the diets of male and female *D. capensis* between 2000 and 2009 (SIMPER Analysis - Primer v.6). N = 95 (55 females, 40 males)

Female dolphins			
Prey species	**Common name**	**% Contribution**	**Cumulative %**
Scomber japonicus	Chub mackerel	56.91	56.91
Sardinops sagax	Sardine	17.20	74.11
Loligo spp.	Chokka squid	12.97	87.08
Trachurus delagoa	Maasbanker	6.95	94.03
Male dolphins			
Prey species	**Common name**	**% Contribution**	**Cumulative %**
Scomber japonicus	Chub mackerel	85.86	85.86
Sardinops sagax	Sardine	4.22	90.08

The similarity between the diets of all female common dolphins was a function of the contributions of four dominant prey species (chub mackerel, sardine, chokka squid and maasbanker), whilst the similarity between male diets was a function of the presence of only two dominant species (chub mackerel and sardine).

Table 2.4 Average total lengths of common prey species recorded in the diet of adult male (N = 30) and female (N = 36) *D. capensis* over the period 2000 to 2009

Prey species	**Average Total Length (cm) Female dolphins**	**Average Total Length (cm) Male dolphins**	**Significant difference between sexes *(P<0.05)**
Fish			
Bregmaceros sp.	2.7	2.58	
Decapterus macarellus	16.21	22.1	
Diaphus sp.	4.93	4.77	
Engraulis encrasicolus	11.42	13.36	
Etrumeus whiteheadi	Absent	17.23	
Exocoetid sp.	34.17	34.81	
Gymnoscopelus cf. bolini	19.48	19.04	
Pagellus bellotti natalensis	13.12	11.99	
Pomatomus saltatrix	25.87	32.79	* (P=0.0416)
Rastrelliger kanagurta	19.95	Absent	
Sardinops sagax	19.51	18.42	
Sarpa salpa	21.98	16.56	*(P=0.0018)
Scomber japonicus	34.11	35.52	*(P=0.0401)
Scombrid sp. *(cf. Euthynnus affinis)*	29.72	31.84	
Sphyraena acutipinnis	20.40	Absent	
Trachurus delagoa	15.11	16.20	*(P=0.0047)
Cephalopods			
Loligo spp.	15.13	12.92	
Lycoteuthis diadema	8.78	8.93	
Sepia sp.	7.42	5.43	
Mean total length of all prey:	17.78	17.91	

The total length of only four prey species in the diet were found to differ significantly between male and female common dolphins (Table 2.4). Males preyed on significantly larger elf (*Pomatomus saltatrix*), chub mackerel (*Scomber japonicus*) and maasbanker (*Trachurus delagoa*) than female dolphins. Conversely, female common dolphins consumed significantly larger strepie (*Sarpa salpa*) than their male counterparts. No correlation was found between dolphin body length and the total length of prey consumed across all three age cohorts ($R^2 = 0.003$).

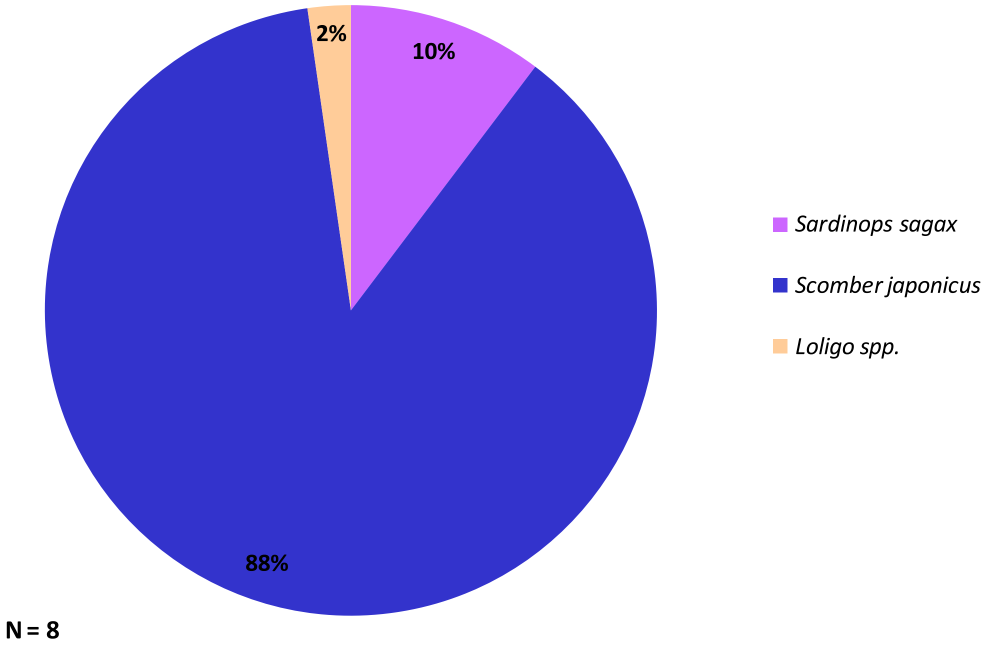

Figure 2.8 Dominant prey species (>1 % mass) in the diet of pregnant and lactating female *D. capensis* between caught in the anti-shark nets off the KwaZulu-Natal coastline over the period 2000 to 2009

The diversity of prey recorded in the diet of adult female dolphins was not evident in the diet of pregnant and lactating females (Figure 2.8) due to the small sample size of this group (6 pregnant females, 2 lactating females). The bulk of the diet of pregnant and lactating female common dolphins was comprised of mackerel (88% by mass) and sardine (10% by mass), with small contributions of maasbanker and chokka squid.

Ontogenetic dietary differences

A high degree of similarity in the species consumed by the different age classes of *D. capensis* was observed although the contribution of each prey species to the overall diet differed (Tables 2.5, 2.6 and 2.7). The IRI values for squid in the diet of calves and juveniles were relatively high in comparison to adults, indicating that squid are a more important food source for younger common dolphins. Sardine was the most important prey species in the diet of calves, closely followed by mackerel and elf. In the diet of juvenile common dolphins, mackerel were dominant, followed by sardine and squid. *Sphyraena acutipinnis* (Sharpfin barracuda) was more common in the diet of calves than it is in the diets of juvenile and adult dolphins. Despite the apparent differences in the main prey consumed by the different developmental stages of the common dolphin population, MDS indicated that there was a high degree of overlap in the diets of adults, juveniles and calves. There was thus little or no resource partitioning between the different ontogenetic stages of common dolphins examined in this study (Figure 2.9). The contribution of the different prey species to the total similarity in diets of the different developmental stages of the dolphin calculated using the SIMPER procedure of PRIMER are indicated in Table 2.8.

Table 2.11 Fish and cephalopod prey of *D. capensis* adults incidentally caught in anti-sharks nets off the KwaZulu-Natal coastline between 2000 and 2009, and their calculated Index of Relative Importance (IRI) values (N = 66; 30 males and 36 females)

Prey species	Number	% Number	Mass (g)	% Mass	Frequency of Occurrence	% FO	IRI	IRI Rank
Fish								
Bremaceros sp.	1	0.104	2.250	0.002	1	1.515	0.161	25
Decapterus macarellus	15	1.566	939.300	0.691	7	10.606	23.933	13
Diaphus sp.	166	17.328	289.310	0.213	12	18.182	318.918	4
Diplodus sargus	1	0.104	90.954	0.067	1	1.515	0.259	23
Engraulis encrasicolus	56	5.846	852.513	0.627	5	7.576	49.034	9
Etrumeus whiteheadi	7	0.731	263.727	0.194	1	1.515	1.401	19
Exocoetidae sp.	25	2.610	7733.000	5.687	9	13.636	113.131	7
Gymnoscopelus cf. bolini	83	8.664	6328.000	4.653	5	7.576	100.889	8
Katsuwonus pelamis	1	0.104	500.000	0.368	1	1.515	0.715	22
Myctophidae sp.	1	0.104	1.491	0.001	1	1.515	0.160	26
Pagellus bellotti natalensis	22	2.296	662.178	0.487	11	16.667	46.390	10
Pomatomus saltatrix	26	2.714	8089.151	5.949	10	15.152	131.250	6
Rastrelliger kanagurta	10	1.044	1007.000	0.741	1	1.515	2.704	17
Sardinops sagax	106	11.065	7288.988	5.360	20	30.303	497.723	2
Sarpa salpa	11	1.148	1203.309	0.885	2	3.030	6.161	15
Scomber japonicus	209	21.816	87181.492	64.111	43	65.152	5598.288	1
Scombridae sp. *(cf. Euthynnus affinis)*	11	1.148	2488.825	1.830	5	7.576	22.564	14
Sphyraena sp. *(cf acutipinnis)*	2	0.209	86.375	0.064	2	3.030	0.825	21
Trachurus delagoa	116	12.109	5079.527	3.735	17	25.758	408.101	3
Valamugil (cf. seheli)	2	0.209	367.000	0.270	2	3.030	1.450	18
Cephalopods								
Enoploteuthis sp.	1	0.104	12.000	0.009	1	1.515	0.172	24
Loligo spp.	35	3.653	4025.358	2.960	20	30.303	200.412	5
Lycoteuthis diadema	41	4.280	1364.526	1.003	4	6.061	32.019	11
Ommastrephes sp.	5	0.522	12.505	0.009	1	1.515	0.805	20
Sepia sp.	5	0.522	116.605	0.086	4	6.061	3.683	16

Table 2.12 Fish and cephalopod prey of juvenile *D. capensis* incidentally caught in anti-shark nets off the KwaZulu-Natal coastline between 2000 and 2009, and their calculated Index of Relative Importance (IRI) values (N = 9)

Prey species	Number	% Number	Mass (g)	% Mass	FO	% FO	IRI	IRI Rank
Fish								
Decapterus macarellus	5	4.348	503.500	3.604	1	11.111	88.356	8
Exocoetidae sp.	4	3.478	1341.000	9.599	1	11.111	145.307	5
Pagellus bellotti natalensis	6	5.217	149.029	1.067	2	22.222	139.649	6
Pomatomus saltatrix	1	0.870	113.632	0.813	1	11.111	18.700	10
Sardinops sagax	43	37.391	2267.403	16.231	2	22.222	1191.605	2
Scomber japonicus	22	19.130	7064.217	50.568	3	33.333	2323.291	1
Scombridae sp. *(cf. Euthynnus affinis)*	4	3.478	871.400	6.238	1	11.111	107.956	7
Sparidae sp.	1	0.870	31.787	0.228	1	11.111	12.190	12
Sphyraena sp. *(cf acutipinnis)*	1	0.870	40.152	0.287	1	11.111	12.855	11
Trachurus delagoa	14	12.174	622.785	4.458	1	11.111	184.800	4
Cephalopods								
Loligo spp.	10	8.696	940.406	6.732	4	44.444	685.663	3
Ommastrephes sp.	4	3.478	24.348	0.174	2	22.222	81.168	9

Table 2.13 Fish and cephalopod prey of *D. capensis* calves incidentally caught in anti-shark nets off the KwaZulu-Natal coastline between 2000 and 2009, and their calculated Index of Relative Importance (IRI) values (N = 20)

Prey species	Number	% Number	Mass (g)	% Mass	FO	% FO	IRI	IRI Rank
Fish								
Ambassis natalensis	2	5.128	9.000	0.695	1	7.143	41.596	9
Apogon sp.	1	2.564	2.000	0.154	1	7.143	19.418	11
Bregmaceros sp.	9	23.077	23.900	1.846	1	7.143	178.021	4
Pagellus bellotti natalensis	2	5.128	122.173	9.437	1	7.143	104.036	8
Pomatomus saltatrix	1	2.564	362.444	27.996	1	7.143	218.283	3
Sardinops sagax	5	12.821	46.154	3.565	3	21.429	351.118	1
Scomber japonicus	1	2.564	539.185	41.647	1	7.143	315.795	2
Sphyraena sp. *(cf. acutipinnis)*	7	17.949	66.667	5.149	1	7.143	164.987	5
Cephalopods								
Loligo spp.	3	7.692	25.641	1.981	2	14.286	138.184	7
Lycoteuthis diademma	1	2.564	35.945	2.776	1	7.143	38.147	10
Sepia sp.	7	17.949	61.538	4.753	1	7.143	162.157	6

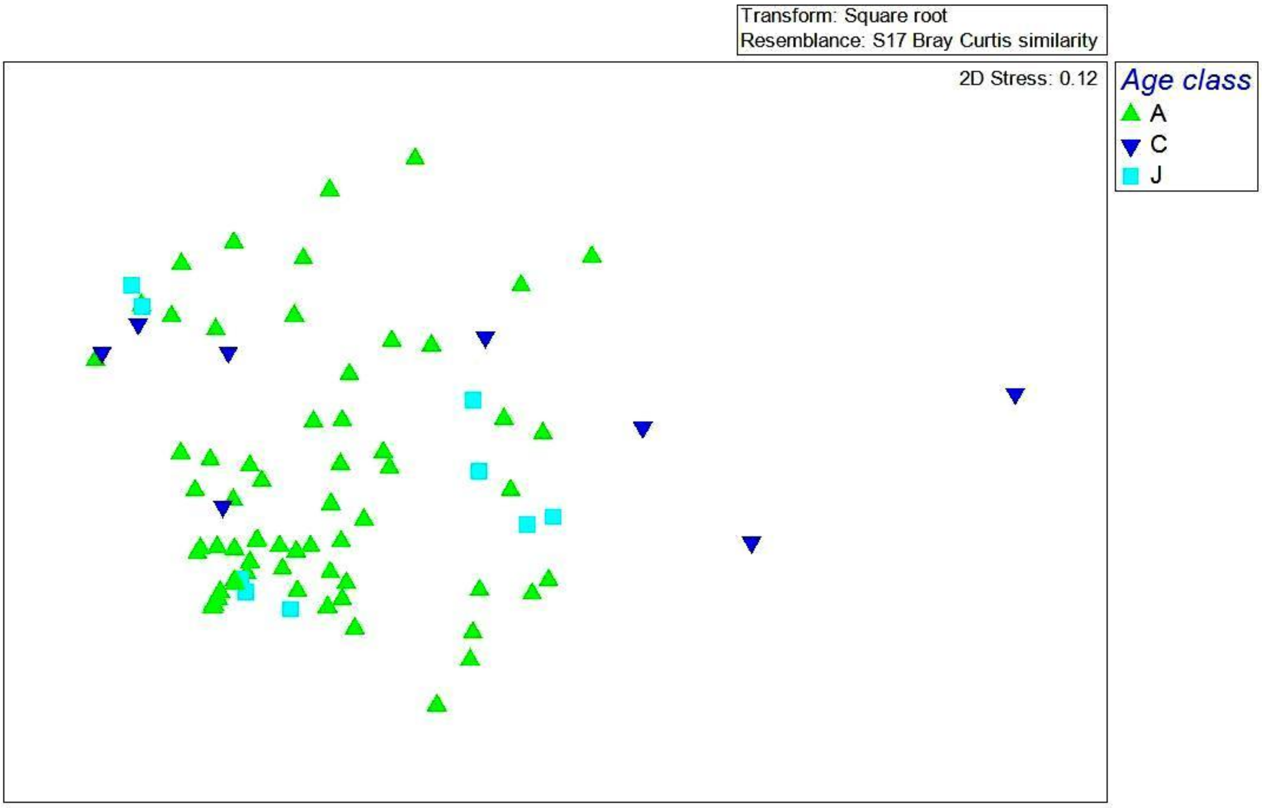

Figure 2.9 MDS ordination for the diet of the different developmental stages of long-beaked Common dolphins incidentally caught in anti-shark nets off the KwaZulu-Natal coastline over the period 2000 to 2009 (A = Adult, J = Juvenile, C = Calf)

Table 2.14 Average Bray-Curtis similarity between the diets of adult, juvenile and calf *D. capensis* incidentally caught in anti-shark nets off the KwaZulu-Natal coastline between 2000 and 2009 (SIMPER Analysis - Primer v.6)

Adults			
Prey species	**Common name**	**% Contribution**	**Cumulative %**
Scomber japonicus	Chub mackerel	77.17	77.17
Sardinops sagax	Sardine	6.54	83.71
Trachurus delagoa	Maasbanker	5.26	88.97
Loligo spp.	Chokka squid	5.17	94.14
Juveniles			
Prey species	**Common name**	**% Contribution**	**Cumulative %**
Scomber japonicus	Chub mackerel	46.08	46.08
Loligo spp.	Chokka squid	34.33	80.41
Sardinops sagax	Sardine	16.56	96.97
Calves			
Prey species	**Common name**	**% Contribution**	**Cumulative %**
Sardinops sagax	Sardine	97.95	97.95

The within-group similarity between the adult dolphins was attributed to four dominant prey species (chub mackerel, sardine, maasbanker and chokka squid) which collectively accounted for 94% of the similarity within the group. The similarity between the diets of juveniles was made up primarily of the contributions of three dominant prey species; chub mackerel, chokka squid and sardine, which combined accounted for up to 97% of the within-group similarity. The presence of sardine alone accounted for the similarity of the diets between all calves during this investigation.

Temporal dietary changes

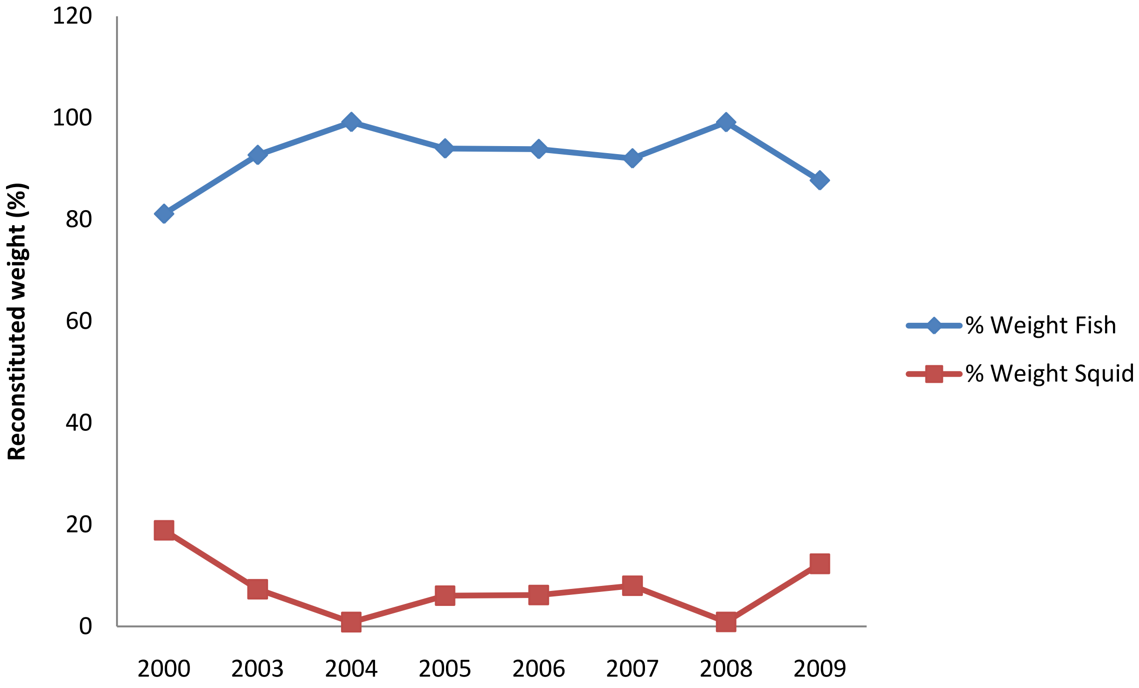

Figure 2.10 Proportional contributions of fish and squid in the diet of *D. capensis* incidentally caught in anti-shark nets off the KwaZulu-Natal coastline between 2000 and 2009. All age cohorts combined.

Fish species constituted the bulk of the prey consumed by the long-beaked common dolphin over the duration of the study, contributing between 80 and 100% of the prey mass, whilst squid prey never formed more than 20% of the diet over the last decade.

Table 2.15 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)

During the Sardine Run (June & July)			
Prey species	**Common name**	**% Contribution**	**Cumulative %**
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
Exoceotid sp.	Flying fish	6.05	92.30
Directly after the Sardine Run (Aug, Sept & Oct)			
Prey species	**Common name**	**% Contribution**	**Cumulative %**
Scomber japonicus	Chub mackerel	78.13	78.13
Sardinops sagax	Sardine	13.78	91.92

The diet of common dolphins caught during the sardine run (June & 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 2.9). Directly after the sardine run, the similarity between individual dolphin diets was attributed to only two dominant species; chub mackerel and sardine (Table 2.9).

Discussion

Annual by-catch trends

The by-catch of common dolphins varies annually, and is likely to depend on the intensity of the sardine run, and the proximity of sardine shoals to the inshore region. The particularly high catches of common dolphins in 2004 and 2005 appear to correspond to particularly strong sardine runs during this period (O'Donoghue 2009). The highest catch of common dolphins in the last decade occurred in 2004, when 30 common dolphins were caught in one year. O'Donoghue (2009) documented that 2004 also exhibited the lowest sea surface temperatures, and the most intense and persistent sardine run. Longer and more intense runs presumably bring the common dolphins into the shallow shelf waters of KwaZulu-Natal and into contact with the anti-shark nets more often, resulting in increased dolphin by-catch. From 2006 onwards, common dolphin catches declined to less than 6 per year, corresponding with the trend of lower sardine abundance in KwaZulu-Natal waters between 2002 and 2006 (O'Donoghue 2009).

Sex bias in net catches

Cockcroft (1990) documented that significantly more mature female common dolphins were caught in the KwaZulu-Natal shark nets than males, and that all calves trapped were either weaned or in the process of weaning. During this study, five of the calves caught were pre-weaning, and their stomachs contained only milk. As in the study of Young (1993), a much higher number of female common dolphins were caught in the anti-shark nets than males during the period 2000 to 2009 (55 females and 40 males). The increased by-catch of female common dolphins may reflect the general sex-ratio of a common dolphin pod. Alternatively, it is possible that females may forage slightly more inshore than their male counterparts, keeping 'nursery' groups containing calves in shallower waters, and thus having a greater likelihood of entanglement in the anti-shark nets (Young 1993). It seems logical that females may use the plentiful food supply offered by the sardine migration to wean their calves and replenish body fat reserves before their next pregnancy (Cockcroft & Peddemors 1990). Young (1993) also postulated that maternal groups may feed closer to the shore than males in order to provide greater protection for calves, isolating them from more violent feeding activity in deeper waters.

Diet composition

The species accumulation curve was calculated in order to determine if an adequate number of samples had been processed to accurately reflect the temporal variation in the diet of *D. capensis* along the KwaZulu-Natal coastline. Cumulative prey curves function on the premise that variations and species richness in the diet will decrease with increasing sample size, creating a curve which reaches an asymptote at an acceptable sample size, where new prey items are rarely added to the diet (Ferry & Cailliet 1996). The calculated predicted maximum number of species within the diet of the common dolphin was 29.88, one more than what was recorded in the stomach contents of the common dolphins during the present study. This suggests that the stomach content results presented here are an accurate reflection of the diet of the common dolphin in KwaZulu-Natal waters.

The bulk of the diet of the common dolphins during this study was comprised of pelagic and epipelagic shoaling fish species (most of which are found above 250m, with the exception of *Trachurus delagoa* which is found at up to 400m), which migrate along the KwaZulu-Natal coastline in high numbers during winter (van der Elst 1995, Heemstra & Heemstra 2004). The long-beaked common dolphin also undertakes a long-distance migration along the south and east coasts during winter, following the movement of these large fish shoals (Cockcroft & Peddemors 1990). This indicates that pod movement is closely linked to that of their preferred prey species (Selzer & Payne 1988, Cockcroft & Peddemors 1990, Brophy *et al*. 2009). Since common dolphins occur in such large pods (sometimes in excess of 5 000 individuals), and use co-operative hunting tactics, they target shoaling species because these are easiest to herd into baitballs (Young 1993). Long-beaked common dolphins along the south-east coast of South Africa appear to be specific in their dietary requirements, with 94.9% of total reconstituted diet being comprised of only nine prey species. The other 19 prey species all constituted less than 1% of the total diet in terms of mass. This suggests that common dolphins are generalist or opportunistic feeders, preying on whichever prey species are most abundant and easily caught locally (Klinowska 1991).

The nine dominant prey species recorded in the stomachs of the common dolphins during this study comprise seven pelagic or epipelagic shoaling fish species and two cephalopod species (Figure 2.3). All of the fish species share a common migration pattern, with movement up the east coast and into the waters of KwaZulu-Natal each winter. *Sardinops sagax* (pilchard/sardine) filter phytoplankton such as dinoflagellates and diatoms, as well as zooplankton and anchovy eggs from the water column, also preying on krill and larval crabs (van der Elst 1995, Heemstra & Heemstra 2004). This is the species predominantly targeted by the South African pelagic fishing fleet (van der Elst 1995), and is the species responsible for the annual ‘sardine run’ phenomenon due to its massive range expansion along the East Coast, where shoals are particularly visible when they move onto the narrow continental shelf off of Durban (Connell 2001). *Scomber japonicus* (Houttuyn 1782) (chub mackerel) is an epipelagic shoaling species found in the surface waters of temperate coastal areas, with shoals being found at depths of up to 200m (van der Elst 1995). This species filters zooplankton from the water column, as well as preying on small fish and squid, and is often found in mixed shoals with other scombrid species, mainly maasbanker and pilchards (van der Elst 1995, Heemstra & Heemstra 2004). It is one of South Africa’s top three commercially landed catches (van der Elst 1995), and spawns off KwaZulu-Natal each winter from July to December (Heemstra & Heemstra 2004).

Diets of male and female common dolphins

Both male and female common dolphins had diets dominated by mackerel (*Scomber japonicus*), with the remaining third of the diet comprised of a suite of pelagic fish and cephalopod prey species. This suggests that both sexes take advantage of the abundant mackerel stocks at this time of year, focusing their feeding effort on the most abundant and easily caught prey items. Although both sexes take advantage of the abundance of large, lipid-rich mackerel, when not eating mackerel, females were more likely to target smaller sardines (10% of female diet vs. 3% of male diet) and squid species, whilst males appeared to prey on larger, faster elf (10% of male diet vs. 2% of female diet). Male common dolphins also preyed on significantly larger elf (*Pomatomus saltatrix*), chub mackerel (*Scomber japonicus*) and maasbanker (*Trachurus delagoa*) than female dolphins, whilst females consumed significantly larger strepie (*Sarpa salpa*) than their male counterparts. The sexual dimorphism observed in common dolphins (males are larger than females by 20 to 30cm –

Best 2007) may explain the larger prey size taken by male common dolphins. No correlation was, however, found between dolphin body length and the total length of prey consumed during this study. Nonetheless, the high degree of overlap in the diets of male and female common dolphins indicates that all adult dolphins feed in the same area, and is reflective of their co-operative hunting tactics (Young 1993). Meynier *et al.* (2008 (a)) also reported a high degree of similarity in the diet of male, female and juvenile common dolphins in the Bay of Biscay, and attributed the slight differences in prey species proportions in the diet to the varying energy requirements of each cohort, as well as their respective foraging abilities. Young (1993) found that male dolphins concentrated on sardine, whilst females had a more diverse diet. There is, however, little evidence to support this finding from the present study.

The results of this study are broadly in agreement with those of Young (1993), who also noted a high relative importance of species such as mackerel, maasbanker and elf in the diet of common dolphins, even though the vast majority of their diet between 1974 and 1992 consisted of sardine. This indicates a strong and persistent presence of larger, shoaling and piscivorous fish species in KwaZulu-Natal waters during winter. Large, highly visible sardine shoals are known to move into KwaZulu-Natal during mid-winter (June and July) each year, with spawning occurring from late June through to December (Connell 2001). Mackerel and other predatory fish species have also been shown to spawn prolifically in KwaZulu-Natal between August and November (Connell 2001). Female dolphins also consumed slightly more squid than males (6% in females and 1% in males), possibly reflecting some differences in prey selection.

Diet of reproductively active females

The diet of pregnant or lactating females is not well represented in this sample, as only eight of the dolphins caught fell into this category (six were pregnant, and two lactating). However, the diet of the pregnant or lactating female common dolphins was similar to that of all adult dolphins, but with a slightly higher proportion of mackerel (87% by mass). The elevated contribution of mackerel may simply be reflective of the inability of such a small sample size to adequately encompass the normal diversity of prey in the diet of adult common dolphins. Alternatively, this may in fact reflect some increased selectivity for mackerel by pregnant and lactating females, who may be making an energetic gain by targeting a smaller number of larger fish, with a higher calorific content than smaller sardine (10.1kJ/g for mackerel as opposed to 8.6kJ/g for sardine) (Young 1993, Young & Cockcroft 1994). The contribution of squid to the diet of lactating females (4.9% by mass) is surprisingly lower than that of all adult females (6% by mass); a result which is likely to be due to the small sample size, and is not consistent with the results of Young (1993), who found a significantly higher proportion of squid in the diet of lactating females. The lactating females did, however, have a higher contribution of squid than the pregnant females (0.6% by mass). Between 1974 and 1992, pregnant and lactating females were found to prey significantly more on squid than other adult dolphins (Young and Cockcroft 1994). Young and Cockcroft (1994) hypothesized that the high water content may make cephalopod prey a valuable component of the diet during lactation. The contribution of sardine in the diet of pregnant and lactating female common dolphins is identical to that of all adult females (10% by mass). The remainder of the diet of pregnant females was made up of *Bregmaceros* sp. and *Diaphus* sp., whilst the remainder of the diet of lactating females was comprised of maasbanker (*Trachurus delagoa*). Brophy *et al*. (2009) suggested that migration into deeper waters to prey on myctophids (rich in lipid content) may also be a strategy employed by females needing to produce milk for suckling calves.

Ontogenetic dietary variation

Whilst Young (1993) found evidence of resource partitioning between adults, juveniles and calves, this result is not corroborated by the present study (Figure 2.9). However, the lack of differentiation between the diets of different ontogenetic stages in this study may be a result of the considerably smaller sample size of juveniles and calves, when compared to the previous study. The results of this study seem to show that juveniles feed within the main pod, preying on the same suite of pelagic fish species, and that calves feed in close association with their mothers, taking sardine and small mackerel as prey items.

All calves < 175cm in total body length had evidence of milk remains in their stomachs, whilst those over 180cm had all started to take fish or cephalopod prey. Therefore it seems weaning is likely to take place during the sardine run, and when calves are near to 180cm in body length, and around 60kg body weight. The onset of the consumption of solid food is thought to occur between the ages of 3 and 6 months in common dolphin calves

(Brophy *et al.* 2009). During this study, the calves generally fed on a higher proportion of cephalopod prey (9.51% by mass) than the adults or juveniles (4.1% and 6.9% by mass respectively). Calves may consume a higher percentage of cephalopod prey because they are feeding in close association with their mothers. Females may still be targeting squid prey because of its higher water content, before having fully weaned their calves (Young 1993). Calf preference for squid may simply be a learned behaviour due to mimicking the foraging strategies of their mothers (Young 1993). Despite the proportion of squid in the diet of calves being higher than that of adults or juveniles, it still constituted < 10% of the total diet. Indeed, the vast majority of the diet of the calves was similar to that of the adults, suggesting that most of the calves caught were already weaned. Only five of the 20 calves in this sample had stomachs containing only milk remains, and were therefore pre-weaning. Young (1993) found that the diet of calves was more similar to that of non-lactating females than lactating females, suggesting that calves may be foraging in “nursery’ groups with sub-adult females, whilst the lactating females join the more intense feeding activity of the main pod. According to the results of this study, it would seem that cows and calves forage separately, often on slightly different prey.

Trends in diet diversity and prey availability

Although common dolphins are generally reported to prey on small, pelagic shoaling fish species (Sekiguchi *et al.* 1992, Young & Cockcroft 1994, Meynier *et al.* 2008 (a,b)), those in KwaZulu-Natal actually exhibit predation on much larger, sometimes predatory fish species including chub mackerel, elf and maasbanker. Sekiguchi *et al.* (1992) report that the diet of common dolphins along the West Coast of South Africa consisted entirely of small fish species such as anchovies and myctophids. It seems the reason for predation on larger fish species in KwaZulu-Natal is the winter migratory patterns of these larger fish species, some of which may use the sardine run as a source of prey as well. Several studies have documented seasonal variations in the diet of common dolphins (Collet 1981, Desportes 1985, Young 1993, Santos *et al.* 2004, Brophy *et al.* 2009). The annual sardine run 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.

Seasonal variation in the contributions of different prey to the diet of common dolphins is a common occurrence throughout their distribution range (Young & Cockcroft 1994, Meynier *et al*. 2008 (a), Brophy *et al.* 2009). Since common dolphins feed opportunistically, their diet is representative of the shoaling characteristics of the most locally-abundant fish and squid prey at any given time (Young & Cockcroft, 1994). The diversity of prey consumed by the long-beaked common dolphin during this investigation increased during the peak sardine run, with sardine not, in fact, forming a significant proportion of the diet (5% by mass). This observation can probably be attributed to the increased incidence of predatory fish attracted to the region in response to the large shoals of sardine. Species such as mackerel, elf, maasbanker and strepie also migrate into KwaZulu-Natal during winter to spawn (van der Elst 1995, Heemstra & Heemstra 2004). 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). Surprisingly, 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 (10.1kJ/g for mackerel, and 8.6kJ/g for sardine) (Young 1993). The vast majority of the winter diet in all years consists of energy-rich fish (mackerel and sardine); a factor which is likely to make this annual long-distance migration into KwaZulu-Natal energetically beneficial. The co-operative hunting tactics employed by common dolphins, whereby some members of the group constantly herd fish into a baitball, whilst other members feed on them, is likely to be energetically expensive, and hence more viable if calorie-rich prey are targeted (Meynier *et al*. 2008 (a)). According to optimal foraging theory (MacArthur & 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 maximise their energy intake rate. Due to the spatial heterogeneity of food resources, 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 (1993) reported that in certain years the proportions of fish and squid in the diet of the common dolphins fluctuates, with squid on occasion forming up to 60% of the total prey weight consumed. The increased incidence of squid in the diet of the dolphins was presumably due to a huge increase in the biomass of squid prey available to the common dolphins in that year in KwaZulu-Natal (Young 1993). During this study, however, squid always constituted a minor component of the prey weight consumed by the common dolphin (<20% by mass), possibly indicating that this prey species is now less abundant in the area along the KwaZulu-Natal coastline in which the dolphins are feeding.

During the years 2000 to 2009, it is apparent that the prey species composition of the diet of the long-beaked common dolphin changed very little, despite interannual and seasonal fluctuations in the proportion of each species to the diet. This pattern was also observed by Young (1993) between 1974 and 1992, although both studies found inter-annual fluctuations in diet composition, which are likely related to fluctuations in prey species availability. The predominance of mackerel in the diet of the common dolphins caught between 2000 and 2009 may also be influenced by the time period at which these animals were caught. During this decade, only 28 dolphins were caught during the peak of the sardine run (June and July), with the majority of catches occurring directly after the sardine run (August, September and October). This pattern of catches occurring predominantly after the period of peak influence of the sardine run is largely due to the new management strategy of the KwaZulu-Natal Sharks Board, whereby the anti-shark nets are raised during the peak of the annual sardine run in order to minimize the by-catch of cetaceans. It is unlikely that the temporal bias in dolphin catches would affect the overall abundance of mackerel and sardine in the diet when results are pooled for the whole catch period. This sampling bias will be further discussed in Chapter 3.

Chapter 3

Historical patterns in the feeding ecology and body condition of the long-beaked common dolphin off KwaZulu-Natal

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Introduction

The ecological role of long-lived, large marine mammal species in marine ecosystems is still poorly understood (Bowen 1997). Long-beaked common dolphins are long-lived mammals, with slow reproduction, and diets which are adaptable and reflective of local and seasonal changes in the suite of available prey species (Dhermain *et al*. 2002, Best 2007; Chapter 2). Assessing their diet over limited time spans may therefore provide little predictive power for the management and protection of the species, and its food resources. Stomach content analysis only provides a snapshot view of the diet, and does not elucidate the long-term feeding habits of marine predators (Lahaye *et al.* 2005). Such long-term dietary data are necessary to gain an understanding of the impacts of climate change, fisheries and environmental degradation, which may operate over longer time frames (Gambaiani *et al.* 2008). To gain a better understanding of the feeding patterns of marine mammal species over longer time frames (e.g. decades), it is necessary to have comparable dietary data sets collected in the same way spanning a number of years or decades. The availability of long-term data on the diet of dolphins is scarce, which makes the specimens collected by the Port Elizabeth Museum over the past four decades invaluable. By comparing the stomach contents of long-beaked common dolphins entangled in the anti-shark nets in KwaZulu-Natal over the past four decades, we are able to obtain unique long-term dietary data for this species along the East Coast of South Africa. In addition to stomach content analyses, a number of additional techniques are available to assess the long-term feeding activities of marine mammals, including fatty acid and stable isotope analyses, and indices of body condition (Walker & Macko 1999, Caon *et al*. 2007, Koopman 2007, Budge *et al.* 2008, Mateo *et al*. 2008).

Stable isotope analysis in marine mammal diet studies

The feeding ecology of cetaceans has traditionally been examined using stomach content analyses. This approach, however, only provides a partial reflection of the food consumed by the animal and fails to consider prey assimilated (Walker & Macko 1999). There are also several sources of error which may result in the over-estimation of certain prey items consumed by the dolphin, as discussed in Chapter 2. The advent of stable isotope analysis has provided a means to study the long-term feeding history of many marine animals (Gorokhova & Hansen 1999, Walker & Macko 1999). In contrast to stomach content analysis, which only reflects prey ingested recently, stable isotope analysis has the potential to provide a record of the nutrients assimilated by the animal over a longer time frame (Michener & Schell 1994, Walker & Macko 1999).

Naturally occurring stable isotope abundances are increasingly being used as tracers to elucidate the cycling of nutrients, carbon, nitrogen and trace elements and identify sources of organic matter and foraging location in ecological studies (Michener & Schell 1994, Gorokhova & Hansen 1999, McKinney *et al*. 2001, Phillips & Gregg 2003). Carbon and nitrogen isotopes are the most commonly used elements in tracing energy flow through food webs (Mateo *et al*. 2008). The ratio between the different isotopes of carbon (^{12}C and ^{13}C) and nitrogen (^{14}N and ^{15}N) in the tissues of organisms closely resembles those of their food sources, with organisms slightly enriched in the heavier isotopes because the lighter isotopes are preferentially used in metabolism (Gorokhova & Hansen 1999). The isotopic composition of any organism depends on its diet, and its position in the food chain. The $\delta^{13}C$ and $\delta\ ^{15}N$ values become more enriched as energy is transferred up the trophic pyramid, with $\delta^{13}C$ and $\delta\ ^{15}N$ values increasing by 1 and 3‰ respectively, between consumers and their food source (Schoeninger & DeNiro 1984). $\delta^{13}C$ signatures can be used to trace the source region of the food, as well as track nutrient flow through the ecosystem (Walker & Macko 1999). Since nitrogen is less abundant than carbon in food sources, a lesser number of metabolic changes are needed before a discernable change in $\delta\ ^{15}N$ signal is seen between the food source and consumer (Walker & Macko 1999). Therefore, $\delta\ ^{15}N$ signatures are more useful in identifying trophic level changes between different species, and documenting the flow of energy through trophic levels (Walker & Macko 1999). Not only are stable isotope analyses useful in food-web studies, but they are also utilized to differentiate between different populations of cetaceans, which feed in different areas. For example, Ohizumi &

Miyazaki (2010) successfully identified offshore and coastal population groups of Dall's porpoises based on differences in their $\delta\ ^{15}N$ and $\delta^{13}C$ isotope ratios, resulting from differences in foraging locality.

The power of stable isotope analysis is that it measures actual assimilation integrated over the time scale of tissue turnover for a particular organism (Michener & Schell 1994). The absolute isotopic values vary among systems depending on the values at the base of the food web (Post 2002). The use of stable isotopes can effectively determine the strength of trophic connections, and thus trace the flow of energy through an ecosystem (Kling *et al*.1992). Due to the differential turnover times of different tissues, isotopic signatures from ingested food sources are incorporated in the body tissues at different rates (Walker & Macko 1999). For this reason, stable isotope analyses of different body organs or tissues will 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 & Macko 1999). Mammalian teeth preserve well and it is possible to use subsamples from each tooth to assess short-term feeding history (Walker & Macko 1999). As a consequence, teeth are often chosen as an ideal tissue for isotopic analyses (Walker & Macko 1999, Niño-Torres *et al*. 2006). Isotopic analysis of individual growth layer groups within the teeth makes it possible to detect changes in diet corresponding to both age of the animal, and fluctuating abundances of prey species over longer time frames (Walker & Macko 1999). Alternatively, using the isotopic signal of the entire tooth will provide an isotopic signature integrated over the animal's entire lifetime, as well as an estimation of trophic position (Walker & Macko 1999, Niño-Torres *et al*. 2006). In essence, stable isotope analyses allow for the determination of feeding patterns between different sexes, age cohorts and geographic regions, as well as long-term dietary shifts within a particular species (Walker & Macko 1999).

Use of blubber thickness as an index of condition

Blubber is one of the most specialised tissues in the body of a marine mammal and performs a variety of functions. It provides insulation and buoyancy in water, assists in the streamlining of body shape, and 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). Blubber is known as a 'biochemically dynamic tissue' (Smith & Worthy 2006), and is of particular importance in cetaceans as it covers almost the entire body, and can make up a significant proportion of the total body mass (Tornero *et al.* 2004, Koopman 2007). Cetacean blubber exhibits a stratified pattern through its depth with an apparent inverse relationship between the intensity of stratification and water temperature (Koopman 2007), but the precise metabolism of fatty acid deposition and withdrawal from the different layers remains poorly understood (Koopman 2007, Smith & Worthy 2006). Blubber thickness can be used as a body condition index (CI) as it 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). Long-term trends in the blubber thickness of Antarctic minke whales (*Balaenoptera bonarensis*) have successfully been employed as an index of change in their diet and their environment (Konishi *et al*. 2008). A long-term trend of declining blubber thickness has been observed in Antarctic minke whales over the past 18 years, possibly due to a decrease in food availability, resulting from increased competition by predators for krill in the Southern Ocean (Konishi *et al*. 2008). Indices of condition which are commonly used are the ratio of blubber mass to body length, the thickness of blubber to body length, and the mass of all the blubber of the animal to its total weight (Ognetov 1990).

Aim

The diet of the common dolphins feeding in the coastal waters of KwaZulu-Natal demonstrates strong inter-annual variability, which likely reflects changes in prey availability (Young 1993; Chapter 2). The spatial and temporal distribution and intensity of the sardine run appear to have changed considerably in recent years, a phenomenon which may have an effect on the winter food resources of the common dolphin in southern African waters. Recent studies indicate a decrease in the intensity of the sardine run between 2002 and 2006, both in terms of sardine presence (O'Donoghue 2009) and sardine egg abundance off the KwaZulu-Natal coast during winter (Connell 2010). 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 cumulative effects in predators may only become apparent over longer time frames.

The aim of this study was to assess the long-term feeding ecology of the long-beaked common dolphins incidentally caught in the anti-shark nets along the KwaZulu-Natal coastline over the past four decades. Data collected during the present study (Chapter 2) will be compared to the results of a similar study conducted by Young and Cockcroft (1994) covering the period 1974 to 1992. Additionally, the δ^{13}C and δ^{15}N isotopic ratios from teeth of *D. capensis* caught in the anti-sharks nets off KwaZulu-Natal over the last 40 years were available from the Port Elizabeth Museum Graham Ross Marine Mammal Collection. These teeth were used to assess whether long-term changes in feeding were reflected in the isotopic signatures of the dentine of the teeth. The long term trends in blubber thickness and blubber total weight records for common dolphins incidentally caught in the anti-shark nets off KwaZulu-Natal dating back to 1970 available from the Port Elizabeth Museum were also assessed. These blubber measurements were used to assess trends in body condition of net-caught common dolphins over the last 40 years.

Materials and Methods

In order to elucidate whether any changes had occurred in the diet of the common dolphins feeding in the waters of KwaZulu-Natal during winter, the data obtained during this study were compared to an 'historical' data set produced during a study which employed identical methodology, and analysed the diet of net-caught common dolphins from KwaZulu-Natal between 1974 and 1992 (Young 1993). One problem which arose was the bias in catch periods of common dolphins between the two studies. During the period in which the 'historical' data were collected, the anti-shark nets were left in the water year-round. Hence animals were caught whenever they moved into the near-shore waters of KwaZulu-Natal. Conversely, during the period over which the current data were collected, the anti-shark nets were being managed differently by the KwaZulu-Natal Sharks Board, in order to reduce the cetacean by-catch associated with the annual sardine run. During the 2000 to 2009 sampling period, the anti-shark nets were lifted from the water, and the beaches closed for swimming, when the first incoming sardine shoals and predator aggregations were observed in the area (Dudley & Cliff 2010). As a consequence, the by-catch of common dolphins was lower during this period, and not all of the dolphins were caught during the peak of the sardine run. However, a lesser number of common dolphins were still caught during June and July (normally the peak sardine run period) during recent years, and therefore it is assumed that the two data sets are still highly comparable.

Stomach content analyses

Stomach contents from 95 common dolphins (55 females, 40 males) caught between 2000 and 2009 (discussed in Chapter 2) were compared to stomach content results obtained by Young (1993) for 297 common dolphins caught in the same area between 1974 and 1992. Between 1974 and 1992, elevated numbers of common dolphins were caught during the peak of the sardine run (June and July), and in the following three months. Conversely, between 2000 and 2009, the majority of catches took place in the months directly after the sardine run (56 dolphins were caught between August and October, and only 28 during June and July). The original data analysed by Young (1993) did not consider temporal patterns in the feeding ecology of common dolphins in relation to the sardine run. Therefore, a subset of the historical data was re-analysed in order to compare the diets of the common dolphins during and after the sardine run.

The otoliths and cephalopod beaks collected during the ‘historical’ study (1974 to 1992) and stored in the Port Elizabeth Museum Marine Mammal Collection we re-analysed and measured as described in Chapter 2. Samples from common dolphins were selected from periods representing catches during the peak sardine run (June and July), directly after the peak of the sardine run (August, September and October) and during other times of the year (any month outside of June to October), with all attempts made to ensure that the two samples had similar demographic and seasonal compositions.

This sub-sample consisted of:

- During the sardine run (June & July): 16 individuals (6 males, 10 females)
- Directly after the sardine run (August, September & October): 19 individuals (6 males, 13 females)
- Other times of the year: 6 individuals (2 males, 4 females)

This sub-sample was used to compare the diet between ‘historical’ (1974 to 1992) and ‘recent’ (2000 to 2009) common dolphin catches, and between the periods inside and outside of the influence of the sardine run. As only one common dolphin was caught outside of the sardine run period (other times of the year) between 2000 and 2009, no comparison was made between ‘historical’ and ‘recent’ dolphin diets for this period.

IRI (Index of Relative Importance) values calculated for the common dolphins in this study (Chapter 2) were added to those reported by Young (1993) in order to represent the variability of the dominant prey species in the diet over the last 30 years.

Fish stock data

In order to relate the changes documented in the diet of the common dolphins to relevant fish stock data, 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 fish stock data for KwaZulu-Natal, egg stock data were used as a proxy for spawner biomass in the area during the period of the sardine run. Sardine and mackerel egg stocks were sampled from the water column over the inshore shelf off of Park Rynie every winter between 1987 and 2009 (Connel 2009, unpublished data). Although egg stock data is not a direct measure of the biomass of these two fish species, it does give an indication of the numbers of the two species moving into the area to spawn. IRI (Index of Relative Importance) values calculated in Chapter 2 for sardine and mackerel in the diet of the common dolphins over the period of this study (2000 to 2009), as well as those presented by Young (1993) for the period 1974 to 1992, were compared to egg stock data for these two species in KwaZulu-Natal over the corresponding years in an attempt to relate the biomass of sardine and mackerel in KwaZulu-Natal waters in winter to the importance of these two species as prey items for the common dolphins.

Stable isotope analysis

Stable isotope analysis was employed as a secondary technique in order to investigate long-term trends in the feeding ecology of common dolphins. Common dolphin teeth accessioned to the Port Elizabeth Museum Graham Ross Marine Mammal Collection from dolphins caught in the anti-shark nets off KwaZulu-Natal since 1980 were used for isotopic analysis. To obtain sufficient material for isotope analysis, 2 or 3 teeth were used per animal. Only teeth from adult animals were selected; males > 220cm, and females > 210cm total body length (Mendolia 1989), ensuring that the pulp cavity was occluded, and that each tooth yielded sufficient dentine for analysis. Dentine is deposited in dolphin teeth throughout the juvenile and early adult life of the dolphin, until the pulp cavity becomes filled (Walker *et al.* 1999). The samples used for this analysis were all from the dentine portion of the tooth. Growth layers (visible in longitudinal sections through teeth) are typically used to age odontocete teeth (Myrick *et al*. 1984). A growth layer group (GLG) consists of a paired band (one hypocalcified and one hypercalcified layer) laid down over the course of a year (IWC Special Issue 3 1980, Hohn 1980). These bands are visible in stained sections (see Figure 3.2). Over time the central pulp cavity of the tooth becomes occluded with the growth of successive dentinal layers (See Figure 3.1). The oldest dentine therefore lies adjacent to the enamel (near the outside of the tooth), and the youngest dentine closest to the central pulp cavity. The thickness of each GLG appears to be age-specific; the thickest GLGs being laid down during the first and second years of life, with GLGs becoming successively thinner with advancing age (Myrick *et al*. 1984). The stresses involved in birth, as well as the disruption to the calf's nutrition which occur at birth, leave a visual marker in the tooth called the neonatal line (IWC 1980, Lockyer 1995). After the deposition of the neonatal line has taken place (representing 0 years/birth), the first GLG begins to be laid down (Murphy & Rogan 2006).

The sectioned teeth drilled in this study closely resembled that shown in Figure 3.2 for a mature short-beaked common dolphin, *Delphinus delphis*. The neonatal line was visually apparent in sectioned teeth in this study. The GLGs formed during the neonatal phase, and during suckling were excluded from the sample because δ^{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 3rd GLG inwards (post-natal dentine) was drilled out (see Figure 3.2). This was done by drilling from the centre of the tooth outwards, and ceasing drilling roughly 0.5mm from the neonatal line. By excluding the pre-weaning GLGs and the cementum, the integrated feeding signal for the entire life of the dolphin, post-suckling is obtained (Niño-Torres *et al*. 2006). The cementum layer was also avoided during drilling as it was particularly thin, and drilling into it may have led to the inclusion of some material from the layers of dentine laid down during suckling.

A total of 16 adult animals were selected (7 males, 9 females), 8 of which represented the 'historical' animals (caught between 1980 and 1992), and 8 of which represented the 'recent' animals (caught between 2000 and 2008). These two categories were selected in order to ascertain whether a shift in trophic-level feeding had occurred over the last three decades. Teeth had been stored in two different ways by the Museum; either cleaned by maceration and then stored dry, or left in a small section of gum and stored in propanol in glass vials. 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 small paper wedges to lift the tip of the tooth if necessary). The mounting medium employed was PEG (polyethylene glycol 4000 – Merck) in crystalline form. The PEG was melted in a small glass beaker on a hot plate, after which a small drop was used to mount the tooth on the glass slide. Mounts were left to set at room temperature in a well-ventilated space for approximately 3 hours. Those teeth stored in propanol were dissected from the gum and the residual tissue removed with a scalpel. The teeth were then rinsed in distilled water and left to dry for at least 48 hours before mounting, to ensure any remaining propanol had evaporated. Once securely mounted, each tooth was sectioned longitudinally using a Buehler Isomet Low Speed saw in the Geology Department, Rhodes University. The tooth sections were then freed from the slide and remaining PEG medium by submerging them in hot distilled water in a glass beaker. Once free of PEG the tooth halves were dried on blotting paper and stored in Eppendorf tubes.

Each sectioned tooth was carefully clamped in a drill-bit head held in a retort stand. The innermost portion of the tooth was then carefully drilled out using an electric dental technicians drill, with care being taken to avoid the cementum, neonatal and pre-weaning layers. Tooth powder was collected in foil cups placed below the mounted tooth, and stored in Eppendorf tubes prior to decalcification.

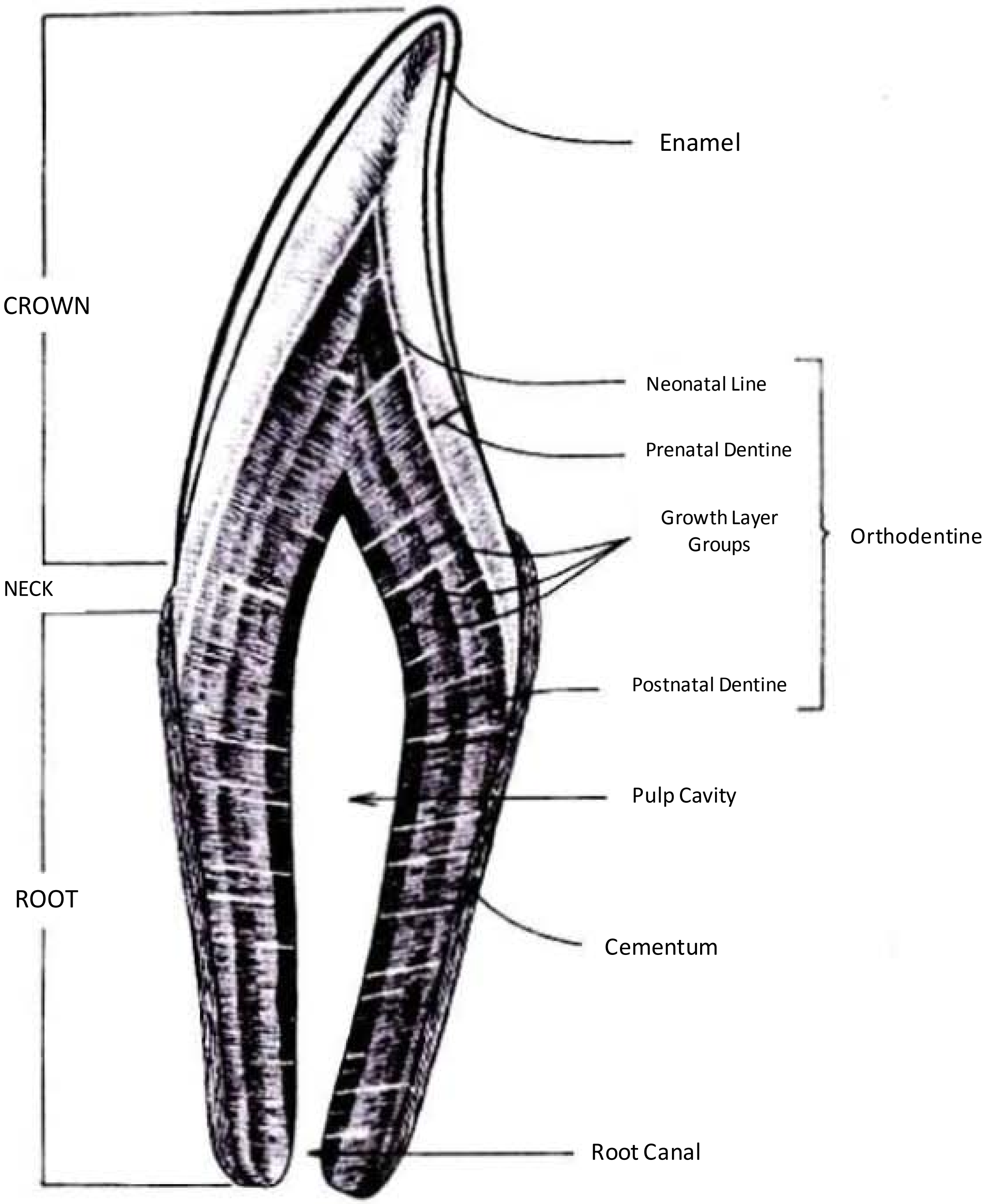

Figure 3.1 Diagrammatic representation of a longitudinal section through a dolphin tooth (after IWC Special Issue 3, 1980)

Figure 3.2 Section through the tooth of a mature common dolphin (*Delphinus delphis*) showing growth layer groups (GLGs). Numbering corresponds to the age in years of the dolphin when the GLG was laid down. 'n' denotes the clear band which forms the neonatal line. This specimen was a 15.5 year old individual which measured 219cm in total body length. Source: Murphy & Rogan (2006)

Decalcification, or acid washing, is a commonly-used procedure employed to eliminate the role of inorganic C in biasing the $\delta^{13}C$ isotopic signatures of organic tissues prior to analysis (Hobson & Welch 1992, Mateo *et al*. 2008). Inorganic (non-dietary) carbon, usually in the form of carbonates, is in comparison to other body tissues, highly enriched in the heavier isotope (^{13}C), and this enrichment introduces a source of bias when bulk samples are analysed for carbon isotopic signal (Mateo *et al*. 2008). To minimize this potential source of error, the inorganic carbonate portions of samples are usually decalcified using an acid wash prior to the stable isotope analyses being conducted. The end result of decalcification/acidification is a lighter $\delta^{13}C$ signature (Mateo *et al*. 2008), which may also introduce bias into results if decalcified samples are being compared to untreated samples. However, if this procedure is conducted systematically on all of the samples in a study (as it was here), the slightly lighter $\delta^{13}C$ will be a feature of all samples, thus ensuring they are still comparable.

The tooth powder was decalcified using 1ml of 1M HCl which was added to each Eppendorf tube. Tubes were closed, shaken for 1 minute, and then left open for 2 hours whilst effervescence took place. After 2 hours, the tubes were closed, shaken again and then centrifuged at 12 000rpm for 2 minutes to ensure that decalcified tooth material formed a pellet. Excess HCl was then 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 000rpm for a further 2 minutes. 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 in the Botany Department, 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 standards IAEA-CH-6 and IAEA-N-1. Based on replicate analyses of samples and standards, the precision levels for $\delta^{13}C$ and $\delta^{1}5N$ for this instrument are 0.10‰ and 0.16‰ respectively. Tooth samples were analysed in duplicate, and the resulting values averaged for each animal.

Blubber thickness records

Historical blubber thickness records were available from the Port Elizabeth Museum Graham Ross Marine Mammal Collection. During the dissection of net-caught common dolphins, blubber thickness was measured at three different points (mid dorsal, mid lateral and mid ventral, in a line just anterior to the dorsal fin) to the nearest 0.1mm using Vernier callipers for each individual animal. Protocols for measuring blubber thickness appear to have changed little since the 1970's, and as a consequence, three measurements are routinely taken along the girth of each animal in accordance with standard dissection techniques employed by the Port Elizabeth Museum. Several studies indicate that blubber thickness should be measured at more than one site on the body of cetaceans, as the distribution of blubber is known to vary according to its function in particular body zones, and is rarely distributed uniformly over the entire body of the animal (Koopman 1998, Evans *et al*. 2003, Dunkin *et al*. 2005). Blubber deposited around the girth (thoracic and abdominal region) appears to be utilised for thermoregulatory purposes, as well as for energy storage, whilst blubber in posterior regions of the body appears to function more in streamlining the peduncle (Koopman 1998). Koopman (1998) states that blubber thickness measurements taken as condition factors should be measured in areas where they are likely to differ most; between the posterior insertion of the flipper and the posterior edge of the dorsal fin, and consequently measurements taken near to or along the girth should reflect most of this variation.

In this study, blubber thickness measurements were taken in order to assess body condition (in terms of stored energy reserves) (Ognetov 1990). Blubber thickness can be used as a condition index (CI) as it represents the stored energy reserves of the animal, and its thickness decreases in times of illness, lactation or starvation, and also changes according to age, sex and season, and may increase during pregnancy due to the energy reserve needed during lactation (Ognetov 1990, Caon *et al*. 2007, Konishi *et al*. 2008). Indices of condition which are commonly used are the ratio of body mass to body length, the thickness of blubber to body length, and the mass of all the blubber of the animal to its total weight (Ognetov 1990). This long-term data set of blubber thickness measurements available from the Port Elizabeth Museum allowed for the calculation of a body condition index (blubber thickness as a percentage of body length) for common dolphins spanning the last 40 years. Also available from the Port Elizabeth Museum were records for blubber total weight for 185 dolphins (84 females and 101 males) caught in the anti-shark nets between 1970 and 2000. Blubber total weight was expressed as a percentage of body weight, and used as an additional indicator of body condition.

Statistical analyses

Dietary differences and stable isotope ratios between the two data sets were assessed using the software packages STATISTICA v. 9.0 (StatSoft Inc.), PRIMER v. 6.0 (Clarke 1993), CANOCO v. 4.5 (ter Braak & Šmilauer 2002), Microsoft Excel 2007 and SigmaPlot v.10.0 (Systat Software Inc.). All age groups were pooled to assess the complete diet of the common dolphins. 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 sub-sample 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 if 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 they belong to. Therefore, the distance between two data point 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 & Šmilauer 2002). T-tests were performed on isotope data 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. 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).

Results

Dietary comparison from stomach contents

The species composition of the diet within the two time periods was 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 differed substantially between the two data sets (Figure 3.3 A and B). Between 1974 and 1992 sardine contributed significantly more (by mass) to the total diet of the common dolphin (T-test P<0.005, N = 297) than chub mackerel. Conversely, significantly more chub mackerel than sardine was recorded in the diet of the dolphins between 2000 and 2009 (T-test P<0.001, N = 95). Additionally, the contribution of Strepie (*Sarpa salpa*) to the diet of the common dolphin fell from 8% of the diet by mass between 1974 and 1992 to 0.8% over the last decade.

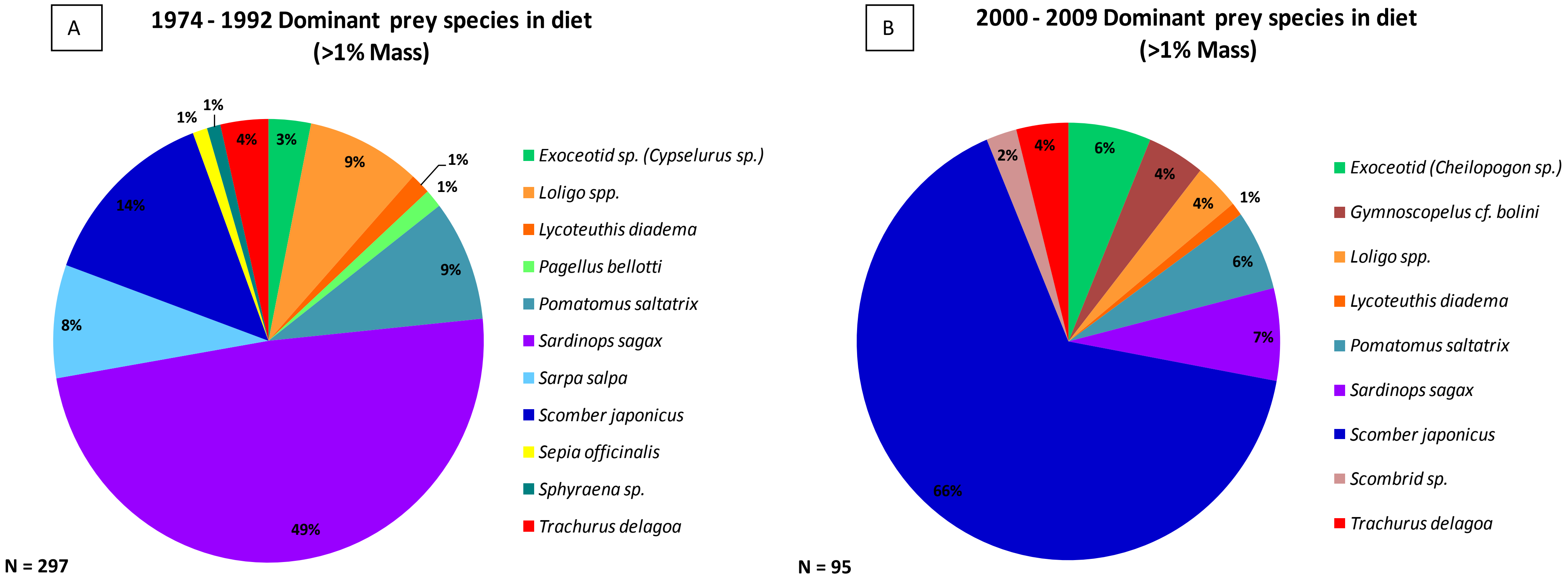

Figure 3.3 Comparison of the diet of *D. capensis* incidentally caught in anti-shark nets off the coast of KwaZulu-Natal over the periods 1974 to1992, and 2000 to 2009 (N = 95)

*The family *Exocoetidae* has been used to refer to *Cheilopogon* sp. (flying fish) in this study, and to what was identified as *Cypselurus sp*. in that of Young (1993).

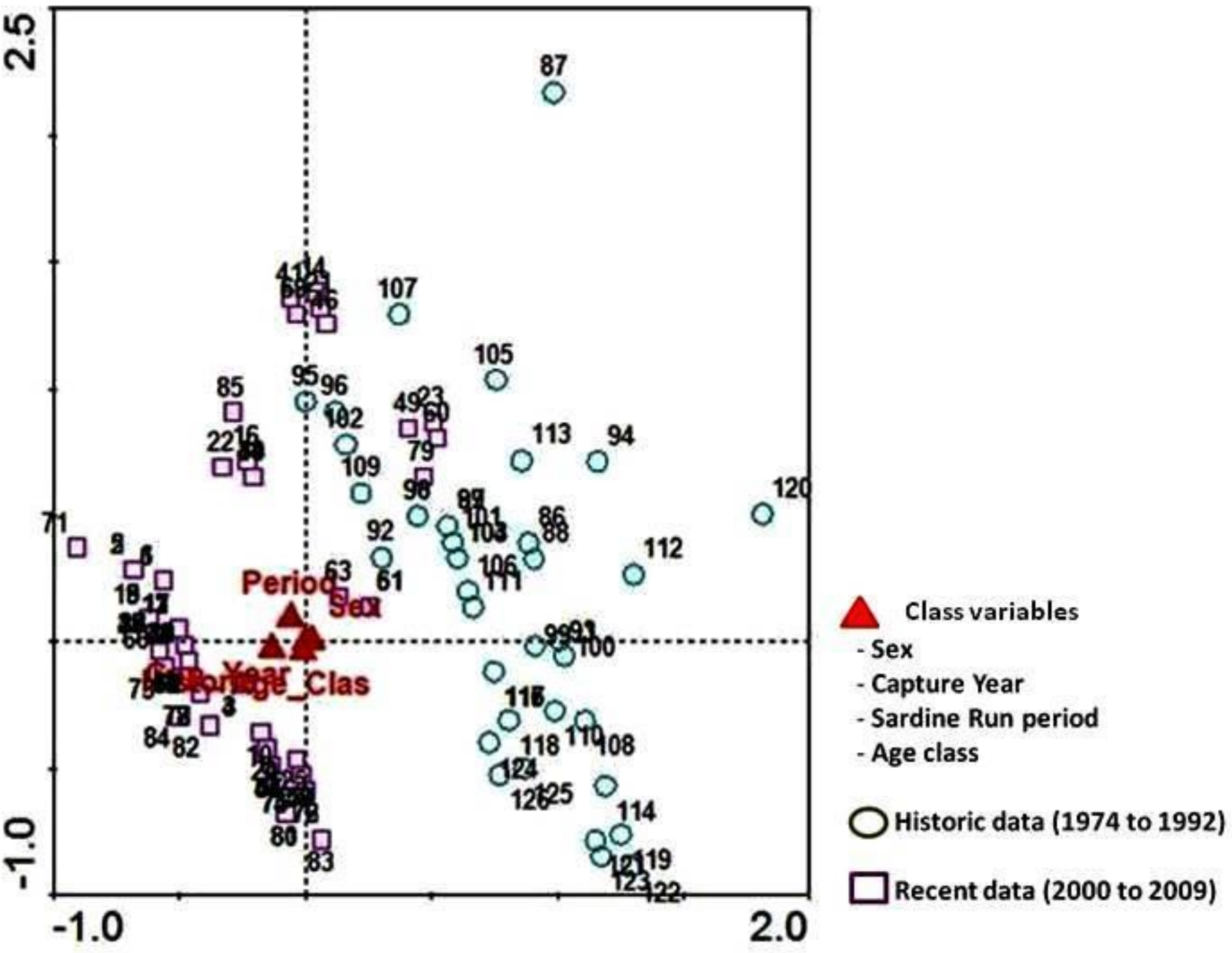

Figure 3.4 Canonical correspondence ordination of historical and recent dietary data for *D. capensis* incidentally caught in anti-shark nets along the coastline of KwaZulu-Natal

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 (Figure 3.4). 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) was particularly dominant in separating the groups (they all fell close to the origin).

In order to assess if the dietary shift observed for the common dolphin over the period 1974 to 2009 was due to biased sampling periods, the diet of the dolphins was separated into three time periods; during the sardine run (June & July), directly after the sardine run (August, September and October) and other times of the year (Figures 3.5, 3.6 and 3.7 below). When examining the trends in diet diversity between dolphins caught during, and directly after the sardine run, different patterns weree evident for the two study periods (Figures 3.5 and 3.6) Between 1974 and 1992, the diversity of the diet of the common dolphins caught during the sardine run was low. In total 12 species were present in the diet although sardine accounted for the bulk of the total diet (64% by mass). Directly after the sardine run, the diet included 15 prey species, with a range of other fish species increasing in their importance in the diet (Figures 3.5 A and 3.4 6). Most noticeably during this period, the proportion of sardine declined from 64% to 42% by mass, with a concurrent increase in the importance of chub mackerel (from 3% to 19%) and elf (from 4% to 13%) in the diet after the sardine run. A very different trend in the diets of common dolphins was observed over the past decade (Figures 3.5 B and 3.6 B). Between 2000 and 2009, the diet was most diverse during the sardine run, consisting of 24 prey species, and containing similar contributions of mackerel (25%), elf (18%), flying fish (13%) and maasbanker (12%). The diversity of the diet of the common dolphins caught after the peak of the sardine run was lower, comprising 19 species, and exhibited an overall predominance of chub mackerel (75% by mass). There was also a wider suite of prey species forming small contributions (11 species) to the diet during the sardine run over the last decade, than there were between 1974 and 1992 (6 species).

Whilst an ANOSIM analysis did not reveal any significant differences between the diets of dolphins caught during the ‘historical’ (1974 – 1992) and ‘recent’ (2000 – 2009) periods (Global R = 0.156), the SIMPER analysis revealed differences in the diet composition between these two time periods (Table 3.1).

Table 3.16 Average Bray-Curtis similarity between the 'recent' (2000 – 2009) and 'historical' (1974 – 1992) diets of *D. capensis* in KwaZulu-Natal (SIMPER Analysis - Primer v.6)

'Recent' common dolphin diet (2000 – 2009)			
Prey species	**Common name**	**% Contribution**	**Cumulative %**
Scomber japonicus	Chub mackerel	71.77	71.77
Sardinops sagax	Sardine	10.65	82.41
Loligo spp.	Chokka squid	6.41	88.82
Trachurus delagoa	Maasbanker	4.67	93.49
'Historical' common dolphin diet (1974 – 1992)			
Prey species	**Common name**	**% Contribution**	**Cumulative %**
Sardinops sagax	Sardine	51.83	51.83
Loligo spp.	Chokka squid	22.44	74.27
Sarpa salpa	Strepie	12.36	86.63
Scomber japonicus	Chub mackerel	4.84	91.47

Over the period 1974 to 1992, the similarity between the diets of all common dolphins caught in the anti-shark nets along the KwaZulu-Natal coastline was a function of four dominant prey species (sardine, chokka squid, strepie and chub mackerel) (Table 3.1). Over the last decade (2000 to 2009), the suite of dominant prey species is similar, but their relative importance in the diet has changed dramatically, with a shift from sardine being the main component previously, to mackerel dominating the diet in recent years. The diets of common dolphins caught in KwaZulu-Natal over the last decade are dominated by chub mackerel, sardine, chokka squid and maasbanker (Table 3.1).

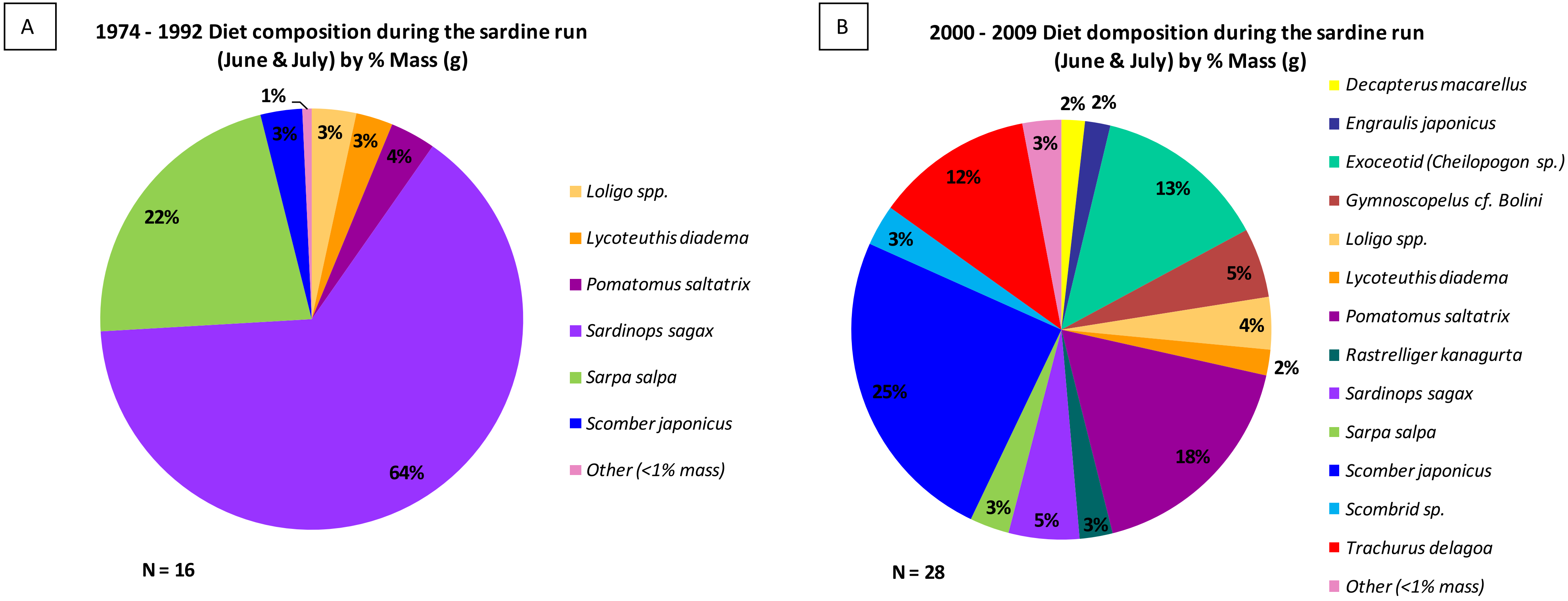

Figure 3.5 Comparison of the diet of *D. capensis* incidentally caught in the anti-shark nets along the KwaZulu-Natal coastline during the sardine run (June and July) between the periods 1974 to 1992 and 2000 to 2009

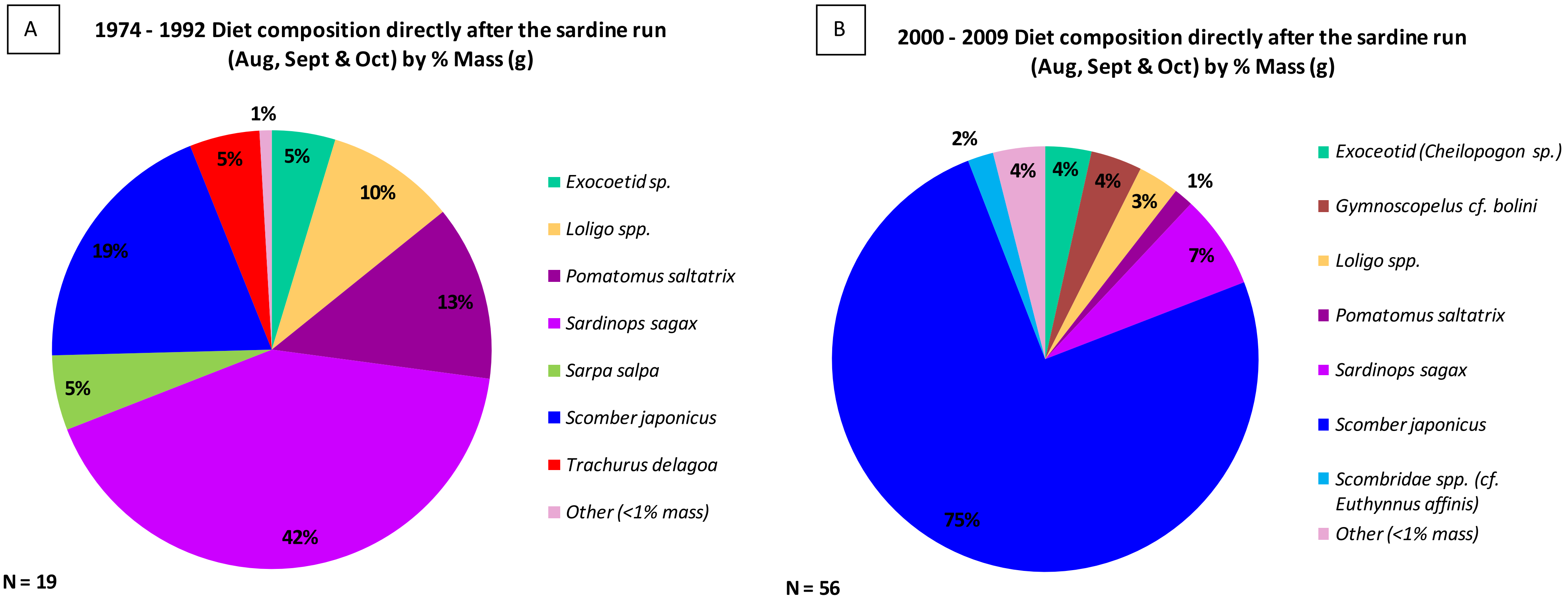

Figure 3.6 Comparison of the diet of *D. capensis* incidentally caught in the anti-shark nets along the KwaZulu-Natal coastline directly after the sardine run (August, September and October) between the periods 1974 to 1992 and 2000 to 2009

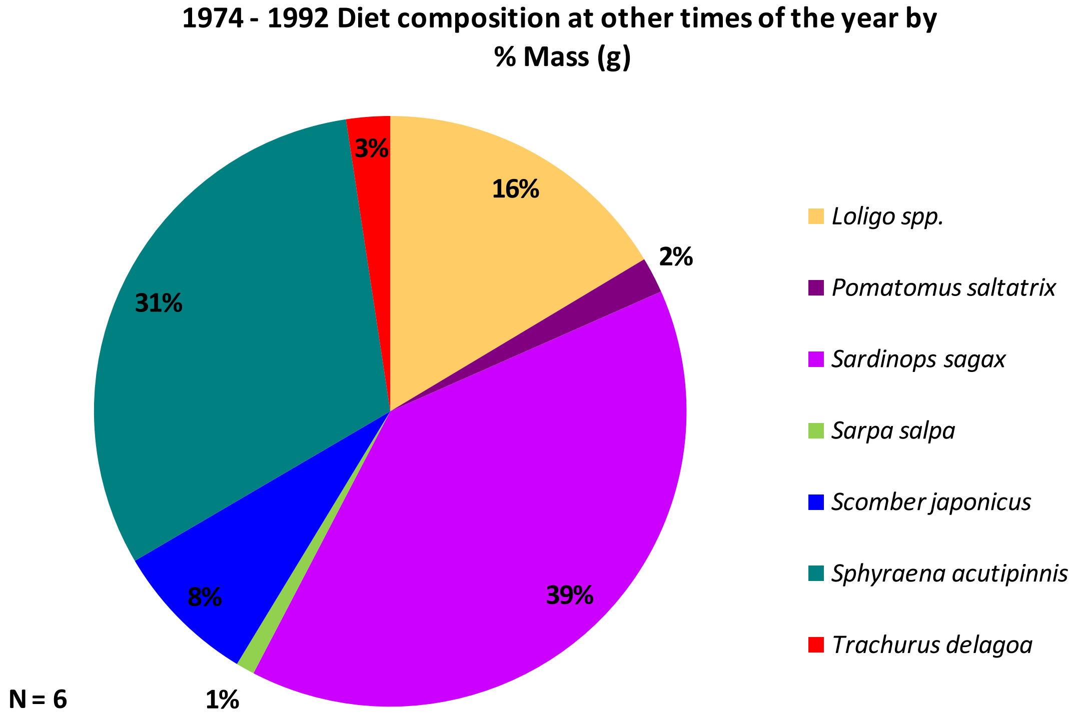

Figure 3.7 Diet composition of *D. capensis* caught in periods outside of the influence of the sardine run between 1972 and 1992 (only historical data shown, as N = 1 for this group between 2000 and 2009)

Common dolphins incidentally caught outside of the influence of the sardine run (Figure 3.7), displayed a diet that was largely comprised of sardines (39% by mass), indicating that sardine stocks were available in KwaZulu-Natal all year round during this period. These dolphins also indicate an important role of sharpfin barracuda (*Sphyraena acutipinnis*) in the diet outside of the sardine run. Chokka 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 (19% by mass) (Figure 3.4 A), but once again forms a much smaller component of the diet in months outside of the influence of the sardine run (8% by mass) (Figure 3.7).

Relating trends in the common dolphin diet to fish stocks

The role of the two dominant prey species (chub mackerel and sardine) in the diet of the common dolphins feeding in KwaZulu-Natal waters was then investigated in relation to long-term trends in fish egg abundance (as a proxy for adult fish biomass) (Figure 3.8).

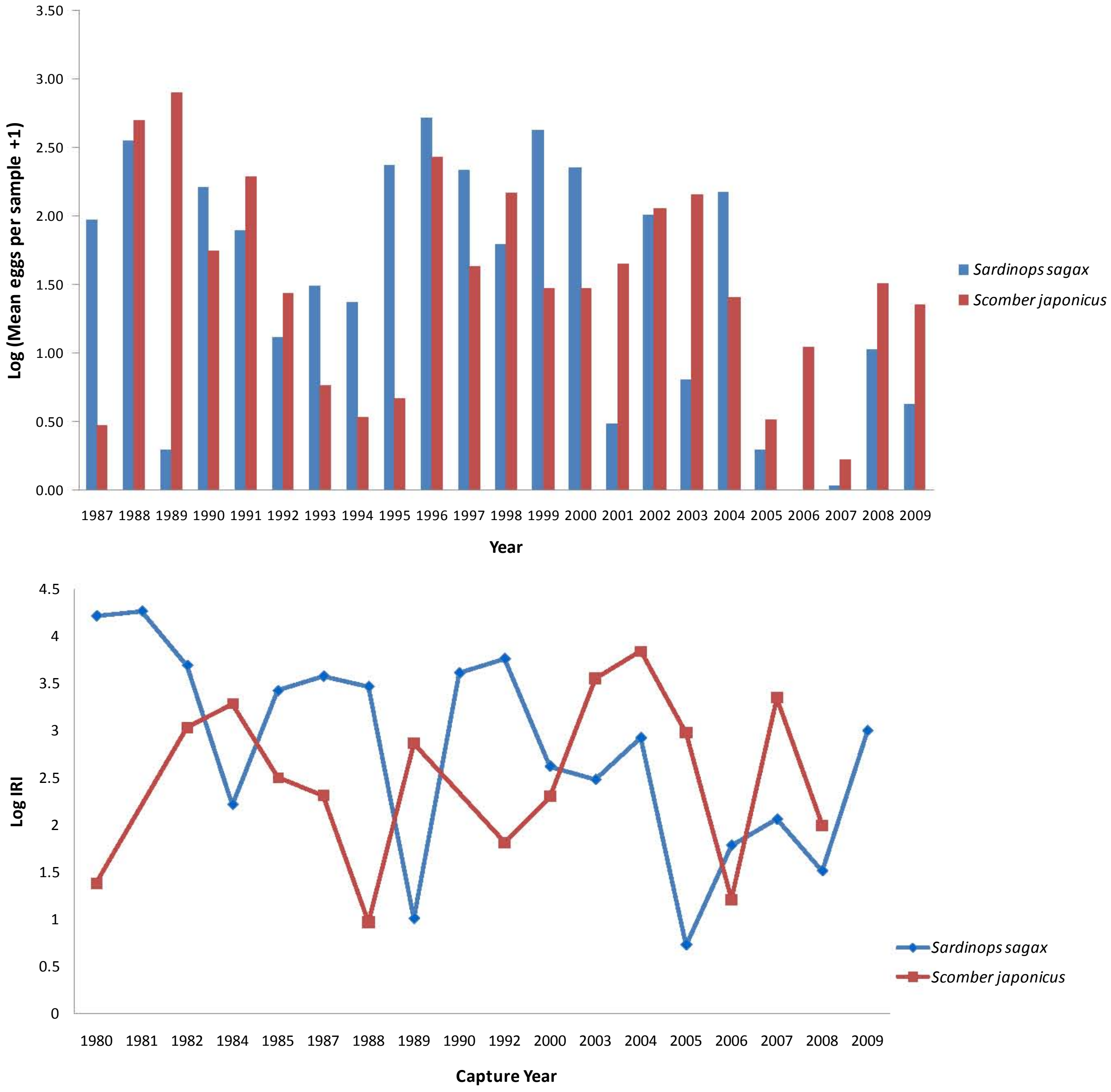

Figure 3.8 Estimates of *Sardinops sagax* (sardine) and *Scomber japonicus* (chub mackerel) egg densities sampled from the water column offshore of Park Rynie, KwaZulu-Natal in mid-winter each year between 1987 and 2009 (Connel 2009, unpublished data), and annual variation in IRI (Index of Relative Importance) values for these two dominant prey species in the diet of *D. capensis* over the periods 1974 to 1992 (Young 1993) and 2000 to 2009.

The estimates of sardine egg abundances in the waters of KwaZulu-Natal were generally equal to or higher than mackerel egg abundances during the 1980's and 1990's. However, from 2001 onwards, a general decline in the sardine numbers was observed, and a corresponding increase in mackerel eggs stocks was seen. During the period 2005 to 2008, sardine egg stocks in the waters off KwaZulu-Natal declined dramatically. Mackerel egg stocks also declined over the same period (notably in 2006 and 2008), however to a much lesser extent. Post-2005, the abundance of mackerel eggs far exceeds that of sardine. The trends observed in both mackerel and sardine egg stocks appear to be paralleled by changes in the IRI values for these two prey species in the diet of the common dolphins in KwaZulu-Natal. 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 except 2006. These parallels signify that the changes observed in the diet of the common dolphins in KwaZulu-Natal may be strongly linked to the size of the stocks of their two most important teleost prey species in KwaZulu-Natal waters.

Natural inter-annual variability in the prey species is a key feature of the diet of the long-beaked common dolphin from KwaZulu-Natal (Young & Cockcroft 1994). As in the study of Young (1993), the results of this study reflect substantial changes in the relative importance of each prey species to the diet between years (Figure 3.9). The long-term trend in the two main prey species during winter (sardine and mackerel), are a gradual decline in sardine importance from the 1980's up until the mid-2000s, with the opposite trend seen in the relative importance of chub mackerel. When long-term trends in the importance of each prey species to the diet are considered (Figure 3.9), 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's and 1990's, 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 to 2009.

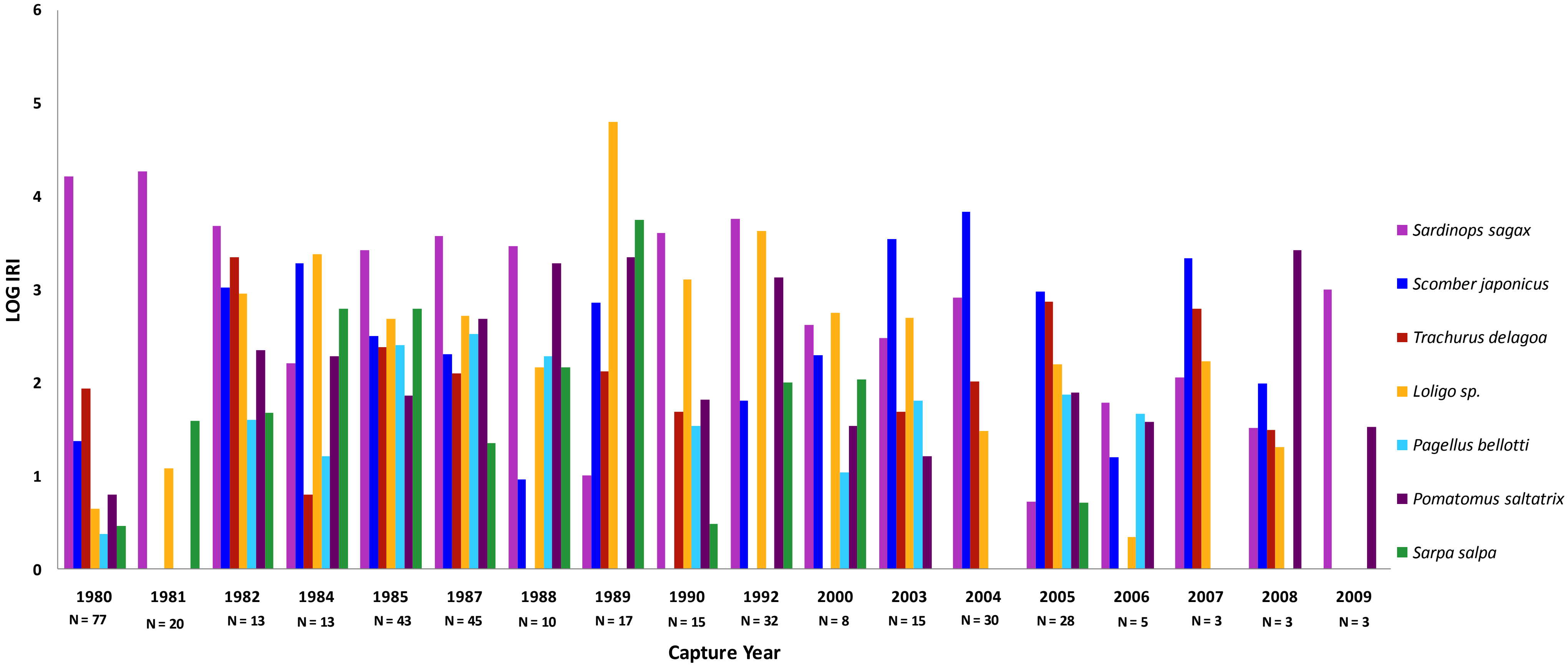

Figure 3.9 Annual variation in LOG IRI (Index of Relative Importance) values for dominant prey species in the diet of *D. capensis* (all age cohorts combined) over the period 1980 – 2009 (including dolphins caught both inside and outside of the sardine run). Only those species contributing >5% of the diet by mass are displayed.

Stable isotope analyses

No significant changes were observed in trophic level feeding of the common dolphins from KwaZulu-Natal waters over the period 1980 to 2008 (Figure 3.10). The average δ^{15}N signature for 'historical' tooth dentine was 13.43 ± 0.7 ‰, whilst that of 'recent' teeth was 13.15 ± 0.3 ‰. The average δ^{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 δ^{15}N, and -13.32 ± 0.6 ‰ for δ^{13}C. No significant difference was found between the δ^{15}N and δ^{13}C isotopic ratios of historical versus recent teeth ($P = 0.575$), with δ^{15}N signatures ranging from 12.59 to 14.57‰ and δ^{13}C signatures ranging from -14.51 to -12.09‰. Likewise, there was no significant difference in either δ^{15}N or δ^{13}C isotopic signals between the male and female common dolphins for which dentine were analysed ($P>0.05$).

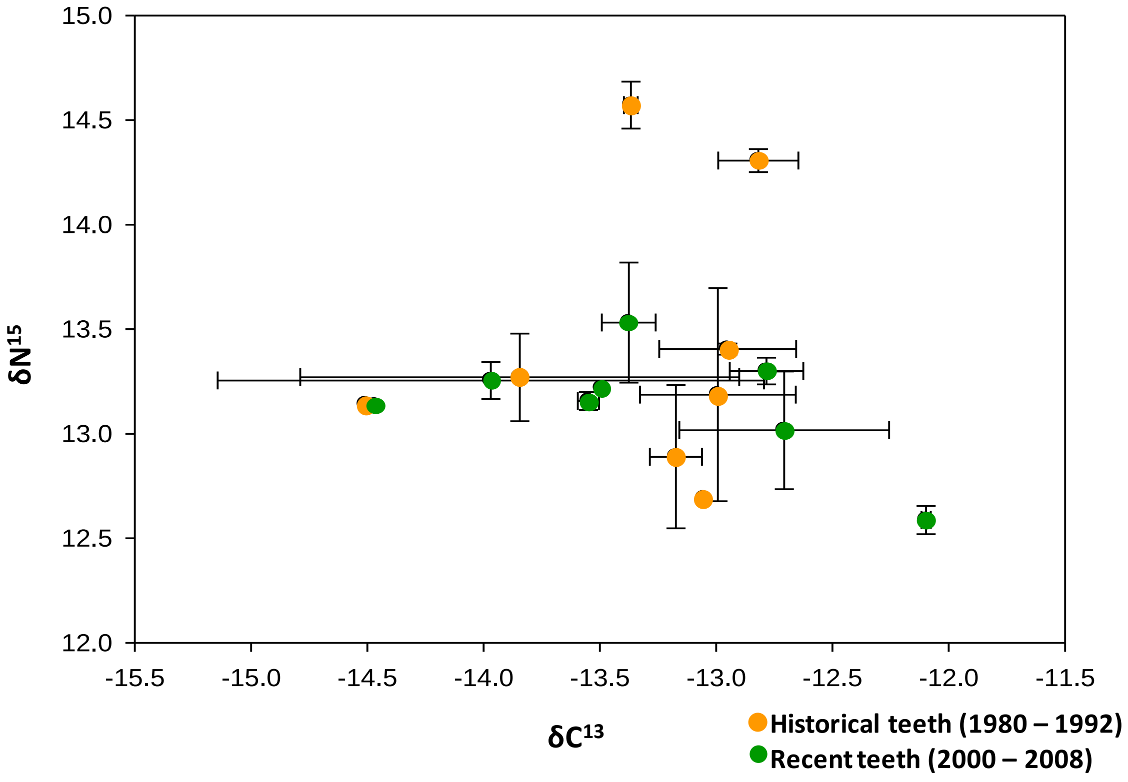

Figure 3.10 Variations in the δN^{15} and δC^{13} isotopic signatures of tissue extracted from the teeth of adult common dolphins incidentally caught in the ant-shark nets along the KwaZulu-Natal coastline over the periods 1980 to 1992 and 2000 to 2008. N = 8 from each period.

Blubber thickness records

Blubber thickness measurements for 78 dolphins dating from 1970 to 2009 were used as a proxy for body condition over the last 40 years.

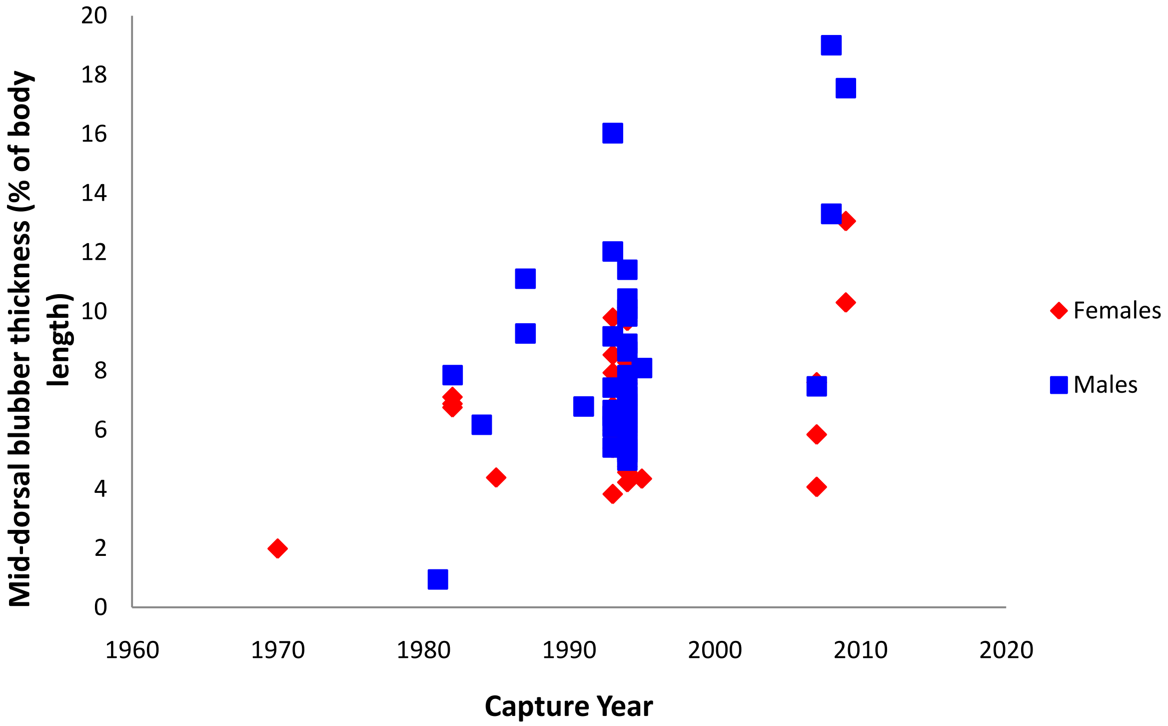

Figure 3.11 Mid-dorsal blubber thickness as a percentage of body length for male and female dolphins caught between 1970 and 2009 ($R^2 = 0.3146$ for males, $R^2 = 0.1034$ for females; $P > 0.05$ in both cases).

Mid-dorsal blubber thickness showed no significant change over the last four decades (Figure 3.11). Similarly, no significant change was observed in blubber thickness at both the mid-lateral and mid-ventral sites ($R^2 = 0.0003$, and $R^2 = 0.0003$ respectively, N = 78). Blubber total weight as a percentage of body weight also showed no significant change over the last 40 years (1970 to 2009) ($R^2 = 0.0016$, N = 185).

Discussion

Diet shift over the last 40 years

During the years 2000 to 2009, it is evident that the overall species composition of the diet of the long-beaked common dolphin changed very little, despite interannual and seasonal fluctuations in the proportion of each prey species to the diet. This pattern was also observed by Young (1993) between the period 1974 and 1992. The most striking difference in the diet composition between the two study periods is that of the most abundant prey species. Between 1974 and 1992 sardine comprised almost half (49% by mass) of the total winter diet of the long-beaked common dolphins in KwaZulu-Natal, whilst more recently, chub mackerel are a far more important component of their diet (66% by mass). Over the period 2000 to 2009, sardine contributed only 7% (by mass) to the total prey consumed by the common dolphin. Chub mackerel importance has risen from only 14% of the diet previously to 66% of the diet over the last decade. Similarly, the contribution of chokka squid to the total diet of the common dolphin has fallen from a mean of 9% previously, to 4% over the last decade. Although the same number of prey species appeared to be consumed over the period of this study, it is evident that the individual percentage contribution of the different species to the diet of the common dolphin has changed in recent years (Figure 3.3).

It is possible that the observed shift in the diet of the common dolphin reflects the new net management policies of the KwaZulu-Natal Sharks Board, whereby nets are removed during peak sardine run activity to reduce cetacean bycatch. The temporal bias in dolphin catches between the two studies was considered as possibly affecting the overall abundance of mackerel and sardine in the diet when results were pooled for the whole catch period, and it was necessary to ensure that data from this study were comparable to those of Young (1993), who analysed data from dolphins caught in the nets mostly during peak sardine run activity between 1974 and 1992. However, when separated into the 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. Although the ANOSIM analysis did not detect any significant differences in dietary composition of common dolphins caught over the last four decade, this is most likely due to the highly similar prey suite consumed between the two time periods. However, when the contribution of each prey species to overall diet is assessed

(SIMPER analysis), it becomes clear that the importance of sardine in the diet has declined, and that of chub mackerel has increased over the last decade. A similar dietary shift was observed in Dall's porpoises (also thought to be opportunistic predators favouring epipelagic foraging) in both the Sea of Japan and the Sea of Okhotsk between the late 1980's and early 1990's (Ohizumi *et al.* 2000). As the stock of Japanese pilchard (*Sardinops melanostictus*) declined, the Dall's porpoise was found to switch to prey predominantly on walleye pollock and Japanese anchovy (Ohizumi *et al.* 2000). This introduction of new prey species to the diet of the Dall's porpoise did not always mirror fluctuations in the catch statistics for these fish stocks in the region (Ohizumi *et al.* 2000).

Decadal changes in winter diet

Patterns in the diet diversity between periods within and outside of the sardine run appear to differ between the two time frames. Between 1974 and 1992, the diversity of the diet was generally low during the sardine run (dominated by sardine), and thereafter increased. The opposite trend was observed over the period 2000 to 2009. During this decade, prey diversity was highest during the sardine run. Young (1993) hypothesized that the increased relative contribution of elf and mackerel during the latter 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 larger predatory fish moving inshore to feed on sardines during this period. The relatively higher diversity of prey found in the diet of the common dolphins in KwaZulu-Natal over the period 2000 to 2009, as opposed to the previous study period, is likely to be a result of the natural variability of this dynamic ecosystem. As in 1992, there is still little information 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 (Young 1993). With the eastward 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 in the following years. Dolphins sampled outside of the winter period of influence of the sardine run between 1974 and 1992 still revealed a high incidence of sardine in the diet. This result is unexpected, given the normal thermal preference of sardine for waters <20˚C. For this reason, dolphins are good environmental indicators, as it is generally thought that sardine stocks have migrated out of KwaZulu-Natal again by the time the sardine run has ended. *Sphyraena acutipinnis* (sharpfin barracuda) makes up one third of the diet outside of the sardine run, and are likely to be locally abundant in the area year-round (Heemstra & Heemstra 2004). Unfortunately, this data cannot be compared with dolphins caught outside of the sardine run between 2000 and 2009, as only one animal was caught during these months within the last decade.

The contribution of *Loligo spp*. (chokka squid) to the diet of the common dolphins in KwaZulu-Natal decreased from 9% of the diet (by mass) between 1974 and 1992, to 4% of the diet over the last decade. This is not a dramatic change in the cephalopod component of the diet, however it could reflect a decline in the availability of squid as a prey item for the common dolphin. The squid fishery located between Plettenberg Bay and Port Elizabeth may impact on the availability of cephalopod prey for common dolphins on the East Coast, as the dolphins target squid of a similar size to that harvested by the commercial fishery (±20cm) (Sauer 1991 In: Young 1993).

Temporal comparison between sardine and mackerel as the dominant prey species

Long-term comparisons between the 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*. 2008). There is a strong spatial bias in the collection of fish stock data from South Africa, with an almost complete absence of data from the East Coast (O’Donoghue 2009). As a consequence, fish egg numbers have been employed as a proxy for prey availability during this investigation. Although egg stocks only function as a rough proxy for fish numbers, they do appear to show some interesting similarities with the IRI values for both sardine and chub mackerel in the diet of the common dolphins. During the 1990’s, sardine egg stocks off Park Rynie, KwaZulu-Natal were relatively high, (especially in the late 1990’s), whilst mackerel egg stocks fell to half that of sardine egg stocks between 1993 and 1995 (Figure 3.8). Sardine egg numbers declined dramatically between 2005 and 2007, whilst mackerel egg numbers increased, and remained at these levels. It is important to note that egg stocks may not be a direct result of the number of sardines moving into the area, as egg numbers are highly dependent on the individual body condition of the fish each year. The IRI values provide a measure of the relative importance of each prey species to the diet of the predator (Young 1993, Young & Cockcroft 1994). During the 1980's and 1990's, sardine IRI values were typically higher than those of the mackerel. However, since 2000 IRI values for mackerel exceeded those for sardine, with exceptions in 2006 and 2009. The fluctuations in the egg stocks (and presumably prey availability) of the two most important prey species for the common dolphin may well explain the recent switch to a predominance of mackerel in the diet during the last decade. O'Donoghue (2009) 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.

A similar trend has also been observed in the diet of sharks caught in the anti-shark nets in KwaZulu-Natal during the annual sardine run. Dudley & 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 & Cliff 2010). Although both shark and common dolphin diet analysis seem 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 beach seine catches of sardine were recorded in 2005, indicating that the shoals were still very 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 characterised by decadal-scale fluctuations in population size (Hutchings *et al.* 2009). Sardine and anchovy stocks appear to fluctuate co-dependently, with the abundance of one stock falling as the other increases. There is almost no pelagic survey data available for chub mackerel stocks in South African waters, but if egg-stocks are a reliable proxy for spawner biomass, then mackerel stocks appear to have been more stable over the last decade than that of sardine. As common dolphins feed opportunistically, the dietary shift observed over the last decade appears to indicate changes in the shoaling characteristics of the most abundant fish prey. Common dolphins may not actively select mackerel over sardine. However, 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. Additionally, because mackerel have a higher calorific value (10.1 kJ/g compared to 8.6kJ/g for sardine) (Young 1993), 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 importance of each prey species to the diet are considered (Figure 3.9), it is apparent that the diet of the common dolphin is extremely variable between years, reflecting their generalist feeding strategy. 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 key feature of their feeding ecology (Young & Cockcroft 1994).

Trophic level

Almost the entire dentinal region of each tooth was used for isotopic analysis in this study. Thus the isotopic ratios recorded represent the integrated feeding over the entire adult life of each dolphin. The deposition of dentin within the tooth is only complete when the pulp cavity is filled (Walker *et al*. 1999, Niño-Torres *et al*. 2006). This process takes many years, and hence the isotopic signatures yielded from the entire central portion of each tooth give an average value for long-term nutrient assimilation (Walker *et al*. 1999). The results of the stable isotope analyses indicate that there have been no significant temporal changes in the stable carbon and nitrogen isotope ratios of common dolphin teeth over the last three decades. Although a significant change was observed in their winter diet during the sardine run over the same time frame, this feeding bout represents only two to three months of their annual diet, and hence is unlikely to be reflected in the isotopic signatures of tissue obtained from their teeth. The isotopic signatures recorded in this study lie close to those reported for common dolphins by Walker and Macko (1999) who gave an average value of 12.4 ± 0.8 for δN^{15} and -14.5 ± 0.3 for δC^{13}, as well as those for inner tooth samples from bottlenose dolphins (16.8 ± 0.2‰ for δN^{15}, and -12.8 ± 0.1‰ for δC^{13}) by Knoff *et al.* (2008).

As in the study by Niño-Torres *et al*. (2006), the close similarity of isotopic signatures for male and female long-beaked common dolphins in this study indicate that both sexes feed on the same food resources, and corroborates the lack of resource partitioning indicated from stomach content results for male and female dolphins in this study (Chapter 2). Whilst stable isotope analysis has proved to be a useful tool in elucidating the trophic functioning of ecosystems around the globe, its interpretations are unfortunately limited to assessments of trophic level, or determinations of the geographic origin of prey species (Samuel & Worthy 2004).

Body condition

The general health and body condition of an animal usually determines its chances of survival and reproductive success, and collectively the survival potential of its population as a whole (Evans *et al.* 2003, Dunkin *et al.* 2005, Caon *et al.* 2007). Indices used to assess body condition reflect how the species copes with environmental stresses, and give a measure of its resilience (Evans *et al.* 2003). In mammals, fluctuations in the stored body fat reserves have serious implications for reproductive success, pregnancy intervals, as well as survival and fecundity (Aguilar & Borrell 1990, Evans *et al.* 2003). Blubber thickness may vary inter-annually with ontogeny, during pregnancy (due to the elevated energy reserves needed to sustain a growing foetus), and also seasonally as a result of food supply and environmental conditions (Dunkin *et al.* 2005, Caon *et al.* 2007). Emaciation dramatically reduces thermal insulation, which can lead to a higher metabolic rate in order to compensate for increased heat loss to the environment, with the combined effect of substantially reducing the dolphin's chances of survival (Dunkin *et al.* 2005). Records of blubber thickness and blubber total weight dating back to 1970 for the common dolphins caught in the anti-shark nets off KwaZulu-Natal reveal no significant trends for male or female animals. Since blubber thickness is used as a proxy for animal condition (Ognetov 1990, Konishi *et al*. 2008), this implies that the body condition and stored fat reserves of the animals have not declined, indicating a relatively healthy population in terms of the dolphins' general condition. Konishi *et al*. (2008) demonstrated that changes in prey availability to cetaceans are reflected in the thickness of their blubber layer. Increased competition for krill with other growing baleen whale populations in the Southern Ocean has been implicated in causing a decline in the body condition of Antarctic minke whales over the past 18 years Konishi *et al*. (2008)

There are, however, certain limitations to using blubber thickness measurements as indices of condition. Whilst blubber thickness is thought to give some measure of the proportional energy reserves of the animal (stored fat), this view may be too simplistic. Cetacean blubber is vertically stratified, and the precise suite of fatty acid components of each layer may change significantly, without resulting in any change in blubber overall depth

(Aguilar & Borrell 1990). The more stable outer stratum provides structural support, whilst the inner layer provides an energy store for rapid mobilisation in times of higher energetic demand (Aguilar & Borrell 1990). Therefore to make accurate assumptions about the general health and body condition of cetaceans, it would be more effective to analyse the chemical composition of the different strata within the blubber (fatty acid profiling). Fatty acid analysis of blubber can provide valuable information about prey type and foraging ecology, based on the knowledge that fatty acid profiles in prey species influence those of their predators, leaving a detectable signal in their stored lipids (Thiemann *et al.* 2004, Thiemann et al. 2008). Some fatty acids from the diet are incorporated into the body tissues of predatory carnivores almost unchanged, allowing us to trace their food sources with a great deal of accuracy (Samuel & Worthy 2004). Future studies of trophic ecology and feeding using by-caught dolphins from South Africa would greatly benefit by combining both stable isotope analyses and fatty acid analysis of blubber lipids, with conventional stomach content analysis, to provide a comprehensive picture of both long and short-term feeding.

Chapter 4

General Discussion

This study aimed to contribute to the available information on the diet of long-beaked common dolphins incidentally caught in anti-shark nets along the East Coast of South Africa. In addition, by combining data obtained during the current investigation with a previous study conducted by Young (1993), long-term patterns in the feeding ecology of long-beaked common dolphins could be assessed. Despite growing evidence that the sardine run has, over the past decade, demonstrated a high degree of unpredictability (O'Donoghue 2009), long-beaked common dolphins have been able to adjust to these fluctuations by switching to other prey species (i.e. chub mackerel). These data confirm the status of the common dolphin both locally and internationally as being an opportunistic predator (Sekiguchi *et al*. 1992, Young & Cockcroft 1994, Das *et al*. 2000, Lauriano *et al*. 2009). Results of both stable isotope and blubber thickness 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. This study has also illustrated the use of a large predator in monitoring environmental change. The changes in the diet of the common dolphin in KwaZulu-Natal over the last ten years correspond well with the variability in the intensity of the sardine run detected by aerial and land-based surveys (O'Donoghue 2009).

Lack of knowledge of the sardine run

The results of the stomach content analyses indicate that chub mackerel formed the dominant component in the diet of long-beaked dolphins over the period 2000 to 2009 (chapter 2). This result is in stark contrast to the study by Young (1993), where sardines were the main prey item consumed by the dolphins between 1974 and 1992. It is suggested that the switch in the main prey items consumed by long-beaked dolphins during winter reflects variations in the strength and timing of the annual sardine run.

Despite the sardine run being the most significant biological event on South Africa's East Coast, and a key event in the feeding ecology and migration patterns of a number of marine predators within the subregion, our current knowledge of its precise environmental controls is notably scarce (Young & Cockcroft 1994, Dudley & Cliff 2010, O'Donoghue *et al.* 2010 (b)). Whilst some progress has been made in determining the environmental parameters which facilitate the movement of sardine shoals up the East Coast (O'Donoghue *et al.* 2010 (a)), very little scientific study has been devoted to understanding the movements and feeding ecology of the predators associated with the sardine run. The paucity of fish stock data from South Africa's East Coast (due mostly to the prohibitive costs of hydroacoustic cruises) (Coetzee *et al*. 2010), means that no accurate assessment exists of the biomass of sardine moving into KwaZulu-Natal waters each winter. Some attempts have been made to estimate the intensity of the sardine run over previous decades, but these have been of little value as they were based on estimates of beach-seine landings (van der Lingen *et al.* 2010). Even in years where no sardines were netted, large shoals of sardine were reported offshore, making beach catches a poor indicator of the strength of the run (van der Lingen *et al.* 2010).

Prior to 2005, only three hydroacoustic cruises had been conducted to assess the sardine abundance off the east coast (in 1986, 1987 and 1990) (Coetzee *et al.* 2010). Unfortunately these surveys were conducted outside periods of peak sardine abundance, and therefore fail to provide accurate estimates of the biomass of sardine associated with the winter sardine run (O'Donoghue 2009). Furthermore, it is unlikely that hydroacoustic surveys to assess the biomass of sardine moving up the coast will take place in the near future, due to the unpredictable timing of the sardine run (O'Donoghue 2009). This lack of scientific study of the intensity and timing of the sardine run has so far been considered unimportant, due to the belief that the sardine run does not involve a significant component of the sardine stock in South African waters (Coetzee *et al*. 2010, Armstrong *et al.* 1991). The main fisheries for sardine are situated on the West and South Coasts, and hence hydroacoustic surveys to estimate the abundance of sardine and other small pelagic fish have been concentrated in these regions (Coetzee *et al*. 2010). The South African sardine stocks have gone through both a collapse (in the 1960's) as a result of high fishing pressure, and a recovery period (between the mid 1990's and 2003) (Coetzee *et al*. 2010). Despite missing the peak sardine run period, the hydroacoustic surveys conducted in 1986 and 1987 estimated sardine biomass on the East Coast at around 30 000 tonnes, during the period of decline in the stock (Coetzee *et al*. 2010).

Although sardine stocks are currently estimated at being similar to pre-collapse levels, the majority of the stock has also undergone an eastward shift towards the South Coast Agulhas Bank area (Fairweather *et al*. 2006, Coetzee *et al*. 2010), indicating some degree of instability in the stock of this highly exploited species. The fluctuations in the South and West Coast sardine stocks do not appear to have had any dramatic impact on the beach seine catches of sardine during the annual sardine run along the south coast, with these catches remaining small each year (between 0 and 700 tonnes) (van der Lingen *et al.* 2010). Given the eastward shift in the sardine population (onto the South Coast) in recent years, Armstrong *et al.* (1991) hypothesized a strengthened sardine run, with higher numbers of sardine moving up the East Coast in Winter. To test this hypothesis, and explore further parameters which may control the movement of sardine into the waters of KwaZulu-Natal, a dedicated research survey was conducted to the region in 2005. The results indicated that despite the bulk movement of the sardine stock into the waters off the South Coast, there had been no increase in the biomass of sardine migrating into the waters of KwaZulu-Natal during winter (an estimated 30 000 tonnes, very close to the previous three estimates). In fact, <11% of the total sardine biomass in South African waters is found on the East Coast during winter (Coetzee *et al*. 2010). Hence it would appear that the strength of the annual sardine run is not related to the size of the stock population on the Agulhas Bank (Hutchings *et al.* 2010).

Another factor possibly affecting the availability of sardine in KwaZulu-Natal during winter is climatic fluctuations. Oceanographic conditions are believed to be the primary driver for triggering the annual sardine run (Crawford *et al.* 2008, O'Donoghue 2009). The migration of sardine up the east coast only occurs when sea-surface temperatures drop below 20˚C (Peschak 2005). Currently, we have very little understanding of how sardine migration patterns may be changing in response to global climate change. To date, most of the knowledge of sardine distribution and the timing of the arrival of these shoals are based on studying the feeding ecology of their predators (e.g. sharks (Dudley & Cliff 2010) and flying seabirds O'Donoghue *et al.* 2010 (b)), as well as recorded data from line fishermen and beach-seine netters (Coetzee *et al*. 2010, Fennessy *et al*. 2010). The long-term recording of ichthyoplankton densities off Park Rynie has provided the most valuable data series to estimate the abundance, and timing of sardine shoals in KwaZulu-Natal waters (using sardine eggs as a proxy for adult spawners) (Connel 2001, O'Donoghue 2009). As useful as this data set may be, it still remains only a proxy for sardine abundance, and it is clear that accurate recording of the timing, intensity and spatial extent of the sardine run is imperative in future years. It must also be stressed that the sardine run does not only comprise the movement of sardine, but also of anchovy, red-eye and east and west-coast round herring, as well as other predatory fish species (van der Lingen *et al.* 2010). The proportional contribution of each of these teleost species to the total biomass of fish moving up the coastline is likely to be highly variable between years. Not only does the sardine run support a range of tourism-based activities, such as boat-based whale-watching and baitball diving, but it also presents a welcome injection of funds into the local community once a year, through beach-seine catches of sardine, and as well as excellent line-fishing for game fish species which follow sardine shoals into KwaZulu-Natal at this time of year (Dicken 2010, Myeza *et al.* 2010). The sardine run is of great importance to the ecology of the east coast of South Africa, and hence it is vitally important that research be conducted on the possible impacts of a weakening of the sardine run on region's marine ecosystems (O'Donoghue 2009).

Climate change and its influence on the sardine run

The annual sardine run takes place when a plume of cold water is pushed up the East Coast by winter storm fronts (Peschak 2005). The arrival of the sardines in KwaZulu-Natal is dependent on a significant drop in SST (to below 21˚C), which usually occurs between May and June each year (O'Donoghue 2009). O'Donoghue (2009) found an inverse and highly significant influence of sea surface temperature on sardine presence in the waters of KwaZulu-Natal. Variability in sardine presence has increased over the last decade, with the lowest sardine abundances being observed between 2002 and 2006 (O'Donoghue 2009). In addition, sardines are failing to reach the KwaZulu-Natal coast more often in recent years (O'Donoghue 2009). This increased unpredictability, and decline in sardine stocks along the East Coast in winter over the last decade is corroborated by the reduced number of sardine eggs found in the water column off Park Rynie over the same period (Connell 2007). O'Donoghue *et al.* (2010 (a)) found that the presence of sardine in KwaZulu-Natal demonstrated significant interannual variability between 2002 and 2006, a result which had not been seen prior to this period. Given the lack of long-term monitoring of the intensity of the sardine run, it is difficult to speculate as to whether this decline in sardine abundance on the East Coast is indicative of a long-term trend. Conversely, de Moor *et al.* (2008) documented a reduction in the estimated sardine stock over the same time frame. O'Donoghue (2009) demonstrated that sardine abundance is highly correlated with declining sea surface temperature along the coastline, corroborating the range extension hypothesis proposed by Armstrong *et al.* (1991). It is thought that the movement of sardines is initiated in the waters of the Eastern Cape, and may be triggered by a series of coastal lows (atmospheric low pressure systems) (O'Donoghue 2009).

O'Donoghue (2009) postulates that changes in the temperature regime of Eastern Cape waters is largely responsible for the variation in the strength and spatial extent of the sardine run along the south and east coasts. This temperature variability is the result of fluctuations in the extent of cold upwelled water from the Port Alfred upwelling cell, and the incursion of warmer Agulhas Current waters along the shelf. The sardine runs experienced over the last decade have been noticeably weaker than in earlier years, but it is not yet apparent whether this is a declining trend, or simply a fluctuation in part of a larger cycle (O'Donoghue 2009). Given the strong climatic control of the sardine run, and the fact that the sardine are at their thermal tolerance limit in the waters of the east coast, it seems intuitive that changes in sea surface temperature, driven by large-scale climatic shifts, could be causing a change in sardine run timing and intensity.

An increase in sea surface temperatures is likely to lead to increased stratification and a deeper thermocline, in turn causing greater water column stability and weakening the influence of nutrient-rich upwelling zones (Roemmich & McGowan 1995). If upwelling of nutrient-rich deep water weakens or ceases, the euphotic zone will become starved of nutrients, plankton production will decline, and the fish stocks which support piscivorous predators will be dramatically reduced – a chain of events which could ultimately lead to cetacean populations becoming unsustainable. If the West Coast sardine stock does in fact contribute to the migration of sardines up the East Coast, the intensity of the sardine migration is likely to diminish if sardine stocks plummet due to weakened West Coast upwelling causing nutrient limitation of surface waters in the region. This could ultimately reduce prey stocks for delphinids species on both the south and east coasts of South Africa.

Rouault *et al.* (2009) argued that the Agulhas Current system had warmed by ± 1.5˚C since 1980 as a result of the intensification of the system under stronger trade winds, coupled with a minor shifting of the westerly wind in a poleward direction. This too may play a role in the annual success of the sardine run on a decadal scale. It is clear that some climatic changes are taking place around South Africa, however no quantification of their effects on the annual sardine run has yet been made. Whilst important data pertaining to the environmental control of the sardine run phenomenon are beginning to be published (O'Donoghue *et al*. 2010 (a), Freon *et al*. 2010, Coetzee *et al*. 2010, Connel 2010, van der Lingen *et al.* 2010), limitations in the spatial and temporal cover of sardine run monitoring remain. Perhaps of even greater urgency is the need for accurate data on the size of fish stocks on the south and east coasts of South Africa, without which it is impossible to predict the possible impacts of climate change on these prey species.

Environmental triggers may be important in controlling the contributions of various prey species to the diet of the common dolphin observed during this, and previous studies. For example, the highest IRI values for chokka squid in the diet of the common dolphins were recorded in 1989 and 1992 (Young 1993). Roberts and Sauer (1994) linked the particularly low sea surface temperatures during 1988 and 1989 (as a result of increased coastal upwelling) to an increased catch of chokka squid in 1989. These authors also stress the possible importance of ENSO (El Niño Southern Oscillation) events on populations of short-lived species such as chokka squid. They propose that El Niño events create stronger westerly winds, which enhance coastal upwelling, and have the knock-on effect of improving chokka squid catches. With climatic variability set to increase under the impacts of global climate change, the suite of prey species available to cetacean predators off South Africa, as well as on a global scale, are likely to undergo substantial changes.

Marine mammals and climate change

Climate change is likely to be associated with changes in the abundance of species at lower levels in the trophic pyramid, setting in motion knock-on effects which are likely to change the prey available to marine predators, including cetaceans (Simmonds & Isaac 2007). Lusseau *et al*. (2004) were the first to successfully link social behaviour in a marine mammal species to climatic changes – they discovered that common bottlenose dolphin and killer whale populations lived in smaller groups under climatically-induced times of food scarcity. This was in response to lower phases of the North Atlantic and Pacific Decadal Oscillations, and demonstrates the adaptability of cetacean social systems (Lusseau *et al*. 2004). However, if climatic events such as ENSO and El Nino intensify under a climate change scenario, it is unlikely that such social adjustments on the part of cetaceans will ensure the survival of their populations. There is already 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 (Learmonth *et al.* 2006). Learmonth *et al.* (2006) proposed that common dolphins may potentially expand their distribution range under a global warming scenario. Macleod *et al*. (2005) documented that common dolphins off the coast of Scotland had increased their range in response to warming of local waters, and concomitantly observed a decrease in white-beaked dolphin numbers (*Lagenorhynchus albirostris,* a species preferring colder waters). Common dolphins generally inhabit warmer waters than those off Scotland (Best 2007), and this range-expansion is the first evidence of a poleward movement of cetaceans in response to changes in ocean temperature (MacLeod *et al*. 2005). Bottlenose dolphins inhabiting the nearshore waters off southern California expanded their range into central Californian waters during a warming El Nino event in 1982, and have since stayed in their new territory well after ocean temperatures returned to normal (Wells & Scott 2002). This behaviour is now thought to reflect a change in the distribution of their prey species in response to the effects of climate change (Wells & Scott 2002). Those cetacean species which cannot readily undertake long-distance migrations to find food, may well be at increasing risk under the impacts of climate change (Simmonds & Isaac 2007), and those which can may find themselves now inhabiting areas in which they are no longer protected by marine laws (MacLeod *et al.* 2005). All cetacean research which informs species management strategies and conservation, such as that undertaken to update the IUCN Red Data List, now need to factor in the increasingly unpredictable possible impacts of global climate change on cetacean populations (Simmonds & Isaac 2007). Hence further research now needs to focus on the ability of cetacean populations to adapt and survive in a rapidly-changing marine environment. 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 prey switching behaviour (Simmonds & Isaac 2007). The extent of their adaptability to these changes is, however, as yet unknown, and difficult to predict (Simmonds & Isaac 2007).

The results of the present study illustrate a high degree of plasticity in the diet of the long-beaked common dolphin along the East Coast of South Africa. These findings are in agreement with previous studies conducted in other regions of the world's oceans (De Pierrepont *et al.* 2005, Lahaye *et al.* 2005, Meynier *et al.* 2008, Stockin 2008). The dramatic increase of chub mackerel in the diet of the common dolphins in KwaZulu-Natal over the last decade appears to reflect the changing dynamics of the winter sardine migration patterns. Results of the gut content analyses suggest a flexible and density-dependent foraging strategy by common dolphins which may allow the species to adapt to environmental change. Also, long-beaked dolphins are thought to be able to travel for hundreds of kilometres to find new feeding grounds (Cockcroft & Peddemors 1990).

Given that sardine distribution is related to sea surface temperature (Coetzee *et al.* 2008), it seems likely that climate change may be responsible, at least in part, for changes in the intensity and timing of the sardine migration. Stocks of at least some commercial pelagic species in South Africa seem to be currently undergoing substantial changes. Adult stock populations of sardine and anchovy were historically found mainly on the south-west coast and Agulhas Bank, and juveniles of the species moved up the West Coast, where the main commercial fisheries are situated (Coetzee *et al.* 2008). However, since 2001, the bulk of the sardine stock has seemingly relocated to the South Coast, meaning that the once-highly productive West Coast fisheries and stock populations are spatially mismatched (Coetzee *et al.* 2008). Changes in the population size of the Pacific sardine (*S. sagax*) were linked to decadal sea surface temperature regime shifts in the North Pacific, and evidence exists that distribution shifts seen in the sardine (*Sardina sardineus*) and anchovy (*E. encrasicolus*) may be related to recent climate change (Alheit *et al*. 2007). Despite the inherent complexity and unpredictability of the southern Benguela Current system, it may also be plausible that climatic changes have triggered a range shift in the South African sardine population.

South African fisheries and potential competition for food with cetaceans

Most of the research into the competitive interactions between common dolphins and fisheries has taken place in the developed world, and focused mainly on the short-beaked form, *D. delphis* (Hall & Lennert 1994, Peltier *et al.* 1994, Aguilar & Silvani 1995, Tregenza *et al.* 1997, Zerbini & Kotas 1998, Notarbartolo di Sciara & Bearzi 2002, Bearzi *et al*. 2003, Lleonart 2005, Bearzi *et al.* 2006). Many authors have documented the negative effects of this competitive interaction for prey species between humans and the common dolphin, often resulting in bycatch of the dolphins in trawl and purse-seine fisheries, or active depredation by fishermen due to the perceived threat of dolphin predation to their livelihoods (Zerbini & Kotas 1998, Notarbartolo di Sciara & Bearzi 2002, Bearzi *et al.* 2003, Lauriano *et al.* 2009). Common dolphin bycatch is common in bottom-set and drifting gillnets in the Celtic Sea, off California and off southern Brazil (Peltier *et al.* 1994, Tregenza *et al.* 1997, Zerbini & Kotas 1998), in the tuna fisheries in the Eastern Pacific Ocean (Hall & Lennert 1994, Peltier *et al.* 1994), and in the pelagic trawl fisheries in the Northeast Atlantic (Tregenza & Collet 1998). In the Mediterranean Sea, the over-exploitation of sardine and anchovy stocks and subsequent prey depletion has resulted in a dramatic decline in the common dolphin (*D. delphis*) population (Bearzi *et al.* 2006). The interactions between humans and marine mammals in the developing world are less well known.

Locally, competition between South African (Cape) fur seals (*Arctocephalus pusillus pusillus*) and commercial fisheries on both the West and South coasts has been documented since the mid-1980s (David, 1987). Since 1943, South Africa's purse-seine fishing industry has targeted anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*), chub mackerel (*Scomber japonicus*), horse mackerel (*Trachurus trachurus*), round herring (*Etrumeus whiteheadi*) and lanternfish (*Lampanyctodes hectoris*), with hake (*Merluccius capensis*) being caught by bottom-trawl (David 1987). David (1987) has demonstrated at least some degree of competition between fisheries and the fur seal population, by calculating the annual consumption of various fish prey of the fur seal (principally anchovy, hake, sardine and horse mackerel), and comparing it to commercial fishery takes of the same species. Intense fishing pressure has already been implicated in the decline of sardine stocks on the South Coast of South Africa, a feature which may correlate with a drop in the intensity of the sardine run observed along the south coast of southern Africa (Baird 1971 In: Young 1993).

The results of this study indicate that the long-beaked common dolphin in South African waters preys on at least four commercially valuable teleost species which sustain considerable commercial fisheries; anchovy, sardine, chub mackerel and round herring, and often in similar size ranges to those caught in commercial fisheries. Commercially caught anchovies (*Engraulis encrasicolus*) average 8cm in length, smaller than those eaten by common dolphins (10 – 11cm), whilst commercially caught sardine (*Sardinops sagax*) and round herring (*Etrumeus whiteheadi*), and those targeted by common dolphins are approximately the same size (17 – 18cm) (Sekiguchi *et al.* 1992). The modal size of commercially-caught sardine (*Sardinops sagax*) was reported as 18cm (Sekiguchi *et al.* 1992), very close to the size taken by common dolphins on both the West (17.9cm) (Sekiguchi *et al.* 1992) and East Coasts (19.2cm in this study). Sekiguchi *et al.* (1992) found that cetacean predators targeted prey sizes similar to the modal fishery catch of the region, and therefore concluded that most cetacean species off the South African coastline employed an "optimal foraging strategy" in their choice of prey species and size of prey. Common dolphins are known to become entangled in both purse-seine and trawl nets on the West and South coasts (Sekiguchi *et al.* 1992), so operational mortalities are already a feature of their interaction with fisheries along this coastline. It is important to note, however, that diet overlap with fishery catches cannot expressly imply that competition actually occurs between the dolphins and the fishery (Santos *et al.* 2004).

If we calculate a very rough estimate of the population consumption of common dolphins in South Africa for sardine (using the formula given in Santos *et al.* 2001), using a population size of common dolphins of 20 000 animals in contact with sardine prey 365 days per year, with a daily consumption of roughly 4.5% of their body weight (Trites *et al.* 1997) (the average body weight across all ages during this study was 108kg), and a diet consisting of 7% sardine (as found during winter between 2000 and 2009), then the annual consumption of sardine by common dolphins in South Africa would be approximately 2 483 tonnes. This constitutes <1% of the total South African sardine stock (estimated at 300 000 tonnes) (Coetzee *et al*. 2010). This low consumption would suggest that there is unlikely to be intense competition between commercial fishers and the long-beaked common dolphin. However, our current knowledge of the status of South Africa fish stocks, the extent of commercial and subsistence fisheries, the extent of dolphin by-catch in local fisheries, as well as the population size of common dolphins in the region, remain inadequate to fully understand their interactions. The management of the South African sardine and anchovy stock depends entirely on data produced by hyro-acoustic surveys, which first commenced in 1984 (de Moor *et al*. 2008). These surveys take place in May and November each year, and only go as far east as Port Alfred (de Moor *et al*. 2008), and for these reasons they fail to survey the sardine biomass moving into KwaZulu-Natal in winter each year.

Chokka squid (*Loligo* spp.) was found to represent a minor component of the diet of the common dolphin in KwaZulu-Natal waters over the last decade. Chokka abundance is sensitive to environmental perturbations, as well as harvesting pressure. The South African chokka fishery is regulated by TAE (Total Allowable Effort), but advances in vessel efficiency and technological equipment have led to increased catches (Strydom & King 2009). Although the South African chokka population is currently larger than ever recorded, it seems it may be heading towards a decline (Strydom & King 2009). Sekiguchi *et al.* (1992) reported that the modal size of chokka squid (*Loligo vulgaris reynaudii*) in the South African trawl fishery was 15-17cm DML (dorsal mantle length). They found that common dolphins from the South African West Coast preyed on squid of around 17.3cm DML, with most of the squid prey actually being larger than those targeted by the commercial squid fishery. The average DML for *Loligo* prey items found in the stomachs of the common dolphins from KwaZulu-Natal between 2000 and 2009 was 15.61cm, although some were calculated as being up to 24cm DML. This could mean that there is potentially some overlap in the size ranges of *chokka squid* targeted both by common dolphins and local fisheries. Hence some overlap between commercial catches and the diet of the common dolphin may occur, but as common dolphins are thought to be opportunistic and adaptable in their feeding (Ross 1984, Young & Cockcroft 1994), this competition is unlikely to result in serious limitations to their survival. The results of this study revealed that the long-beaked common dolphins feeding in KwaZulu-Natal during winter have targeted teleost fish to a greater degree than squid over the last 10 years. Although the stocks of clupeid species may be able to support both common dolphins and small commercial fisheries at present, there is cause for concern if fisheries expand, indicating a need for long-term studies to monitor these interactions.

Opportunistic foraging strategy in common dolphins

Inter-annual variability in prey stocks is an underlying feature of the dietary composition of the long-beaked common dolphin in South African waters. The results of this study, and that of Young (1993), demonstrate a highly flexible diet for this cetacean predator, and one which consists of the most abundant, and hence easily caught, prey species in any given region. As the suite of pelagic fish stocks may change in composition and abundance from year to year, especially during such periods as the sardine run where spawning migrations may take place, the diet of the common dolphin changes in accordance with the suite of prey available. Common dolphins are clearly able to undertake long-distance migrations in order to exploit abundant food resources (such as we see during the annual sardine run in South Africa), but are also able to adapt their diet to prey on the suite of teleost and cephalopod species available in any locality. For this reason, the species should be considered highly opportunistic in its feeding ecology. It is also for this reason that the common dolphin may possess a lifestyle with a higher degree of adaptability than most other large mammals, and this plasticity in dietary requirements and ability to travel long distances to find food may enhance its survival capabilities under the possible impacts of future climate change. Whilst the common dolphin may be able to adapt to changes in its suite of prey species, it will not be able to avoid the impacts of prey depletion which result from human fishing pressures and environmental degradation.

Conclusions

A clear shift was detected in the diet of the long-beaked common dolphins feeding in the sardine run, away from reliance on sardine and towards a diet dominated by chub mackerel. However, this dietary shift appears to have had no impact on their general body condition, as no long-term changes in body condition or trophic level of feeding were detected over the last four decades. This evidence confirms that common dolphins exhibit a high degree of plasticity and opportunism in their feeding ecology, with their diet reflecting the local abundance of epipelagic shoaling fish species. Hence the shift detected in the winter diet is likely to be simply due to a change in the numerical abundance of their different prey species in the waters of KwaZulu-Natal. Possible competition between common dolphins and expanding local fisheries warrants further study in the future, and it is clear that a more thorough understanding of sardine run dynamics will greatly aid in assessing the importance of this annual event in the yearly diet of the common dolphin in South Africa. In addition, a new population assessment of common dolphins in South African waters is needed, both to quantify their potential for competition with fisheries for food resources, and to assess their population status to inform conservation and management decisions involving this species. In light of the recent proposal by the IWC sub-committee on small cetaceans that the common dolphin should be regarded as one global ‘super-species’ (IWC 2009 Annex L), it seems that further comparative studies (genetic, phylogeographic, morphological and ecological) are imperative in helping to resolve the taxonomic confusion within the genus, as well as to enable the IWC to identify meaningful stock units around which to focus conservation efforts. To date, the IUCN still lists the long-beaked form, *Delphinus capensis*, as “Data Deficient”, making long-term studies such as this of particular importance in understanding its ecology.

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