THE SARDINE RUN:
INVESTIGATING SARDINE AND PREDATOR DISTRIBUTION IN RELATION TO ENVIRONMENTAL CONDITIONS USING GIS AND REMOTELY SENSED PRODUCTS.

by

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As the candidate's supervisor I have approved this thesis/dissertation for submission.

Signed: Name: V.M. PEDDEMORS Date: 23rd December 2009

ABSTRACT

The sardine run is a spectacular but poorly understood natural phenomenon. This research aims to broaden scientific knowledge pertaining to sardine, *Sardinops sagax*, distribution, both in relation to their predators and environmental conditions. Sardine distribution was closely related to sea temperature. Sardines were sighted every year along the Lower Wild Coast, where continental shelf conditions were cooled by the Port Alfred upwelling cell. To the north of Mbashe River, shelf conditions were dominated by the warm Agulhas Current, and sardine distribution varied annually in close relation with sea temperature conditions. Along this coastline sardine abundance always peaked between Waterfall Bluff and Port St Johns with favourable conditions caused by the westward inflection of the coastline and the shelf bathymetry. Topographically-induced upwelling was concluded to be the cause of cooler sea temperatures and elevated chl a concentrations. Although chl a concentration appeared to be associated with east coast sardine distribution, the uncertainty with regards data accuracy hindered their usefulness as a predictor of suitable biological conditions for sardine. Sardine northward movement along the KZN coastline was impeded adjacent to the Durban Eddy, where they were forced shorewards by the warm conditions. This coincided with the peak in beach seine catches. The Cape Gannet, *Morus capensis*, was very closely associated with sardine along the entire east coast. Their abundance declined substantially adjacent to the Durban Eddy. Prevailing atmospheric conditions affected gannet behaviour: they travelled more frequently during strong alongshore winds and foraged more upon cessation of such winds. Gannets were closely associated with feeding dolphins at both coarse and fine scales, and responded to changes in dolphin behaviour. Common dolphin, *Delphinus capensis*, abundance and group size peaked between Waterfall Bluff and Port St Johns. Along this stretch of coastline they travelled more slowly, and in pods more perpendicular to the bathymetry of the region. Bottlenose dolphin, *Tursiops aduncus*, abundance increased during the sardine run with the influx of a migrant stock which reached the KZN Mid South Coast. Humpback Whale, *Megaptera novaeangliae*, and sardine distributions did not appear to be related.

PREFACE

The experimental work described in this thesis was carried out in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, from July 2005 to July 2009, under the supervision of Professor Victor M Peddemors.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

DECLARATION 1 - PLAGIARISM

I, Sean O'Donoghue, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.

2. This thesis has not been submitted for any degree or examination at any other university.

3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis (include publications in preparation, submitted, *in press* and published and give details of the contributions of each author to the experimental work and writing of each publication)

Publication 1:
O'Donoghue SH, Drapeau L and Peddemors VM (in press) An investigation of broad-scale distribution patterns of sardines and their predators in relation to remotely sensed environmental conditions. *African Journal of Marine Science*.

O'Donoghue – data collection (aerial surveys), data capture, analyses, writing, intellectual input
Drapeau – data collection (remote sensing time series), writing (remote sensing methods)
Peddemors – data collection (aerial surveys), writing, intellectual input

Publication 2
O'Donoghue SH, Drapeau L, Dudley SFJ and Peddemors VM (in press) The KwaZulu-Natal sardine run: shoal distribution in relation to near-shore environmental conditions, 1997 to 2007. *African Journal of Marine Science*.

O'Donoghue – data collection (climate), data capture, analyses, writing, intellectual input
Drapeau – analyses (GLM and GAM modelling), writing
Dudley – data collection (KZNSB oceanographic), writing, intellectual input
Peddemors – writing, intellectual input

Publication 3
O'Donoghue SH, Whittington P, Peddemors VM and Dyer BM (submitted) The 2005 sardine run survey II: Avian and marine mammal predators associated with the sardine run. *African Journal Marine Science.*

O'Donoghue – data collection (remote sensed time series), data capture, analyses, writing, intellectual input
Whittington – data collection (ornithological survey), data capture, analyses, writing, intellectual input (bird data)
Peddemors – data collection (mammal survey), writing, intellectual input
Dyer – data collection (ornithological survey)

Publication 4
O'Donoghue SH, Peddemors VM (submitted) Fine-scale sardine run distribution and predator behaviour along the Eastern Cape 'Wild Coast' in relation to environmental conditions.

O'Donoghue – data collection (aerial survey, climate data), data capture, analyses, writing, intellectual input
Peddemors – writing, intellectual input

Publication 5
O'Donoghue SH, Peddemors VM (in prep) Differences in predator behaviour along the Eastern Cape 'Wild Coast' in relation to the annual sardine run. *African Zoology*

O'Donoghue – data collection (point survey), data capture, analyses, writing, intellectual input
Peddemors – data collection (CTD survey), writing, intellectual

Signed:

CONTENTS

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This thesis would not have been possible without the energy and enthusiasm that Professor Vic Peddemors brought to the University of Durban, Westville, in 2002. Vic's interest in the sardine run has been long-term, and his motivation and hard work resulted in the initiation of the UKZN sardine run research programme. I would like to thank him both for his role as the programme director, and for his guidance and tireless dedication as my supervisor and in preparing this thesis. Finally, I would like to thank him for the six wonderful years of sardine run research that I've been fortunate enough to participate in.

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This sardine run research has required much cross-discipline collaboration, without which, very little meaningful new information would have emerged. I would like to thank all scientists with whom I've been fortunate enough to collaborate, especially Laurent Drapeau for his help and tuition in the remote sensing aspects of this research. The University of KwaZulu-Natal is also thanked for providing the GIS training necessary to extract useful information hidden in unwieldy and daunting long-term data series. The Director and staff of Marine and Coastal Management are thanked for their help in supplying data and for giving advice readily. Special thanks in this respect are expressed towards Carl van der Lingen and Janet Coetzee. Similarly, the CEO and staff of the KwaZulu-Natal Sharks Board are thanked for the provision of archived data and help with collecting current data during aerial surveys of the east coast. Sheldon Dudley is especially thanked for his help, as is Allan Connell, formerly of the C.S.I.R. for sharing his vast experience. Our appreciation is extended to Mike Roberts of MCM for the loan of his CTD. Special thanks to Malcolm Smale of the Bayworld Centre for Research & Education for his enthusiasm during fieldwork collecting the CTD data and ongoing support for this research. Other sources of data included historic climate data kindly provided by the South African Weather Service, remotely sensed data via the remote sensing server for marine sciences and the South African Hydrographic Office for supplying the bathymetric charts.

Sardine run research happens for a short period of time once a year. To maximise field research productivity a lot of help is need from willing and dedicated volunteers. In this respect I would like to thank researchers on the 2005 FRS *Africaner* ornithological survey, especially Phillip Whittington and Bruce Dyer, and Maleeha Mahomed for her help with the marine mammal survey. Maleeha is thanked again, repeatedly, for her enthusiasm and help with the aerial surveys, as is Ruwen Pillay. Field trips would not be possible without the assistance of experts in their crafts, especially the gyrocopter and microlight pilots who managed to keep me safely in the air, and skippers of small inflatable craft whose exert seamanship ensured that we were able to return to land safely every day. In this regard special thanks are extended to Blue Wilderness Dive Expeditions for their ongoing support of research via subsidised boat and skipper time during this project.

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CHAPTER ONE: INTRODUCTION

The annual movement of South African Sardine, *Sardinops sagax* (Jenyns 1842), up the east coast of South Africa is popularly known as the 'sardine run.' Scientific information pertaining to the spatial and temporal distribution of sardines and their predators is scarce, yet it is potentially one of the most important biotic events on the east coast of South Africa.

From an ecological perspective, the influx of thousands of tonnes of sardine must provide a substantial input of nutrients into coastal waters that are oligotrophic in nature (Carter and d'Aubrey 1988; Meyer *et al.* 2002). The large numbers of predators associated with the sardine run suggests that this event is of ecological significance to these predators, for example female common dolphin, *Delphinus capensis*, use this temporary abundance of fish to wean their young (Cockcroft 1990). There is also evidence to suggest that various fish species e.g. elf (*Pomatomus saltatrix*), geelbek (*Atractoscion aequidens*) and garrick (or leervis, *Lichia amia*), time their spawning migrations to coincide with the run (Garratt 1988; Griffiths 1987).

From a human perspective, the sardine run supports a small KwaZulu-Natal (KZN) beach seine fishery with annual landings of less than 1000 tonnes (Cliff and Dudley 1992; Smith 1987), and an east coast recreational fishery targeting gamefish associated with the run. It also impacts upon the daily operations of the KwaZulu-Natal Sharks Board (KZNSB), which strives to remove the netting installations protecting KZN bathing beaches (known locally as 'shark nets') prior to the arrival of the predators associated with the run (Davis *et al.* 1989). Additionally, the sardine run has become a mainstay of winter tourism-related activities on the KZN coast during the past ten years (Manana 2008) and has brought considerable economic benefits to small towns along the Eastern Cape coastline (Dicken in press).

Given the apparent importance of the sardine run to both the south-east coast nearshore ecology and regional socio-economy, it is surprising that so little research has been conducted on this phenomenon. This PhD research is an attempt to redress this situation by investigating the movement of sardines and their predators along the east coast of South Africa in relation to environmental variables. It is hoped that an improved understanding of the mechanism of sardine movement during the sardine run will facilitate management decisions, both from an ecological and tourism perspective.

Sardine biology

Sardines prefer water temperatures between 14 and 20 °C (Barange *et al.* 1999) and their presence has been correlated with large scale thermal frontal features (Coetzee 1996). They are widely spread over the Agulhas Bank (the wide continental shelf to the south of the subcontinent) with a tendency for larger fish to inhabit deeper water towards the shelf edge and for smaller fish to stay near the coast (Armstrong *et al.* 1987).

Sardines are omnivorous (van der Lingen 2002, van der Lingen *et al.* 2006a) and primarily filter feeders, with particle size determining when they switch to particulate feeding (van der Lingen 1994, 1995). The size frequency and the composition of food in their environment is reflected within sardine stomachs (van der Lingen 1996, 1999), and consists mostly of calanoid and cyclopoid copepods less than 1.2mm. Despite its relatively moderate biomass, the plankton of the South African east coast provides suitable food for sardines (Carter and Schleyer 1988).

Sardines start spawning when they are about 18 months and approximately 19 cm standard length (Armstrong *et al.* 1987), although van der Lingen (*et al.* 2006b) have demonstrated substantial variability in sardine spawning with regards their length-at-maturity (17.0 +/- 0.03 to 19.1 +/- 0.05 cm). Their spawning range is between the Western Cape and the Natal Bight (Beckley and Hewitson 1994; van der Lingen and Huggett 2003), with an east coast seasonal peak during spring and early summer (Anders 1975; Connell 1996, 2001). Sardine eggs and larvae are found on the KZN continental shelf as far north as the Thukela River (Fig. 1) and until January (Beckley and Naidoo, 2003; Connell 1996; Naidoo 1998).

The reason why sardines move northwards into KZN waters remains elusive, as there do not seem to be obvious benefits in terms of feeding and reproduction. Armstrong *et al.* (1991) proposed that the sardine run is initiated as an extension of the sardine's habitable range due to the seasonal cooling of the east coast inshore waters to the sardine's preferred temperature range. Sardine northward movement is best described in terms of the environmental conditions associated with distinct regions along the South African south-east and east coasts.

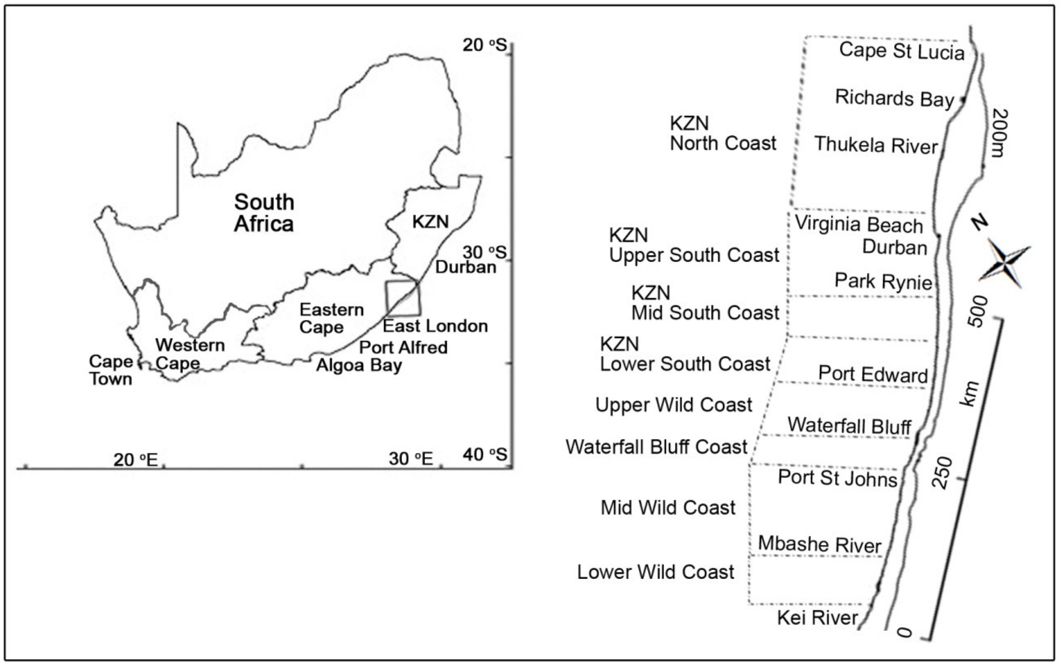

Figure 1. South African political map showing the provincial boundaries and (square) the location of the Wild Coast along the Eastern Cape. The map on the right shows the study area in greater detail, including the zones into which the coastline was divided for analyses and the 200 m isobath.

Environmental conditions

During the austral summer young sardine of approximately 15 to 20 cm caudal length (+ 1yr cohort) are frequently concentrated in the shallow bays of the Western and Eastern Cape, e.g. Algoa Bay (Fig 1) (Armstrong *et al.* 1987). Within these bays onshore winds generate cool and productive upwelling conditions (Schumann *et al.* 1988). With the onset of winter these conditions are disrupted by the eastward passage of low pressure frontal systems with strong SW winds. The dissipation of the summer thermocline across the continental shelf coincides with the eastward movement of sardines (Baird 1971). Sardines are thought to utilise a thin strip of cool water that stretches up the east coast on the shoreward side of the warm, poleward flowing Agulhas Current at the edge of the continental shelf. Swimming speed whilst feeding ranges between 0.15 and 0.65 $m.s^{-1}$ (van der Lingen 1995). This gives a theoretical maximum distance covered during a 24 hour period of between 12.96 and 56.16 km.

The south-east and east coasts are generally considered nutrient poor and have been speculated to represent poor conditions for sardine moving up the coast. However, careful consideration of various environmental features along this stretch of coast indicates that there may be locally enhanced productivity. For example, there is some evidence for a topographically induced upwelling cell near Port Alfred (Fig. 1), which frequently reaches as far north as the Mbashe River (Lutjeharms *et* al. 2000a). Primary production is enhanced due to the upwelling of nutrient-enriched water. This presumably provides suitable habitat for sardine occupation and is possibly a conduit for sardine northward movement each winter.

Northwards of the Port Alfred upwelling cell the continental shelf narrows considerably. Shelf conditions are dominated by the Agulhas Current and nearshore current direction is usually in a south-westerly direction. Conditions do not appear to be suitable for sardine habitation because there is poor retention of the primary productivity along the largely straight coastline. Despite this, sardines have been recorded across the continental shelf (Armstrong *et al.* 1991).

Whillier (1962) investigated current structures within gentle convolutions of the coastline and concluded that small-scale gyres could exist, potentially allowing for retention of primary productivity and providing refuge for sardines from the Agulhas Current. One example is the westward inflection of the coastline at Waterfall Bluff (Fig. 1). Here the Agulhas Current is located further offshore (Schumann 1987), while seabed sedimentation patterns are suggestive of northward flowing inshore counter-currents (Flemming 1980) typically associated with topographically-induced upwelling cells (Gill and Schumann 1979).

It is thought that this part of the coastline may be important for sardine distribution, and may act as a holding area for sardines, providing them with suitable habitat and refuge from the Agulhas Current, until favourable conditions occur for northward movement. This theory is known as the 'gateway hypothesis' (VM Peddemors, 2003, *pers comm.*) and it has not yet been tested. The success of the sardine run along the KZN coastline, about 80 km to the north of Waterfall Bluff (Fig. 1), may rely upon the 'Waterfall Bluff Gateway' being open for sardine northward progression.

Favourable conditions for sardine northward progression could include the movement of the Agulhas Current further from shore, or the development of a subsurface or nearshore return current. There is also a popular notion that sardine northward progression is aided by the passage of low pressure fontal systems, which travel up the coast during this time of year. The role of environmental conditions affecting the movement of the sardine run through the Waterfall Bluff Coast will be examined in this thesis.

To the north of Waterfall Bluff the continental shelf waters are again dominated by the Agulhas Current, with a mean winter temperature of 23 °C (Christensen 1980), and current speeds in excess of 1 $m.s^{-1}$ frequently within five kilometres of the shore (Schumann 1981). The trajectory of the Agulhas Current is extremely stable with the current core found in its normal position 80 % of the time (Beal and Bryden 1999; Grundlingh 1983). This suggests that conditions are unsuitable for sardine habitation along this stretch of coastline.

The effect of local wind forcing on continental shelf currents appears to be minimal (Schumann 1981), although Heydorn *et al.* (1978) did postulate about the possibility of a nearshore regime, within one kilometre of the coast, where longshore water movement could be driven by swell conditions. During the sardine run months this would amount to movement in a northerly direction as swells generated in the roaring forties travel up the coast. Temperature variability in the surface layers occurs and is driven by wind forcing, including sea- breezes.

Near Durban (Fig. 1), there is a semi-permanent cyclonic gyre termed the Durban Eddy. Here warm Agulhas Current water flows onto the shelf to within at least 6 km from shore (Pearce *et al.* 1978; Schumann 1982) and the dominant nearshore current direction is from south to north. Schumann (1988) recorded dramatic temperature decreases throughout the water column in this region when current direction changed to southwards, and considered this stretch of coastline to be transitional between the Agulhas Current dominated shelf to the south and the wind dominated shelf to the north.

The continental shelf is considerably wider along the KZN North Coast (Fig. 1), due to the westward inflection of the coastline to form the Natal Bight. The Agulhas Current flows further from shore (> 40 km compared with ~ 15 km along the South Coast), while current conditions across the shelf are a lot more variable. Alongshore NE or SW winds precede the initiation of currents of a similar direction by approximately 18 hours (Schumann 1981). Important features along this stretch of coastline, in terms of sea temperature and nutrient input, are the kinematically-driven upwelling cell near Cape St Lucia (Fig. 1), sheer-edge features along the inshore edge of the Agulhas Current and the Thukela River.

Sea temperature within the Natal Bight is frequently lower and nutrient and chlorophyll a concentration higher compared with the KZN south coast (Lutjeharms *et al.* 2000b; Meyer *et al.* 2002), hence it would appear to be more suitable habitat for sardines to occupy. Although sardine eggs have been sampled from the Thukela Bank, off the Thukela River (Beckley and Hewitson 1994), and sardines often remain off the KZN coastline as late as November (Connell 1996; van der Elst 1988), little is known about the northward limit of the sardine run. The width of the shelf in the Natal Bight potentially provides sardines with space to evade predators and would make detecting sardine presence a lot more difficult than on the narrow shelf to the south of the Durban Eddy. This may be why so little is known about sardine distribution in this region.

Changing environmental conditions up the east coast of South Africa must affect sardine distribution both in terms of how far north they progress each year, and their distance from shore. Unfortunately, hydroaccoustic cruises to determine sardine distribution during the sardine run are prohibitively expensive, and prior to 2005 have been limited to three cruises during the 1986 and 1987 sardine runs (Armstrong *et al.* 1991), none of which took place during peak sardine run activity on the KZN coast. In the absence of such data, one has to use a proxy for sardine presence to determine sardine distribution. Historically, predators of the sardine run have been used in this way. Although there has been a dearth of research on the sardine run per se, substantial research has been conducted upon animals associated with this phenomenon (mostly cetacean and shark species) caught in the KZN shark nets (Cliff *et al.* 1989; Cliff and Dudley 1991, 1992; Cockcroft 1990, 1992; Peddemors 1995). Additional data have been obtained through information acquired from the local recreational fishery, with regards the movement of predatory fish species associated with the run (van der Elst 1981, 1988). Another valuable source of data has been the long-term (approximately 20 years) ichthyoplankton sampling project off Park Rynie (Fig. 1), where valuable information about the timing (and to a lesser degree the strength) of the sardine run along this stretch of coastline has been inferred from the abundance and cross-shelf distribution of sardine eggs (Connell 2001).

In this thesis, I have used Fréon's definition of the sardine run: "The sardine run can be defined as the winter migration of a variable fraction, about 10 %, of the South African population of sardine (*Sardinops sagax*), and to a lesser extent that of west coast roundherring (*Etrumeus whiteheadi*) and anchovy (*Engraulis encrasicolus*), from the Agulhas Bank up the narrow east coast continental shelf to Durban, and beyond, during the early austral winter. Associated with the sardine migration are foraging top predators, including sea birds, marine mammals and piscivore teleostean and chondrichthyan fish." For a comprehensive account of oceanographic conditions along the South African east coast, the reader is referred to Lutjeharms (2006).

Predators associated with the Sardine Run

Despite the above research, little is known about the distributions of seabird and marine mammal predators associated with the sardine run along the KZN coastline. Much less still is known about their distribution along the Eastern Cape 'Wild Coast' (Fig. 1). An understanding of the relationship between each predator and the sardine run is crucial, given their potential importance as drivers of the sardine run northwards, as well as their charismatic role in sardine run tourism. This study focuses upon the three most abundant seabird and marine mammal predators of the sardine run, i.e. the Cape Gannet, *Morus capensis* (Lichtenstein 1823), the Long-beaked Common Dolphin, *Delphinus capensis* (Gray 1828), and the Indo-Pacific Bottlenose Dolphin, *Tursiops aduncus* (Ehrenberg 1833).

Cape gannets are non-breeding winter visitors to KZN (Broekhuysen *et al.* 1961, Crawford *et al.* 1983). Their foraging distribution conforms to sardine distribution along the southern and western coasts of South Africa (Crawford 1996; Crawford and Shelton 1981; Pichegru *et al.* 2007). Since 2001, sardines have comprised 72% of gannet diet on the east coast of South Africa (Crawford *et al.* 2007). The South African Anchovy, *Engraulis encrasicolus*, at 17%, constitutes the second most important prey item, highlighting the dependence of gannets on pelagic shoaling fish abundance and distribution (Berruti and Colclough 1987; Klages *et al.* 1992).

Currently, the largest gannetry in the world (98 000 breeding pairs) (Crawford *et al.* 2007) is located at Bird Island in Algoa Bay (Fig. 1). The increase in the size of this gannetry over the past ten years has been coincident with an eastward shift in the sardine stock across the Agulhas Bank (Coetzee *et al.* 2008; van der Lingen *et al.* 2005); suggesting a direct correlation between increased gannet population with increased sardine availability within the Bird Island gannets' foraging range. Gannets are central place foragers during their summer breeding period and the foraging behaviour of Bird Island gannets has been well studied (Ropert-Coudert *et al.* 2004a). Gannets leave their nests at sunrise and travel to feeding grounds where they forage during the morning. This is followed by a bout of sitting to digest their catch lasting between 1.48 and 2.79 hours. Thereafter they forage again prior to travelling back to the nest to deliver food to their chicks. Gannet foraging during the sardine run, however, has received scant attention. Research presented in this thesis attempts to fill this knowledge gap.

It is hypothesized that gannets locate fish shoals by observing movements of other birds and that they are attracted by the sight of other gannets diving (Crawford 2005). The plunge dive, which gannets use to catch their prey, has been described in fine detail by Ropert-Coudert *et al.* (2004b): gannets dive from approximately 30m height and decelerate very little upon entering the water. The birds use their momentum to descend at an average rate of 2.87 +/- 1.53 $m.s^{-1}$. Prey is sometimes pursued under water using either the wings or feet, and the birds use their positive buoyancy to glide passively to the surface.

Cape gannets follow dense fish shoals up the east coast, with some gannets reaching the coast of Mozambique (Berutti 1995; Klages *et al.* 1994). Numbers of gannet involved in the sardine migration seem to be variable. Even historically there appears to have been considerable inter-annual variation in gannet abundance and distribution, with large numbers recorded off the coast of KwaZulu-Natal in 1954, but followed by only three birds being sighted during a 10-day period of observation in 1955 (Davies 1956). Interestingly, the sardine shoals recorded during the 1955 migration were nearly as large as those recorded in 1954. The reason for this reported interannual difference in gannet abundance is not known.

Long-beaked Common Dolphin are resident throughout the year within the 200 m isobath along the Eastern Cape coastline as far north as East London (Cockcroft and Peddemors 1990). Common dolphin diet is dominated by sardine, roundherring (*Etrumeus* sp.), anchovy and species of squid, particularly chokka, *Loligo vulgaris raynaudii* (Young and Cockcroft 1994). During winter common dolphin move northwards along the Wild Coast and into KZN coastal waters in association with the sardine run (Cockcroft and Peddemors 1990). Common dolphin utilisation of the sardine run has been well documented (Peddemors 1999; Young and Cockcroft 1994). Their largest aggregations between East London and Durban have typically been recorded in the Port St Johns region (Cockcroft and Peddemors 1990).

Although common dolphin distribution corresponds with that of sardine on the Wild Coast and KZN (Cockcroft and Peddemors 1990), analysis of their diet has not always reflected this (Young and Cockcroft 1994) suggesting that common dolphins in these waters may shift their prey in years of low sardine activity. Surprisingly, no direct correlation between sardine and common dolphin distribution and abundance has previously been made for these waters, even though common dolphins are considered a major indicator species as to the progression of the sardine run up the coast and whether shark nets in KZN should be removed (Dudley and Cliff, in press).

A second delphinid species considered to be an indicator of the sardine movement is the Indo-Pacific Bottlenose Dolphin. These dolphins are resident throughout the South African south east coast with a distribution that is strongly skewed towards shore and is thought to be related to water depths of less than 30m (Ross *et al.* 1987, 1989). Each winter, KZN bottlenose dolphin abundance is thought to increase with the arrival of a genetically-distinct (Natoli *et al.* 2008) migratory stock from the south (Peddemors *et al.* submitted). Stomach content analysis of bottlenose dolphins captured along the KZN coastline indicates that this species does not utilise sardines as a major source of prey (Cockcroft *et al.* 1990b). However, other fish species that migrate up the east coast in association with the sardine run, e.g. elf, *Pomatomus saltatrix*, do form a significant part of bottlenose dolphin diet (Peddemors and Cockcroft 1997). The extent to which resident and migrant stocks of bottlenose dolphins associate with the sardine run is not known. The enigmatic relationship of these delphinids with the sardine run is therefore of interest and they have been included in these analyses.

The most abundant Mysticete along the east coast during winter is the humpback Whale, *Megaptera novaeangliae* (Borowski 1781). The prevalence of humpback whale feeding on sardines during their northward breeding migration is not known. Historical records show that whale stomachs examined in Durban (n = 38) were either empty or contained euphausiids (Bannister and Baker 1967; Matthews 1938). Although they are often sighted in close proximity to sardine run activity (pers. obs.), there are no reliable reports of them feeding upon sardines. Considering reports of southern hemisphere humpback whales feeding on shoaling fish elsewhere in the world (Kaufman 2009), it seems incongruent that these whales are not utilising this abundant food source during their northward movement up the east coast of South Africa. To determine any association between humpback whale distribution and that of the sardine run, and because of their importance as a charismatic species marketed by sardine run tourism organisations, humpback whales have been included in these analyses.

Methods used in this study

The findings reported in this thesis are based upon various survey methods, including broad and fine scale aerial and ship-based surveys, point surveys conducted from cliffs and incidental reporting of field staff at the KZN Sharks Board.

Aerial surveys were conducted along both the KZN and Eastern Cape coastlines using standardized methods developed for cetacean surveys in this region (Cockcroft and Peddemors 1990; Cockcroft *et al.* 1992; Ross *et al.* 1989). One advantage of using a standardised methodology is that results are comparable. All flights were made by flying along the coast at 230 m above the shoreline. The surf zone was therefore consistently at the bottom of the search area. A 1 km strip width was used as historical aerial surveys in these waters indicated that 90% of bottlenose dolphins were present within this nearshore zone (Ross *et al.* 1989). The aircraft pilot and data recorder searched beyond this strip width for any large dolphin or gannet aggregations and/or oil slicks indicating sardine presence. Although it is recognised that this survey design may result in missed sightings further offshore due to the decrease in sighting efficiency with increasing distance from the transect line, an ability to compare data with historical aerial survey data, and the historical concept of the sardine run constituting a sliver of fish and associated predator movement close inshore, led to this survey design. Unfortunately, a downfall of this survey design is that it is impossible to use these aerial surveys to determine the distance from shore of the sardine run along the east coast.

A unique opportunity to survey offshore abundance and distribution of the sardine run arose via a ship-based hydro-acoustic survey for sardines in 2005. The FRS *Africana* surveyed the area between East London and Richards Bay (Fig. 1) in a systematic grid pattern to ascertain abundance, distribution and biomass of sardines, their prey and predators during the sardine run period. Predator searches were conducted from the flying bridge of the FRS *Africana* during these survey tracks using standard ship-based cetacean and ornithological methodology (Cockcroft *et al.* 1990a; Tasker *et al.* 1984). Data obtained from this cruise were used to determine the alongshore and offshore distribution of predators along the east coast and correlated with their prey distribution and environmental conditions.

Finally, the fine-scale movements and behaviour of predators were investigated by conducting point surveys from cliffs along the Wild Coast using standardised methodology (Würsig 1986; Würsig and Würsig 1980). The advantage of monitoring animals from a fixed station is that for a relatively low cost one can generate a substantial fine-scale time-series database, but a disadvantage is the limited spatial coverage (Evans and Hammond 2004). Because of the high inherent variability in the sardine run, the time between counts was kept short in order to generate a high sample number.

Using the above surveys, I describe the spatio-temporal distribution of sardines and predators during the sardine run along both the KZN and Eastern Cape coastlines. Distribution was compared with environmental variables, including remotely sensed sea surface temperature (SST) and chlorophyll a (chl a) concentration. SST was derived using two data sets: The first set was obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua satellite. MODIS Level-1 daily satellite images were extracted from the SeaWiFS data server (http:// oceancolor.gsfc.nasa.gov/SeaWiFS.html). The Level 1 data set is part of the 33 data sets that comprise the ECS data collection (http://modis.gsfc.nasa.gov/). Daily maps during the study period were compiled at a 1 km scale on a cylindrical equidistant map projection. Data sets are available in Hierarchical Data Format (HDF) from the Jet Propulsion Laboratory Physical Oceanography Distributed Active Archive Centre (JPL PO.DAAC). The second set was constructed from the European Meteosat series of geostationary satellites. The Meteosat thermal sensor has poor spatial resolution of 5 km at nadir, but has a high image acquisition rate; a full view centred on 0° of longitude is obtained every 30 min enhancing the chances of achieving a complete daily SST description. Full details of the processing procedure for SST images from geostationary satellites and their application to coastal upwelling areas are described in Demarcq *et al.* (1989).

The main problem with using remotely sensed SST to describe oceanographic conditions along the east coast is that conditions below the surface are not adequately described. Upwelling of cool water that does not reach the sea surface and thermoclines are not visible to satellite imagery. There are, however, no other long-term temperature datasets with similar spatial coverage available for this region. In the absence of sub-surface measurements, data from satellite imagery become the only available source of information to create a large-scale, time-series set of sea surface temperature (SST) conditions during the sardine run.

A second problem with using remotely sensed SST is that there is a loss of data along the shoreline equating spatially to approximately 2 km for MODIS satellite data and 4.5 km for METEOSAT data. Although this results in a lack of data for the actual surveyed area, the outer edge of the surveyed area is approximately 1.4 km from shore, and therefore only 600 m from the first reliable remotely sensed MODIS data. Along the KZN coastline SST measurements, made by KZNSB field staff whilst they serviced the net installations, were used to supplement the loss of remotely sensed nearshore data. Other sea temperature measurements used to confirm the accuracy of remotely sensed SST during this study, included continuous measurements made during the 2005 hydrographic survey and the deployment of a continuous temperature and depth recorder (CTD) off Waterfall Bluff to specifically investigate the role of sub-surface temperatures in regulating the Waterfall Bluff Gateway.

The chl a concentration time series were derived using the available ten years of chl a data (Oct 1997–2007) from SeaWiFS on board the OrbView-2 satellite. These data were produced by the NASA project using the OC4 algorithm suitable for use in the coastal zone (O'Reilly *et al.* 2000), and are available as a level 3 product for the study region from the Goddard Earth Sciences Distributed Active Archive Centre. The data are used in three-day running mean composites with an approximately 4.5 km spatial resolution. This data set was used for a coarse scale description of the coastal primary production dynamics. Data sets are available in HDF from the NASA Goddard Space Flight Centre Distributed Active Archive Centre (GSFC DAAC) 2.1.3.

As with the SST data, there is a similar strip along the coastline where chl a data is unavailable. Furthermore, there is the possibility of bias in these data due to inaccuracy caused by riverine input and suspended sediments in the water column (Walters and Schumann 1985). There is, unfortunately, no way of verifying the accuracy of the ocean colour satellite imagery at present, although new research initiatives are being made to quantify this inaccuracy across the region and to modify the algorithms that are used to determine chl a concentration. Despite these apparent problems, remotely sensed chl a data could potentially be used to predict sardine presence and its usefulness is examined in this thesis. In mitigation of the above problems, the majority of the sardine run data were acquired during the dry season when the inflationary effect of terrigenous input should be at a minimum (Carter and Schleyer 1988; Malan and Schumann 1979).

Other environmental data used in these analyses include oceanographic measurements made by KZNSB field staff along the KZN coastline and the use of archived climate data, obtained from the South African Weather Service. The influence of environmental and biological variables upon sardine distribution along the KZN coastline are investigated using multivariate statistics, Generalised Linear Models (GLM) and Generalised Additive Models (GAM).

Data Collection:

During this research I participated in the collection or collation of the data for each of the five stand-alone papers. In the broad scale aerial surveys of Chapter 2, I participated in two of the twenty years of data collection. In the investigation into sardine nearshore distribution along the KZN coastline of Chapter 3, I collated all data from the KZNSB and the South African Weather Service. For the FRS *Africana* survey of Chapter 4, I collated all predator and remotely sensed data. For the fine scale aerial surveys of Chapter 5, I collected two of the three years' data and for the cliff surveys of chapter 6 I collected all of the data.

Aims of the Research

Firstly, this study aims to describe the coarse and fine scale spatio-temporal distribution of sardines and their predators along the Eastern Cape and KZN coastlines. This would improve the ability of custodians of this coastline to develop suitable management-related protocols regarding both conservation and exploitation (fishery and tourism) of the fauna involved in the sardine run.

The spatio-temporal distribution will be compared to oceanographic conditions to determine the role these conditions have in regulating the timing and intensity of the sardine run. It is envisaged that satellite imagery will become a useful tool for predicting sardine presence along the east coast, particularly the arrival of sardines along the KZN coastline in future years. An ability to correlate these remotely sensed data to the sardine run, and hence make predictions of sardine movement, would be valuable to organisers of sardine run tourism marketing ventures, the small beach-seine fishery targeting sardines, and to the KZNSB in ensuring the timely removal of their nets ahead of increased predator activity associated with this phenomenon.

The actual biomass of sardines moving up the coast each year is unknown, although Armstrong *et al.* (1991) estimate that it is approximately 13 % of the total sardine biomass. Regular hydro-acoustic surveys are prohibitively expensive for what appears to be a relatively small proportion of the standing stock of sardines on the SE coast of South Africa and which is of limited economic value. Additionally, the irregular timing of the event and requirement for long-term reservations of ship time imply that regular hydro-acoustic surveys are unlikely to occur. The opportunity to participate on one such survey in 2005, at the initiation of this research project, therefore presented a unique chance to collect data on the offshore extent and distribution of the fish and associated predators during the sardine run. These data provide further understanding of the movements of sardines and their predators up the east coast of South Africa, the relative proportions of the total biomass and whether the nearshore activity generally considered as the ‘sardine run’ is as important a biological event as has been previously hypothesised.

A final aim is to investigate the relationship between predators of the sardine run, specifically between gannets and dolphins, and whether they are passively accumulating at a shared resource (sardines), or whether the presence of one species initiates a change in behaviour of the other species. This investigation will progress on to fine-scale research into the feeding dynamics of these predators using underwater video analysis. The latter is intended to be conducted as follow-up work upon conclusion of this Ph.D thesis.

CHAPTER TWO

An investigation of broad-scale distribution patterns of sardines and their predators in relation to remotely sensed environmental conditions.

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ABSTRACT

The annual movements of sardine, *Sardinops sagax*, and their predators up the east coast of South Africa during the sardine run was investigated via aerial surveys from 1988 to 2005, and compared with remotely sensed SST and chl a data. Sardine sighting rates were highest within the Waterfall Bluff Bight, where conditions appeared to be most favourable. Sardine and predator sightings decreased significantly northwards of Mdoni on the KZN coast, while the proportion of nearshore sightings increased. The causal mechanism of the inshore aggregation by sardines is suggested to be the influx of warm Agulhas Current water from the Durban Eddy. Cape gannet, *Morus capensis*, common dolphin, *Delphinus capensis*, and sardine distributions were associated. There was a clear increase in bottlenose dolphin, *Tursiops aduncus*, sightings upon commencement of the sardine run. These dolphins were considered to consist of a migratory stock that enters KZN waters every winter and joins the resident stock there. SST was associated with sardine and predator distribution. These results form part of a growing body of knowledge addressing the need to understand the sardine run as a phenomenon and its value to the east coast ecosystem.

KEY WORDS: bottlenose dolphin, Cape gannet, chlorophyll a, common dolphin, *Delphinus capensis*, environment, MODIS, *Morus capensis*, remote sensing, sardine run, *Sardinops sagax*, SST, *Tursiops aduncus*

INTRODUCTION

The annual movement of South African Sardine, *Sardinops sagax*, (Jenyns 1842) up the east coast of South Africa remains a poorly understood phenomenon. Scientific information pertaining to the spatial and temporal distribution of sardines and their predators, including migratory dolphin and seabird species, during the sardine run is scarce, yet this spectacular marine event rivals the Serengeti wildebeest migration in terms of predator concentration, and has become a mainstay of tourism-related activities during the past ten years.

Sardines occur across the Agulhas Bank off the southern African south and west coasts throughout the year. Two to three year old fish occupy deeper water towards the edge of the continental shelf and younger fish, i.e. the one year cohort, occupy shallower water, often in bays from November to March (Armstrong *et al.* 1987; Barange *et al.* 1999). With the onset of winter, sardines move eastwards along the continental shelf and usually reach the KwaZulu-Natal (KZN) coastline by July (O'Donoghue *et al.* in press). Armstrong *et al.* (1991) proposed that the sardine run is initiated as an extension of the sardine's habitable range due to the seasonal cooling of the South African east coast inshore waters to the sardine's preferred temperature range, which Barange and Hampton (1997) reported as being between 14 and 20 °C. Along the South African east coast the continental shelf narrows considerably (Fig. 1A), with shelf waters heavily influenced by the warm, southward-flowing Agulhas Current (Schumann 1987). Sardines are thought to utilise a thin strip of cool water that stretches up the South African east coast shorewards of the Agulhas Current. This thin strip is frequently visible in infra-red satellite imagery. In the absence of sub-surface measurements, data from satellite imagery becomes the only available source of information to create a large-scale, time-series set of sea surface temperature (SST) conditions during the sardine run.

South African east coast shelf waters are characteristically nutrient-poor, although it is thought that two persistent, topographically-induced upwelling cells, one located in the Natal Bight off the KZN North Coast and the other off Port Alfred (Fig. 1A), drive the pelagic ecosystem (Beckley and Hewitson 1994; Lutjeharms *et al.* 2000a). Primary production is enhanced due to the retention of nutrient-enriched upwelled water within gyres associated with these upwelling cells (Lutjeharms *et al.* 2000b; Meyer *et al.* 2002). Between these two gyres the coastline appears largely straight with little upwelling, nutrient enrichment or retention of primary productivity. Consequently, conditions for sardine occupation are poor.

However, Whillier (1962) investigated current structures within gentle convolutions of the coastline and concluded that small-scale gyres could exist, potentially allowing for retention of primary productivity and providing refuge for sardines from the Agulhas Current. One example is the westward inflection of the coastline forming the Waterfall Bluff Bight (Fig. 1D). Here the Agulhas Current is located further offshore (Schumann 1987), while seabed sedimentation patterns are suggestive of northward flowing inshore counter-currents (Flemming 1980), typically associated with topographically-induced upwelling cells (Gill and Schumann 1979). Whether sardines preferentially inhabit these areas, and what effect these areas have upon the retention of primary production, is currently not known.

Since 2001, the sardine run has been promoted as a tourist attraction on the KZN Lower South Coast (Fig. 1C). However, marketing efforts are hampered by the unpredictable nature of the sardine run, which in latter years has frequently failed to reach the KZN coastline (O'Donoghue *et al.* op cit.). An improved understanding of the sardine run would help with predicting the timing of a run, or of non-event years, which would be a useful tool for planning marketing strategies.

This paper aims to advance the current understanding of the spatial and temporal distribution patterns of sardines and their predators in relation to environmental factors. We have therefore compiled a SST and chl a concentration time-series data set from satellite images to investigate the relationship between these variables and sardine distribution along the east coast, including Waterfall Bluff.

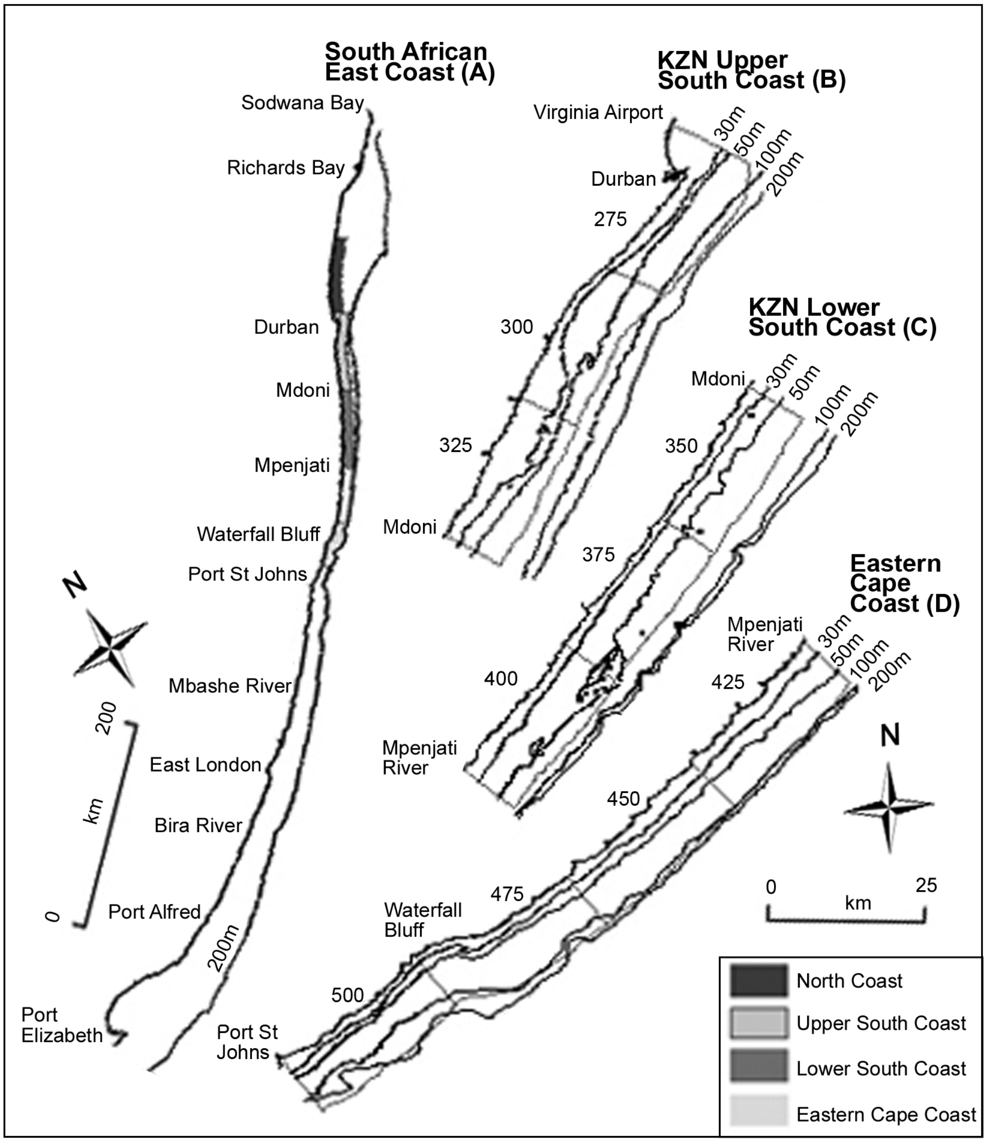


Figure 1. South African East Coast (A) showing the 200 m isobath, the KwaZulu-Natal / Eastern Cape border (dashed line) and the widening of the continental shelf north of Durban known as the 'Natal Bight'. In four shades of grey scale are the four coastal zones into which data were classified for analyses. Three of these zones (B – D) show the 30, 50, 100 and 200 m isobaths and the ~ 25 km segments (numbered) used to calculate standardised sighting rates, with numbers indicating each segment's relative position southwards along the survey transect from Sodwana Bay.

METHODS

Aerial surveys

Long-shore aerial surveys were conducted along the South African east coast (Fig. 1A) from 1988 to 2005 between the months of April to August. One kilometre fixed strip-width line transects were flown at approximately 175 km.h^{-1} at an altitude of 250 m, as per Leatherwood *et al.* (1982). Flight path was directly over the coastline so that two observers on the seaward side of the aircraft could observe from the back line of breakers seawards. A pilot and data recorder scanned further offshore to a distance of approximately 10 km for secondary sightings.

Upon making an observation, which consisted of sardine or predator activity, the following data were recorded: identification of species to the highest possible taxonomic level and location, count, behaviour and direction of travel. From 2003 onwards the longshore position of each sighting was recorded via GPS. Prior to this, the position of the sighting was marked upon a map. Similarly, from 2003 the angle of the sighting from the horizontal plane was recorded via a hand-held inclinometer as the sighting was perpendicular to the aircraft in order to estimate distance of the sighting offshore. Prior to 2003, the distance offshore was estimated; hence an offshore index was employed to minimise bias using the following distance classes from shore (m): 0 – 100, 101 – 1000 and > 1000.

The following environmental conditions were recorded at the commencement of each flight, and in response to any changes in conditions during the flight: atmospheric pressure, wind direction, wind speed, sea state and cloud cover. Morning transects were usually flown from north to south, which negated glare.

To estimate the depth of the water column below the sightings, a range of depth classes were obtained from 1:50 000 SAN bathymetric charts for the South African east coast. The isobaths on these charts were used to create the following depth classes (m) in this study: 0 – 15, 16 – 30, 31 – 50 and > 50. Each sighting was assigned a depth class corresponding to its locality.

Counts of groups of predators comprising 50 individuals or less were made by circling the group (if need be) until consensus was reached between the two observers. Larger group abundances were estimated by counting a sample of the entire group and multiplying up the count as per Cockcroft and Peddemors (1990).

The high concentrations of predators associated with sardine run events dramatically improved offshore detection of feeding aggregations and clearly identified the approximate longshore extent of the 'run,' as predator abundance is significantly higher where sardines are present (O'Donoghue and Peddemors, submitted).

The coastline was divided into 10 segments each approximately 25 km long x 5 km wide (segments 275 to 500 in Figure 1) to calculate a standardised sighting rate and to include sufficient samples for the estimation of environmental parameters from 4 km^2 Meteosat pixel resolution. A count of the number of sightings (per species) within each segment during each transect was divided by the length of the segment to give a sighting rate per kilometre for that segment. If the entire segment was not covered during the flight, but the distance flown within the segment was greater than 10 km, then it was considered to be representative of the segment and the sighting rate for that segment was calculated *pro rata* using the distance flown. An aerial survey was used in this analysis if at least 100 km of coastline was surveyed in a flight.

Environmental conditions

Oceanographic conditions were described using remotely sensed data. Sea surface temperature (°C) data were derived using two sets of remotely sensed images. The first set was obtained from the moderate resolution imaging spectroradiometer (MODIS) Aqua satellite. We extracted MODIS Level-1 daily satellite images on the SeaWiFS data server (http:// oceancolor.gsfc.nasa.gov /SeaWiFS.html). The Level 1 data set is part of the 33 data sets that comprise the ECS data collection (http://modis.gsfc.nasa.gov/). Daily maps from 10/05/2003 to 30/06/2006 were compiled at a 1 km scale on a cylindrical equidistant map projection. Data sets are available in Hierarchical Data Format (HDF) from the Jet Propulsion Laboratory Physical Oceanography Distributed Active Archive Centre (JPL PO.DAAC). The second set was constructed from the European Meteosat series of geostationary satellites. The Meteosat thermal sensor has poor spatial resolution of 5 km at nadir, but has a high image acquisition rate—a full view centred on 0° of longitude, is obtained every 30 minutes enhancing the chances of achieving a complete, daily SST description. Full details of the processing procedure for SST images from geostationary satellites and their application to coastal upwelling areas are given by Demarcq *et al.* (1989). Daily images were used from 01/01/1988 to 31/08/2003.

The Chlorophyll a (chl a) concentration time series was elaborated using the available seven years of chl a data (Oct 1997–2004) from SeaWiFS on board the OrbView-2 satellite. It was obtained for the study region from the Goddard Earth Sciences Distributed Active Archive Centre. These data were produced by the NASA project using the OC4 algorithm suitable for use in the coastal zone (O'Reilly *et al*. 2000), and available as a level 3 product. The data used were three-day running mean composites with approximately 4.5 km spatial resolution. This data set was used for large scale description of the coastal primary production dynamics. Data sets are available in HDF from the NASA Goddard Space Flight Centre Distributed Active Archive Centre (GSFC DAAC) 2.1.3.

Remotely sensed data were checked for outliers; values of SST > 30.0 °C and chl a concentration > 19.9 mg.m^{-3} were considered to be unrealistic based upon findings presented for this region (Heydorn *et al.* 1978; Shannon *et al.* 1984). For the purposes of these analyses only data within 10 km of the shoreline were used as there were no sightings beyond this distance. To illustrate the variability in SST and chl a concentration between years, seasons and along the east coast of South Africa, a Hovmőller plot was produced for both SST and chlorophyll a concentration.

Statistical analyses

All statistical analyses were performed using SPSS version 15. Because sighting rates per segment did not follow a normal distribution, the Kruskal-Wallis H-test was used to investigate whether there were any significant differences in sighting rates of sardines and predators between months and between the three coastal zones defined in Figure 2, namely KZN Upper South Coast, KZN Lower South Coast and Eastern Cape Coast.

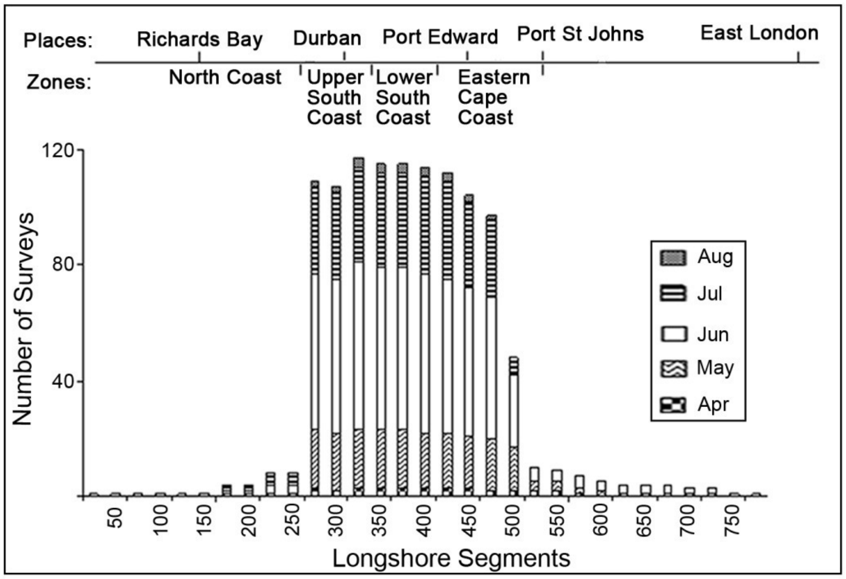


Figure 2. Total number of surveys conducted within each longshore transect segment per month. The approximate locations of towns along the survey strip, and coastal zones into which aerial survey data were divided (see Fig. 1), are superimposed above.

Counts of predators were not always conducted during surveys, as indicated by the difference between the number of sightings and the number of counts (Table 1). Analysis of changes in group size between months and between coastal zones, including the North Coast zone from Richards Bay to the Upper South Coast (Fig. 1A), was therefore conducted using only sightings for which a minimum of ten counts of group size were available for both zone and month. The Kruskal-Wallis H-test was used to test for significant differences. Because of the low number of common dolphin sightings, comparisons of group size between months were made by pooling April and May data and comparing these against pooled June and July data. Similarly, common dolphin data obtained from the Eastern Cape were pooled and compared with KZN data. The Mann-Whitney U-test was used to test the pooled data for significant differences.

Table 1. Total numbers of observations (Obs.) of sardine and their predators per coastal zone. Also given is the number of observations for which group size was determined (Counts), for which estimates of distance from shore were available (Distance), and for which both group size and distance from shore were available (Distance + Count) during aerial surveys made between April and August, 1988 - 2005.

Species	Coastal Zone	Obs.	Counts	Distance	Distance + Count
Sardine	North Coast	16	-	14	-
	Upper South Coast	90	-	64	-
	Lower South Coast	159	-	101	-
	Eastern Cape Coast	226	-	139	-
Cape Gannet	North Coast	31	24	17	15
	Upper South Coast	141	89	44	15
	Lower South Coast	489	309	153	44
	Eastern Cape Coast	577	308	243	79
Common Dolphin	North Coast	5	5	4	4
	Upper South Coast	4	1	2	0
	Lower South Coast	15	10	11	6
	Eastern Cape Coast	74	55	56	43
Bottlenose Dolphin	North Coast	32	28	11	11
	Upper South Coast	203	194	85	79
	Lower South Coast	292	267	137	117
	Eastern Cape Coast	337	301	148	121

Distance from shore was not always recorded during the surveys and is indicated by the difference between the number of sightings and the distance, (Table 1). Consequently, it was not possible to use sighting rates to investigate changes in the offshore distribution of sardines and predators along the coastline. Instead, using only sightings for which this distance or an estimate thereof was given, the percentage frequency occurrence of sardines or predators within the offshore index classes was calculated for each coastal zone. We made the assumption that sighting efficiency across the strip-width did not change along the trackline. The percentage occurrence of each species within each depth class was similarly computed. Because the Agulhas Current is found further from shore in the region from Waterfall Bluff to Port St Johns (Segment 500 in Fig. 1D) offshore distances and depths of predators observed within this region were analysed separately to the remainder of the Eastern Cape zone.

Associations between the sighting rates of sardines, predators and environmental variables were investigated using the Spearman's Rank Bivariate Correlations test. This test is appropriate when comparing a set of bivariate measurements that do not meet the assumptions of normality or homoscedasticity required for correlation tests. The data set was split by month and by coastal zone. Daily sighting rates within each zone were compared with concurrent mean SST and chl a concentration values. Any cases with missing data were excluded from the analyses.

RESULTS

Aerial surveys

A total of 121 aerial surveys were conducted over a total distance of 26 218 km, giving a mean distance surveyed per year of 1409.5 +/- 651.4 km and a mean distance per survey of 221.3 +/- 60.5 km. The years

2001, 1995 and 2003 had 14, 10 and 9 flights respectively, while 1999, 2004 and 1989 had 2, 3 and 3 flights. All other years had from 4 to 8 flights. The mean distance surveyed per month was 459.7 +/- 134.9 km.

Although the entire surveyed coastline was between Sodwana Bay and Bira River (Fig. 1A), the majority (85 %) of the surveys were conducted between Virginia Airport and Port St Johns (Figs 1 and 2). Therefore, only segments 275 to 500 were used for sighting rate comparisons.

Sightings

The number of sightings and counts that were conducted per species, and where an estimate of distance from shore was available, is given in Table 1. There were 3311 sightings, of which 2927 were identified to species level (Table 2). The following four species comprised 93% of the identified sightings, and are the focus of these analyses: South African sardine, Cape gannet, *Morus capensis* (Lichtenstein 1823), Long-beaked common dolphin, *Delphinus capensis* Gray 1828, and Indian Ocean bottlenose dolphin, *Tursiops aduncus* (Ehrenberg 1833). The lack of reliability of sightings of sub-surface predators e.g. sharks and gamefish precluded an analysis of their distribution.

Sardines were rarely directly observed, however their presence was inferred by oil slicks on the sea surface (although it is possible that these could also have come from other small pelagic fish species), dark uniformly-edged patches visible through the water column, shimmering surface eruptions as sardines escaped sub-surface predation and aggregations of gannets $\geq$ 1000 either diving or sitting on the water following feeding bouts.

Alongshore-temporal distribution

Sardines were first sighted during May along the Eastern Cape coastline (Fig. 3). Sighting rate increased significantly during June (χ^2 = 14.149; $p < 0.001$) when sardines reached the Upper and Lower South Coasts but decreased significantly northwards ($\chi^2 \geq 5.135$; $p \leq 0.023$). Sighting rates peaked during June along the Eastern Cape and Lower South Coasts and during July along the Upper South Coast. During July sighting rates did not differ between the three coastal zones ($p \geq 0.05$). Sighting rates declined thereafter with sardines not sighted on the Upper South Coast during August.

Cape gannets were sighted within each coastal zone from May to July (Fig. 3), although the two gannet sightings along Upper South Coast during May were both in the southern-most segment. During May, sighting rate increased significantly southwards ($\chi^2 \geq 6.048$; $p \leq 0.014$). Sighting rate increased significantly in all zones from May to June ($\chi^2 \geq 10.728$; $p \leq 0.001$). During June and July gannet sighting rate was significantly lower along the Upper South Coast compared with the Lower South and Eastern Cape Coasts ($\chi^2 \geq 7.72$; $p \leq 0.005$). Gannet sighting rate within the Lower South and the Eastern Cape Coasts declined from June to July, but peaked during July on the Upper South Coast.

Gannet group size was substantially larger within coastal zones during months when sardines were present (Table 3). During June, group size along the KZN Upper and Lower South Coasts was significantly smaller than along the KZN North and the Eastern Cape Coast ($\chi^2 \geq 6.857$; $p \leq 0.009$). Mean gannet group size was greatest within all coastal zones during June but median group size along the Upper South and Lower South Coasts was significantly larger during July ($\chi^2 \geq 6.059$; $p \leq 0.014$). By July, there was no difference in gannet group size throughout the study area.

Common dolphin sighting rates ($\chi^2 \geq 4.618$; $p \leq 0.021$) and mean group size ($z = -2.871$; $p = 0.004$) were significantly higher during June/ July than during April/ May (Table 3). Along the KZN coastline, common dolphins were first sighted during June. Both sighting rate ($\chi^2 \geq 7.280$; $p \leq 0.004$) and group size ($z = -2.017$; $p = 0.044$) was significantly larger along the Eastern Cape Coast than along the KZN coastline.

Bottlenose dolphins were sighted within all coastal zones each month from April to August (Fig. 3). Sighting rates did not differ between the three zones during April and May ($p > 0.05$). From May to June, sighting rates increased along the Lower South (χ^2 = 13.782; $p < 0.001$) and Eastern Cape (χ^2 = 10.322; $p = 0.035$) coasts, with sighting rates along both of these coasts being significantly higher than along the Upper South Coast (χ^2 = 11.835; $p = 0001$). Eastern Cape and Lower South Coast sighting rates peaked during August. Sighting rates along the Upper South Coast did not differ much during any month ($p > 0.05$).

Table 2. Number of observations per species from aerial surveys flown between 1988 and 2005 for the months of April to August between Durban and Port St Johns.

Sighting type	**Species name**	**sightings**
Whale Shark	*Rhinocodon typus*	3
Devil Ray	*Mobula* spp	3
Manta Ray	*Manta birostris*	34
Shark unidentified	-	46
Sardine -assumed	*Sardinops sagax*	634
East Coast Roundherring	*Etrumeus teres*	1
Small shoaling fish	-	23
Garrick	*Lichia amia*	1
Queen Mackerel	*Scomberomorus plurilineatus*	8
Predatory fish	-	7
Loggerhead Turtle	*Caretta caretta*	2
Turtle unidentified	-	24
Cape Gannet	*Morus capensis*	1195
Cape Cormorant	*Phalacrocorax capensis*	1
Skua, gull or tern	-	4
Birds unidentified	-	1
Humpback Whale	*Megaptera novaeangliae*	108
Southern-right Whale	*Balaena glacialis*	4
Minke Whale	*Balaenoptera acutorostrata*	6
False Killer Whale	*Pseudorca crassidens*	1
Whale unidentified	-	34
Common Dolphin	*Delphinus capensis*	114
Bottlenose Dolphin	*Tursiops aduncus*	830
Humpback Dolphin	*Sousa plumbea*	8
Spotted Dolphin	*Stenella attenuata*	1
Rissos Dolphin	*Grampus griseus*	1
Dolphin unidentified	-	194
South African Fur Seal	*Arctocephalus pusillus p.*	11

Bottlenose dolphin group size (Table 3) did not change significantly between zones from April to May ($p > 0.05$). During June, group size increased within each zone southwards from the Upper South Coast ($\chi^2 \geq 6.428$; $p \leq 0.011$). Group size increased along the Upper South Coast during June ($\chi^2 = 6.428$; $p < 0.011$) and again during July ($\chi^2 = 4.071$; $p < 0.044$). During July, Upper South Coast group size was significantly larger than North Coast group size ($\chi^2 \geq 8.773$; $p \leq 0.003$), and not different from Lower South Coast group size, but smaller than Eastern Cape Coast group size ($\chi^2 = 5.672$; $p < 0.017$). By August there was no significant difference in bottlenose dolphin group size from the Upper South to the Eastern Cape Coasts. Group size did not change along the North Coast ($p > 0.05$).

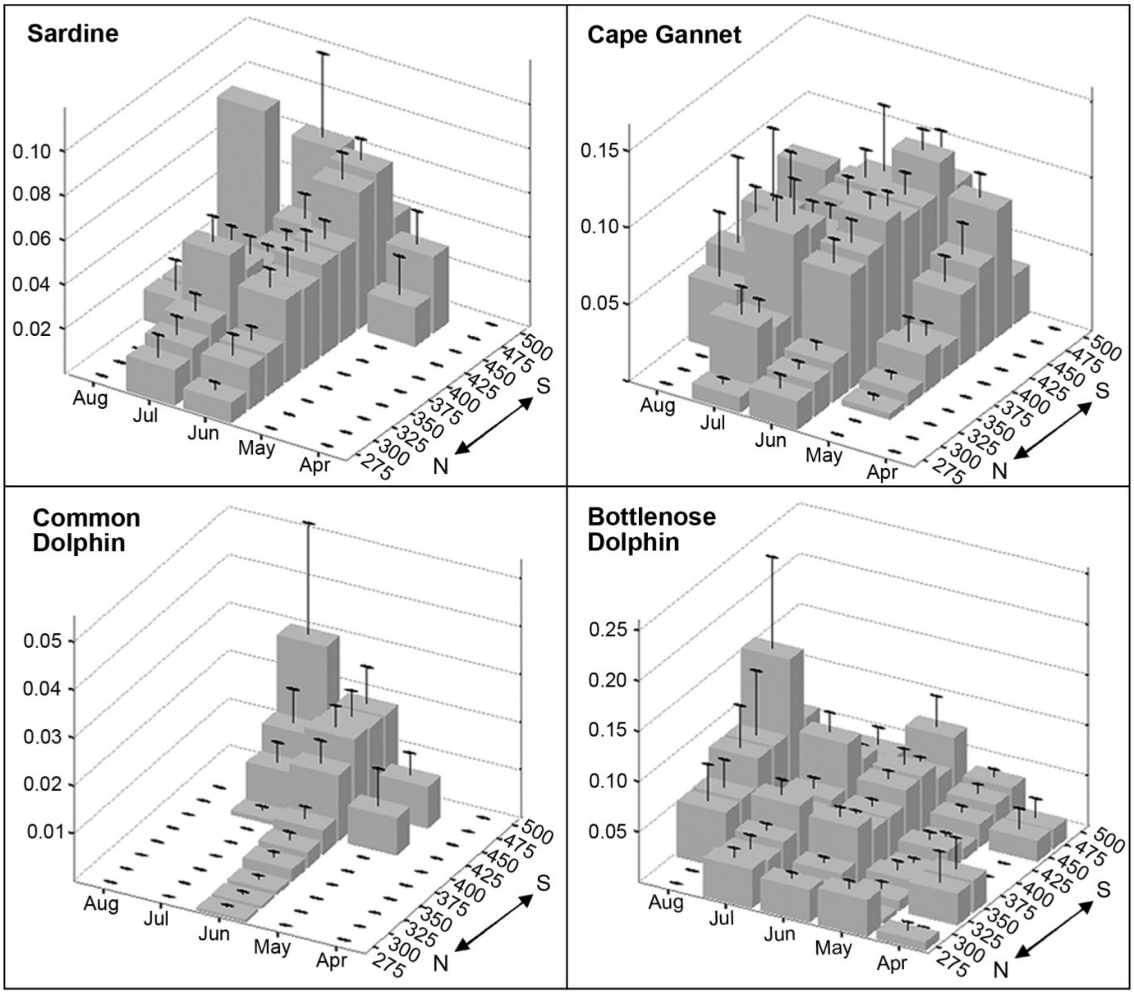


Figure 3. Mean sardine and predator sighting rates (sightings per km) per year from 1988 to 2005 against month (x-axis) and longshore segment (y-axis). Segments 275 – 325 = Upper South Coast, 350 – 400 = Lower South Coast and 425 – 500 = Eastern Cape Coast, of which segments 475 – 500 were from Waterfall Bluff southwards. Error bars denote 1S.E.

Table 3. Descriptive statistics of predator group size per coastal zone per month derived from aerial surveys between Durban and Port St Johns from 1988 to 2005.

Species	Zone	Month	N =	Mean	Std. Dev.	Median	Max
Cape Gannet	North Coast	Jun	12	1090.0	956.3	1000	3000
		Jul	12	174.0	213.0	150	750
	Upper South Coast	Jun	61	200.0	807.0	8	4500
		Jul	27	61.2	61.8	40	250
	Lower South Coast	May	10	6.1	5.9	4	20
		Jun	176	191.0	739.6	17	6000
		Jul	106	128.7	320.7	40	3000
		Aug	15	3.6	3.0	3	12
	Eastern Cape Coast	May	67	255.5	688.6	8	4000
		Jun	154	1082.4	2251.2	100	15 000
		Jul	79	259.0	689.9	50	4000
		Aug	8	6.1	6.6	4	20
Common Dolphin	KZN	-	16	661.6	703.3	600	2500
	Eastern Cape	-	57	1412.5	1385.0	800	5000
	-	May	7	244.3	211.1	300	500
	-	Jun/Jul	66	1354.3	1323.3	800	5000
Bottlenose Dolphin	North Coast	Apr	6	34.2	23.3	30	80
		Jun	10	149.9	200.9	63	650
		Jul	12	27.7	36.0	13	135
	Upper South Coast	Apr	8	17.1	16.4	12	50
		May	20	24.3	17.7	20	80
		Jun	104	65.0	95.6	35	600
		Jul	55	80.0	95.4	50	603
		Aug	7	58.9	37.9	43	106
	Lower South Coast	Apr	4	13.5	11.5	10	30
		May	21	35.4	34.9	28	150
		Jun	146	84.8	90.0	54	600
		Jul	81	115.2	184.6	51	1230
		Aug	15	84.6	79.4	38	240
	Eastern Cape Coast	Apr	3	30.0	21.8	20	55
		May	44	67.7	86.3	31	350
		Jun	149	165	220.4	75	1280
		Jul	89	226.8	372.0	80	2500
		Aug	16	129.8	96.6	100	380

Offshore distribution

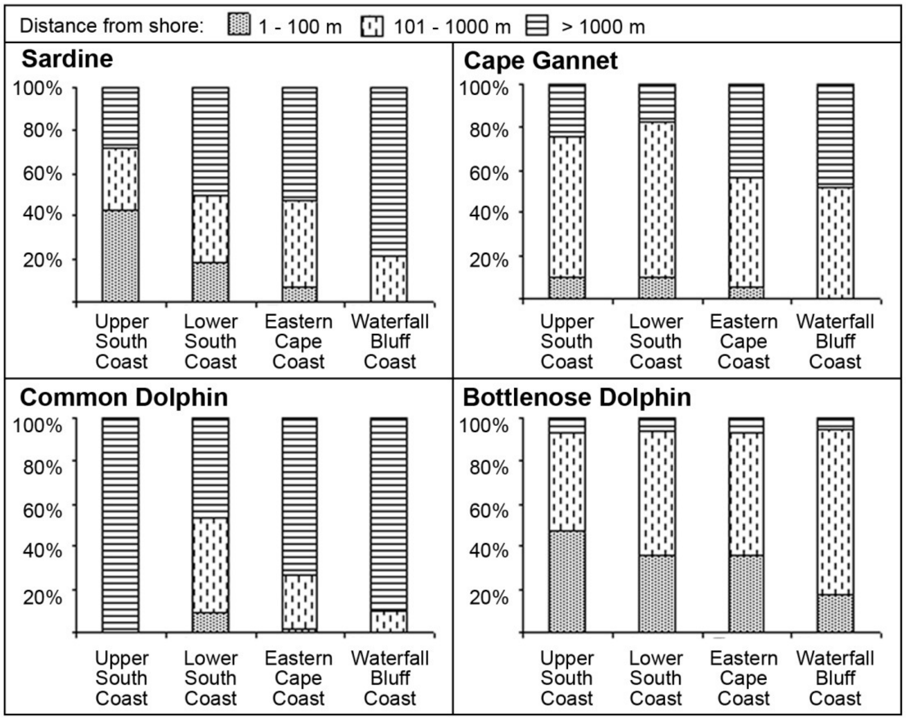
Sardines were sighted closer to shore in the north (Fig. 4). Off the Upper South Coast 43 % of sardine sightings were within 100 m of the shoreline, while only 28 % were beyond 1000 m from shore. This is diametrically opposed to the region south of Waterfall Bluff, where no sardines were seen within 100 m and 79 % of the sightings were beyond 1000 m from shore.

In all four zones, between 51 and 72 % of gannet sightings were between 100 and 1000 m from shore (Fig. 4). Although sightings > 1000 m from shore increased with increasing latitude, the trend was less pronounced when compared with sardine sightings. Less than 10 % of gannet sightings were within 100 m of the shore.

Common dolphins were sighted further from the shore than the other species (Fig. 4). There was some evidence of common dolphins occurring closer to shore with decreasing latitude, although all sightings off the Upper South Coast occurred > 1000 m from shore. The percentage frequency of common dolphins within 1000 m of the shore increased from 10 % off Waterfall Bluff to 54 % off the Lower South Coast, of which 9 % were within 100m. Mean group size for common dolphins > 1000 m from shore was 1524.9 +/- 1248.3 (n = 28). This was significantly larger (z = -2.598; p = 0.009) than mean group size within 1 km of the shore, which was 823.6 +/- 1217.6 (n = 11).

At least 95 % of the bottlenose dolphin sightings were within 1000 m of the shore in all four coastal zones (Fig. 4). To the north of Waterfall Bluff, 36 % of bottlenose dolphin sightings were within 100 m of the shoreline. To the south this declined to 18 %.

Figure 4. Percent relative frequency of the occurrence of sardine and predator sightings within three distance classes from shore within the four coastal zones. Waterfall Bluff is a sub-zone of the Eastern Cape zone (see Figs 1 and 2).



Depth distribution

The frequency of occurrence of sardine sightings in water depths greater than 30 m declined from 67 % off Waterfall Bluff to 15 % along the Upper South Coast, where 45 % of sightings were in water depths of less than 15 m (Fig. 5). Along the entire KZN South Coast, 86 % of gannet sightings were in water depths of less than 30 m. This declined to 40 % off Waterfall Bluff.

Between 62 and 100 % of the Eastern Cape common dolphin sightings were in water depths greater than 30 m. This declined to 33 % along the Lower South Coast (Fig. 5). For bottlenose dolphins, less than 6 % of the sightings north of Waterfall Bluff were in water depths of greater than 30 m (Fig 5). South of Waterfall Bluff this increased to 21 %.

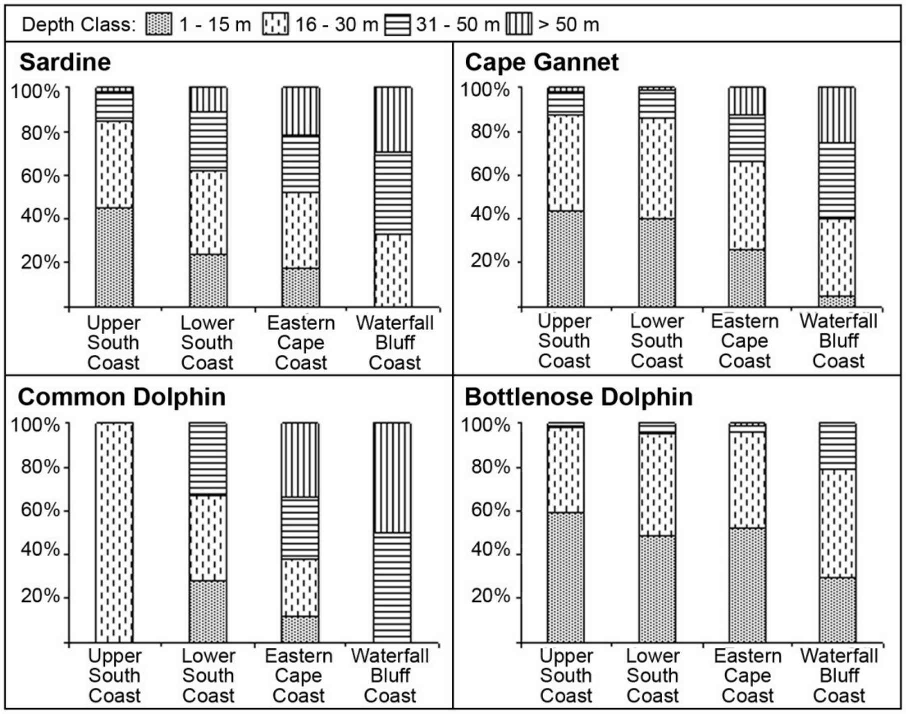


Figure 5. Percent relative frequency of the occurrence of sardine and predator sightings within four water column depth classes within the four coastal zones. Waterfall Bluff is a sub-zone of the Eastern Cape zone (see Figs 1 and 2).

Environmental conditions

Sea surface temperature within 5 km of the shoreline decreased significantly each month from April to August ($\chi^2 \geq 28.751$; $p \leq 0.001$) and southwards within each coastal zone ($\chi^2 \geq 12.956$; $p \leq 0.001$). This is evident in the Hovmőller plot from around June (Fig. 6) with winter cooling most pronounced from the Eastern Cape Coast southwards. The cooler temperatures associated with the Port Alfred upwelling cell are clearly apparent, with considerable variability between years in the strength and northward extent of the winter cooling; between 1999 to 2002 this cooling was only weakly evident beyond East London. Along the Upper South Coast, SST was highest in the segment immediately north of Mdoni ($\chi^2 = 10.302$; $p = 0.006$). Water temperature below 21 °C was only recorded once (in 2003) in this region during the time series.

Chl a concentration within 5 km of the shoreline was highest during the summer months from Mbashe River southwards (Fig. 7). Conversely, along the Lower and Upper South Coasts chl a concentration was lowest during the summer months. Generally the chl a concentration varied less in these two regions during the winter compared with the summer. Between Mbashe River and Waterfall Bluff, chl a concentration varied considerably between years.

There was a significant increase in chl a concentration within each of the three coastal zones from April to July ($\chi^2 \geq 4.420$; $p \leq 0.036$), but no differences occurred from July to October ($p > 0.05$), following which, concentrations usually decreased to below 0.5 mg.m^{-3}. During June and July, chl a concentration decreased from Mbashe River northwards, with significantly lower concentrations between Waterfall Bluff and Durban compared with south of Waterfall Bluff ($\chi^2 = 25.172$; $p < 0.001$).

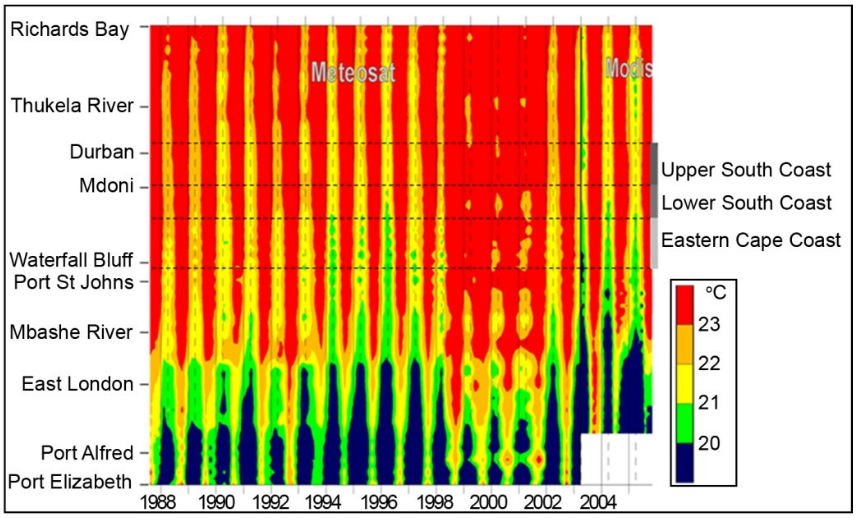


Figure 6. Sea surface temperature (℃) from 1988 to 2005 (x-axis) between Port Elizabeth and Richards Bay (y-axis). The solid and dashed vertical lines denote the 1st of June and September respectively for that year. Data prior to 2003 were derived from Meteosat images, and subsequently from MODIS. The coastal zones in the study area are indicated by horizontal dashed lines and the three greyscale boxes on the right axis. Figure reproduced with permission from Fréon *et al.* (in press).

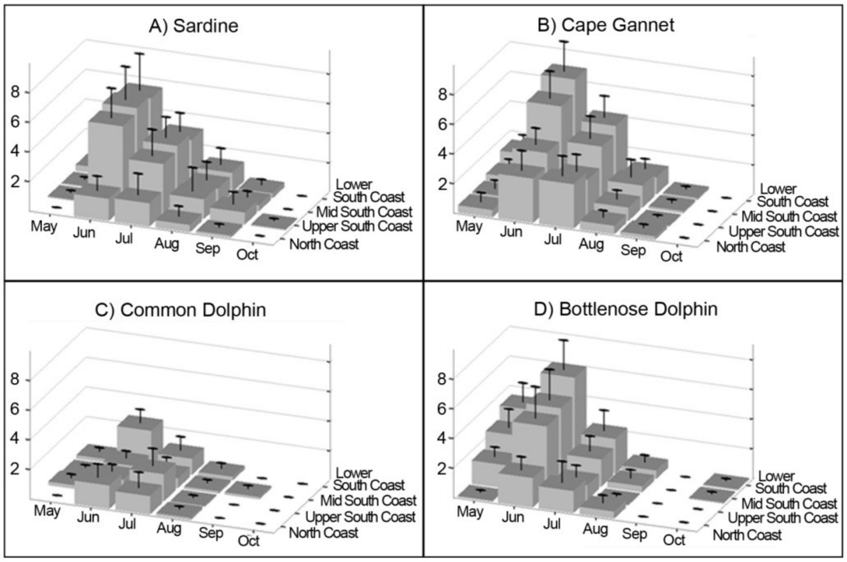


Figure 7. Chlorophyll a concentration (mg.m^{-3}) from 1998 to 2005 between Port Elizabeth and Richards Bay. The solid and dashed vertical lines denote the 1st June and September respectively for that year. The longshore extents of the coastal zones in the study area are shown with horizontal dashed lines and in the three greyscale boxes on the right axis.

Biological and environmental associations

From May to July along the Eastern Cape and the Lower South coasts, sardine, Cape Gannet and common dolphin sighting rates were significantly associated (Table 4). Gannet and sardine sighting rates were significantly associated during all months in every zone. Bottlenose dolphin sighting rate was significantly associated with sardine and gannet sighting rates during June, and along the Upper and Lower South coasts.

Sardine and gannet sighting rates were significantly, inversely associated with SST during May and June respectively (Table 4). The following species' sighting rates were significantly inversely associated with SST: sardines along the Upper South Coast, gannets along all three zones, and bottlenose dolphins from the Lower South to the Eastern Cape Coasts. Sardine sighting rate was significantly associated with chl a along the Lower South Coast.

Table 4. Spearman's Rank correlations between day-scale sardine and predator sighting rates and concurrent remotely sensed environmental variables. Data are separated into coastal zones and months. Variables: SST – sea surface temperature (°C), CHL – chlorophyll a concentration (mg.m^{-3}).

Associations across all months within zones:				
Zone	**Var1**	**Var2**	**p =**	**r =**
Upper South Coast	Sardine	SST	0.050	- 0.206
	Gannet	Sardine	< 0.001	0.512
	Gannet	SST	< 0.001	- 0.371
	Bottlenose Dolphin	Sardine	0.021	0.220
Lower South Coast	Sardine	CHL	0.023	0.363
	Gannet	Sardine	< 0.001	0.563
	Gannet	Common Dolphin	0.001	0.317
	Gannet	Bottlenose Dolphin	< 0.001	0.402
	Gannet	SST	0.002	- 0.312
	Common Dolphin	Sardine	< 0.001	0.347
	Bottlenose Dolphin	Sardine	< 0.001	0.385
	Bottlenose Dolphin	SST	0.016	- 0.241
Eastern Cape Coast	Gannet	Sardine	< 0.001	0.564
	Gannet	Common Dolphin	< 0.001	0.368
	Gannet	SST	0.015	- 0.248
	Common Dolphin	Sardine	< 0.001	0.398
	Bottlenose Dolphin	SST	0.032	- 0.220
Associations across all zones within months:				
Month	**Var1**	**Var2**	**p =**	**r =**
May	Sardine	SST	0.002	- 0.423
	Gannet	Sardine	< 0.001	0.475
	Gannet	Common Dolphin	0.007	0.345
	Common Dolphin	Sardine	< 0.001	0.454
June	Gannet	Sardine	< 0.001	0.549
	Gannet	Common Dolphin	< 0.001	0.411
	Gannet	Bottlenose Dolphin	< 0.001	0.317
	Gannet	SST	< 0.001	- 0.318
	Common Dolphin	Sardine	< 0.001	0.401
	Bottlenose Dolphin	Sardine	< 0.001	0.336
Jul	Gannet	Sardine	0.001	0.455
	Gannet	Common Dolphin	0.014	0.269
	Common Dolphin	Sardine	0.042	0.223
Aug	Gannet	Sardine	0.018	0.759

DISCUSSION

Aerial surveys were conducted using standardized methods developed for cetacean surveys in this region (Cockcroft and Peddemors 1990; Cockcroft *et al.* 1992; Ross *et al.* 1989). The 1 km strip width would have resulted in some missed sightings offshore due to the decrease in sighting efficiency with increasing distance from the transect line. We assumed that the decrease in sighting efficiency was constant over time and along the entire surveyed coast, due to the standardised methods used. A decrease in sighting efficiency would mean that smaller groups would not have been seen offshore, resulting in an apparent bias for larger groups offshore. There was no evidence of this for gannets and bottlenose dolphins, but common dolphin group size did decrease along the KZN coastline, which raises the possibility that some sightings of smaller groups further than 1 km from shore may have been missed. It was not possible for us to account for this possibility with the methodology that we employed.

Environmental conditions

Temporal and spatial patterns of sea surface temperature and chlorophyll a concentration reported in this study are comparable with those previously recorded along the east coast (Lutjeharms *et al.* 2000b; Pearce *et al.* 1978; Schumann 1987). The high chl a concentration associated with the two upwelling cells at Cape St Lucia and Port Alfred have been well documented previously (Carter and Schleyer 1988; Lutjeharms *et al.* 1989, 2000b), although the values reported in our study are slightly higher. When measurements within 5 km of the shoreline were excluded, our results are similar to those reported by the above authors.

An investigation into the accuracy of ocean colour products in this region is currently being planned to quantify the inflationary effect that pixel-contamination by land or riverine input (Walters and Schumann 1985) have upon remotely sensed chl a concentrations. The majority of the sardine run data were acquired during the dry season, when terrigenous input is usually at a minimum (Lutjeharms *et al.* 1989; Malan and Schumann 1979). Given the above, we believe that these data are the best available representation of chl a in the study area.

Sardine distribution

Sardine arrival corresponded with the seasonal cooling of inshore waters along the coast, as has been previously reported (Baird 1971; Barange *et al.* 1999; Crawford 1981). Sardine spatio-temporal distribution and their inverse association with SST are consistent with the range-extension hypothesis of Armstrong *et al.* (1991). The inverse association between sardines and SST occurred during May and along the Upper South Coast, i.e. where or when SSTs were warmest, suggesting limitation to sardine distribution due to sea temperature.

The peak in sardine sighting rates and distance from shore southwards of Waterfall Bluff, combined with the significantly cooler SST and higher chl a concentration values in this region, support the hypothesis that the Waterfall Bluff Bight provides the most suitable habitat for sardines within our study area. This would be due to the Agulhas Current flowing further from shore.

The decrease in sardine sighting rate in the Mdoni area, and the peak in rates immediately south of this region during July, suggest that sardine northward movement is constrained here. The pronounced sardine movement towards shore in this region has also been reported by O'Donoghue *et al.* (op cit.) and occurred during the 2005 FRS *Africana* hydroaccoustic survey, where sardines were only detected by the inflatable boat deployed to survey shallow water within a kilometre of the shoreline (Coetzee *et al.* in press).

To explain this concentration of sardines close to the shore on the Upper South Coast, it is necessary to consider several possibilities. KZN alongshore SST, measured up to 10 km from shore, peaked along the Upper South Coast (see Fig. 5 in Chapter 3). In this region, a cyclonic lee-eddy, termed the Durban Eddy, draws warm Agulhas Current water, with a mean regional winter temperature of 23 °C (Christensen 1980), onto the shelf to within at least 6 km from shore (Pearce *et al.* 1978; Schumann 1982). Concurrent SST measurements, from shark netting installations protecting the KZN coastline (approximately 300 – 500 m from shore), revealed a similar peak in mean SST in the Mdoni region (Cliff *et al.* 1989; O'Donoghue *et al.* op cit.), although mean SST was slightly lower, i.e. below 21 °C, than that reported from the satellite imagery presented in this study. It would appear that this increase in SST at the shark nets is related to the increase in SST from the shoreward-flowing Durban Eddy, although suitable oceanographic measurements are needed to confirm this.

Along the Upper South Coast, the dominant inshore current direction is from south to north (Schumann 1982). This should provide sardines with respite from the physical exertion of swimming against the southward-flowing Agulhas Current. If current avoidance was the reason for sardine shoreward movement along the Upper South Coast, then one would expect sardines to be relieved of this constraint at Mdoni. Similarly, if shoreward movement was due to predators, then sardines should be freed of this latter constraint from Mdoni northwards (ignoring the possible influence of predation from other predators such as sharks and gamefish). We believe that the most probable scenario is that the sardines are forced shorewards as they encounter the warm, oligotrophic Agulhas Current water brought inshore by the Durban Eddy, and that this restricts their northward movement. Our data suggest that sardine northward movement is usually over by July with a decline in sighting rate occurring from July to August. This is consistent with the findings of O'Donoghue *et al.* (op cit.).

There was little association between chl a concentration and sardine sighting rates. This is hardly surprising as primary productivity in this region is highly variable both spatially and temporally (Carter and Schleyer 1988) and occurs on different scales to those used in this study. Additionally, only surface chl a concentration was measured via satellite, and subsurface chl a maxima, which may be more closely associated with sardine distribution than surface chl a, may occur in these regions. Despite these limitations, however, it is apparent that food availability (as represented by chl a concentration) north of Waterfall Bluff is lower than further south.

Predator distribution

Cape gannets are non-breeding winter visitors to the KZN coastline (Broekhuysen *et al.* 1961; Crawford *et al.* 1983). Their foraging distribution conforms to sardine distribution on the southern and western South African Coasts (Crawford 1996; Crawford and Shelton 1981, Pichegru *et al.* 2007), whilst the dietary importance of sardines has been well documented (Batchelor and Ross 1984; Klages *et al.* 1992) with sardines accounting for 72 % of the Cape gannet diet on the east coast (Crawford *et al.* 2005). Although gannets were sighted further up the coastline earlier than sardines, they were the only species that was associated with sardines within every zone and during each month, and they emerge as the primary biological indicator of sardine presence. Gannet and sardine distribution did, however, diverge along the KZN Upper South Coast nearshore, which may be a behavioural response to the difficulty posed by foraging within the shallow surf zone, in terms of prey visibility and plunge-diving onto the shallow benthos.

Common dolphins only occur inshore along the east coast during the winter months, when they appear to follow the sardine run (Peddemors 1999). The increase in common dolphin group size along the Eastern Cape Coast during June and July occurred in tandem with the arrival of sardines. Group size was comparable to that reported by Cockcroft and Peddemors (1990). It seems likely that the large groups sighted across the Waterfall Bluff Bight split up into smaller groups along the KZN coastline, possibly to forage efficiently on smaller shoals of sardines concentrated close to the shoreline. Such changes in foraging strategy corroborate a hypothesis that pelagic dolphins feeding on shoaling fish in the open ocean, i.e. across the continental shelf south of Waterfall Bluff, require large group sizes to efficiently find their prey, while dolphins living in shallower nearshore environments forage in smaller groups (Norris and Dohl 1980).

The resident status of bottlenose dolphins throughout the study area (Cockcroft *et al.* 1991) and their nearshore distribution (Ross *et al.* 1987) resulted in them being sighted during every month of the survey. The similarity of group size between the zones is typical for resident bottlenose dolphins along this coast (Ross *et al.* 1989). The increase in both sighting rate and group size from June to August on the Lower South and Eastern Cape coasts, but with no increase in sighting rate along the Upper South Coast and no increase in group size along the North Coast, suggests an influx of dolphins from somewhere south of Port St Johns. This has been proposed by Peddemors *et al.* (submitted), and is substantiated by the peak in bottlenose dolphin catches occurring within the NSB shark nets from June to October (Cockcroft 1990). A 'migratory stock' has been identified as being genetically distinct from resident KZN bottlenose dolphins (Natoli *et al.* 2008), and is the likely cause of increased sighting rates and group sizes reported in our study.

Of the three predators, bottlenose dolphin distribution was least similar to sardine distribution. In KZN, bottlenose dolphins feed upon a wide range of prey species (72 species found in stomach contents), but of these, six species constituted over 60 % by mass of bottlenose dolphin diet (Cockcroft and Ross 1990). Sardines did not comprise a major portion of bottlenose dolphin diet, hence their seemingly lower dependence upon sardines as a source of food in this study. However, the significant association between bottlenose dolphins and sardines does support the suggestion that the migratory stock may either prey upon sardines or other fishes associated with the sardine run e.g. elf, *Pomatomus saltatrix* (Peddemors and Cockcroft 1997; Fennessey *et al.* submitted). To resolve this, any investigations of bottlenose dolphin stomach contents should, if possible, differentiate between the migratory and resident stocks.

This study confirms the seasonal nature of the sardine run as well as the association between sardine distribution and SST. Changes in sardine distribution along the east coast have been described in detail, especially in the Waterfall Bluff and Mdoni regions. It is apparent, however, that the sardine run as a phenomenon is already fully constituted upon reaching Port St Johns. Fine scale aerial surveys along the Eastern Cape coastline are, therefore, being undertaken in an attempt to broaden knowledge pertaining to this important ecological event in this region.

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CHAPTER THREE

The KwaZulu-Natal sardine run: shoal distribution in relation to near-shore environmental conditions, 1997 to 2007

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ABSTRACT

The nearshore presence of South African sardine, *Sardinops sagax*, along the KwaZulu-Natal (KZN) coast was investigated using sightings data collected by the KZN Sharks Board from 1997 to 2007. The spatio-temporal distribution of sardines was described in relation to that of their predators and to environmental conditions, including oceanographic and atmospheric variables, and subjected to GLM and GAM analyses. Variables describing spatio-temporal conditions performed best in the models ($R^2 = 0.52$) with seasonal effects, specifically the months of June and July, having the highest probability of sardine presence. The contribution of the years 2003, 2006 and 2007, and the KZN North Coast, was significantly lower. The predator variables were highly significant ($R^2 = 0.48$) with the Cape gannet, *Morus capensis*, the sharks/ gamefish group and common dolphin, *Delphinus capensis*, respectively, most closely associated with sardine presence. Environmental variables were not as influential in the GLM models ($R^2 = 0.23$), but some variables were useful in describing conditions favouring sardine presence, namely calm current conditions, light NW landbreezes and stable atmospheric conditions. Increasing SST, moderate north to south currents, large swells and turbid water had a negative impact upon sardine presence. NE and NW winds and north to south currents had a cooling effect upon nearshore sea surface temperatures, whilst SE winds and increasing air temperatures caused nearshore warming. Results are discussed in the context of developing an understanding of the mechanisms that govern fine scale movements of sardine shoals during the run.

KEYWORDS: bottlenose dolphin, Cape gannet, common dolphin, *Delphinus capensis*, *Morus capensis*, sardines, sardine run, *Sardinops sagax*, sea surface temperature, SST, *Tursiops aduncus*

INTRODUCTION

The annual northward movement of South African sardine, *Sardinops sagax* (Jenyns 1842), along the east coast of South Africa is known as the ‘sardine run.’ The influence of biological or environmental conditions upon sardine movement along the KwaZulu-Natal (KZN) coastline remains poorly understood. Despite a lack of predictability and considerable interannual variability, its proximity to shore enables a local beach seine-net fishery to harvest sardines. The run also impacts upon the daily operations of the KwaZulu-Natal Sharks Board (KZNSB), which strives to remove the netting installations protecting KZN bathing beaches (known locally as ‘shark nets’) prior to the arrival of the predators associated with the run. An improved understanding of the sardine run, leading to better prediction of the movement of the shoals, would greatly benefit the fishery, the KZNSB and participants in a burgeoning tourism industry focused on the run.

Sardines prefer water temperatures between 14 and 20 °C (Barange and Hampton 1997). Each austral winter nearshore sea temperature along the South African south east coast drops to within this range. The seasonal nature of the sardine run, combined with the results of three hydro-acoustic surveys, led Armstrong *et al.* (1991) to hypothesise that the northward movement of sardines is a range extension controlled by temperature. Along the KZN coast, however, sardines were found in water warmer than 20 °C, leading these authors to propose that factors beside temperature may exert control over the movement of sardines along the KZN coastline, possibly including predation pressure.

The KZN coast comprises different oceanographic regions, each driven by distinct environmental forces. The shelf waters of the KZN Mid to Lower South Coasts (Fig. 1) are dominated by the warm, poleward flowing Agulhas Current, which has a mean winter temperature of 23 °C (Christensen 1980). Here current speeds in excess of 1 $m.s^{-1}$ frequently occur within five kilometres of the shore (Schumann 1981). The trajectory of the Agulhas Current is extremely stable with the current core found immediately offshore of the shelf break 80 % of the time (Beal and Bryden 1999; Gründlingh 1983). This suggests that conditions are normally unsuitable for sardine habitation along this stretch of coastline.

The effect of local wind forcing on currents appears to be minimal (Schumann 1981), although Heydorn *et al.* (1978) did postulate about the possibility of a nearshore regime, within 1 km of the coast, where longshore water movement could be driven by swell conditions. During the winter months this would amount to movement in a northerly direction as swells generated in the roaring forties travel up the coast. Sardines do move closer to shore as they travel northwards along the KZN coastline (O’Donoghue *et al.* in press, a), but whether this is in response to environmental conditions (i.e. avoidance of the Agulhas Current) or biological conditions (i.e. predation pressure) is not known.

Along the KZN Upper South Coast (Fig. 1), there is a semi-permanent cyclonic gyre termed the Durban eddy. Here warm Agulhas Current water flows onto the shelf and the dominant nearshore current direction is from south to north (Schumann 1982). This stretch of coastline is considered to be transitional from the Agulhas Current dominated shelf to the south and the wind dominated shelf to the north.

The North Coast continental shelf is considerably wider (> 40 km compared with ~ 15 km along the South Coast), with the Agulhas Current flowing further from shore. Current conditions across the shelf are subsequently a lot more variable. Wind affects current conditions, with alongshore NE or SW winds preceding the initiation of currents of a similar direction by approximately 18 hours (Schumann 1981). To the north of this region sea temperature is frequently lower and nutrient and chlorophyll a concentration frequently higher compared with the KZN south coast (Lutjeharms *et al.* 2000; Meyer *et al.* 2002). This region would therefore appear to be more suitable habitat for sardines to occupy, but the extent to which they utilise the KZN North Coast is unknown.

These distinct oceanographic regions along the KZN coastline may affect sardine movement and distribution. This study describes the spatial and temporal variability in sardine nearshore distribution between 1997 and 2007. Sardine distribution was compared with concurrent oceanographic and climate data, using generalized linear modelling (GLM) and generalised additive modelling (GAM) procedures to investigate which variables are associated with sardine nearshore presence in an attempt to improve our understanding of the sardine run.

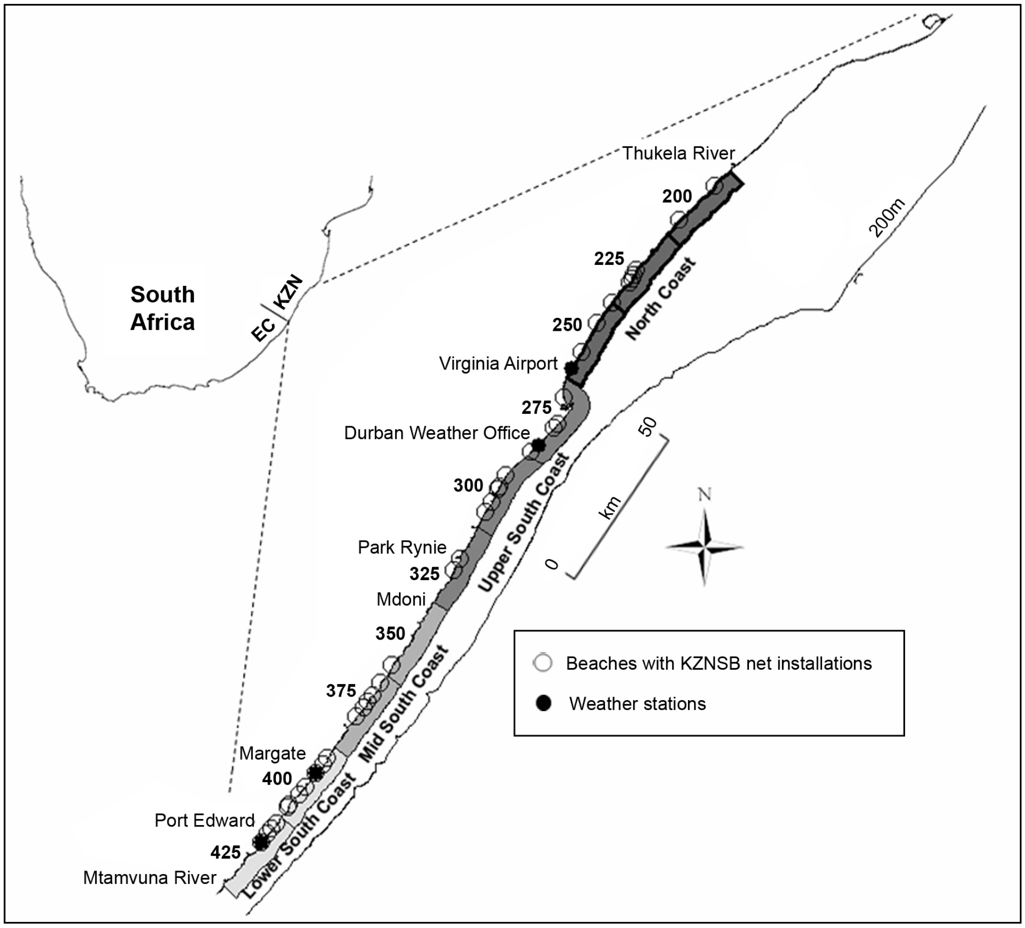

Figure 1. KwaZulu-Natal coastline showing the four coastal zones (grayscale shades with oblique labels) into which the KZN Sharks Board field staff sightings data were divided. These zones were sub-divided into smaller ~ 25 km segments (numbered) to describe SST measured at beaches with KZNSB shark net installations. Historical climate data were obtained from the weather stations. The 200 m isobath indicates the continental shelf margin.

METHODS

Sightings data

Whilst working, KZNSB field staff recorded observations of sardine run activity either from boats at the shark nets or from shore-based observation points, including the presence of sardine shoals and aggregations of predators normally associated with the shoals. Details included date, time, location, estimated distance from shore, species identification to the highest possible taxonomic level, an approximate count, behaviour and the direction of travel. When beach-seine netters landed a catch of sardine the KZNSB field staff recorded the approximate volume and value of the catch.

In this analysis sardine sightings were logged as “sardine assumed” unless a) there was confirmation of their presence in beach-seine or cast-net catches, b) there was concentrated predator feeding during a period of sardine run activity or c) there was a confirmed sardine sighting within the same vicinity and within one day of the assumed sardine sighting. If any one of the above criteria was met then an observation of “sardine confirmed” was recorded.

Only KZNSB observations recorded between the Thukela and Mtamvuna rivers were retained for analysis (Fig. 1). Sightings data were not collected systematically. To minimise bias due to variability between observers in terms of counts and reporting fidelity, all sardine and predator data were pooled into three-day periods and scored as either present or absent within the following four coastal zones in KZN (Fig. 1): North Coast (NC), Upper South Coast (USC), Mid South Coast (MSC) and Lower South Coast (LSC). These zones followed the description of the regions in the introduction, and those used in concurrent, standardised aerial survey data (O'Donoghue *et al.* op. cit., a), with which these results were compared. The only deviation from the zones used in the analysis of the aerial survey data, was the sub-division of the coastline from Mdoni to Mtamvuna River (Fig. 1) into two coastal zones (MSC and LSC). This arbitrary sub-division was made because of the length of the coastline, the high number of beaches containing shark net installations and the large number of locations at which beach-seine netting occurred (Table 1).

We assumed that sardine presence, or other sardine run activity, within any coastal zone during any three-day period was reported. This assumption was tested by comparison with the aerial survey data previously referred to (O'Donoghue *et al.* op. cit., a). The presence of sardines within any given coastal zone was recorded on 52 occasions in this study, in close agreement (96%) with the 54 occasions reported during the KZNSB aerial surveys.

Table 1. For each coastal zone in this study the following is given: the length of coastline, the number of beaches that have KZNSB shark nets and the number of beaches at which beach-seine netting was recorded.

Coastal zone	Length (km)	KZNSB net installations	Seine netting locations
KZN North Coast	75.4	8	3
KZN Upper South Coast	78.9	9	27
KZN Mid South Coast	49.8	6	21
KZN Lower South Coast	42.7	12	14

Longshore distribution per month

All three-day sighting periods of confirmed or assumed sardine presence were summed per coastal zone and per month for each year. Because these data were not normally distributed, the Kruskal-Wallis H-test was used to test for significant differences between zones and months. Predator sightings data were analysed similarly.

Distance from shore

Differences in the distance from shore of sardines and predators between coastal zones were investigated using only observations where an estimate of distance from shore was available (n = 255, 882, 909 and 1065 for the North Coast, Upper South Coast, Mid South Coast and Lower South Coast zones respectively). This distance was not measured but was estimated in relation to "backline" (the line of breakers most distant from shore) and the position of the shark nets, which are located approximately 400m from shore. Hence these reference points were used as the basis for the following three categories to which observations were ascribed: 1) less than 100 m (from shore to backline), 2) from backline to 1km offshore (approximately twice the distance of the shark nets from shore) and 3) greater than 1km from the shore. The percentage occurrence of observations within each of these three categories within each zone was then computed.

Oceanographic data

Oceanographic variables were recorded when KZNSB staff serviced the shark nets approximately twenty times per month. They included sea surface temperature (SST), measured with a hand-held thermometer accurate to 0.1 °C, water clarity (visibility) estimated in metres looking vertically down the shark net, swell height in 0.5 m increments and current direction and estimated strength (speed). Current direction was predominantly from north to south or south to north and speed was estimated as calm, light, moderate or strong.

All SST values in excess of 24 °C were compared with measurements from adjacent beaches for that day and discarded if the difference was > 2 °C. Mean SSTs from 1997 to 2007 were computed per month and per longshore coastal zone. Each zone was subdivided into smaller segments, approximately 25 km in length (Fig. 1), which correspond with those used in the KZNSB aerial survey data. This was done for comparative purposes and to improve the spatial resolution for the chart depicting mean SST per month along the coastline.

Climate data

Historical weather data from 1997 to 2007 were obtained from the South African Weather Service for the following weather stations from north to south (Fig. 1): Virginia Airport (altitude = 14 m), Durban Weather Office (14 m), Margate (154 m) and Port Edward (11 m). Their locations along the KZN coastline corresponded with the four zones from North to South respectively, except for Margate, which was marginally south of the southern border of the Mid South Coast. The conditions recorded at each weather station were assumed to be representative of conditions within each corresponding coastal zone. The following daily weather variables were available: maximum and minimum air temperature (°C), atmospheric pressure (millibars) and total rainfall (only measurements ≥ 0.1 mm were retained). Average wind speed (m.s^{-1}) and direction (10 ° increments from true north) were measured thrice daily at 08h00, 14h00 and 20h00.

GLM analyses

Sardine and predator presence was described using a suite of spatio-temporal variables (Year, Month and Coastal Zone). The influence of biological and environmental variables upon sardine presence, and the relationship between SST and other environmental variables, was investigated using generalised linear models and generalised additive models.

Due to the binomial nature of the dependent variable (sardine being present or absent) we fitted a generalised linear model. In the general linear model a response variable Y is linearly associated with values of X variables by:

$$Y = b0 + b1X1 + b2X2 + ... + bkXk + e \qquad (1)$$

where ‘e’ stands for the error variability not accounted by the predictors. In the generalized linear model the following relationship is assumed:

$$Y = g\ (b0 + b1X1 + b2X2 + ... + bkXk) + e, \qquad (2)$$

$$\text{so that: } f\ (muy) = b0 + b1X1 + b2X2 + ... + bkXk \qquad (3)$$

where ‘muy’ stands for the expected value of y where e is the error and g is the link function. In the spatio-temporal analysis the model was set with a binomial distribution of the dependent variable and a probit link function (f(z)=invnorm(z), where ‘invnorm’ is the inverse of the standard normal cumulative distribution function).

A similar modelling procedure was used to investigate the influence of the presence of sardine run predators upon sardine presence. To further explore the relationship between presence/absence of predators and sardines we used a Classification Tree analysis. This is one of the main techniques in Data Mining and its goal is to explain responses of our binomial dependent variable (sardine). The Classification and Regression Tree criteria (Breiman *et al.* 1984) for splitting the nodes were selected. This method constructs a Classification and Regression Tree to predict continuous dependent variables (regression) and categorical predictor variables (classification). Using this method, all possible splits for each predictor variable at each node are examined to find the split producing the largest improvement in goodness of fit (or equivalently, the largest reduction in lack of fit). The Goodness of fit was computed according to the Chi-square value. The Chi-square measure is similar to the standard Chi-square value computed for the expected and observed classifications (with priors adjusted for misclassification cost). The computation was conducted using Statistica 7.0. Illustration of the relative importance of each species was produced with a deviation plot at each node. Although humpback whales were not considered to be closely associated with the 2005 sardine run during ship-based sardine run surveys (O’Donoghue *et al.* submitted, b), they were included in the classification tree analysis for comparison with sardine predators.

A Friedman ANOVA analysis with Kendall’s coefficient of concordance was used to detect whether there was any significant difference between the mean ranks of each predator observation when paired with sardine presence or absence within each three-day sighting period per zone. This method is useful for conducting an ANOVA analysis when the assumption of normality is not met (Friedman 1937). A lack of significant difference would indicate similar distributions.

The influence of environmental variables upon sardine presence with data pooled across three-day sighting periods was investigated. For both atmospheric pressure and maximum/ minimum air temperature, the median, maximum and minimum values were obtained from the three daily measurements for each sighting period for each zone. Rainfall was similarly summed over three days. The mean, maximum and minimum SST values per coastal zone were obtained from the KZNSB data for each three-day period.

Non-continuous, estimated or categorical variables were manipulated as follows: the daily values recorded at each shark net installation for water clarity, swell height and current direction and speed were assigned to one of the index classes in Table 2. The modal class obtained for each variable per zone per day was determined, and its frequency of occurrence over each three-day sighting period was then summed. This effectively gave a maximum of three and a minimum of zero occurrences for each index class per variable, providing a comparative measure of conditions over three days for that variable. If data for more than one day in any three-day period were missing, then that three-day period was scored as *no data.* For the wind data, each of the nine measurements made during each three-day sighting period was assigned to one of the index classes in Table 2. Wind direction is stated using direction from which the wind originates. The frequency of occurrence of each wind index class within each zone over each three-day sighting period was summed. The same criterion for *no data* cases was applied.

Table 2. Oceanographic and climate variables (coded into index classes) used in the environmental GLM analyses. The “value” rows denote the range of values for each class. Each wind direction class was combined with each wind strength class to give 16 possible wind conditions e.g. NE2 would be a NE wind of between 5 and 9.9 knots. All wind classes had n = 2684 observations.

Water clarity – metres	Index	Viz1	Viz2	Viz3	
	n =	2124	2084	1762	
	value	0 – 3	4 – 6	> 6	
Current direction	Index	Cdir_Calm	Cdir_NtoS	Cdir_StoN	
	n =	2238	2340	2254	
	value	calm	southward	northward	
Current speed (boat drift speed)	Index	Csp_Calm	Csp_Weak	Csp_Mod	Csp_Str
	n =	2150	2340	2109	1983
	value	calm	weak	moderate	strong
Swell height – metres	Index	Swell05	Swell10	Swell15	
	n =	2068	2296	2117	
	value	0 – 0.5	1	≥ 1.5	
Wind direction – ° from true north	Index	NE	SE	SW	NW
	value	10 – 100	110 – 170	180 – 260	270 - 360
Wind strength – knots (m.s^{-1})	Index	1	2	3	4
	value	0 – 4.9 (0–2.5)	5 – 9.9 (2.6–5.1)	10 – 14.9 (5.2–7.7)	> 15.0 (>7.8)

General linear models (GLM) are frequently used within the fisheries-ecosystem management context (Maravelias and Reid 1995; Swartzman *et al.* 1992) and were used by Agenbag *et al.* (2003) to determine the relationship between sardine distribution and sea temperature. Our GLM analysis investigating the influence of environmental variables upon sardine presence was constrained by using only data characteristic of the sardine run period. This was done to exclude environmental conditions prior to the start of the sardine run that would not have been typical of when sardines were likely to be present. These were identified from the spatio-temporal GLM as having a probability of sardine presence > 0.5 and were as follows: months = "June" or "July", years = "1997 to 2002" and "2004 to 2005" and zones = "Upper, Mid and Lower South Coasts". Any cases containing missing environmental data were discarded. Both the continuous and the coded variables were fitted to a GLM model of sardine presence/ absence using a binomial distribution and a probit link function employing a stepwise selection procedure. The resulting significant variables were investigated further using GAM plots to identify the nature of their association with sardine presence.

Finally, we investigated the relationship between climate and oceanographic variables and minimum SST measured at the shark nets. Minimum SST was used as that represented the best possible conditions for sardines, in terms of temperature. There was no need to code these data into three-day sighting periods, so daily measurements were used. These variables were fitted to a GLM model using Splus 2000 professional statistical software. The GLM procedure of Splus is built to fit Generalised Linear models, an extension of linear models to data with error distributions other than normal or Gaussian. By using GLM, we can fit data with Gaussian, binomial, Poisson, gamma, or inverse Gaussian errors. Because we fitted a General Linear Model, we used a Gaussian distribution, an identity link function and a stepwise selection approach. Adding and dropping terms is a useful method for selecting the best model. The step function provides an automatic procedure for conducting stepwise model selection by estimating at each selection step which variable will contribute the most to the R^2 value. Significant variables were investigated using GAM plots as above.

RESULTS

Sightings data

KZNSB field staff made 6581 observations of sardine run activity between 1st May and 30th October from 1997 until 2007 (Table 3). The following species contributed 83 % of the total number of observations: South African sardine (assumed or confirmed), *Sardinops sagax*, Cape gannet, *Morus capensis* (Lichtenstein 1823), Long-beaked common dolphin, *Delphinus capensis* Gray 1828, Indo-Pacific bottlenose dolphin, *Tursiops aduncus* (Ehrenberg 1833), and humpback whale, *Megaptera novaeangliae* (Borowski 1781). Subsurface predators, specifically all shark and gamefish species, contributed a further 6 % towards the total sightings. Because they were difficult to detect and identify, they were grouped together and included only in the classification tree analyses, as were humpback whales.

The 6581 KZNSB field staff observations were then assigned into three-day sighting periods. Over the entire study period there was a total of 671 three-day sighting periods, with four zones per sighting period. This created 2684 observations or either present or absent for each species. Sardines were present on 443 occasions. There were 498 Cape gannet, 150 shark and gamefish, 151 common dolphin, 406 bottlenose dolphin and 178 humpback whale observations.

Longshore distribution per month

Sardines were rarely present along the KZN South Coast during May (Fig. 2A). During June, sardine presence along the North Coast was substantially lower than along the Upper, Mid and Lower South coasts ($p \leq 0.015$; $\chi^2 \geq 10.528$), but not during July. From August onwards sardine presence declined along the entire KZN Coast.

Gannets were present in all coastal zones from May to September (Fig. 2B). Presence increased within each zone from May to June ($p \leq 0.001$; $\chi^2 \geq 11.138$). During June gannet presence was significantly higher along the Mid and Lower South Coasts compared with the Upper South and North coasts ($p \leq 0.045$; $\chi^2 \geq 6.185$), but not during July. By August gannet presence had declined within all coastal zones ($p \leq 0.015$; $\chi^2 \geq 5.949$).

Common dolphin presence (Fig. 2C) within the south coast zones increased from May to June ($p \leq 0.021$; $\chi^2 \geq 5.345$). Presence along the Lower South Coast during June was significantly higher than along the Mid and Upper South Coasts ($p \leq 0.005$; $\chi^2 \geq 10.689$), but not during July. Common dolphin presence declined along the whole coast from August ($p \leq 0.013$; $\chi^2 \geq 8.686$).

Table 3. Species list and numbers of observations reported by KwaZulu-Natal Sharks Board field staff during May to October from 1997 to 2007.

Common name	**Species name**	**Obs.**
Whale Shark	*Rhincodon typus*	6
Copper Shark (Bronze Whaler)	*Carcharhinus brachyurus*	37
Spinner Shark	*C. brevipinna*	18
Dusky Shark	*C. obscurus*	12
Hammerhead Shark	*Sphyrna* sp.	1
Great White Shark	*Carcharodon carcharias*	4
Raggedtooth Shark	*Carcharias taurus*	8
Diamond Ray	*Gymnura natalensis*	2
Manta	*Manta birostris*	1
Sharks (unidentified)	-	146
Roundherring	*Etrumeus*	7
Sardine (confirmed)	*Sardinops sagax*	822
Sardine (assumed)	-	1368
Cape Anchovy	*Engraulis encrasicolus*	2
Baitfish (with sardine)	-	60
Baitfish	-	118
Elf (shad)	*Pomatomus saltatrix*	33
Giant Kob (Daga Salmon)	*Argyrosomus japonicus*	1
Geelbek	*Atractoscion aequidens*	7
Kingfish	*Caranx* sp.	4
Bonito	*Sarda* sp.	6
King Mackerel	*Scomberomorus commerson*	10
Queen Mackerel	*S. plurilineatus*	3
Garrick (Leervis)	*Lichia amia*	10
Yellowfin Tuna	*Thunnus albacares*	5
Gamefish (unidentified)	-	75
African Penguin	*Spheniscus demersus*	2
Albatrosses and petrels	-	6
Cape Gannet	*Morus capensis*	1736
Skuas, gulls and terns	-	22
Birds (unidentified)	-	7
Southern Right Whale	*Eubalaena australis*	22
Humpback Whale	*Megaptera novaeangliae*	282
Dwarf Minke Whale	*Balaenoptera acutorostrata*	9
Whales (unidentified)	-	80
Indo-Pacific Humpback Dolphin	*Sousa plumbea*	4
Indo-Pacific Bottlenose Dolphin	*Tursiops aduncus*	987
Long-beaked Common Dolphin	*Delphinus capenis*	272
Killer Whale	*Orcinus orca*	4
Dolphins (unidentified)	-	374
South African Fur Seal	*Arctocephalus pusillus p.*	8
Total sightings:		**6581**

Bottlenose dolphins were present in each zone from May to August (Fig. 2D). During May bottlenose dolphin presence was lower along the North Coast compared with the South Coast zones ($p = 0.001$; $\chi^2 = 11.499$). From May to June bottlenose dolphin presence increased significantly within all coastal zones ($p \leq 0.01$; $\chi^2 \geq 7.777$).

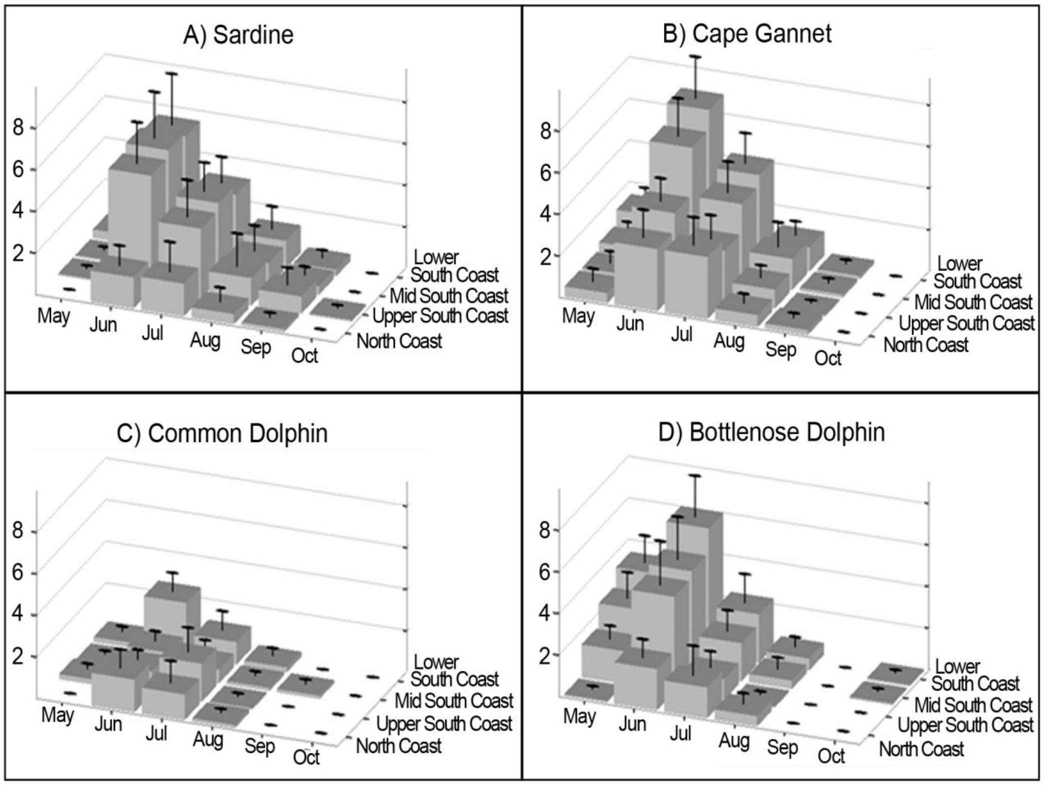

Figure 2. Mean annual number of KZNSB field staff observations per month (y-axis) of sardines (A) and predator species (B – D) within coastal zones (z-axis) along the KwaZulu-Natal coastline between 1997 and 2007. Error bars denote 95 % confidence interval.

Distance from shore

The percentage of sardines present between the shore and backline increased from 70 % to 86 % from the Lower to the Upper South coasts and declined to 51 % along the North Coast (Fig. 3A). The number of sardine nettings along the coastline was very similar with an increase northwards to the Upper South Coast and then a decline along the North Coast (Fig. 4). The percentage of sardines present further than 1 km from shore increased from 3 % along the Upper South Coast to 51 % along the North Coast.

Gannet distance from shore was similar to sardines, although they tended to occur further from shore (Fig. 3B). Common dolphins moved further from shore northwards along the KZN coast (Fig. 3C). There was no obvious change in bottlenose dolphin distance from shore along the coastline (Fig. 3D). At least 90 % of all bottlenose dolphin records were within 1 km of the shoreline and ≥ 53 % of observations were near backline.

SST conditions

SST from 1997 to 2007 (Fig. 5) decreased every month from May to August within each 25 km segment along the coast ($p \leq 0.001$; $\chi^2 \geq 35.627$). During these months SST increased slightly from the North

Coast to the Upper South Coast, and then declined significantly within each zone southwards to the Lower South Coast ($p \leq 0.032$; $\chi^2 \geq 4.601$). Mean SST along the Mid and Lower South Coasts was below 21 °C from June, and along the entire coast from July, onwards. SST increased from September onwards in all coastal zones, with the highest mean temperatures in February (not shown).

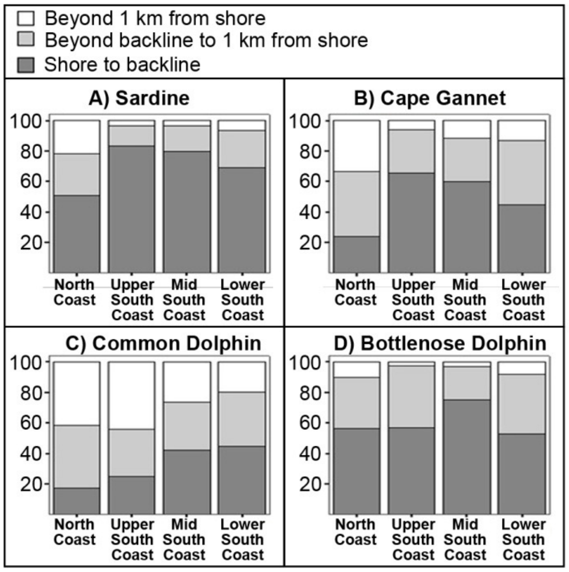

Figure 3. Percentage frequency distribution within three distance classes from shore of sardines (A) and predators (B – D) within four coastal zones along the KZN coastline.

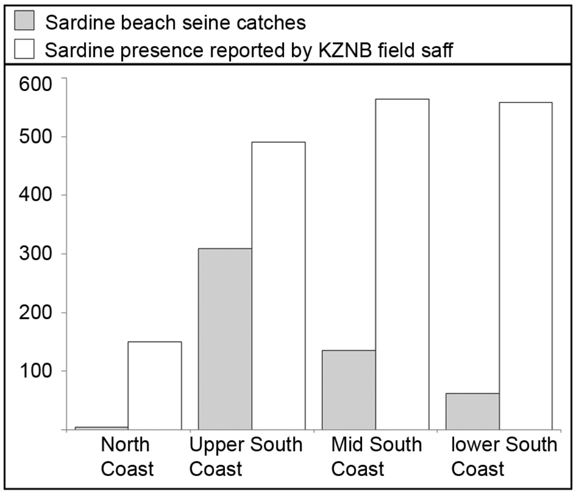

Figure 4. Total number of sardine catches in beach seine nets and observations of sardine by KZNSB field staff between 1997 and 2007 within four coastal zones along the KZN coastline.

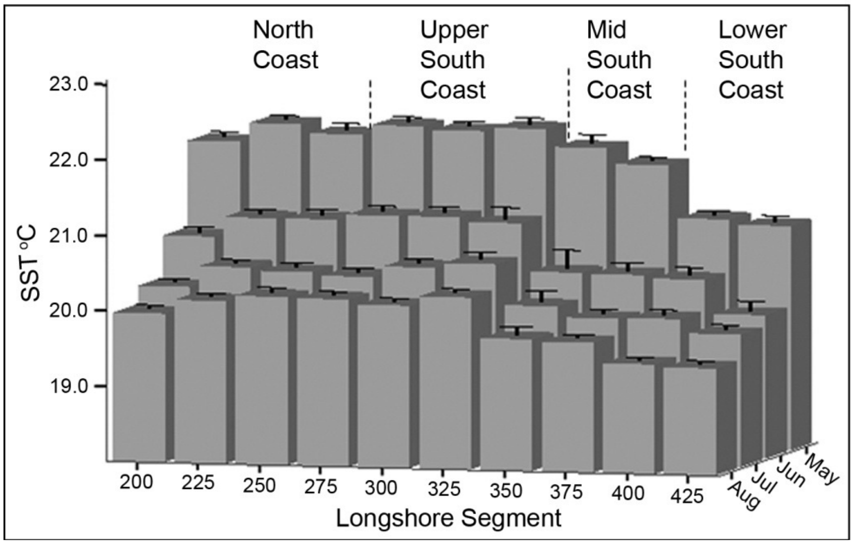

Figure 5. Mean sea surface temperatures (°C) measured at the shark nets between 1997 and 2007 along the KZN coastline per month and per longshore segment of coastline. The boundaries of the coastal zones are indicated by the dashed lines.

GLM analyses

In describing sardine distribution, all three spatio-temporal variables were significant ($n = 2420$; $p < 0.0001$ and $F = 235.8$, 25.3 and 38.0 for month, year and zone respectively) with $R^2 = 0.52$. The highest probability of sardine presence was during June and July and during 2004 (Fig. 6). The lowest probability was during May, September and October, during the years 2003, 2006 and 2007 and along the KZN North Coast.

The predator variables were significant in describing sardine presence in the second GLM analysis ($n = 2684$, $p < 0.01$, $F = 83.60$) with $R^2 = 0.48$. In the classification tree (Fig. 7) the predators successfully predicted 90 % of the variability in sardine presence (2442 out of 2684 observations), with the most successful predators being the gannets, the sharks group and common dolphins, respectively. Of the predator species, however, only gannet and sardine mean ranks did not differ in the Friedman ANOVA ($n = 2684$, $\chi^2 = 2.35$, $p > 0.05$).

The environmental variables had a significant influence upon sardine presence ($n = 504$, $R^2 = 0.23$). The signs preceding the coefficients in Table 4 indicate the direction of the impact of significant variables upon the probability of sardine presence, with a positive coefficient indicating a positive effect. Persistent light NW winds, calm current conditions, higher minimum atmospheric temperatures and higher atmospheric pressure were associated with increased sardine presence. Increasing SST, southward flowing currents of moderate strength, poor water clarity and large swells had a negative impact upon sardine presence.

The relationship between the continuous environmental variables and sardine presence is apparent in Figure 8, where maximum air temperature (Fig. 8E) and atmospheric pressure (Fig. 8D) had a positive linear effect, and maximum SST (Fig. 8A) had an inverse linear effect. For minimum SST (Fig. 8B) there was no effect upon sardine presence below ~ 20 °C. Above this temperature sardine presence declined. For mean SST (Fig. 8C) sardine presence increased until ~ 21 °C and then declined.

The environmental variables that had a significant effect upon minimum SST are listed in Table 5 ($n = 504$, $R^2 = 0.35$). In Table 6 the direction and relative impact of these significant variables can be perused, with negative coefficients inversely related to SST. Examples of these included NE winds (Fig. 9A-C) and current direction from north to south (Fig. 9D). SE winds (Fig. 9A-C), increasing maximum atmospheric temperature, the maximum wind speed and rainfall (Fig. 10A-C) were associated with warmer sea conditions.

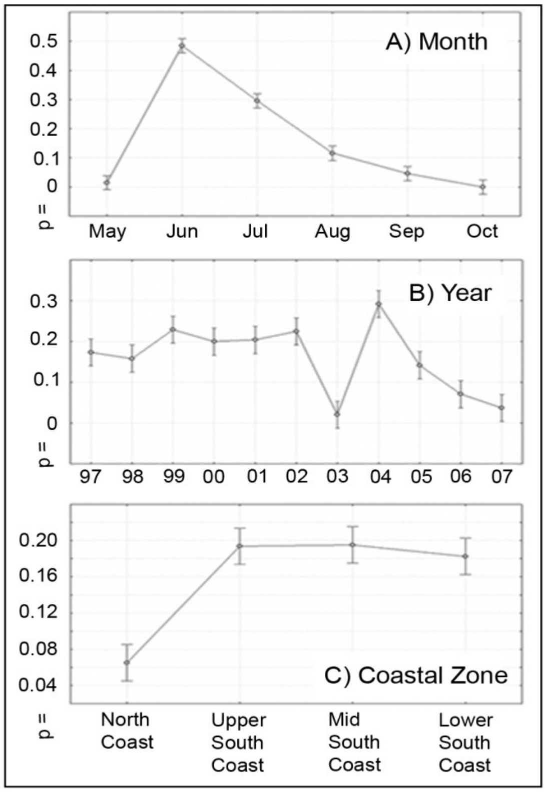

Figure 6. Spatio-temporal GLM analysis output showing the probability of sardine presence by (A) month, (B) year and (C) coastal zone. Error bars denote 95 % confidence intervals.

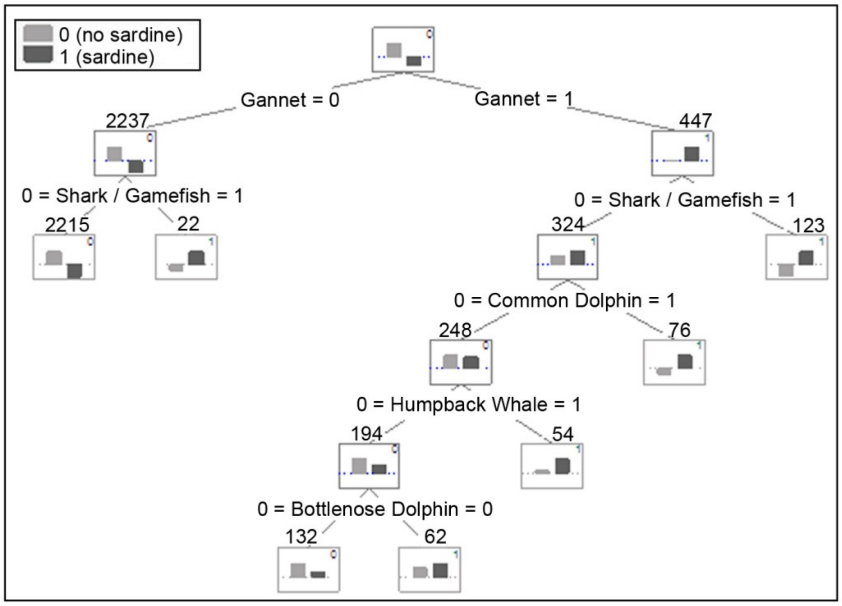

Figure 7. Classification tree showing the relative influence of the presence and absence of each predator species as predictors of sardine presence. Numbers above the node boxes refer to the number of observations of the species in the diagonal branch above.

Table 4. GLM output showing the influence of environmental variables upon sardine presence determined that the variables listed below had a significant effect. Index classes: “Viz1” – water clarity ≤ 3m; “Cdir” – current direction; “NtoS” – north to south; “Csp_Mod” – current speed moderate; “Swell15” – 1.5m swell; “Median_airtemp_min” and Median_ATM – the median value obtained over each three day sighting period for minimum air temperature and for atmospheric pressure, respectively; “NW1” – NW wind < 5kts. D.F. = degrees of freedom

Variable	D.F.	F =	p =	Coefficients
Intercept				-45.52
SST_mean	262	26.08	< 0.001	-0.57
Viz1	267	5.96	0.015	-0.30
Cdir_calm	271	222.00	< 0.001	1.21
Cdir_NtoS	270	4.37	0.038	-0.54
Csp_mod	269	10.32	0.001	-0.80
Swell15	268	3.35	0.068	-0.49
Median_airtemp_min	265	6.32	0.012	0.59
Median_ATM	263	4.25	0.040	0.35
NW1	272	21.32	< 0.001	0.41

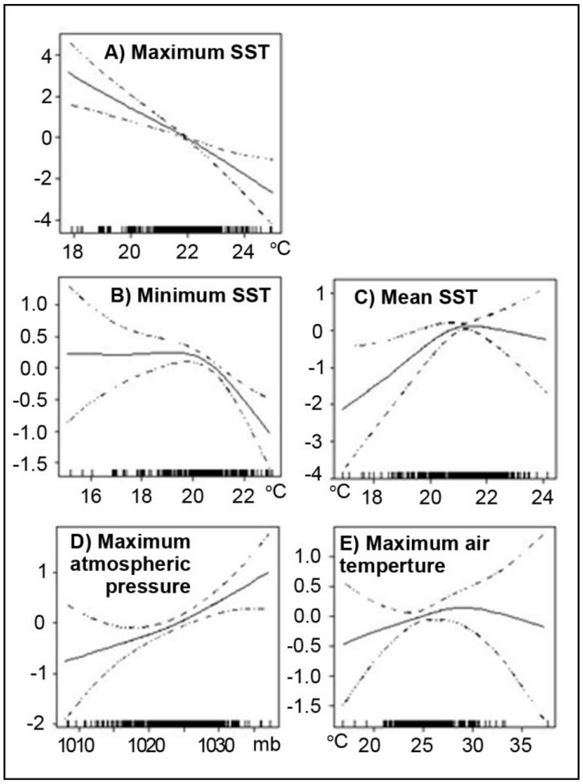

Figure 8. GAM plots investigating the effect of the following continuous environmental variables upon sardine presence during three day sighting periods: A) maximum SST, B) minimum SST, C) mean SST, D) maximum atmospheric pressure and E) maximum air temperature.

Table 5. GLM output showing the influence of environmental variables upon minimum SST

Variable	**D.F.**	**F =**	**p =**
Wind direction at 8am	259	2.88	0.023
Wind speed at 8am	258	0.20	0.657
Direction of maximum wind speed during day	254	5.16	< 0.001
Maximum wind speed during day	253	6.51	0.011
Direction of max wind speed of previous day	249	2.13	0.078
Maximum wind speed of previous day	248	0.06	0.800
Maximum air temperature	247	7.61	0.006
Minimum air temperature	246	3.00	0.085
Atmospheric pressure	245	0.50	0.479
Rainfall	244	5.61	0.019
Current direction	242	9.05	< 0.001
Current speed	239	1.29	0.280
Swell height	233	1.29	0.263
Maximum water clarity	219	1.31	0.203
Modal water clarity	217	0.02	0.979

Table 6. Standard Error, t-value and coefficients of significant variables in the GLM for minimum SST.

Variable	**Std. Error**	**t =**	**Coefficient**
(Intercept)	0.860	20.559	17.680
Wind direction at 8am: NE	0.177	-1.121	-0.199
Wind direction at 8am: SE	0.193	1.443	0.278
Wind direction at 8am: SW	0.070	2.149	0.151
Wind direction at 8am: NW	0.040	0.314	0.012
Direction of max wind speed during day: NE	0.552	-0.850	-0.469
Direction of max wind speed during day: SE	0.194	0.142	0.027
Direction of max wind speed during day: SW	0.104	-1.731	-0.180
Direction of max wind speed during day: NW	0.074	-2.112	-0.156
Maximum wind speed during day	0.038	1.463	0.056
Maximum air temperature	0.031	3.488	0.107
Rainfall	0.009	2.426	0.021
Current direction north to south	0.082	-4.118	-0.339
Current direction south to north	0.051	-0.137	-0.006

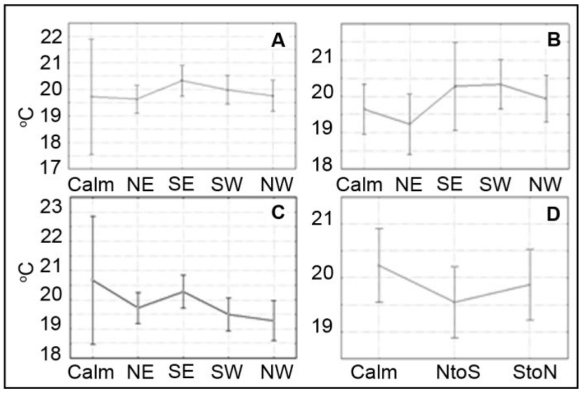

Figure 9. GLM analysis investigating the effect of wind and current direction upon SST at the shark nets along the KZN south coast during June and July. A) direction of maximum wind speed of preceding day, B) wind direction during SST measurement, C) direction of maximum wind speed during day of measurement and D) current direction at the shark nets. “NtoS” represents an alongshore current in a southerly direction.

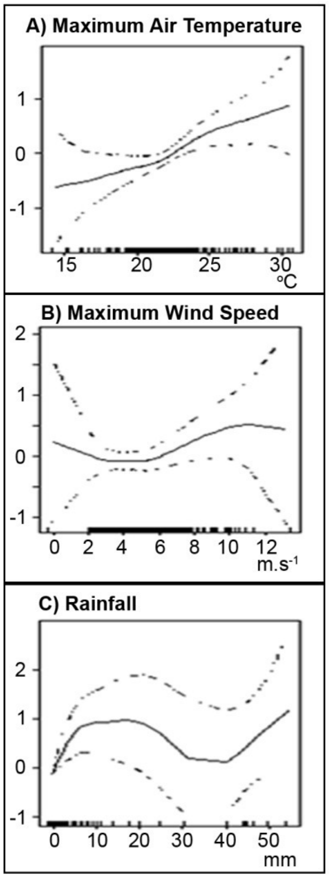

Figure 10. GAM plots investigating the effect of the following continuous variables upon SST at the shark nets along the KZN south coast during June and July: A) maximum air temperature, B) maximum wind speed and C) rainfall.

DISCUSSION

Limitations of the sightings data set

The pooling of data into three-day sighting periods constrained the temporal resolution of analyses with regards changes in predator longshore distribution, especially for highly mobile predators e.g. common dolphins. The data used in this study are biased towards shore, but it was assumed that this bias was similar for the four zones and that these data could, therefore, be used comparatively.

Limitations of the environmental data sets

The removal of shark nets immediately prior to the arrival of the sardine run meant that KZNSB staff conducted observations from shore for the remainder of the sardine run. This resulted in the loss of the most pertinent oceanographic data, which limited the amount of data available for the GLM analyses. The KZNSB measurements are the only reliable data available for nearshore (< 1km) oceanographic conditions in the study area and hence they have been used in these analyses.

The sea temperature data consist of surface measurements at the shark nets in water depths of between 10 and 14 m. This shallow zone is well mixed (Schumann 1988) so temperature measurements should be representative of conditions through the water column. The large number of SST measurements, obtained over 11 years, and the removal of outliers, gave a robust representation of conditions at the shark nets (Fig. 5). The trend over time and alongshore resembled that obtained using remotely sensed SST data within 5km of the shoreline in O'Donoghue *et al.* op. cit., a), and conforms to known SST distribution along the KZN coastline (Lutjeharms *et al.* 2000).

The other oceanographic variables: water clarity, swell height and current direction and strength (speed), consisted of subjective estimations made by the KZNSB field staff. The use of broadly defined indices should have minimised the effect of observer bias in these estimations. The resultant semi-quantitative, ordinal variables were useful for detecting the direction of the main effects (i.e. positive or negative) of parameters upon sardine presence in the GLM analyses, but it was not possible to quantify the magnitude of these effects.

Wind speed values measured at land-based weather stations underestimate those on the adjacent continental shelf (Schumann 1992). The close proximity of the shark nets to the shoreline and the employment of a wind speed index should have minimised errors due to land effects, as wind speed categories would have been broader than the difference between land-based measurements and conditions at the shark nets,.

Rainfall was recorded along the coastline, and as such, does not reflect runoff from rainfall occurring inland. However, during winter KZN rainfall is largely restricted to coastal regions (Diab *et al.* 1991), as the rain-bearing low pressure systems are deflected away from the country by a persistent high pressure system, which tends to dominate conditions over land (Harrison 1986). Hence runoff from inland is normally at a minimum during the survey months and rainfall measures used in this study can be considered representative.

Sardine sightings

The arrival of the sardine run during June corresponded with a significant decline in mean SST along the KZN Mid and Lower South Coasts from ≥ 21.0 °C during May to ≤ 20.4 °C. The seasonal nature of the sardine run was strongly confirmed by the spatio-temporal GLM analysis with the months of June and July emerging with the highest probability of sardine presence. The strong presence recorded during 2004 is consistent with other studies (O'Donoghue and Peddemors submitted, b). During this year the strongest, most persistent run and the coolest sea temperature conditions were recorded.

The recent variability in sardine presence per year is evident in Figure 6B. From 2002 until 2006 sardine presence differed significantly each year, with four of the last five years having the lowest presence of the time series. This pattern compares favourably with the mean number of sardine eggs collected per year at Park Rynie (Fig. 1) along the KZN Upper South Coast (Connell 2007). As our time series spans only eleven years, it is not possible to determine whether the above pattern is part of a longer term trend or cycle. However, given the lack of significant difference prior to 2002, this does suggest some change in sardine distribution on South Africa's East Coast, especially as it corresponds temporally with a decline in estimated biomass of the sardine stock (de Moor *et al.* 2008).

Sardine presence along the North Coast was significantly lower than along the Upper South Coast (Fig. 2A), while proximity to shore peaked within the latter zone (Fig. 3A). This corroborated findings by O'Donoghue *et al.* op. cit., a). The peak in mean SST along the Upper South Coast during the sardine run (Fig. 5) is contiguous with warming that occurs 6 km from shore due to the Durban Eddy (Pearce *et al.* 1978) and may, therefore, be related to this oceanographic feature. Whether sardines move into the surf zone to avoid this warm water is not known, and data confirming a temperature difference between the surf zone and beyond 100 m from the shore have not been collected. Connell (2007), however, hypothesized that the cool, nightly land breezes persistent along this coast during winter might have a cooling effect upon surf zone temperatures.

Regardless of the cause, this shoreward sardine movement has an important consequence for the beach-seine net fishery, which is restricted to the vicinity of the surf zone. Catches of sardines peaked along the Upper South Coast (Fig. 4), as sardine availability presumably increased. It should, however, be noted that the proximity of Durban as a market could be skewing fishing effort.

The environmental data, while significant, did not account for much of the variability in sardine presence ($R^2 = 0.23$). Certain variables do, however, provide an important insight into conditions favouring sardine presence. SST had an inverse and highly significant influence. The nature of the influence is apparent in the GAM plot of maximum SST and in the limiting effect above 20 °C for minimum SST. This is consistent with sardine's preferred temperature range (Barange and Hampton, 1997). Sea currents had a significant effect with calm current conditions most favourable for sardine presence and moderate current speeds from north to south most detrimental. As sardine movement during the run is northwards, this counter current effect is expected.

Additional environmental conditions positively associated with sardine presence were increasing air temperatures, increasing atmospheric pressure and a high incidence of light NW land breezes. This combination of variables suggests that sardine presence visible to land-based observers is higher during periods between cold fronts with calm atmospheric conditions resulting in calm nearshore current conditions. It is further supported by the inverse effect of large swells and low water clarity, which would be associated with the passage of cold fronts.

Wind direction, wind speed, current direction, air temperature and rainfall all significantly affected minimum SST measured at the shark nets. Current and wind direction effects dominated, with NE wind and currents from north to south having a cooling effect upon SST. Pearce *et al.* (1978) found a strong correlation between local winds and current speed in water depths of less than 20 m. Schumann (1988) recorded dramatic temperature decreases of up to 5 °C throughout the water column approximately 5 km from shore along the coastline south of Durban when current direction changed to southwards.

Schumann (1986) described how cool water is brought up onto the continental shelf in the bottom boundary layer due to Ekman veering. NE winds cause the surface water layer to move away from shore allowing the cool water to reach the surface. This process occurs along much of the South African east coastline (Schumann 1988, Schumann *et al.* 1988). Conversely, SW winds push warm Agulhas Current surface water towards shore causing inshore temperatures to increase, which would negatively impact upon sardine presence. The effects of local wind forcing evident in the GLM analyses are consistent with the above findings.

Increasing maximum air temperature, SE winds, wind speeds in excess of 6 $m.s^{-1}$ and rainfall had a warming effect upon SST. Schumann (1981) reported increased variation in surface layer sea temperatures driven by local wind forcing, including sea breezes. The latter three variables are all associated with the passage of frontal systems where warm surface waters would be pushed shoreward resulting in warmer SSTs at the shark nets.

When NW land breezes were recorded as the maximum wind speed for the day, they had a cooling effect upon SST. This cooling should have been greatest in the vicinity of the well mixed surf zone. Sardines are often sighted close inshore during early mornings, suggesting that they could be utilising cooler conditions (A. Connell 2009 *pers. comm.*). In this study the highest percentage of sardine observations within the surf zone was along the Upper South Coast where temperatures across the continental shelf are warmest. Surf zone temperatures were not recorded so it was not possible to determine whether the cooling effect measured at the shark nets was accentuated in surf zone measurements.

Predator sightings

Predator sightings explained more of the variability in sardine presence than did environmental variables, however the use of predators as sighting cues for the presence of sardines probably inflated the R^2 value, so that these data cannot be compared with the environmental data to determine which had the greater effect upon sardine presence. This analysis does, however, provide some insight into the relative importance of the predators with regards predicting sardine presence along the KZN coastline.

As is the case on the Eastern Cape coastline (O'Donoghue *et al.* op. cit., a, b; O'Donoghue and Peddemors op cit., b), the Cape Gannet was the predator species most closely associated with sardine presence along the KZN coastline. This was evident in the predator GLM analysis, Friedman's ANOVA and in the classification tree, and it is clearly evident in the similarity between sardine and gannet presence in Figures 2A and 2B. The only obvious difference was the significant decline in gannet presence from the Mid to Upper South Coasts during June, and the smaller percentage of gannets present within 100 m of the shore. This pattern is very similar to gannet abundance reported by O'Donoghue *et al.* op cit., a), in which abundance was inversely associated with SST.

In the present study SST was significantly higher along the Upper South Coast than along the Mid and Lower South Coasts (Fig.5). It is not clear why significantly fewer gannets were associated with sardines along the Upper South Coast during June, although the movement of sardine into the surf zone may have been a contributory factor. There is evidence to suggest that gannet foraging is limited by the depth of the water column (O'Donoghue and Peddemors, in prep, a), presumably because of the danger of plunge-diving into shallow water where visibility is obscured by suspended sediments and foam from the breakers. Despite these differences in distribution, the Cape Gannet is confirmed as the most useful indicator of sardine run activity along the KZN coastline.

The nearshore presence of common dolphins along the South African East Coast during winter is significantly associated with sardine presence (Cockcroft and Peddemors 1990; Ross 1984), and common dolphin utilisation of the sardine run has been well documented (Peddemors 1999; Young and Cockcroft 1994). These findings are consistent with the emergence of the common dolphin as the second most important species predicting sardine presence in the classification tree. This is despite the decline in their abundance recorded as they head northwards into KZN waters (O'Donoghue *et al.* op. cit., b), where common dolphin tend to occur slightly further offshore than sardines. The tendency for sardines to occur within or adjacent to the surf zone on the KZN coast may account for the overall decrease in common dolphin presence there, but also may explain the relative increase in their occurrence along the North Coast where sardines tend to occur further from shore.

The significant increase in bottlenose dolphin presence along the KZN South Coast from May to June suggests a regional increase in dolphin abundance. A similar increase was recorded by O'Donoghue *et al.* (op. cit., b), and is considered to represent the influx of a genetically distinct migratory stock from the south (Natoli *et al.* 2008). The resident stock does not appear to associate with the sardine run, whereas the migrant stock does (O'Donoghue *et al.* op. cit., b). The residence status of bottlenose dolphins on the KZN coastline and the fact that this study did not differentiate between resident and migrant stocks may explain why the bottlenose dolphin was the species least likely to predict sardine presence in the classification tree. Bottlenose dolphin and humpback whale performance in the classification tree analysis was appropriate for species that are not considered to be major predators of sardines during the sardine run.

This study has substantially improved description of the spatio-temporal characteristics of the sardine run off the KZN coast, and our understanding of the influence of environmental and biological variables upon sardine distribution. To elaborate upon findings in this study, fine scale measurements of sea temperatures along the Upper South Coast between the surf zone and the shark nets are being conducted to assess whether there is a gradient in temperatures which sardines may be utilising.

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CHAPTER FOUR

The 2005 sardine run survey II: Avian and marine mammal predators associated with the sardine run

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ABSTRACT

During the 2005 FRS *Africana* survey opportunistic predator surveys were conducted to determine abundance and distribution of South African east coast marine mammals and seabirds in relation to each other, to clupeids and to oceanographic variables. Species' distributions were primarily separated by latitude, with Bryde's whale, *Balaenoptera edeni*, African penguin, *Spheniscus demersus*, Cape cormorant, *Phalacrocorax capensis* and anchovy, *Engraulis encrasicolus*, predominantly found in the cool southern part of the surveyed region. Peak sardine run activity occurred within 4 km of shore at the northward limit of a strip of cool nearshore water (< 21 °C) stretching up the east coast. The principal predators within this activity were common dolphins, *Delphinus capensis,* and Cape gannets, *Morus capensis*, and their nearshore distribution was strongly correlated with sardine, *Sardinops sagax*, and east coast roundherring, *Etrumeus teres,* density. Density of these latter two clupeids was strongly, inversely correlated with sea temperature and positively correlated with chlorophyll a concentration. Northward movement of the sardine run was concluded to be regulated by the interacting effects of the warm Agulhas Current and the northward extent of cool water derived from an upwelling cell in the southern part of the surveyed area. Along the KZN coastline sardines were the dominant clupeid species and their distribution was strongly skewed towards shore, resulting in particularly intense sardine run activity during the survey period. It was along this stretch of coastline that the highest abundance of bottlenose dolphin, *Tursiops aduncus*, was detected.

KEYWORDS

Anchovy, bottlenose dolphin, Cape gannet, chlorophyll a, common dolphin, *Delphinus capensis*, east coast roundherring, *Engraulis encrasicolus*, Etrumeus *teres*, *Etrumeus whiteheadi,* hydrographic survey, marine mammal, *Morus capensis*, sardines, sardine run, *Sardinops sagax*, seabird, remote sensing, sea surface temperature, SST, *Tursiops aduncus*, west coast roundherring

INTRODUCTION

The annual movement of the South African sardine, *Sardinops sagax* (Jenyns 1842), up the east coast of South Africa is a spectacular and, thus far, largely unpredictable event that is known locally as the "sardine run". This phenomenon has become an important annual event for regional economies, particularly with respect to tourism focussed on the sardine run itself (Dicken in press; Myeza *et al.* in press), tourism related to swimming at shark-netted beaches in KwaZulu-Natal (KZN) (Dudley and Cliff in press) and short-term employment opportunities based on the actual sardine run itself (Myeza *et al.* op cit.).

Additionally, the sardine run is considered to constitute an important ecological event for the subtropical coastal waters of KZN, which are considered relatively impoverished due to low nutrient levels and a lack of substantial upwelling phenomena (Carter and d'Aubrey 1988; Meyer *et al.* 2002). Although biodiversity and endemism of fishes is highest in this area of South Africa (Turpie *et al.* 2000), the biomass is low in comparison to the Southern and Western Cape waters. The influx of tonnes of sardine into these waters therefore probably provides an important annual injection of nutrients. Sardines provide an important food source for numerous predators, which include piscivorous fishes, birds and marine mammals (Cockcroft and Peddemors 1990; Crawford *et al.* 1991, 2008; van der Elst 1981, 1988). Many predatory fishes are associated with the sardine run (Garrat 1988, Fennessey *et al.* in press), as are sharks (Dudley and Cliff, in press), seabirds and cetaceans (O'Donoghue *et al.* in press, a, b; Peddemors 1999). The annual movement of sardines into the nearshore waters of KZN is undoubtedly the most important biological phenomenon occurring along this coast.

Surprisingly, almost nothing is known about the oceanographic features driving this fish movement and it has been postulated that sea temperature is the primary factor affecting the spread of fish into KZN (Armstrong *et al.* 1991). Recent GIS analysis of sardine and associated predator distribution in KZN confirms that mean sea surface temperatures below 21 ºC are required for the sardine run to occur (O'Donoghue *et al.* op cit., b). However, the data with which these analyses were conducted were confined to sea surface data acquired by satellite imagery and only the coastal strip was surveyed due to aerial survey offshore limitations. The offshore distribution of sardines and predators, plus the oceanographic conditions at depth, are still largely unknown during the course of the sardine run.

Our current understanding of the occurrence and population structure of sardine off the east coast was derived from three hydro-acoustic and mid-waters trawl surveys in August 1986, June 1987 and June 1990 (Armstrong *et al.* op cit.). Unfortunately, each of these three surveys were conducted during periods outside of peak sardine abundance in KZN, leading to limitations in developing an understanding of the oceanographic influences on the sardine run itself.

The recent eastward shift of the sardine stock towards the Eastern Cape (Fig. 1)(van der Lingen *et al.* 2005) has further emphasised the need for a comprehensive understanding of the distribution of the sardine run off the east coast, especially given the potential growth in tourism associated with this event. During May and June, sardines move northward through the Eastern Cape coastal waters towards Port St Johns (O'Donoghue *et al.* op cit., b) (Fig. 1), and apparently range across the continental shelf (Armstrong *et al.* op cit.). As they continue northwards within the narrowing continental shelf, which reaches a minimum width of approximately 9 km near Waterfall Bluff (Fig. 1), they are accompanied by dense concentrations of predators including long-beaked common dolphin, *Delphinus capensis* Gray 1828, and Cape gannet, *Morus capensis* (Lichtenstein 1823), (O'Donoghue *et al.* op cit., b).

Aerial surveys of sardine and their predators during the sardine run have historically been conducted along the coastline, but no reliable information exists of sardine activity further than approximately 4 km from the shore. Additionally, although the sardine run is occasionally observed north of Durban (O'Donoghue *et al.* op cit., a), and sardine eggs have been sampled from the Thukela Bank (Beckley and Hewitson 1994), off the Thukela River (Fig. 1), little is known about the northward limit of the sardine run. This highlights the requirement of a larger-scale survey to be undertaken during the actual sardine run phenomenon in both the alongshore and offshore spatial scales.

In 2005 the FRS *Africana* undertook a multi-disciplinary research cruise to survey the sardine run during its movement up the coast. Clupeid distribution during this cruise, including sardine, has been described in Coetzee *et al.* (in press). This paper investigates the abundance and distribution of marine mammals and seabirds in relation to that of clupeids as well as oceanographic and other environmental variables, with the aim of determining how far offshore and how far north the sardine run occurs along the east coast.

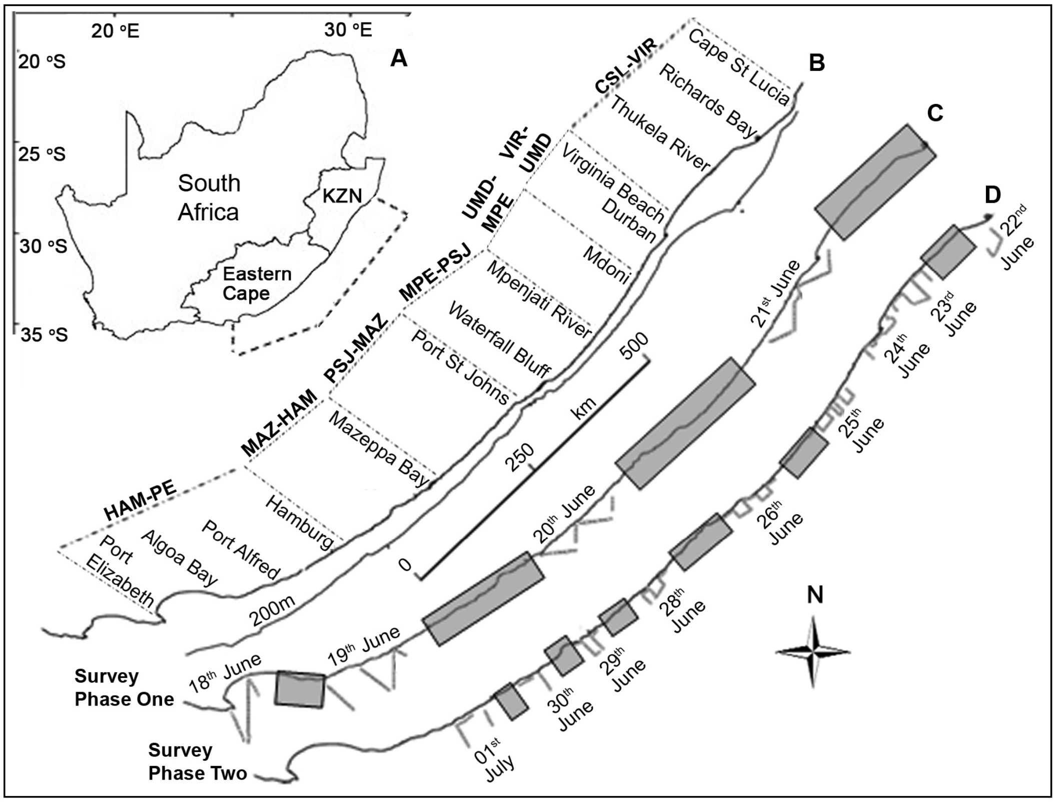

Figure 1. The 2005 FRS *Africana* predator visual surveys conducted along the KwaZulu-Natal (KZN) and Eastern Cape coastlines, delineated by the bounding box (A). (B) indicates division of the coast into seven regions and includes the 200 m isobath indicating the edge of the continental shelf. (C) and (D) detail the survey transect lines per date for Phases One and Two and the area not surveyed for predators (shaded boxes) during the night.

METHODS

Survey design:

The sardine run survey was primarily designed to investigate the abundance, size-structure and distribution of east coast clupeid shoals. Marine mammal and seabird surveys were conducted opportunistically between transect stations with no dedicated time allocated to these surveys. The sardine run survey was split into three phases: Phase One consisted of northward cross-shelf zigzag transects from Port Elizabeth to Richards Bay from the 18th to the 21st June (Fig. 1) to determine a suitable spatial grid pattern for Phase Two. Phase Two consisted of randomly determined transects running perpendicular from the coast out to the continental shelf edge from Richards Bay to Port Alfred from the 22nd June to the 1st July. The dedicated predator surveys were terminated at the end of Phase Two off Port Alfred.

Marine Mammal Survey

Marine mammal surveys were conducted using standardised methods (Eberhardt *et al.*1979). Recordings of marine mammals were made by two dedicated observers searching the ocean ahead of the ship in an arc 10 ° either side of their respective forward quarter. Searches were conducted alternating between using the unaided eye and 10 x 50 binoculars from the flying bridge of the FRS *Africana* (eye height = 17

m) during daylight hours. At the start of each transect leg the following environmental conditions were recorded: Beaufort Sea State, wind direction and strength and the extent of the visibility from the ship. Observations were only prematurely terminated if the sea state exceeded six or if visibility was less than two nautical miles. Any observations made during trawls, whilst off track or at CTD stations were recorded as incidental. Upon each sighting the following physical data were recorded: time, vessel location using a GPS, the angle of the sighting relative to the ship's trackline and the angle of declination via a handheld inclinometer. Observations were identified to the highest possible taxonomic level and the best estimate of three counts was used to determine group size. Other biological information collected simultaneously included behavioural state, direction of travel and associations with other predators (if any) seen within 100m of the primary sighting.

Seabird survey

Seabird surveys were conducted using standardised methods (Tasker *et al.* 1984). Observations of all avian species were made from the flying deck of the FRS *Africana* by two dedicated and experienced observers in a separate team from, but concurrent with, the mammal surveys. Counts were made for the duration of ten minutes with a period of twenty minutes between counts and covered an arc of 180° forward of the observation platform. All birds estimated by eye to be within 300 m of the ship were included in the counts. Individual birds suspected of following the ship and thus periodically circling around it were only counted once. The presence of species that were not recorded during the counts but that were seen between counts or at a distance greater than 300 m from the ship was also noted, as well as all feeding aggregations with numbers estimated whenever possible. No bird counts were made during the proportion of the survey that was carried out at night (Fig. 1).

Two Cape gannets were caught during the survey for telemetry studies. One was approached from downwind in an inflatable boat and caught by throwing a hoop net over the bird. The hoop net consisted of a large mesh net attached around a hoop with floats. The second bird was caught by throwing a sardine from the boat and netting the bird as it emerged after diving for the fish. Both birds were fitted with ST-10 Microwave Telemetry satellite transmitters. These devices, weighing approximately 30 g, were attached under the bird's central tail feathers using glue and cable ties. The battery was switched on for eight hours in each 24 hour cycle and has an expected lifespan of 6–8 weeks, depending on use. The first bird was caught at 31° 44.09'S 29° 26.31'E on 22 June 2005. The second bird was caught on 23 June 2005 at 31° 44.88'S 29° 24.93'E and was colour-dyed with pink on the left wing and purple on the right wing.

Survey Data Analyses

To summarise the broad-scale patterns of clupeid and predator distribution, and their association with environmental conditions, we employed methods successfully used by Tynan *et al.* (2005) and Ainley *et al.* (1992). All non-incidental marine mammal sightings made whilst on transect and during transits were retained for analyses provided survey criteria were satisfied. The location of each sighting was calculated using Pythagoras software and these data were then entered into a GIS document using ESRI's ArcView 9 software. The Euclidean distance of each sighting from shore was then computed. The water column depth of each sighting was determined using the South African Hydrographic Office 1:50 000 National Series charts, specifically SAN 126 – 132 and 135 (available from http://www.sanho.co.za). These charts give coastal bathymetry using depth classes, of which the following have been used in these analyses: 0, 15, 30, 50, 100, 200, 500 and 1000m. The depth class of each sighting was obtained by performing a spatial join and the results were used to describe mammal distribution in relation to depth. Marine mammal behaviour was classified according to three basic categories: travelling, feeding and 'other' (including socialising and resting).

Due to the paucity of the data, sightings from phases one and two were pooled. To compare predator, clupeid and environmental variable distributions the survey area was divided into a grid. The blocks within this grid needed to be large enough to contain sufficient surveyed ocean to avoid bias when calculating predator encounter rates, but small enough to address the aims of this study. To enable spatial analysis, the coastline was divided into longshore regions, the breaks largely following breaks in surveys per day, as well as changes in the bathymetry and the biogeography of the coastline, as identified by Turpie *et. al.* 2000, and locations identified by O'Donoghue *et al.* (op cit., b) as being of potential importance to sardine distribution. The locations at which the coastline was divided were as follows (see Fig. 1): Cape St Lucia (CSL), Virginia Beach (VIR), Mdoni (UMD), Mpenjati River (MPE), Port St Johns (PSJ), Mazeppa Bay (MAZ), Hamburg (HAM) and Port Elizabeth (PE). Offshore spatial distribution of sightings was facilitated through dividing the survey grid into the following classes of distance from shore (kilometres): 0.1 – 4, 4.1 – 8, 8.1 – 16 and > 16.0. All sightings, transect tracklines and environmental data were ascribed to one of the above blocks using the spatial join function in the GIS document.

The following environmental variables were obtained from the FRS *Africana* ship's log: GPS position, time, ship speed, water column depth and sea surface temperature (SST). The total distance surveyed within each block of the grid was computed from the ship's log data using the calculate length function within X-tools Pro (version 4.2.0) (http://www.xtoolspro.com) with the data in the WGS84 UTM zone 32S projection. To calculate the abundance rate for each species within each block of the grid, the counts that were made when survey criteria were met, during both phases of the survey, were summed and divided by the total distance surveyed within that block, giving an abundance rate per kilometre (km^{-1}).

Seabird counts were similarly treated with the data from phases one and two pooled. Only ten-minute counts that were made when the ship was underway with a mean speed of no less than three nautical miles per hour, and with no directional changes greater than ninety degrees, were retained for analyses. This was to minimise bias that can arise when counting highly mobile subjects at sea (Tasker *et al.* 1984). The distance covered in each ten minute count was computed in the manner described above. The surveyed area of each ten minute count was then calculated by multiplying its length by its width i.e. 600 m (300 m on each side of the boat). All ten minute counts and their calculated areas were then assigned to blocks in the survey grid. The counts in each block for each species were then summed and divided by the total area surveyed within that block to give an abundance rate per square kilometre (km^{-2}). Because the transect strip width was only 300 m, the ship's location was used when calculating the Euclidean distance of each seabird sighting from shore as well as its depth, which was obtained from the ship's log.

Clupeid surveys

Hydroaccoustic surveys were conducted via continuous acoustic sampling to a depth of 250 m using a Simrad EK60 echo sounder with Midwater trawls conducted to identify targets. Further details of the methods used in the hydroaccoustic survey are described in Coetzee *et al.* (in press). Clupeid distribution and density along the east coast was determined by interpolating the density point data obtained during the cruise using the natural neighbour method with a cell size = 0.019 km within the GIS document. In order to compare clupeid and predator distributions, only those clupeid data that were obtained within valid predator transects were used. Zonal statistics were used to calculate the mean and maximum density of each clupeid species per block of the survey grid. Clupeid distribution from phases one and two are presented separately to illustrate the movement of the fish between phases. During Phase Two a workboat was deployed each day to investigate the nearshore clupeid distribution and density by towing a SIMRAD EY500 echo-sounder in depths inaccessible to the FRS *Africana*. These data were used for day-scale comparisons with the predator survey data.

Environmental data

The mean latitude and depth of the trackline for each valid survey was computed using the ship's log data and assigned to a block in the survey grid for comparison with the sightings rate data. All remotely sensed SST and chlorophyll a (chl a) concentration data were downloaded from the Remote Sensing Server for Sciences website (www.rsmarinesa.org.za) where they are available as level 3 data compiled on a 1 km grid scale from the Moderate Resolution Imaging Spectrometer (MODIS) sensor. To circumvent data loss due to cloud cover the three-day weighted-average (SST) and five-day weighted average (chl a) images were used. SST and chlorophyll a concentration along the survey transects were determined by performing a zonal statistics analysis within a 1000 m buffer zone on each side of the transect line. The buffer zone was used to ensure that there were sufficient data points included within each zone. Composite images showing SST and chl a concentration across the continental shelf pertaining to that day's survey were then produced. The accuracy of the remotely sensed sea surface temperature data was investigating by comparing mean temperatures obtained within each survey block against those obtained using the ship's log data.

Statistical analyses

All statistical analyses were performed using SPSS version 15.0. Descriptive statistics were used to present the distribution, abundance and behaviour of species during the survey period. To compare predator and clupeid distributions, a Hierarchical Cluster Analysis (HCA) was performed. The aim of an HCA analysis is to identify subgroups of similar cases in a population. This is achieved by identifying cases (or clusters) where within group variation (or distance) is minimised and between group variation is maximised. Our cluster method employed a between-groups linkage measuring the squared Euclidean distance for interval data and standardising variables using Z-values. An output of this analysis is a dendrogram, which provides a visual representation of clusters of species with similar distributions. The shorter the distance between joining lines in the dendogram, the closer the association between species' distributions. The resulting dendogram was then tested by conducting Spearman's Rank Bivariate correlations of these species' distributions with the environmental variables.

RESULTS

The total distance completed in suitable conditions during Phases One and Two of the marine mammal surveys was 434 and 635 km respectively. There was a total of 28.3 hours of valid seabird observation periods with 12.7 and 15.6 hours in Phases One and Two respectively. This equated to a total survey area of 149 and 186 km^2 respectively. The total distances and areas surveyed within each block of the survey grid are shown in Figure 2. Blocks further than 16 km from shore between Virginia Beach and Mazeppa Bay had a total of fewer than 15 km of surveyed tracklines within them. This was because of the narrowness of the continental shelf in this region. To minimise bias when calculating abundance rates, these blocks were added to their 8.1 - 16.0 km classes.

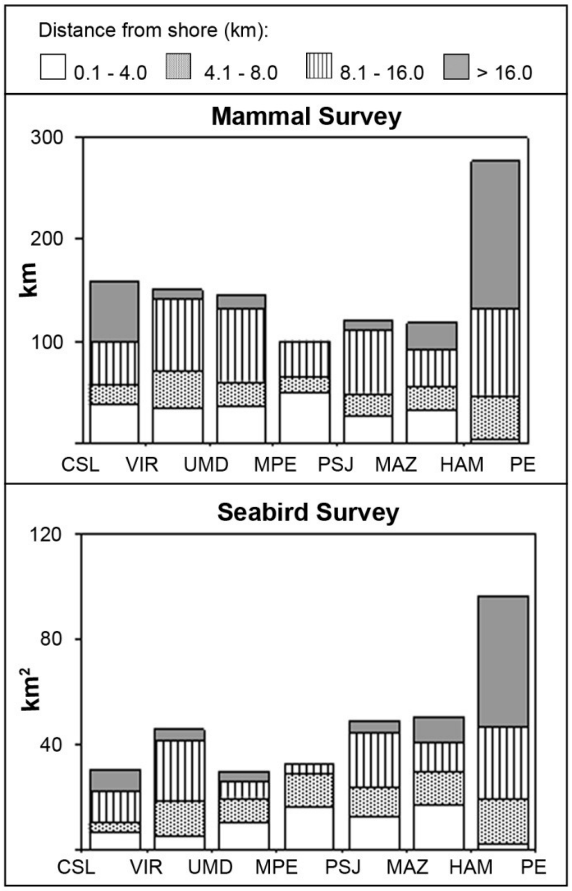

Figure 2. Total mammal survey transect distance (km) and seabird survey transect area (km^2), for Phases One and Two combined, covered during the 2005 FRS *Africana* predator survey. The x-axis locations follow the divisions shown in Figure 1.

Similarly, a paucity of data for the 0.1 - 4.0 km class between Hamburg and Port Elizabeth led to it being joined to the 4.1 to 8.0 km class. This left of total of 23 survey blocks in which distributions were compared. The total counts of marine mammal and seabird species observed during Phases One and Two of the survey, as well as their abbreviations used in these analyses, are given in Table 1.

Mammal distribution

Long-beaked common dolphins were the most abundant marine mammals (Table 1) with a median pod size of 400 individuals, and ranging from 50 to 3000 individuals. The majority of sightings (13) consisted of schools of 100 to 500 individuals. Abundance rates were highest between Mpenjati River and Mazeppa Bay (Fig. 3) with a maximum of 142 km^{-1} sighted within 4 km of the shore between Port St Johns and Mazeppa Bay. Abundance rates were an order of magnitude lower north of Mpenjati River and there were no sightings north of Virginia Beach. The median common dolphin distance from shore was 2.9 km and the range was between 50 m and 12 km. They were observed feeding on six occasions, of which five were within 4 km of the shore. Feeding common dolphins were associated with feeding gannets four times with a minimum gannet abundance of 350 during these associations.

Table 1. Sightings from Phases One (18th – 21st June) and Two (22nd June – 01st July) of the 2005 FRS *Africana* marine mammal and seabird surveys. Numbers in parentheses indicate number of sightings followed by the total number of individuals counted.

Common name	Scientific name	Phase One	Phase Two
Long-beaked Common Dolphin	*Delphinus capensis*	(2) 900	(15) 8570
Indo-pacific Bottlenose Dolphin	*Tursiops aduncus*	0	(7) 675
Humpback Whale	*Megaptera novaeangliae*	(14) 28	(70) 132
Dwarf Minke Whale	*Balaenoptera acutorostrata*	(1) 2	(6) 6
Bryde's Whale	*B. edeni*	(3) 3	0
South African Fur Seal	*Arctocephalus pusillus p.*	(7) 11	(4) 25
Cape Gannet	*Morus capensis*	(52) 1271	(44) 7176
White-chinned Petrel	*Procellaria aequinoctialis*	(46) 494	(29) 194
Swift Tern	*Sterna bergii*	(9) 17	(10) 19
Antarctic Tern	*S. vittata*	(2) 3	(3) 5
Indian Yellow-nosed Albatross	*Thalassarche carteri*	(32) 102	(20) 71
Black-browed Albatross	*T. melanophris*	(6) 6	(4) 4
Shy Albatross	*T. cauta*	(4) 4	(3) 4
Sooty Shearwater	*Puffinus griseus*	(7) 7	(10) 10
Subantarctic Skua	*Catharacta antarctica*	(10) 14	(5) 12
Arctic Skua	*Stercorarius parasiticus*	0	(1) 1
African Penguin	*Spheniscus demersus*	(5) 12	(1) 1
Antarctic Prion	*Pachyptila desolata*	(7) 20	(1) 1
Cape Cormorant	*Phalacrocorax capensis*	(5) 11	0
Southern Giant Petrel	*Macronectes giganteus*	(2) 2	(1) 1
Pintado Petrel	*Daption capense*	(1) 1	(1) 1
Great-winged Petrel	*Pterodroma macroptera*	(2) 2	0
Soft-plumaged Petrel	*P. mollis*	0	(1) 1
Wilson's Storm Petrel	*Oceanites oceanicus*	(4) 6	0
Unidentified Giant Petrel	-	(1) 1	0
Southern Pochard	*Netta erythrophthalma*	0	(1) 3
Feral Pigeon	*Columba livia*	(2) 3	0

There were seven Indian Ocean bottlenose dolphin (*Tursiops aduncus*) sightings totalling 675 individuals (Table 1). All were sighted during Phase Two between Mdoni and Port St Johns (Fig. 3). Their median pod size consisted of 80 individuals, but ranged from 20 to 250. Their median distance from shore was 1.1 km with a maximum of 2.3 km, and never in water exceeding 30 m depth. There was one sighting of a pod of eight individuals 5.3 km from shore, 42 km south of Mazeppa Bay, but these were considered to belong to the offshore stock (see Peddemors 1999) and were, therefore, not included in the above descriptive statistics. Bottlenose dolphins were observed feeding three times; each time in association with Cape gannets whose abundance always exceeded 200 individuals at these sightings.

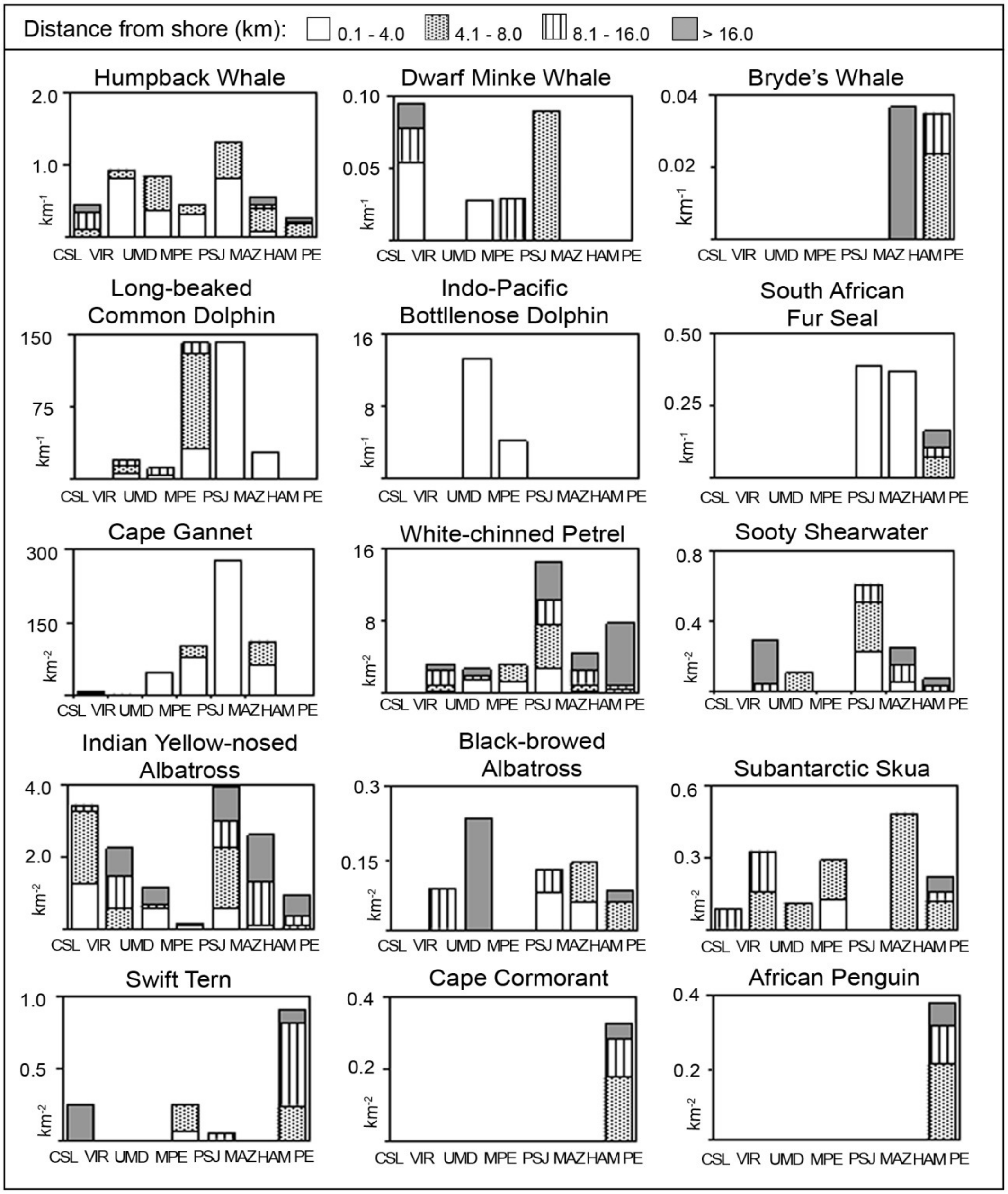

Figure 3. Marine mammal sighting rates (km^{-1}) and seabird density (km^{-2}) along the South African east coast during the sardine run. Locations follow demarcations indicated in Figure 1.

Humpback whales, *Megaptera novaeangliae,* were the most frequently encountered mammals and the most abundant mysticete species (Table 1). They had a median group size of 2 individuals and a range from one to eight. Humpback whales were sighted along the entire coast with their maximum abundance occurring within 4 km of the shore (Fig. 3). Of the 56 observations of travelling animals, 43 were moving in a northerly direction.

The other mysticete species were encountered far less abundantly (Table 1). Dwarf minke whales, *Balaenoptera acutorostrata acutorostrata,* were sighted alone on six occasions. The seventh sighting consisted of two individuals between Port St Johns and Mazeppa Bay. They were sighted most frequently (four times) between Cape St Lucia and Virginia Beach. Minke whales were recorded between 1.7 and 16.7 km from shore. Bryde's whales, *B. edeni,* were sighted three times: twice near Port Elizabeth and once off Mazeppa Bay. These sightings were 5.3, 13.9 and 15.1 km from shore respectively. There was one incidental sighting of a southern right whale, *Eubalaena australis*, 28 km north of Mazeppa Bay and 1.7 km from shore.

Thirty-six South African fur seals (*Arctocepahlus pusillus pusillus*) were encountered. Sixty-four percent of sightings were of single animals, most of these being seen between Port Elizabeth and Hamburg with a median distance of 12.3 km from shore. However, their highest abundance rates were recorded between Port St Johns and Hamburg within 4 km of the shore (Fig. 3). There were no sightings of fur seals north of Port St Johns.

Bird distribution

During the 2005 winter survey, 20 species of seabirds were recorded comprising seven coastal, eleven offshore, one freshwater and one terrestrial species (Table 1). The coastal species can be further broken down to four resident breeders, two summer migrants and two winter migrants. The offshore species consisted largely of oceanic birds that breed on subantarctic islands during the austral summer, some of which wander widely outside of their breeding season. The other categories relate to unusual sightings: three very lost southern pochards, *Netta erythrophthalma,* recorded *c.* 850 m off the coast approximately 60 km north of Durban, and two feral pigeons, *Columba livia,* that alighted on the ship just outside Algoa Bay (Fig. 1). Of the species observed, only three (the Cape gannet, white-chinned petrel *Procellaria aequinoctialis* and swift tern *Sterna bergii*) were recorded regularly around sardine shoals.

The Cape gannet was the most abundant seabird species encountered during both phases of the survey (Table 1). The highest gannet abundance, 274 km^{-2}, was recorded between Port St Johns and Mazeppa Bay within 4 km of the shore (Fig. 3). Gannet abundance declined northwards of Port St Johns with 46 km^{-2} sighted between Mdoni and Mpenjati River, also within 4 km of the shore. North of Mdoni gannet abundance was very low with a maximum of 5 km^{-2} between Cape St Lucia and Virginia Beach sighted further than 16 km from shore. Gannet median distance from shore was 2.9 km and they ranged from 0.8 to 25.7 km from shore.

Unfortunately, both satellite transmitters failed to return information on movements of the tagged birds. Both devices were working when fitted and the reasons for their failure are not known. However, the satellite-tagged bird that was also colour-dyed was seen one day (24th June) after capture at 31° 27.836'S 29° 49.510'E (W. Bernard pers. comm.[1]), 50 km north and east of where it had been tagged. It was also seen from the FRS *Africana* to the south of the Mtentu River mouth at 31° 17.49'S 30° 02.06'E on 26 June 2005 (PAW and BMD pers. obs.). This location was 78 km north and east of the place of capture and 28 km from the site of the observation made two days previously.

Cape gannets occurred in large feeding groups of up to 3000 birds, usually in the company of common dolphins, and often with white-chinned petrels, swift terns and occasionally humpback whales. A feeding flock of gannets would typically comprise birds circling up to 30 m above the water, many diving and foraging and varying proportions of birds sitting on the water surface, presumably having fed. Cape gannets observed in feeding aggregations and along transects were predominantly in adult plumage. Juveniles comprised between 0 and 6% of birds in feeding groups, averaging 2 %.

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White-chinned petrels were recorded in the second highest densities after the Cape gannet and were present in all but the Virginia Beach to Cape St Lucia section (Fig. 3). Peak numbers occurred between Mazeppa Bay and Port St Johns and birds were present in all distance classes. In Phase One, 472 were recorded compared to 250 in Phase Two. In Phase One, 75 % of sightings were made between Port Elizabeth and Hamburg, mostly offshore. This did not coincide with any clupeid distributions (see below) or those of any marine mammals. Most were recorded where sea surface temperature was 20 °C or higher. In Phase Two, only 5 % of sightings were in this area, the majority (68 %) being in the Mazeppa Bay to Port St Johns section. Although white-chinned petrels were recorded in high densities coinciding with the alongshore regions of highest fish density, the birds tended to be further offshore of where the fish shoals were located.

Swift tern distribution followed a similar pattern to that of white-chinned petrel. All but one of those recorded in Phase One were between Port Elizabeth and Hamburg and coincided with the occurrence of South African anchovy (*Engraulis encrasicolus*). In Phase Two, most were found between Mazeppa Bay and Port St Johns. Between Cape St Lucia and Virginia Beach swift tern were only seen in the furthest offshore block.

Yellow-nosed albatross, *Thalassarche carteri,* was the most frequently recorded albatross, with densities approaching 4 km^{-2}. They were found throughout the area and in all distance classes but were uncommon between Port St Johns and Mpenjati River (Fig. 3). Adults comprised about 60 % of those recorded. In Phase One, most adults were seen between Port Elizabeth and Hamburg, while the highest numbers of immature birds were in the northern-most longshore region between Virginia Beach and Cape St Lucia. By Phase Two, adults appeared to have moved northward, with distribution patterns being similar for both age groups, although adult distribution was still skewed southward exhibiting a more pronounced peak in the Mazeppa Bay to Port St Johns section. There did not appear to be any obvious similarity with the distributions of clupeid fish or marine mammals, most Indian yellow-nosed albatrosses tending to be further offshore. Black-browed albatross, *T. melanophris,* was comparatively scarce; ten birds, all immature, being recorded during the survey, five in each phase.

Sooty shearwaters *Puffinus griseus* were found in low densities through most of the survey area but most frequently between Mazeppa Bay and Port St Johns (Fig. 3), and were spread within all blocks from inshore to offshore. Five were recorded in Phase One, 16 in Phase Two. In Phase Two of the survey, the distribution of this species was similar to that of sardine and anchovy in the Mazeppa Bay to Port St Johns section. Subantarctic skuas, *Catharacta antarctica,* were recorded in low densities throughout the journey (10 in Phase One and 27 in Phase Two – Table 1), except for between Mazeppa Bay and Port St Johns, where they were not recorded (Fig 3). They did not appear to be associated with any clupeid species or marine mammals.

All 13 African penguins, *Spheniscus demersus,* recorded on the survey were between Port Elizabeth and Hamburg, with twelve seen during Phase One (Fig. 3). They were found where sardine, west coast roundherring, *Etrumeus whiteheadi*, and anchovy densities were high. Cape cormorant, *Phalacrocorax capensis,* was uncommon with four sightings totalling eleven birds recorded between Port Elizabeth and Hamburg in Phase One and one incidental sighting of six birds between Hamburg and Mazeppa Bay in Phase Two. Like the African penguin, they were limited to the southern region of the survey area. Antarctic prion, *Pachyptila desolata,* was only recorded between Port Elizabeth and Mazeppa Bay. Most observations were in the Port Elizabeth to Hamburg section and all but one was seen on the second day of Phase One of the survey. Their distribution did not appear to overlap with that of any pelagic fish species or marine mammals and there was no obvious relation to any environmental variables.

Clupeid distribution

Sardines appeared to be distributed in two major patches during Phase One of the survey, namely between Algoa Bay and Hamburg, and in the region immediately south of Mazeppa Bay (Fig. 4). During Phase Two sardine were found at lower densities and were spread between the coastline between Hamburg and Waterfall Bluff. This distribution was reflected in their mean densities within survey blocks, which was highest between 4 and 8 km from shore during Phase One of the survey, and within 4 km of the shore by Phase Two (Fig. 5). Sardine nearshore distribution, recorded by the working boat, differed from that recorded on the FRS *Africana* (Fig. 5) with mean density between Mdoni and Mpenjati River three times higher than within any other nearshore block, and undoubtedly constitutes the nearshore movement of sardines in what is locally known as the 'sardine run'.

Although the distribution and abundance of east coast round herring, *E. teres*, shifted slightly northward between the two phases of the survey (Fig 4), their maximum mean density was continually recorded in the longshore zone between Port St Johns and Mazeppa Bay, within 4 km of the shore (Fig. 5). West coast roundherring longshore distribution shifted substantially northward between the two phases of the survey (Fig. 5). During Phase One they were only recorded south of Mazeppa Bay, but by Phase Two they were recorded almost as far north as the Mpenjati River, although their highest densities were still between Hamburg and Port Elizabeth. Anchovy density was always highest between Hamburg and Port Elizabeth, although they were recorded off Mazeppa Bay during Phase Two.

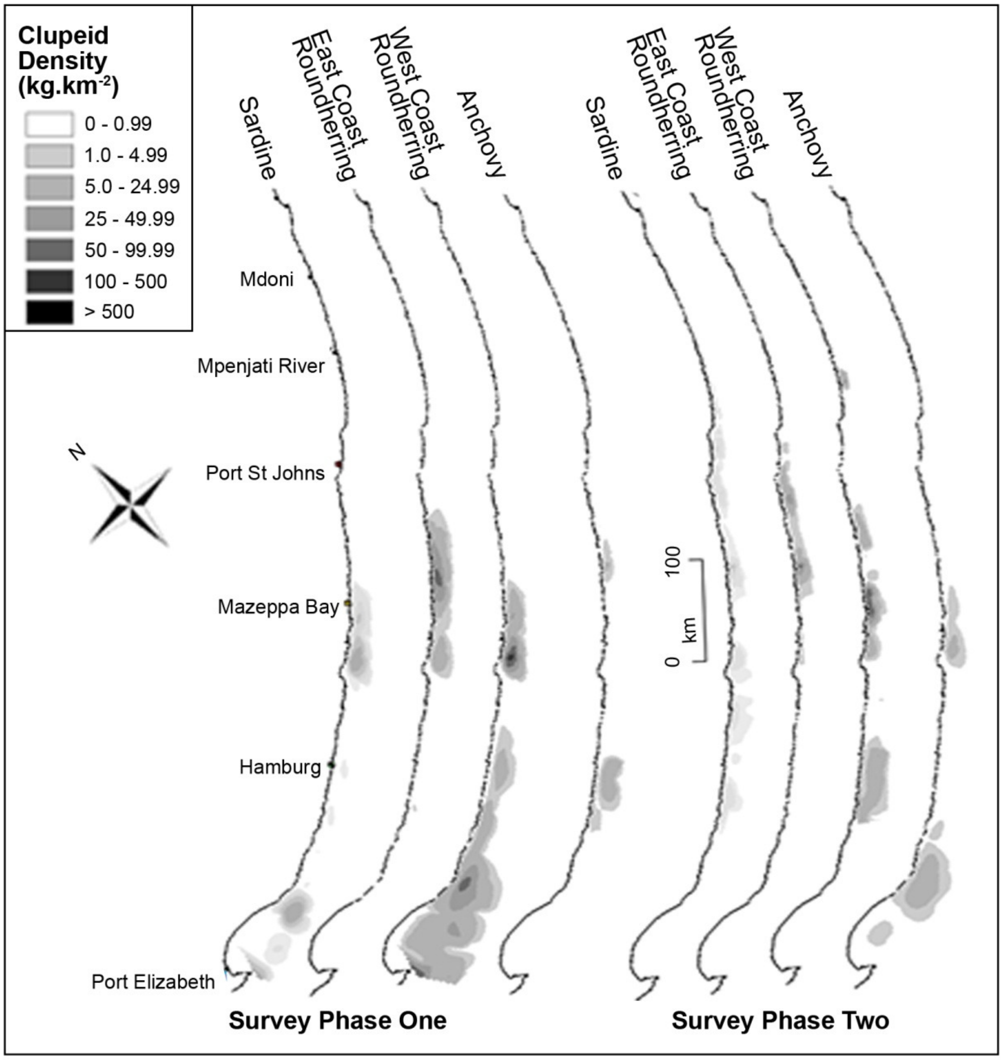

Figure 4. Clupeid density (kg.km^{-2}) along the east coast of South Africa interpolated from data collected during Phases One and Two of the 2005 FRS *Africana* sardine run survey. Data from the working boat are not included in this chart. Data courtesy of J. Coetzee (MCM).

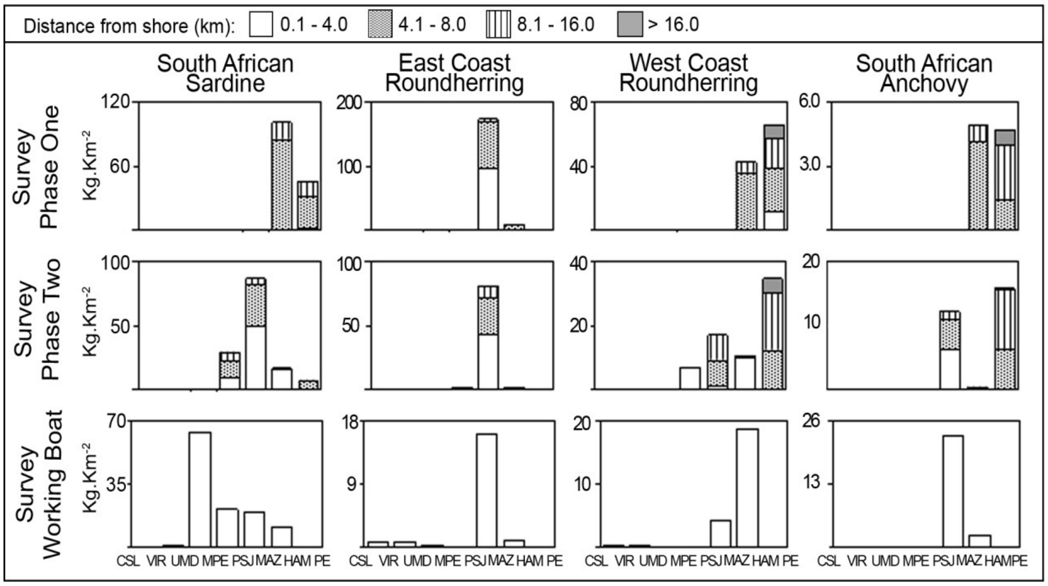

Figure 5. Mean clupeid density (kg.km^{-2}) per longshore segment of coastline (x-axis) and within distance classes from shore (groupings within bars).

Environmental conditions

There was no significant difference (z = -0.755; p = 0.450; n = 110) between mean sea surface temperatures recorded by satellite images (mean = 21.8 +/- 1.6 °C) and ship-board sensors (mean = 21.5 +/- 1.8 °C), with these measures significantly correlated (r = 0.762; $p < 0.001$). Satellite images of SST can therefore be considered representative of conditions at the time of the surveys.

Mean sea surface temperatures were strongly, inversely correlated with increasing latitude (r = -0.760; $p < 0.01$). The satellite images clearly show a band of water cooler than 21 °C stretching up the coast to the Mazeppa Bay region during both phases of the survey (Fig. 6). North of Mazeppa Bay during Phase One there were large patches of water within 8 km of the shore where SST was below 22 °C. By Phase Two, water temperatures along the coast between Mazeppa Bay and Virginia Beach had warmed with the intrusion of water ≥ 23 °C, except for between Mpenjati River and Port St Johns, where small patches below 22 °C were recorded. SST increased with distance from shore and was strongly, inversely correlated with maximum chlorophyll a concentration (r = -0.711; $p < 0.001$). During Phase One elevated chl a concentrations were recorded in a broad band between Hamburg and Mazeppa Bay, with large patches exceeding 4 mg.m^{-3} (Fig. 7). From Mazeppa Bay to Waterfall Bluff chl a concentration was mostly below 2 mg.m^{-3}. By Phase Two mean chl a concentration had declined and was restricted to a narrow strip along the coast.

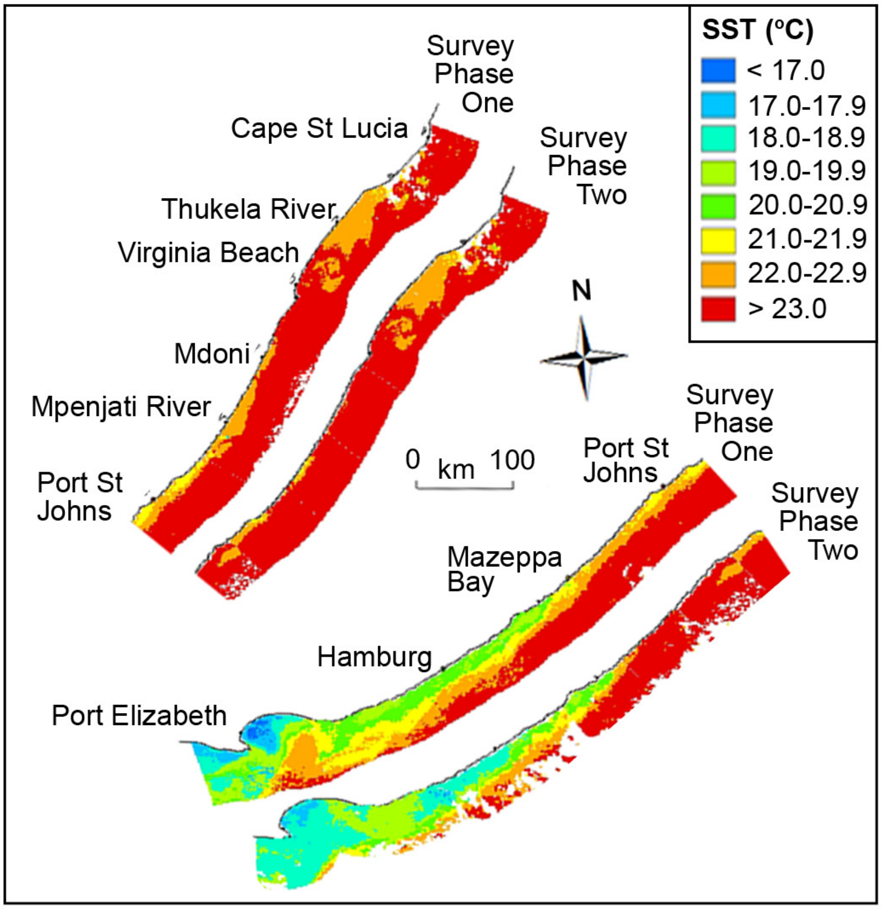

Figure 6. Remotely sensed sea surface temperatures (°C) from the 18th June – 1st July 2005. This composite image was derived from images obtained for each stretch of coastline surveyed on the survey day. White patches within the images indicate no data due to cloud cover.

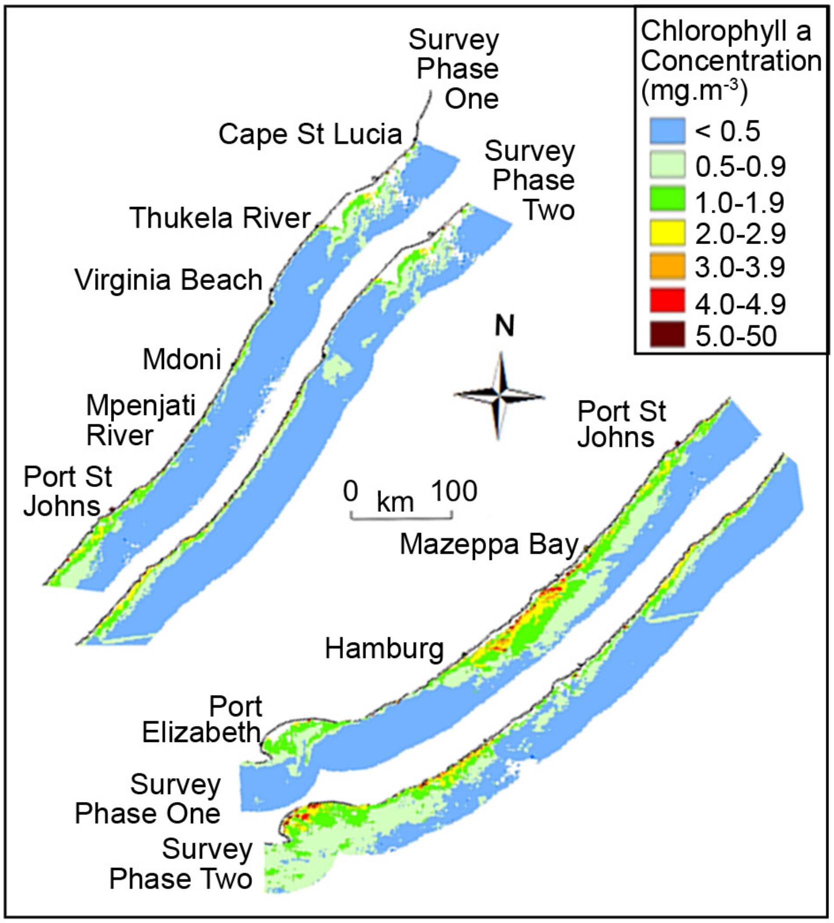

Figure 7. Remotely sensed daily chlorophyll a concentration (mg.m^{-3}) obtained for each stretch of coastline surveyed on the day. White patches within the images indicate no data due to cloud cover.

Comparing distributions

Penguins, Cape cormorants, west coast roundherring and Bryde's whales were grouped into an assemblage that appeared to be related to their longshore distribution (Fig. 8). Bryde's whale abundance was modestly correlated with penguin and Cape cormorant abundance ($r = 0.610$; $p = 0.003$), but not with west coast roundherring density. Abundance for both penguin and Cape cormorant was modestly correlated with west coast roundherring and anchovy density ($r \geq 0.504$; $p \leq 0.017$), with all species from this assemblage inversely correlated with both latitude ($-0.773 \leq r \leq -0.513$; $p \leq 0.012$) and SST ($-0.773 \leq r \leq -0.414$; $p \leq 0.044$). West coast roundherring density was modestly correlated with mean chlorophyll a concentration ($r = 0.519$; $p = 0.011$).

The next assemblage consisted of sardine, east coast roundherring and anchovy. Each of these species' densities was correlated with each other ($0.614 \leq r \leq 0.867$; $p \leq 0.002$), inversely correlated with mean SST ($r = -0.699, -0.456, -0.720$ respectively; $p \leq 0.029$), latitude ($r = -0.620, -0.476, -0.746$; $p \leq 0.022$) and positively correlated with mean chlorophyll a concentration ($r = 0.689, 0.574, 0.645$; $p \leq 0.004$).

The final assemblage consisted of common dolphins, Cape gannets, fur seals and humpback whales (Fig. 8). Amongst these predators, common dolphin and Cape gannet abundance was modestly correlated ($r = 0.567$; $p = 0.005$) with peak abundance for both of these species occurring along the same stretch of coastline, and the same distance from shore as that of east coast roundherring and sardine. When testing only within the 4 km strip nearest to shore along the east coast, gannet and common dolphin abundance was strongly correlated with sardine and east coast roundherring density ($r \geq 0.880$; $p \leq 0.021$; $n = 6$). Fur seal abundance was correlated with anchovy, west and east coast roundherring densities ($r = 0.684$, 0.653, 0.431 respectively; $p \leq 0.045$), and inversely correlated with SST ($r = -0.583$; $p = 0.004$) and latitude ($r = -0.588$; $p = 0.007$). Bottlenose dolphins were not included in any assemblage.

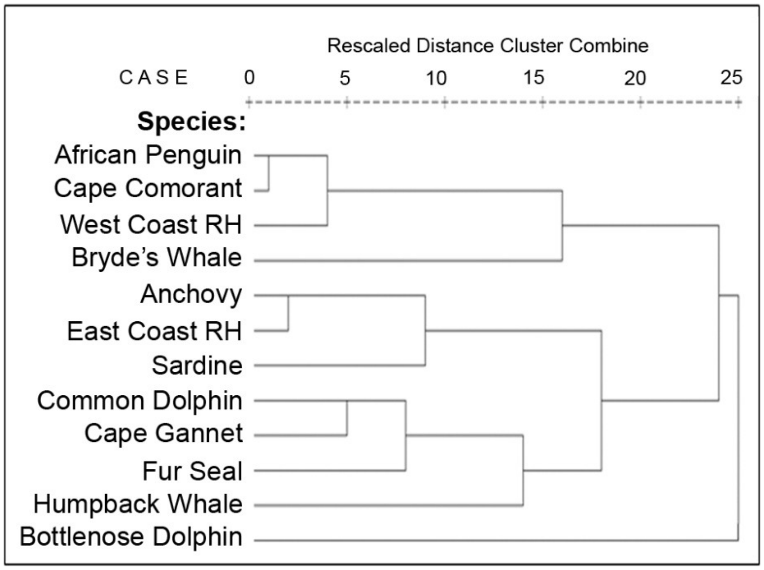

Figure 8. Hierarchical cluster analysis of sardine run-associated predator sighting rates and clupeid density rates.

DISCUSSION

The data used in this study are based upon a single cruise consisting of two passes along the east coast. The predator data were missing from the majority of one of those passes (Phase One) due to travel during the night along the coastline north of Port St Johns (Fig. 1). As such, any findings from this study can provide, at best, a "snapshot" view of the 2005 sardine run. Nonetheless, given the paucity of data on the offshore extent of the sardine run, we believe that these data do contribute to the development of an overall understanding of the sardine run on the east coast, particularly when taken into consideration with previous attempts to survey this phenomenon (Armstrong et al. 1991). These data also represent the first analysis of avian and cetacean fauna along the east coast of South Africa during this time of year.

Common dolphins are found over the continental shelf year round off the south and south-east coasts of South Africa, only coming inshore off the east coast during the winter months when following sardines (Peddemors 1999). During this time their diet is dominated by fish (88.8 %), predominantly the clupeid species detected during this cruise (Young and Cockcroft 1994). To the south of Port St Johns, common dolphin offshore distribution was significantly skewed shorewards, with peak abundance occurring within 4km of the shoreline between Port St Johns and Mazeppa Bay. The strong nearshore correlation between common dolphin distribution and east coast roundherring and sardine densities during Phase Two was therefore expected.

To the north of Port St Johns, common dolphins were spread across the continental shelf, with high abundance recorded between Port St. Johns and Mpenjati, despite relatively low clupeid abundance. This stretch of coastline contains the Waterfall Bluff Bight, where sighting rates for common dolphin, Cape gannet and sardine have previously been found to be significantly higher and further from shore than the adjacent coastlines (O'Donoghue *et al.* op cit., b; O'Donoghue and Peddemors, unpublished data). Their distribution in the lee of the bight may relate to favourable oceanographic conditions, frequently visible as cooler sea surface temperature and elevated chl a concentration in satellite imagery. The high abundance recorded during this survey may be evidence for common dolphin habituation to this part of the coastline, and should be investigated further.

Although group size for the majority of the common dolphin sightings were within the range previously reported for this species (Findlay et al. 1992), median group size recorded in our study was larger than the mean group size of 267 animals reported in the above study. The larger median and range of group sizes reported in our study concur more with those reported by Cockcroft and Peddemors (1990), suggesting that group size increases during this time of plentiful prey.

Indian Ocean bottlenose dolphins are considered to be the most ubiquitous coastal dolphin species on the east coast of southern Africa (Peddemors 1993). Bottlenose dolphin distribution is known to be highly skewed towards the shore with a preference for water depths of less than 30 m and usually within 1 km of the shore (Ross *et al.* 1987). During this survey, the median distance from shore was 1.1 km, with bottlenose dolphins never in water depths exceeding 30 m. The inability of the *Africana* to survey close to shore would likely result in an underestimation of bottlenose dolphin occurrence in the nearshore zone, but the data obtained during this study confirm the nearshore nature of this species' distribution, even during the sardine run.

Although bottlenose dolphins do not extensively feed on sardines (Cockcroft and Ross 1990), they are known to be associated with the sardine run (O'Donoghue *et al.* op cit., b; O'Donoghue unpublished data) where they are thought to feed upon fish species, e.g. elf, *Pomatomus saltatrix* (Cockcroft and Ross 1990), that follow the sardine run northwards (Fennessey *et al.* in press; van der Elst 1988). This lack of reliance on clupeids *per se* was highlighted by the low correlations of bottlenose dolphins with other species in the hierarchical cluster analysis. This research survey did not collect data on fish species primarily constituting bottlenose dolphin prey, but it is likely that clupeid abundance and distribution would affect these predatory fishes, in turn affecting bottlenose dolphins, It was not surprising, therefore, that the greatest bottlenose dolphin abundance occurred along the same stretch of coastline where the greatest sardine abundance was recorded by the working boat, and where concentrated sardine run activity was reported to be occurring near the shore (O'Donoghue *et al.* op cit., a)

Bottlenose dolphin group size was within the range previously reported for this species off the east coast of South Africa (Peddemors 1999) suggesting that these sightings represent animals resident along this stretch of coast (Cockcroft et al. 1991) rather than the larger groups of the genetically distinct migratory stock (Natoli et al. 2008).

Humpback whales were the most frequently encountered mammal and most abundant mysticete during this survey, confirming their status as the most abundant large cetacean on this coast. All humpback whales encountered were migrating along the east coast of Africa toward their tropical breeding grounds off Mozambique from their feeding grounds in Antarctic waters. Humpback whales are not considered to use the sardine run as a feeding opportunity, with no historical confirmed report of active feeding. The lack of correlation between humpback whale abundance and clupeid abundance corroborates the apparent lack of feeding on the variety of pelagic shoaling fish encountered during their north-bound migration.

The nearshore distribution of humpback whale sightings corresponds to that reported further northwards off Cape Vidal (Findlay and Best 1996a) suggesting that north-bound whales keep inshore of the powerful south-flowing Agulhas Current to reduce energy expenditure during their migration. The median group size of 2 individuals within a range up to eight whales is similar to that reported for both the east (Findlay and Best 1996b, 2006) and west (Best et al. 1995) coasts of southern Africa.

The other mysticete species were encountered far less abundantly. The predominantly single individual sightings of dwarf minke whales concur with previously reported dwarf minke whale behaviour (Zirbini et al. 1997). Their distribution over the continental shelf corresponds with previously reported distribution for minke whales, with dwarf minke whales found over the shelf in primarily shallow water and ordinary minke whales within deep oceanic water (Zirbini et al. 1997). In all areas of their range, they have been primarily seen in coastal waters from late winter to summer (Arnold et al. 1987; Best 1982; Zerbini et al. 1997).

Bryde's whales, *B. edeni,* were sighted three times: twice near Port Elizabeth and once off Mazeppa Bay. The southern nature of these sightings during the survey confirm the distribution range of Bryde's whales being primary south and west of East London (Best 2001) with all three sightings being within the offshore range of the so-called 'inshore population' (Best 1977). The correlation of Bryde's whale with African penguin and Cape cormorant abundance highlights the interrelationship between these predators whose normal range constitutes the Agulhas Bank but move east and northwards during the winter months following the sardine run.

Fur seals were most frequently sighted south of Hamburg, but their highest abundance occurred between Port St Johns and Mazeppa Bay, where their distribution was modestly correlated with that of east and west coast roundherring and anchovy. Although fur seals on the east coast of South Africa appear to feed predominantly upon benthic and demersal species (Castley *et al.* 1991), on the south coast their diet has historically contained high levels of anchovy and sardine (David 1987). The correlation between fur seal abundance and clupeid density was corroborated by the nearshore distribution of fur seals north of Hamburg where the sardine run was confined to within 4 km of the coast. Although fewer sightings of fur seals were made north of Hamburg, they were found in larger groups. To the south of Hamburg, fur seals were distributed further from shore and were usually seen as single individuals. Such distribution is more usual for fur seals foraging on the Agulhas Bank as the likely colony of origin for these fur seals is Bird Island in Algoa Bay. The distances travelled by fur seals during the sardine run are well within those previously reported for the west coast where the average distance travelled for fur seals collected at sea was 323 km and 519 km for females and males, respectively (Oosthuizen 1991).

Cape gannets of all age groups are known to follow dense fish shoals, including sardine, with some reaching the coast of Mozambique (Berutti 1995; Klages 1994). Numbers following the sardine run seem variable: large numbers were recorded off the coast of KwaZulu-Natal in 1954, but during a 10-day period of observation in 1955 only three birds were seen. The sardine shoals recorded during 1955 were nearly as large as those recorded in 1954 (Davies 1956). Cape gannets are non-breeding winter visitors to KZN (Broekhuysen *et al.* 1961). The importance of sardine to the diet of these birds has been well documented (Berruti and Colclough 1987; Crawford *et al.* 2007; Klages *et al.* 1992) and their association with the sardine run has also been reported (O'Donoghue *et al.* op cit., a, b). The high gannet abundance recorded between Port St Johns and Mazeppa Bay within 4 km of the shore, and their strong correlation with sardine, east coast roundherring and common dolphins is typical of their close association with the run. Similarly, the decline in their abundance north of Mdoni has also been described by O'Donoghue *et al.* (op cit., a, b) where it was attributed to a decline in sardine abundance from Durban northwards. To the north of Durban, the highest recorded gannet abundance was further than 16 km from shore, indicating that birds spread out over the wide continental shelf. This was in stark contrast to the movement of the birds up the KZN South Coast, when the majority of sightings were within 4 km of the shore. Gannets are thought to follow sardine movement towards shore along the KZN coastline, particularly between Mdoni and Virginia Beach (O'Donoghue *et al.* op cit., a, b).

The paucity of juvenile Cape gannets during the 2005 survey is interesting and suggests that most juveniles had already dispersed elsewhere. Birds ringed as nestlings are known to reach Mozambique on the east coast and north of Angola on the west coast (Crawford *et al.* 1983). Gannets seem to locate shoals by observing movements of other birds and are attracted by the sight of other gannets diving (Crawford 2005). They were also observed following common dolphins and plunge-diving over both feeding common and bottlenose dolphins (BMD, PAW and VP pers. obs.). Whether any species benefits from these aggregations remains to be answered.

White-chinned petrels are often associated with feeding groups of fur seal, common dolphin and Bryde's whale in the southern Benguela, where their main food is offal and discarded fish from trawlers (Jackson 1988). In our study, there was no obvious correlation between White-chinned petrel distribution and that of the above mentioned marine mammals. Nevertheless, it was often observed within the vicinity of pelagic fish shoals.

The major food source of the Swift Tern is pelagic shoaling fish, principally sardine and anchovy (Crawford & Dyer 1995), near which swift tern were frequently sighted during this survey.

Although the Yellow-nosed albatross probably feeds primarily on fish, including sardine, anchovy and the roundherring (Crawford *et al.* 1991), there is little evidence to suggest that they were targeting these fish species during the survey. The four pelagic fish species recorded in the survey were estimated to comprise 20 % by mass to the diet of the Yellow-nosed albatross in south-western Africa (Crawford *et al.* 1991) but generally the diet of this albatross in southern Africa is poorly known (Ryan 2005a).

There was no indication during the survey that the distribution of sooty shearwater followed that of any marine mammals, although it has been associated with feeding groups of fur seals, common dolphins and Bryde's whales in the southern Benguela (Jackson 1988; Ryan 2005b). In the latter region, the main diet of the sooty shearwater was small fish, including anchovy, which comprised 33 % by mass (Jackson 1988; Ryan 2005b).

Subantarctic skuas are mainly winter visitors to southern Africa from their subantarctic breeding grounds. Their diet in southern Africa is little known (Crawford *et al.* 1991). They kleptoparasitise other bird species including Cape gannets, white-chinned petrels, gulls and terns (Wanless & Ryan 2005) but there was little evidence for any association with the distributions of other bird species during this survey.

The main prey items of the African penguin are sardine and anchovy (Crawford 2004) but in the 2005 sardine run survey, the birds did not appear to follow this prey north of Hamburg and they are generally rare east of Algoa Bay (Wilkinson *et al.* 1999). It is thought that some African penguins, primarily birds in their first year, do follow the migrating sardines northwards and come ashore, mostly in a state of starvation, when the sardine shoals dissipate. A total of 99 such birds were found along the KwaZulu-Natal coast between 1981 and 1999 (Wilkinson *et al.* 1999).

The Cape cormorant is said to be a regular visitor in varying numbers between June and November to KwaZulu-Natal, where they are associated with the winter sardine run (Cyrus and Robson 1980; Taylor *et al.* 1999). In the south-western Cape, anchovy and sardine accounted for 87 % of the diet of Cape cormorants between 1984 and 1992 (Crawford & Dyer 1995). It is likely that these species were also being targeted by the cormorants during the current survey. Only two birds were recorded east of Algoa. Cape cormorants form large flocks when feeding (Davies 1956) and would have been obvious had they been present. It is not clear why so few Cape cormorant were sighted along this east coast.

Although feeding on small fish, the main food of the Antarctic prion is zooplankton (Ryan and Rose 1989) so this species is unlikely to have been associating with the sardine run.

One of the aims of this study was to determine the longshore and offshore extent of the sardine run during 2005. The strong, inverse relationship between the clupeid species' density, SST and latitude, and the peak in sardine and east coast roundherring density within 4 km of the shore at the northern end of the strip of cool water stretching up the east coast are suggestive of temperature control imposed by the warm Agulhas Current. Nearshore sea temperatures in the Mazeppa Bay region and to the south are cooled by a persistent upwelling cell (Lutjeharms *et al.* 2000). The northward extent of this upwelling cell varies, which presumably affects clupeid distribution, and consequently the two principal predators of the sardine run, the common dolphin and Cape gannet.

Virtually no clupeids were detected by the FRS *Africana* beyond the 30 m isobath to the north of Mpenjati River. The working boat, surveying only in water shallower than 30 m, recorded the highest sardine density between Mpenjati River and Mdoni, suggesting that sardine distribution was skewed shorewards along the KZN coastline. This was corroborated by reports of concentrated KZN sardine run activity, including large numbers of feeding predators, for the entire period that the cruise ship was in KZN coastal waters (unpublished data). The low predator abundance recorded across the KZN continental shelf further emphasises the nearshore skew in sardine distribution.. These findings support those reported in (O'Donoghue *et al.* op cit., b), where it was suggested that sardines are forced shorewards by the warm Durban Eddy, from Mdoni northwards. This would explain the peak in sardine abundance to the south of Mdoni as the northward movement of fish would have been impeded.

The distribution patterns of marine mammals and seabirds observed during the sardine run cruise were typical for these species, with latitude and temperature effects dominating. It is evident that along the Eastern Cape coastline, all four clupeid species constitute what is commonly called the sardine run, but that sardine and east coast roundherring, during this year at least, were the principal clupeids up the east coast. Along the KZN coastline, sardine emerged as the dominant clupeid with a distribution that was very strongly skewed towards shoreline. Future attempts to establish the abundance of sardines along the east coast should, therefore, ensure that this nearshore zone is surveyed.

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CHAPTER FIVE

Fine-scale sardine run distribution and predator behaviour along the Eastern Cape 'Wild Coast' in relation to environmental conditions.

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ABSTRACT

Information pertaining to the distribution of the sardine run along the Eastern Cape 'Wild Coast' (South Africa) is scarce despite its ecological importance and a rapid increase in regional tourism. In redress, daily aerial surveys were conducted each June from 2004 to 2006. Sardines, *Sardinops sagax*, were sighted along the Lower Wild Coast every year, but their abundance declined northwards in tandem with increasing sea temperature, especially above 21 °C. Waterfall Bluff emerged as an important area of coastline by providing sardines with suitable conditions and thereby causing high predator abundance. Cape Gannet, *Morus capensis*, were very closely associated with sardine distribution. Gannets travelled more frequently during strong alongshore winds and fed more frequently following storms. Common Dolphins, *Delphinus capensis*, were closely associated with sardines and feeding gannets along the Lower Wild Coast. Bottlenose Dolphin, *Tursiops aduncus*, group size increased with the commencement of the sardine run and abundance was low during the weak run of 2006. Atmospheric and oceanographic features affect the movement of sardines along the Wild Coast, which in turn influence predator activity. The Wild Coast appears crucial in regulating the annual sardine run up into KZN waters.

Keywords: Cape gannet, chlorophyll a, *Delphinus capensis*, distribution, Eastern Cape, Indo-Pacific bottlenose dolphin, long-beaked common dolphin, *Morus capensis*, sardine run, *Sardinops sagax*, sea surface temperature, *Tursiops aduncus*, Waterfall Bluff, Wild Coast

INTRODUCTION

The annual movement of South African Sardine, *Sardinops sagax* (Jenyns 1842), up the east coast of South Africa and into KwaZulu-Natal (KZN) coastal waters (Fig. 1) is known as the ‘sardine run’. Historically the sardine run has been utilised by a local beach-seine and recreational fishery, and in recent years, has become increasingly important as an international tourism event (Dicken in press). The recent spate of weak sardine run events along the KZN coastline (O’Donoghue *et al.* in press, a) has reinforced the need for an understanding of this phenomenon.

It is believed that sardine northward movement is initiated in the Eastern Cape, and that events occurring on the stretch of coastline, known as the Wild Coast (Fig. 1), influence whether the sardine and their associated predators reach KZN. A fine-scale investigation of the movement and behaviour of sardine and their predators in this formative coastal region is therefore critical to better understanding the sardine run.

During the austral summer young sardines (+ 1yr old cohort) are frequently concentrated in the shallow bays of the Eastern Cape, e.g. Algoa Bay (Fig 1) (Armstrong *et al.* 1987; Smale 1983), within which onshore winds generate cool and productive upwelling conditions (Schumann *et al.* 1988), with temperatures within sardine preferred range of 14 to 20 °C (Barange and Hampton 1997). With the onset of winter these conditions are disrupted by the passage of severe low pressure weather systems termed ‘coastal lows’. These systems have a periodicity of between 3.8 and 5.9 days (Hunter 1988), and are frequently accompanied by strong SW winds. The summer thermocline across the continental shelf dissipates and extensive mixing occurs through the water column (Schumann *et al.* 1988). This coincides with the eastward movement of sardine, which most frequently consist of the 1 – 2 year old cohort (Baird 1971). The seasonality of sardine movement into cool water led Armstrong *et al*. (1991) to propose that the run was an extension of the sardines’ habitable range up the coast.

Along the Eastern Cape coastline, centred in the Port Alfred region but usually reaching as far north as the Mbashe River (Fig. 1), is a semi-permanent upwelling cell of cool nutrient-enriched water (Lutjeharms *et al.* 2000). This presumably provides suitable habitat for sardine occupation, although the predominant nearshore current direction is usually in a south-westerly direction due to the pole-ward flowing, warm Agulhas Current. There are, however, occasional barotropic current reversals associated with strong winds out of the south west (Schumann 1987), which may aid sardine northward movement.

To the north of the Port Alfred upwelling cell the continental shelf narrows considerably, to a minimum of around 9 km between Waterfall Bluff and Port Edward (Fig. 1). The influence of the Agulhas Current increases along the largely straight coastline, with little retention of primary productivity or zooplankton grazers (Carter and Schleyer 1988) and, therefore, presumably representing habitat of deteriorating quality for sardines. At Waterfall Bluff, however, there is a westward inflection of the coastline. In the lee of the resulting bight, shelf conditions are less influenced by the Agulhas Current with sediment bed-form patterns suggestive of either slack current, or current conditions counter to the flow of the Agulhas Current (Flemming 1980), which is found further from shore (Schumann 1987). This part of the coastline may therefore be a holding area for sardines, providing them with suitable habitat and refuge from the Agulhas Current, until favourable conditions occur for northward movement. To the north of Waterfall Bluff, the continental shelf conditions are again dominated by the Agulhas Current. Consequently, the Waterfall Bluff Bight is thought to be crucial to the success of the sardine run along the KZN coastline, which begins at Port Edward, about 80 km to the north (Fig. 1).

Sardine nearshore distribution, in relation to environmental conditions, has not been studied along the Wild Coast. Within KZN, the probability of sardine presence decreases when mean sea surface temperatures (SST) exceed 21 °C with sardines sighted more frequently during periods of stable atmospheric conditions (O’Donoghue *et al.* op cit., a). The nature of the association between sardine distribution and the passage of coastal lows, however, remains enigmatic. There exists the popular perception that sardines may use nearshore current reversals induced by these coastal lows (Schumann 1988) to move up the coast. We investigated this perception by using a fine-scale data set monitoring sardine and predator movements in relation to daily local environmental conditions including those typical during and following the passage of coastal lows.

Sardine are followed up the Eastern Cape coastline by Cape gannet, *Morus capensis* (Lichtenstein 1823), from their summer breeding colony in Algoa Bay (Fig. 1). The dietary importance of sardine to gannet has been well established (Batchelor and Ross 1984; Crawford *et al.* 2007; Klages *et al.* 1992), as is the close nature of their association with the sardine run along the KZN coastline (O'Donoghue *et al.* op cit., a; O'Donoghue *et al.* in press, b). Much less, however, is known about gannet distribution along the Wild Coast, its relation to sardine and associated predator distribution, and about gannet movement and behaviour in relation to environmental variables.

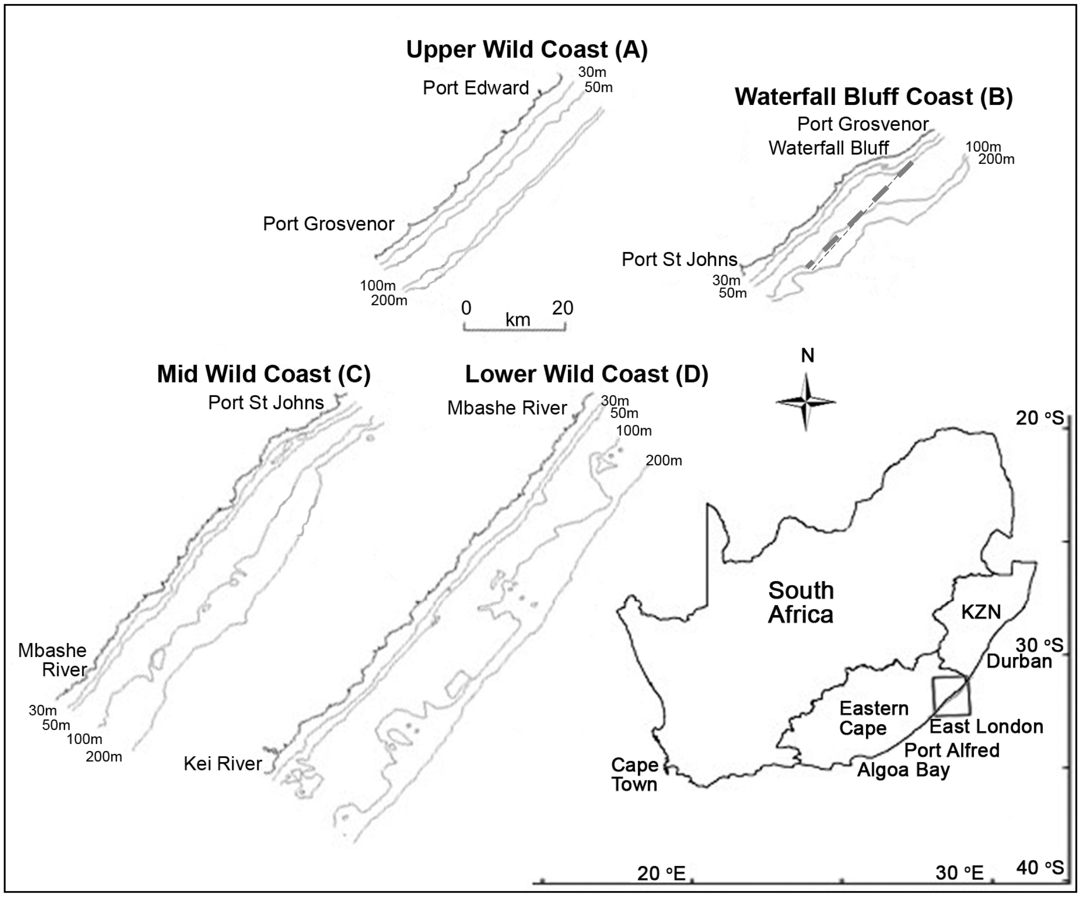

Figure 1. Exploded view of the four coastal zones (A – D) along the Eastern Cape "Wild Coast" (denoted by the box in the insert map of South Africa) into which sardine run aerial survey data were divided and analysed. Also shown are the 30, 50, 100 and 200m isobaths. The dashed line in (B) represents the location of a current line on the 18th June 2005.

Long-beaked common dolphin, *Delphinus capensis* Gray 1828, are resident throughout the year along the Eastern Cape coastline (Fig. 1) as far north as East London (Cockcroft and Peddemors 1990; Peddemors 1999). During winter they move northwards along the Wild Coast and into KZN coastal waters in association with the sardine run, and are considered to be the sardine run's most important mammalian predator (O'Donoghue *et al.* op cit., a, b). However, by the time common dolphin reach the KZN coast their abundance is significantly lower than along the Wild Coast, highlighting the need to better understand their role in the dynamics of the sardine run.

Indo-Pacific bottlenose dolphin, *Tursiops aduncus* (Ehrenberg 1833), are resident throughout the South African south east coast with their distribution being nearshore (Ross *et al.* 1987; Ross *et al.* 1989) and confined to water depths of less than 30 m. Each winter, KZN bottlenose dolphin abundance increases (O'Donoghue *et al.* op cit., a) with the arrival of a migratory stock (Natoli *et al.* 2008) from the south, supposedly from beyond the Wild Coast. Their distribution has been significantly associated with the KZN sardine run (O'Donoghue *et al.* op cit., a; Peddemors 1999; Peddemors *et al.* submitted). From stomach content analysis of resident bottlenose dolphin captured along the KZN coastline (Cockcroft and Ross 1990), it would appear that they do not utilise sardine as a major source of prey. However, other fish species that migrate up the east coast in association with the sardine run, e.g. elf, *Pomatomus saltatrix* (Linnaeus 1766), do form a significant part of bottlenose dolphin diet (Peddemors and Cockcroft 1997). A possible difference in dietary preference between the resident and migratory bottlenose dolphin stocks has been hypothesised (O'Donoghue *et al.* op. cit, b), with the migratory bottlenose dolphin stock potentially feeding more on sardine, but this requires further investigation. The apparent close association between the movement of the migratory stock of bottlenose dolphin and the sardine, and the enigmatic relationship of these delphinids with the sardine run, suggests these relationships are worthy of further investigation.

Humpback Whale, *Megaptera novaeangliae* (Borowski 1781), traverse the Wild Coast on their northward breeding migration during winter (Best *et al.* 1998). Although humpback whales are often sighted in close proximity to sardine run activity, there are no reliable reports of them actively feeding upon sardine. Any association with the sardine run is thought, in KZN at least, to be coincidental. Nevertheless, they are the most abundant Mysticete along the Wild Coast during the sardine run (O'Donoghue *et al.* submitted, c), and as such, have been included in these analyses.

This study reports on fine-scale movements and inter-specific interactions between sardines and their predators using daily flights along the Wild Coast to survey sardine run activity. Data are correlated with local environmental conditions at a smaller spatio-temporal scale than have been previously reported in an attempt to better understand the biological and environmental parameters affecting the movement of sardines and their predators.

METHODS

Aerial surveys

Aerial surveys were conducted both opportunistically and weather permitting from micro-light aircraft along the Wild Coast shoreline during the month of June between 2004 and 2006 (Fig. 1). The 1 km fixed strip-width line transect methods were the same as those used during Chapter Two, except for the following: The single passenger (researcher) was responsible for searching the survey strip, taking an inclinometer reading of the angle of animal sightings from the horizontal plane and identifying, counting and recording the species observed. The pilot searched beyond the survey strip for sardine run activity and provided a GPS position and a second count for each observation.

Each transect strip was divided into 5 x 5 km bins. The number of sardine sightings within a bin was summed and divided by five to give a sighting rate per kilometre for each bin per survey. For predators, the total number of individuals counted within a bin gave the abundance per kilometre for each bin. The Cape Gannet was the only predator for which there was sufficient data to sub-divide abundance into the following three behaviour classes: "Feeding" including all observations of circling above and diving onto prey, "Resting" where gannets were observed sitting on the water, including post feeding bouts, and "Travelling" where gannets were observed flying in a straight line without any indication of their typical foraging flight pattern (Nelson 1978).

Sardine sighting, predator abundance and gannet behaviour rates for each bin were ascribed to a suite of temporal, spatial and environmental predictors, and subjected to statistical analyses to determine whether differences in rates within predictor classes were significant. The temporal predictors included: (1) "SR", which compared predator rates before the commencement of, and during the sardine run and (2) survey "Year".

Spatially, each bin was ascribed to one of the following four zones along the Wild Coast: Upper Wild Coast, Waterfall Bluff Coast, Mid Wild Coast and Lower Wild Coast (Fig. 1). The segregation of the coastline into these zones follows the description of continental shelf oceanographic and bathymetric conditions in the introduction. The distance of each observation from shore was calculated by applying the equation: tan (Radians) * height (m) to the inclinometer reading of each observation. An estimate of the depth of the water column below each observation was obtained using 1:50 000 SAN bathymetric charts for the study area. The isobaths for the following depth classes on these charts were used in this study: 0 – 15 m, 16 – 30 m, 31 – 50 m and > 50 m (Fig. 1). The suite of environmental predictors included variables calculated from the following climate and oceanographic data.

Climate data

Climate data were obtained from the South African Weather Service (www.weathersa.co.za), for the Port Edward (altitude = 11 m) and East London (125 m) weather stations (Fig. 1). The weather conditions recorded at these two stations were assumed to be representative of overall conditions between them. Recorded data included: atmospheric pressure (millibars – measured at 8am) and average wind speed ($m.s^{-1}$) and direction (10° increments from true north) measured thrice daily at 08h00, 14h00 and 20h00.

Maximum daily wind speed and direction were obtained from the weather station nearest each sighting for both the day of the observation and the previous day. Wind speed was converted into knots ($1\ m.s^{-1} = 1.94$ knots) and ascribed to one of the following three classes: (0 – 10, 11 – 20 or 21 – 40 knots). Wind direction was simplified to: NE (10 – 90°), SE (100 – 170°), SW (180 – 260°) and NW (270 – 360°).

Daily atmospheric pressure readings were used to record the change in atmospheric pressure from each previous day (increase or decrease) during the study period. Each observation's temporal position relative to the cycle of coastal lows propagating north-eastwards along the coastline was classified as follows: "during" the passage of a low pressure/ cold front system, one "day after" and "between" systems. "During" was characterised by the commencement of SW winds following a period of decreasing atmospheric pressure. "Day after" was identified by the day of the cessation of SW winds, increasing atmospheric pressure and usually a peak in swell size. "Between" consisted of all other survey days that did not fit into these two categories

Oceanographic data

Oceanographic conditions were described using remotely sensed data derived from the Moderate Resolution Imaging Spectroradiometer Aqua Satellite (MODIS). All data were obtained from the Remote Sensing Server for Marine Sciences website (www.rsmarinesa.org.za), where they are freely available as level 4 products at a 1 km^2 resolution. Three-day weighted average composites ($day^{-1} * 1$, $day * 3$, $day^{+1} * 1$) of sea surface temperature (°C) and chlorophyll a concentration (chl a, $mg.m^{-3}$) were used to mitigate the effects of cloud cover. Due to the problem of coastal "bleed-off" in satellite images, there was an approximately two pixel-width strip, i.e. 2 km, of no-data along the coast. As sightings were predominantly within this 2 km strip along the coast, a 5 km^2 survey bin size was chosen to provide an estimation of oceanographic conditions surrounding observations. Using the ArcGIS 9 zonal statistics tool, the mean values for SST and chl a concentration were computed for each bin.

Statistical analyses

Sardine sighting rates, predator abundance (including gannet behaviour) and predator group size were described using the spatial, temporal and environmental variables described above. Differences between classes of these variables were tested for significance using non-parametric inferential statistical methods suitable for when data do not conform to a normal distribution. Associations between sardine distribution, predator distribution and remotely sensed variables were investigated using simple Spearman's Rank Bivariate Correlations with the data separated into separate coastal zones. The relationship between sardine and predator distribution and gannet behaviour was summarised within a Hierarchical Cluster Analysis (as used in Chapter 4), which employed an average linkage method between groups using the squared Euclidean distance measure and with values transformed by their Z-scores.

RESULTS

Aerial surveys: 2004

The dates of each aerial survey, distances surveyed per coastal zone and the total sightings per species are provided in Table 1. Aerial surveys commenced ten days before the arrival of the 2004 sardine run along the Lower Wild Coast on the 19th June. A total of 32 flights were undertaken, during which 19 aerial surveys were successfully completed. This was the only year in which aerial surveys preceded the arrival of the sardine run, so comparisons of predator abundance rates before and during the sardine run were restricted to this year. The 2004 sardine run reached the KZN coastline on the 24th June (unpublished data). It therefore covered the approximately 250 km long coastline in six days, at a mean rate of just over 40 km per day (Fig. 2).

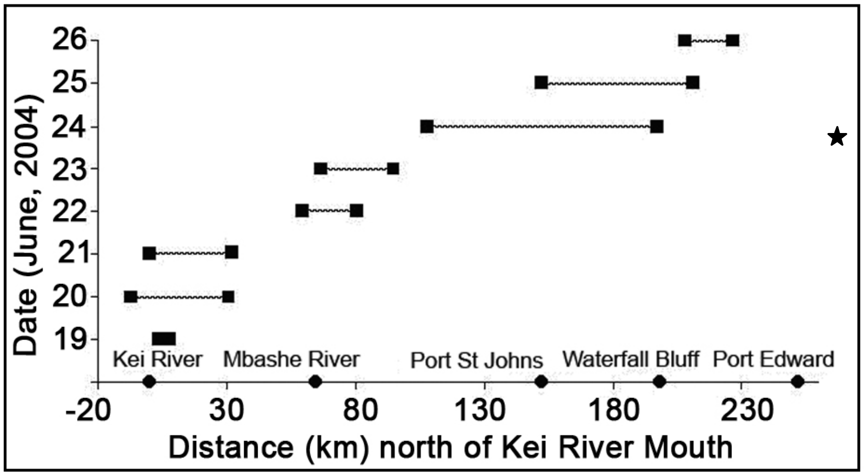

Figure 2. Daily movement and extent of the 2004 sardine run activity along the Eastern Cape "Wild Coast" as identified by feeding aggregations of predators. The x-axis gives the distance northwards from the Kei River mouth with superimposed place names. The asterisk denotes the first sighting of advanced sardine shoals in KZN.

Aerial surveys: 2005

The 2005 surveys commenced on the 16th June, four days after the sardine run reached the KZN coastline (O'Donoghue *et al.* op cit., a), and were largely restricted to the Waterfall Bluff and Mid Wild coasts (Table 1). A total of 22 flights were undertaken, during which 9 aerial surveys were successfully completed. Comparisons of abundance rates between zones during 2005 were restricted to the two central zones to avoid bias resulting from low sample size in other coastal zones.

On the 18th June, during the peak of the sardine run activity along the Waterfall Bluff Coast, a current line was observed extending southwards from the northern end of Waterfall Bluff (dashed line in Fig. 1B), with concentrated sardine run activity sighted along the shoreward side of this line. An overlay of SST conditions
for this day showed that this line corresponded with an increase in water temperature from less than 21 °C on the shoreward side, to above 22 °C on the seaward side.

Aerial surveys: 2006

The 2006 surveys commenced on 16 June, but were limited to the coastline north of Port St Johns (Fig. 1). A total of 8 flights were undertaken, during which 8 aerial surveys were successfully completed. At the time, there was very little sardine run activity throughout this region, with feeding aggregations of predators apparently predating upon roundherring of the genus *Etrumeus* (direct observation by D Wong 2006 pers. comm.).

Table 1. Distances surveyed per coastal zone (km) and number of sardine and predator sightings by date during aerial surveys along the Eastern Cape Wild Coast between 2004 and 2006.

Date	Upper Wild Coast	Waterfall Bluff Coast	Mid Wild Coast	Lower Wild Coast	Sardine	Cape Gannet	Common Dolphin	Bottlenose Dolphin	Humpback Whale
2004_06_09	-	-	-	40.6	0	7	2	6	0
2004_06_10	-	-	-	40.6	0	10	0	10	0
2004_06_11	-	-	-	38.3	0	4	0	5	0
2004_06_12	-	-	-	36.1	0	6	0	3	0
2004_06_14	-	-	-	36.1	0	2	1	6	0
2004_06_15	-	-	-	36.1	0	6	2	5	2
2004_06_16	-	-	-	36.1	0	6	0	6	0
2004_06_18	-	-	-	36.1	0	4	0	7	1
2004_06_19	-	-	-	36.1	1	7	0	7	2
2004_06_20	-	-	-	40.6	6	18	3	9	1
2004_06_21	-	-	-	44.6	4	17	3	2	1
2004_06_22	-	-	-	88.3	6	43	0	8	0
2004_06_23	-	-	15.2	31.7	4	19	2	7	0
2004_06_24	-	23.8	70.3	-	17	35	7	10	3
2004_06_25	3.3	51.9	55.9	-	5	16	4	13	3
2004_06_26	19.1	35.4	-	-	7	18	1	5	2
2004_06_28	-	35.5	-	-	1	8	1	4	0
2004_06_29	3.3	55.3	-	-	5	10	1	2	2
2004_06_30	-	45.2	-	-	6	7	4	7	1
2004 total:	**25.7**	**247.1**	**141.4**	**541.3**	**62**	**243**	**31**	**122**	**18**
2005_06_16	-	-	19.4		0	7	0	0	0
2005_06_17	-	39.2	-	-	10	24	0	6	0
2005_06_18	2.3	55.3	-	-	14	23	2	6	0
2005_06_20	2.3	55.3	-	-	10	19	3	2	2
2005_06_22	-	-	30.7	-	7	14	2	5	0
2005_06_23	2.3	53.9	-	-	4	25	0	2	1
2005_06_24	-	-	33.7	-	0	17	3	6	1
2005_06_26	-	-	71.9	23.5	6	32	5	21	3
2005_06_28	-	27.2	39.8	-	0	32	0	11	1
2005 total:	**6.9**	**230.9**	**195.5**	**23.5**	**51**	**193**	**15**	**59**	**8**
2006_06_16	28.6	7.0	-	-	0	3	1	1	0
2006_06_17	2.3	55.3	-	-	2	6	0	0	1
2006_06_18	2.3	28.1	-	-	0	2	1	0	3
2006_06_19	2.3	36.4	-	-	3	3	0	1	2
2006_06_20	2.3	28.1	-	-	0	0	1	0	5
2006_06_21	2.3	29.1	-	-	1	1	1	0	0
2006_06_24	2.3	29.1	-	-	0	1	0	0	1
2006_06_26	35.8	28.1	-	-	1	1	1	2	2
2006 total:	**78.2**	**241.2**	**-**	**-**	**7**	**17**	**5**	**4**	**14**
Total	**110.7**	**719.0**	**336.9**	**564.8**	**120**	**453**	**51**	**185**	**40**

Temporal distribution

Gannet abundance ($z = -6.31$; $p < 0.001$), gannet group size ($z = -7.704$; $p < 0.001$) and bottlenose dolphin group size ($z = -4.175$; $p < 0.001$) increased significantly following the commencement of the 2004 sardine run along the Lower Wild Coast (Fig. 3). There were too few common dolphin and humpback whale sightings prior to the commencement of the sardine run to consider for this comparison.

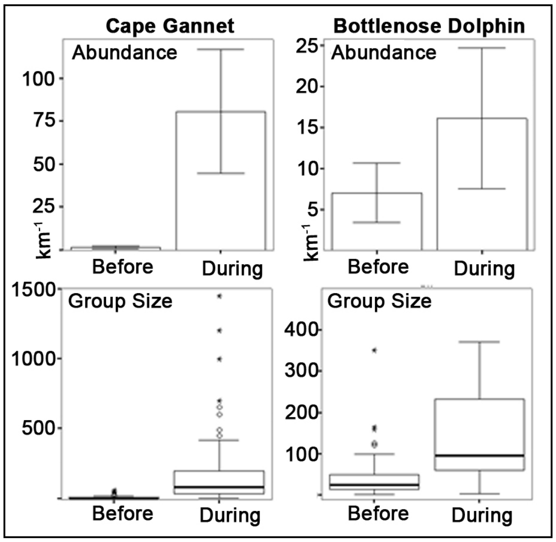

Figure 3. Cape Gannet and bottlenose dolphin abundance (per km) and group size before the commencement of, and during, the 2004 sardine run along the Lower Wild Coast. Error bars denote the 95 % confidence intervals.

Inter-annual sighting rates highlighted the reduced sardine and predator activity in 2006 compared with 2004 and 2006 along the Waterfall Bluff Coast (Fig. 4); sardine ($\chi^2 = 10.33$; $p = 0.006$), gannet ($\chi^2 = 21.73$; $p < 0.001$) and bottlenose dolphin ($\chi^2 = 17.54$; $p < 0.001$) rates were significantly higher during both 2004 and 2005 than during 2006. Gannet abundance (Fig. 5) for all three behaviour classes at Waterfall Bluff was significantly lower during 2006 than during the previous years ($\chi^2 \geq 12.142$; $p \leq 0.002$), except for resting gannets during 2004. The Mid Wild Coast was not surveyed in 2006, however sardine sighting ($z = -2.47$; $p = 0.013$) and common dolphin abundance ($z = -1.98$; $p = 0.047$) rates during 2004 were significantly higher here than during 2005 (Fig. 4). Gannet group size along the Mid Wild Coast was significantly smaller ($z = -6.85$; $p < 0.001$) during 2005 than during 2004 (Fig. 6).

Spatial predictors

Substantial longshore spatial variation in both sardine distribution and predator abundance occurred along the Wild Coast (Fig. 4). Sardine sighting rate ($z = -2.88$; $p = 0.004$) decreased from the Waterfall Bluff Coast to the Mid Wild Coast during 2005. The focus on the Waterfall Bluff Coast in 2006 (Table 1) led to an inability to realistically compare zones in 2006. Waterfall Bluff consistently had the largest group sizes for gannets and common dolphins (Fig. 6). Gannet behaviour differed between years (Fig. 5): during 2004 travelling gannet abundance was highest along the Lower Wild Coast and lowest at Waterfall Bluff, whilst the converse was true for feeding gannet abundance. For each year, feeding gannet abundance was highest at Waterfall Bluff.

Mean sardine, gannet and common dolphin distance from shore was greatest at Waterfall Bluff (Fig. 7). This distance was significantly further than for sardines along the Upper Wild Coast (χ^2 = 13.47; p = 0.004) and gannets along the Upper and Lower Wild coasts (χ^2 = 31.39; $p < 0.001$). Bottlenose dolphin distance from shore was greatest along the Lower Wild Coast (χ^2 =34.08; $p < 0.001$),

Analysis of water depths (Fig. 8) indicated that sardines were in deeper water along the Waterfall Bluff Coast compared with the Lower Wild Coast (χ^2 = 10.62; p = 0.014). Gannets along the Waterfall Bluff to Mid Wild coasts were in deeper water than along the Lower Wild Coast (χ^2 = 10.82; p = 0.013). Common (χ^2 = 36.75; $p < 0.001$) and bottlenose (χ^2 = 153.35; $p < 0.001$) dolphins were sighted in shallower water along the Lower Wild Coast than within the other three zones.

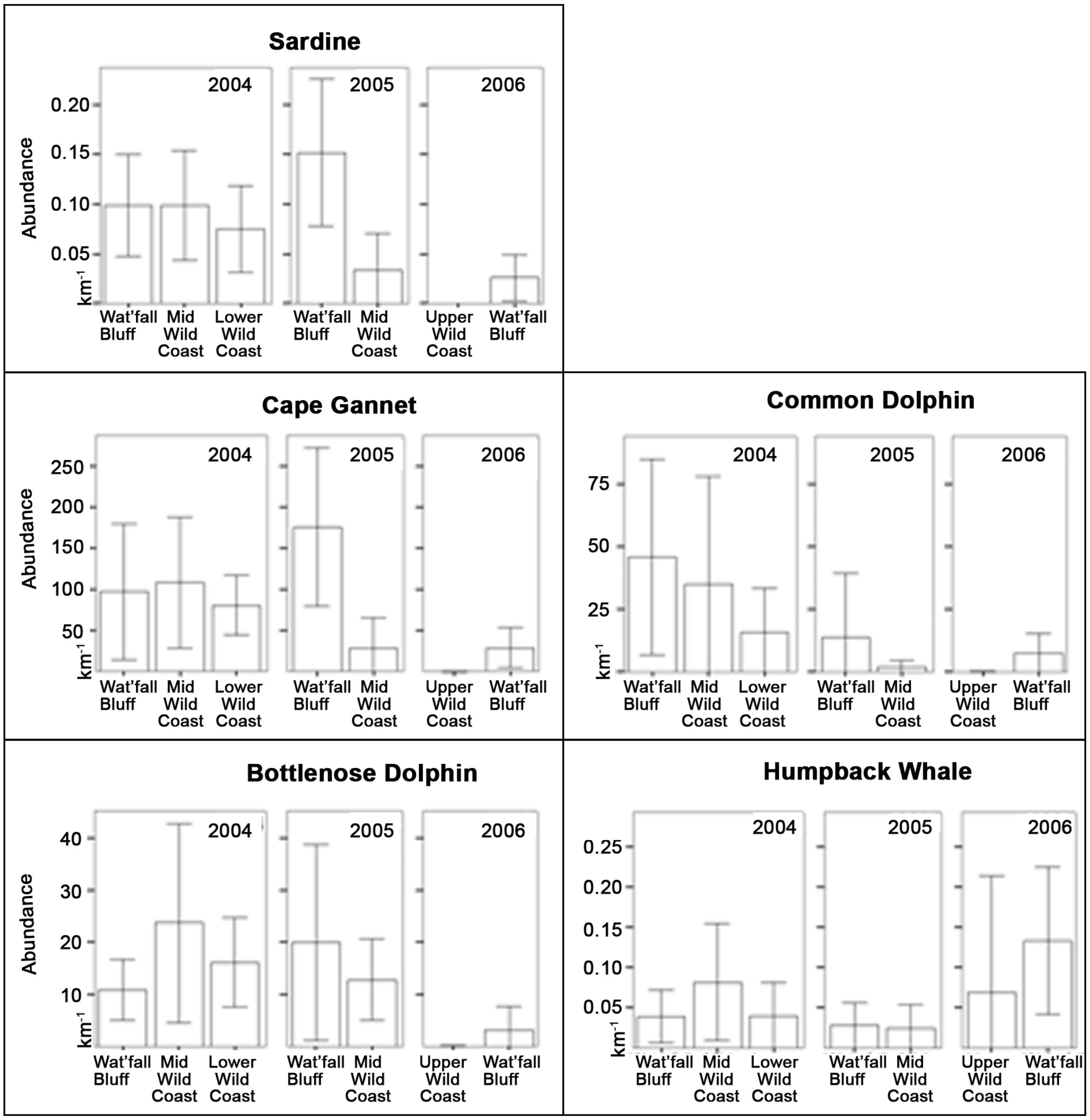

Figure 4. Sardine sighting rate and predator abundance (per km) within coastal zones (x-axes) during the years 2004 to 2006. Error bars denote the 95 % confidence intervals.

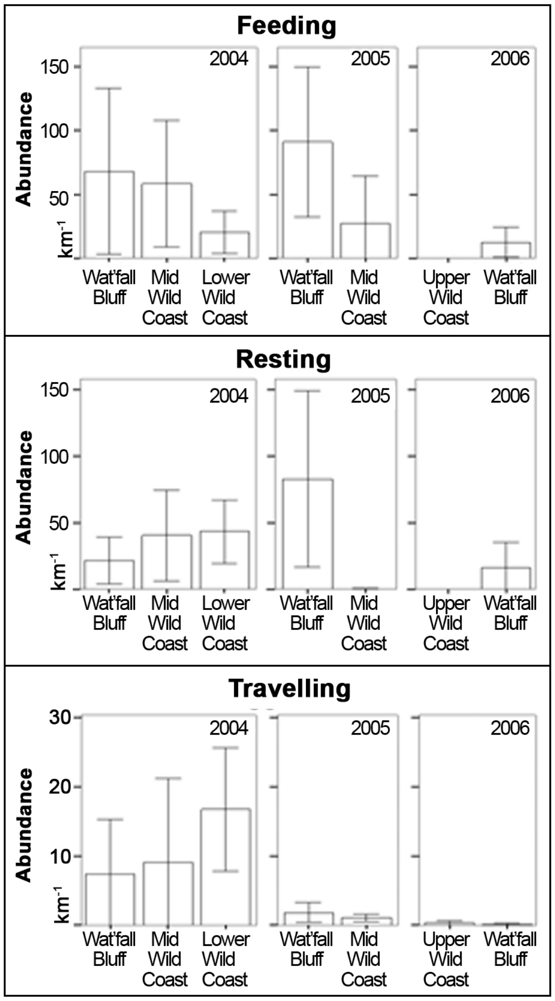

Figure 5. Gannet abundance (per km) for three behaviour classes within coastal zones (x-axes) during the years 2004 to 2006. Error bars denote the 95 % confidence intervals.

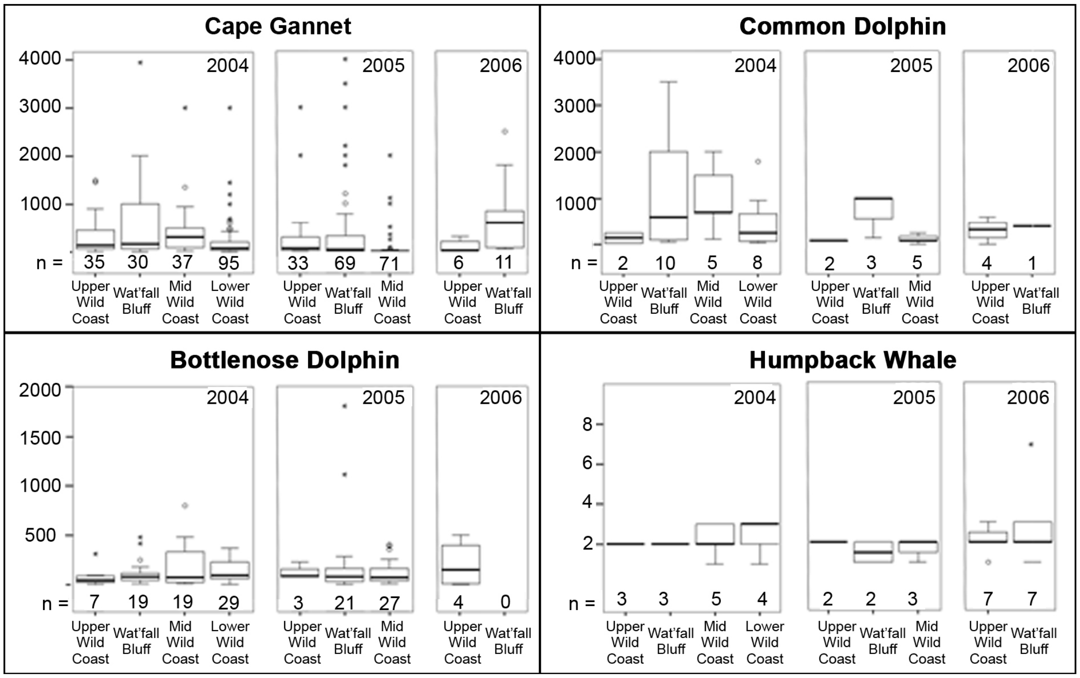

Figure 6. Predator group size within coastal zones (x-axes) along the Eastern Cape 'Wild Coast' from 2004 to 2006. Circles and stars represent outliers and extreme values respectively.

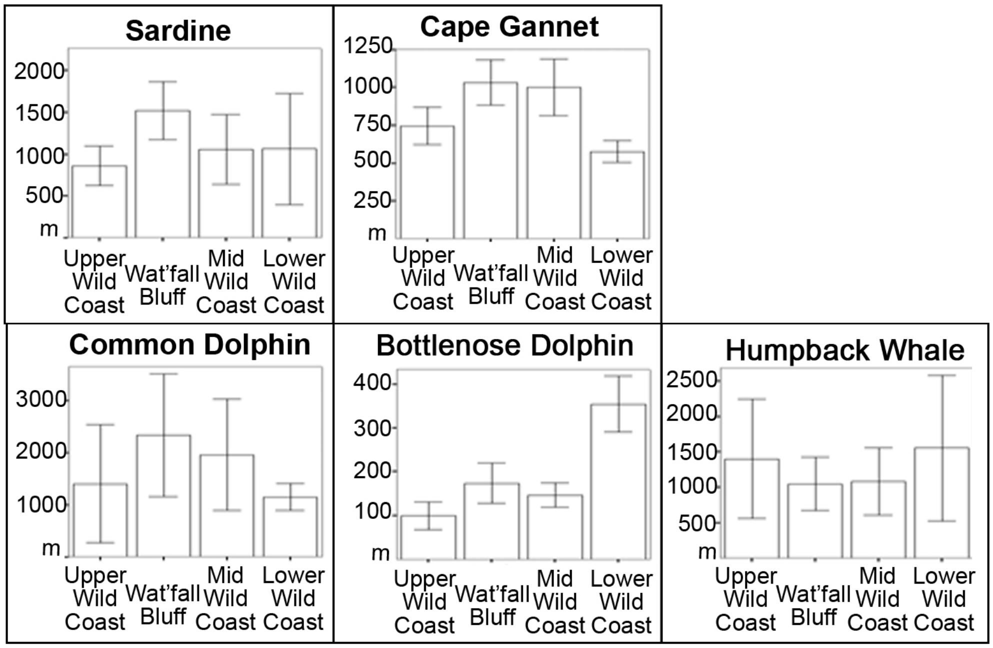

Figure 7. Mean sardine and predator distance from shore within coastal zones (x-axes) along the Eastern Cape 'Wild Coast'. Error bars denote the 95 % confidence intervals.

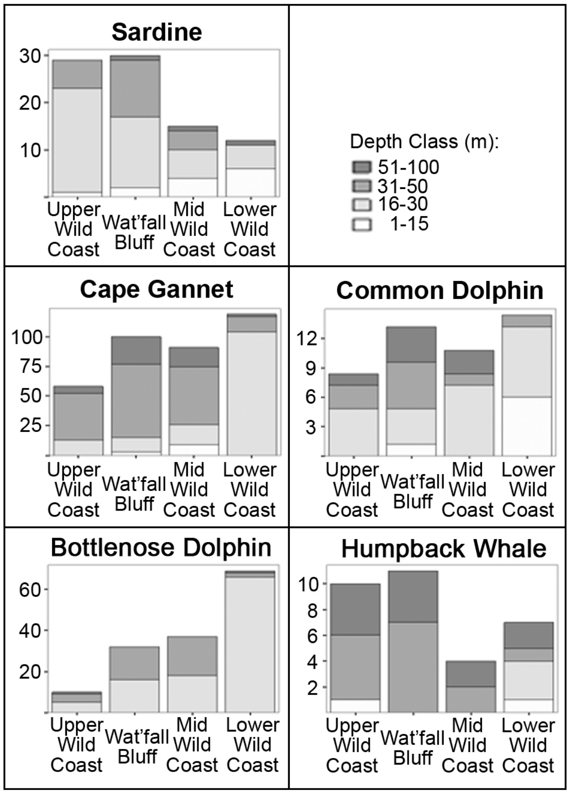

Figure 8. Number of sardine and predator sightings per depth class (m) within coastal zones along the Eastern Cape 'Wild Coast.'

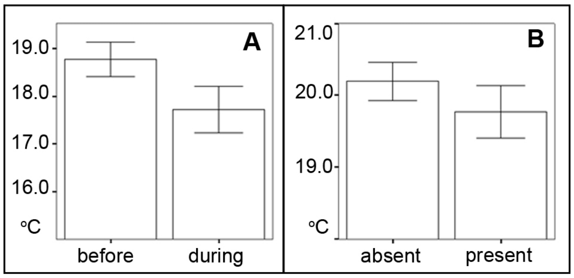

Figure 9. Mean sea surface temperature A) before the commencement of, and during the 2004 sardine run along the Lower Wild Coast and B) where sardines were absent from aerial survey bins compared with where they were present. Error bars denote the 95 % confidence intervals.

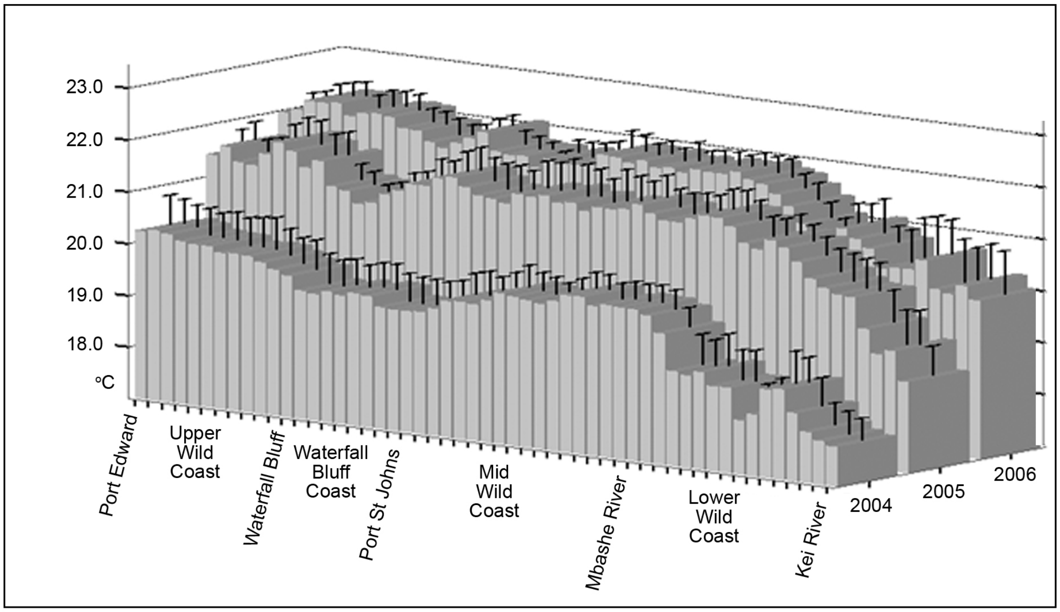

Figure 10. Mean sea surface temperature (℃) within 5 x 5 km survey bins along the Eastern Cape 'Wild Coast' from 2004 to 2006. Error bars denote the 95 % confidence intervals.

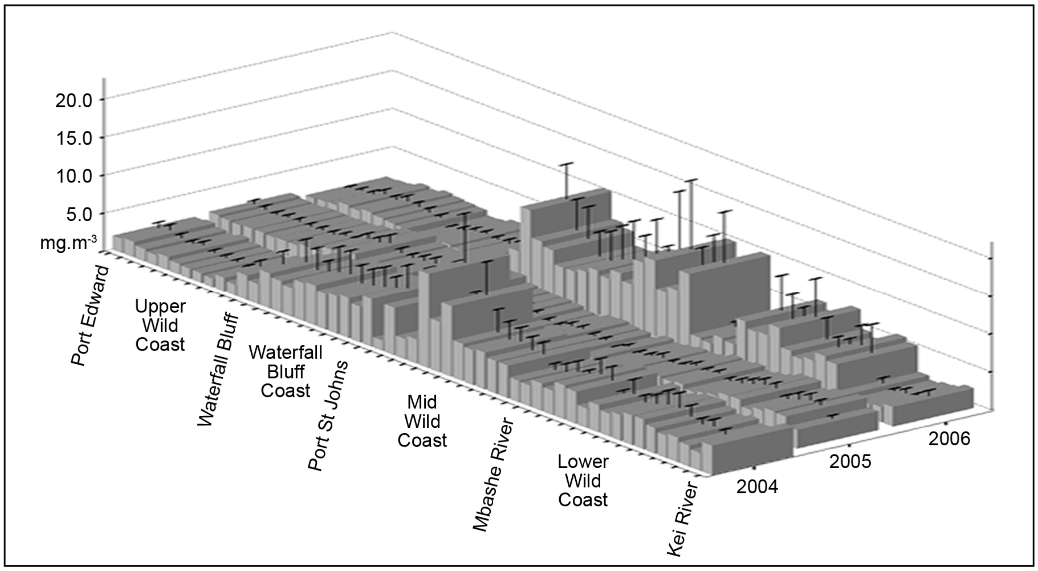

Figure 11. Mean chlorophyll a concentration (mg.m^{-3}) within 5 x 5 km survey bins along the Eastern Cape 'Wild Coast' from 2004 to 2006. Error bars denote the 95 % confidence intervals.

Environmental Predictors

Mean SST (Fig. 9) cooled significantly prior to the commencement of the 2004 sardine run ($z = -4.37$; $p < 0.001$). Over the three years, SST was cooler where sardines were present compared with where they were absent ($z = -2.15$; $p = 0.031$). During 2004 mean SST was well below 21 °C along the entire Wild Coast, whereas during 2005 only the Waterfall Bluff and Lower Wild coasts were below 21 °C (Fig. 10). During 2006, SST below 21°C was only recorded along the Lower Wild Coast. Mean SST during 2004 was significantly cooler than during either 2005 or 2006 for both Waterfall Bluff and the Mid Wild Coast zones ($\chi^2 = 228.70$; $p < 0.001$ and $\chi^2 = 371.95$; $p < 0.001$, respectively). There was a significant trend over all years for SST to increase northwards ($\chi^2 \geq 32.24$; $p < 0.001$).

Mean chl a concentration varied substantially between years and between zones without any obvious trend (Fig. 11). During 2006 no surveys were flown south of Port St Johns, so it was not possible to verify if the high values recorded within the satellite image for this zone were due to poor water clarity. Neither of the weather stations recorded substantial rainfall during this period, so it is unlikely that riverine input would have been the cause for the high chl a values reported.

Sardine sighting rate and feeding gannet abundance increased during periods of increasing atmospheric pressure ($z \geq -2.51$; $p \geq 0.012$), and on the day following the passage of a coastal low ($\chi^2 \geq 8.24$; $p \leq 0.016$). Travelling gannet abundance was higher during SW and NE winds compared with NW winds ($\chi^2 = 8.12$; $p = 0.017$). Travelling and resting gannet abundance increased during strong winds ($\chi^2 \geq 6.96$; $p \leq 0.031$) and large swells ($z \geq -2.03$; $p \leq 0.042$)

Associations

The presence of sardine (Fig. 12) significantly increased gannet ($z = -10.618$; $p = 0.001$) and common dolphin ($z = -5.84$; $p \leq 0.001$) abundance, whilst the presence of common dolphins significantly increased gannet abundance ($z = -4.866$; $p \leq 0.001$). Gannet feeding rates were strongly correlated with sardine presence in every coastal zone ($r \geq 0.80$; $p < 0.001$). Common dolphin abundance along the Lower Wild Coast was correlated with feeding gannet abundance and sardine sighting rate ($r = 0.57$ and 0.58 respectively; $p < 0.001$). Gannet resting and feeding rates were correlated ($r = 0.46$; $p = 0.002$). A summary of these associations for the whole coast is presented graphically in Figure 13.

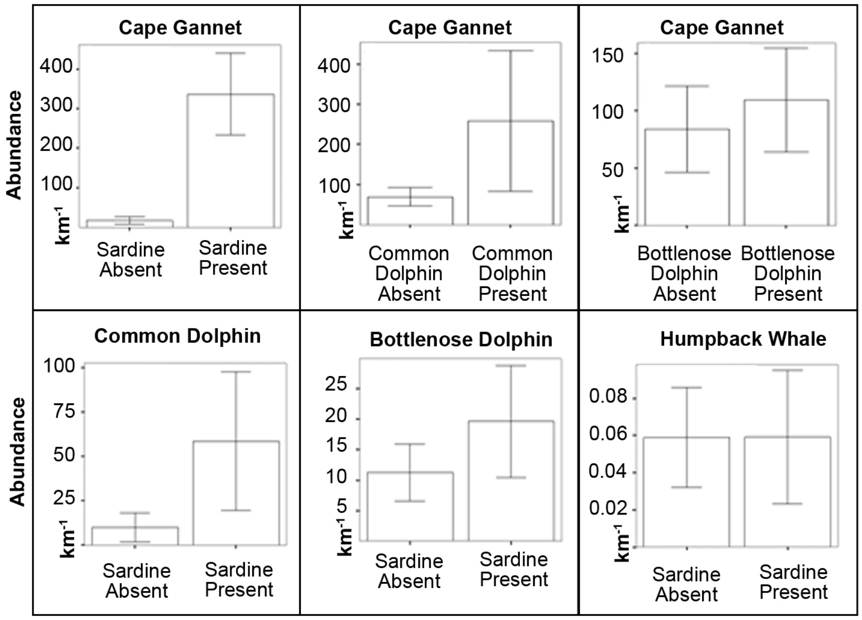

Figure 12. Mean predator abundance per km when sardines, or another predator, were either present or absent (x-axes) during aerial surveys of the Eastern Cape 'Wild Coast'. Error bars denote the 95 % confidence intervals.

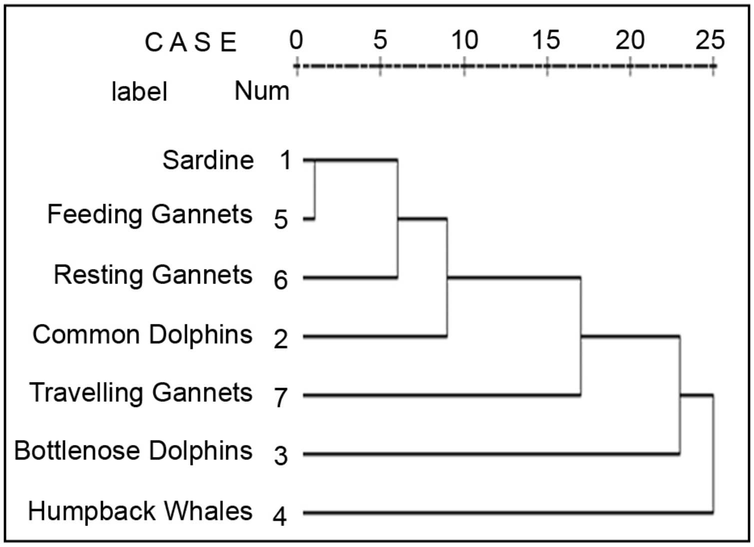

Figure 13. Hierarchical Cluster Analysis comparing sardine sighting and predator abundance per km, including gannet behaviour classes, from aerial surveys of the Eastern Cape ‘Wild Coast’ from 2004 to 2006. The shorter the distance between labels, the closer their association.

DISCUSSION

The methods used in this study and in recent broad scale aerial surveys along the Upper Wild Coast (O'Donoghue *et al.* op cit., b) were standardised to facilitate comparison of species' distributions between these two studies. As the Wild Coast aerial surveys in this study were flown in small aircraft, they did not cover the entire coastline. As such, only coastal zones with sufficient survey coverage could be analysed. Despite this, these data have proven useful in better understanding interactions between the animals and their environment.

There was substantial inter-annual variability in the sighting rates, speed of travel and distance travelled by the sardines and their predators during this study. The 2004 sardine run was exceptional in terms of the speed of movement up the Wild Coast, the cool ocean temperatures prevailing during this movement and of the length of the run in KZN as reported by O'Donoghue *et al.* (op cit., a, b). Mean sardine northward distance travelled per day in 2004 was 40 km, which is equivalent to 1.7 $km.h^{-1}$. This is within the range of swimming speeds of feeding sardines (0.6 – 2.4 $km.h^{-1}$) reported by van der Lingen (1995) in laboratory experiments. The rapid sardine movement up the coast inevitably will have led to the lack of longshore trends for 2004, in terms of difference in sardine abundance between coastal zones.

Although curtailed in terms of temporal length, the 2005 sardine run was particularly intense along the KZN South Coast, the Waterfall Bluff Coast and off the Lower Wild Coast near the Mbashe River (O'Donoghue *et al.* op cit., a, b, c). The high sardine sighting rates off the Waterfall Bluff and Lower Wild coasts and the low rates along the Mid Wild Coast obtained during this study concur with the above. High and low sighting rates occurred where mean SST was below and above 21 °C respectively.

During 2006, intense sardine run activity was observed moving northwards along the Lower Wild Coast on the 13 and 14th June with the first confirmed report of sardine presence along the KZN coastline on the 20th June (unpublished data), indicating that the sardine run had already commenced by the start of the 2006 aerial surveys. In comparison with the previous two years, 2006 was clearly a weak run along the Waterfall Bluff Coast and a very weak run in KZN (O'Donoghue *et al.* op cit., b). The dissipation of the sardine run to the north of the Lower Wild Coast corresponded with an increase in mean SST to above 21 °C for each zone.

Along the KZN coastline, sardine presence declines significantly when minimum and mean SSTs exceed 20 and 21 °C respectively (O'Donoghue *et al.* op cit., a). Within the transect survey bins along the Wild Coast, sardines were seldom sighted when mean SST was above 21 °C with mean SST usually lower than 20 °C when sardines were present. These data add to the growing body of evidence suggesting that temperature becomes a significant factor limiting sardine run distribution, and the variation in sardine distribution per year strongly suggests that this occurs along the Wild Coast with at least the Lower Wild Coast experiencing a sardine run each year.

The watershed in sardine run distribution must, therefore, come from a point of the coastline northwards of the termination of the Port Alfred upwelling cell. Temporally, the northward extent of the penetration of this upwelled water along the coast varies; Lutjeharms *et al.* (2000) found that outcropped water was visible almost as far north as Port St Johns within 5 % of the satellite images they analysed. The interaction between water upwelled in the Port Alfred cell, upwelling of cool water via Eckman drift near the shore following NE winds (Schumann *et al.* 1982) and the intrusion of warm Agulhas Current water onto the shelf results in much variation in temperature along the Wild Coast. This presumably causes variation in the biomass of sardine that reaches the Waterfall Bluff Coast and progresses northward.

The distance of sardine shoals from shore was greatest along the Waterfall Bluff Coast, with sardines significantly closer to shore along the Upper Wild Coast. This offshore distribution is supported by recent data using fixed-wing aerial and ship-based surveys (O'Donoghue *et al.* op cit., b, c) along this coastline. Their increased sighting rate and distance from shore and the lower SSTs apparent in this region support the hypothesis that this part of the coastline provides a refuge for sardine, which may be using the Waterfall Bluff Bight to avoid the warm Agulhas Current. The KZN component of the sardine run may then be dependent upon how much sardine reaches Waterfall Bluff and whether oceanographic conditions allow the prerequisite cooler water beyond this point. The current line off Waterfall Bluff has previously been observed during fixed-wing aerial surveys (O'Donoghue *et al.* op cit., b). These authors suggested that it represents a situation where the Agulhas Current is flowing close to the coastline and is constraining sardine movement northwards through what these authors termed the ‘Waterfall Bluff Gateway’. Sea surface temperature and predator distribution during these surveys support this hypothesis.

The significant increase in gannet abundance and group size following the arrival of the sardine run has been well documented from the southern KZN to the Waterfall Bluff coasts (O’Donoghue *et al.* op cit., a, b), with good agreement in gannet group size between these studies. The sudden and substantial increase in gannets within all behavioural classes upon commencement of the 2004 sardine run suggests that the Wild Coast receives a substantial influx of these predators from the south. The similarity in the response of sardines and gannets within the suite of temporal and spatial variables, and the strong association between feeding gannets and sardines within all the coastal zones, confirm that the close association that exists between these two species along the KZN coastline is, if anything, even stronger along the Wild Coast. Analysis of stomach contents of gannets at the nearest colony, Bird Island in Algoa Bay, indicates a strong preference for sardines at this time of year (Klages *et al.* 1992) corroborating this apparent close relationship between gannets and sardines.

The modal water depth where gannets were feeding was between the 30 and 50 m isobaths for all zones except the Lower Wild Coast and they travelled significantly more during alongshore than during across shore winds. Given that sardine exhibit more of an alongshore than across shore distribution range along the Wild Coast, due to the confining effects of the narrow bathymetry and the Agulhas Current, it is likely that gannets use these winds to forage efficiently over large stretches of coastline. The frequent occurrence of both NE and SW winds would thus provide a mechanism that would allow birds to remain closely associated with sardine shoals. The increase in gannet feeding rates following the passage of a coastal low may have been due to hunger following a period of reduced feeding ability, as gannets are seldom observed feeding in large aggregations in wind conditions greater than Force 4 (Nelson 1978), which typically occur during the passage of coastal lows. The increased feeding rate may, therefore, not necessarily be a true reflection of increased sardine abundance. Further fine-scale data collection should be continued to ascertain the role of cold fronts on sardine abundance and distribution.

Common dolphin group size was comparable with that recorded during both standardised aerial and ship-based (O’Donoghue *et al.* op cit., b, c) transect survey data, although historical data report larger common dolphin groups of between 50 and 10 000 seen during the sardine run (Cockcroft and Peddemors 1990). The current range in group sizes is within that reported by (Findlay *et al.* 1992) suggesting that the mean of 1 193 dolphins reported by Cockcroft and Peddemors (1990) may have been skewed by a small number of very large common dolphin aggregations.

Common dolphin abundance and group size peaked along the Waterfall Bluff Coast. It is possible that common dolphins have learnt that sardines occur more frequently, and in greater abundance, along this coast, so that the dolphins preferentially occupy this area. Group size along the Upper Wild Coast was smaller than along the Waterfall Bluff Coast. This decline is known to continue northwards into KZN (O’Donoghue *et al.* op cit., b). This smaller group size may be linked to prey availability and dolphin foraging strategies. If only a small proportion of the sardine biomass moves up the coast into KZN, then there would be less incentive to follow them and insufficient prey for large numbers of dolphin. Alternatively, increased prey density in the narrow coastal strip off the Upper Wild Coast and KZN would require fewer dolphins to participate in cooperative foraging strategies (Gaskin 1982) and allow groups to reduce in size.

Bottlenose dolphin group size along the Lower Wild Coast prior to the commencement of the sardine run was comparable with results from aerial and ship-based surveys of the sardine run (O’Donoghue *et al.* op cit., b, c). These group sizes correspond to those reported for resident bottlenose dolphins off KZN (Peddemors 1999). Mean group size following the commencement of the 2004 sardine run was comparable with, but slightly lower than the 199 ± 323.1 previously recorded for the migratory stock. The significant increase in bottlenose dolphin group size with the arrival of the run, their higher abundance rate when sardines were present in their surveys bins, and their significantly lower abundance rate during the weak sardine run in 2006, suggests some association between bottlenose dolphins and the sardine run. Any further investigation of bottlenose dolphin association with the sardine run should attempt to differentiate between resident and migratory dolphins, although simple morphometric differentiation appears impossible (Peddemors 1995). This study has highlighted the requirement for a new analysis of stomach contents linked to differentiation of stock to determine the prevalence of sardines in the diet of migratory and resident bottlenose dolphins.

Bottlenose dolphin distribution was strongly skewed towards shore with only 3 out of 149 sightings further than 1.1 km from shore, and only two sightings in water deeper than 30 m. The strong skew in bottlenose dolphin distribution towards shore and in water depths of less than 30 m is consistent with their known diurnal distribution (Ross *et al.* 1987; Ross *et al.* 1989). Although bottlenose dolphins were further from shore along the Lower Wild Coast, compared with the Mid Wild to Waterfall Bluff coasts, they were still in shallower water than for the other three zones, thereby adding support to the hypothesis that depth limits bottlenose dolphin distribution.

The largest marine mammal off the coast during the sardine run, the humpback whale, showed the least variability in their response to the predictor variables. There was no significant difference in group size or abundance rate prior to, and upon commencement of, the sardine run. Abundance rates did not differ significantly between either years or coastal zones. These data all infer that humpback whale movements up the east coast of South Africa are unlikely to be influenced by the presence of sardines.

The associations between the species, obtained from the Spearman's Rank correlations, and by comparing their sighting and abundance rates, are presented in the dendogram produced by the Hierarchical Cluster Analysis. Clearly feeding and resting Cape gannets and common dolphins are closely associated with sardines, while bottlenose dolphins and humpback whales are less so. This is supported by the findings of the other analyses. It is also evident that common dolphins are closely associated with Cape gannets, however this study suggests that gannet behaviour is important in this relationship. The strong association reported for these predators during the coarse scale aerial surveys (Chapter 2) is replicated here at a finer scale and suggests interaction between these species. This will become the focus of the next chapter of this thesis.

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CHAPTER SIX

Differences in predator behaviour along the Eastern Cape 'Wild Coast,' in relation to the annual sardine run.

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ABSTRACT

Previous research has shown the importance of environmental conditions in regulating the movement of South African sardine, *Sardinops sagax*, up the east coast of South Africa, particularly the seasonal cooling of nearshore sea temperatures. This then regulates the abundance of predators following the sardine. Less is known about how predator abundance differs at fine scales, both temporally and spatially and between behaviour types, hence this research using a theodolite during point surveys from cliffs along the Eastern Cape 'Wild Coast'. The sardine run arrived along the Lower Wild Coast following a period of nearshore cooling of sea temperatures to below 18 °C. Northward movement of the sardine run was constrained by an increase in sea temperature to above 21.5 °C, with concentrated predator feeding observed at the well developed thermal front at the northern boundary of the cool water, and significantly lower predator abundance recorded at sites north of this front. Cape gannet, *Morus capensis*, feeding abundance was highest in the early morning, and during the middle part of the day they rested. Gannets travelled more during alongshore winds, than during across shore winds. Long-beaked common dolphin, *Delphinus capensis*, travel speed and pod shape changed significantly at Waterfall Bluff, where they were sighted further from shore. An increase in common dolphin nearshore feeding occurred within a patch of water in the lee of the Waterfall Bluff Bight that was cooler than adjacent waters, and was thought to be related to an intrusion of cool water onto the shelf that was probably topographic in origin. It was hypothesised that the intrusion of cool water may have been an insight into the mechanism of the Waterfall Bluff Gateway, which is thought to regulate the success of the sardine run along the KwaZulu-Natal coastline.

KEYWORDS

behaviour, bottlenose dolphin, Cape gannet, common dolphin, *Delphinus capensis*, distribution, *Morus capensis*, sardine, sardine run, *Sardinops sagax*, sea surface temperature, SST, *Tursiops aduncus*

INTRODUCTION

The movement of South African sardine, *Sardinops sagax* (Jenyns 1842), and their predators up the east coast of South Africa is known as the sardine run. This spectacular natural phenomenon has been described as the marine equivalent of the wildebeest migration in East Africa (O'Donoghue *et al.* in press, b), yet until recently, little information has existed as to the factors driving this movement. Sardine distribution is controlled by temperature (Armstrong *et al.* 1991). Temperature is affected by upwelling processes along the coastline (Schumann 1988) in combination with prevailing wind conditions which warm or cool surface water. Surface temperature has been measured using remote sensing techniques and shown to be inversely related to sardine distribution (O'Donoghue *et al.* op cit., b; O'Donoghue and Peddemors submitted).

Sardine abundance and distribution plays an important role in the diet and life history of several predators (Beckley and van der Lingen 1999). O'Donoghue *et al.* (op. cit., b) have shown that sardine abundance and distribution also regulates the large-scale along-shore abundance and distribution of marine apex predators on the South African East Coast, particularly along the KwaZulu-Natal (KZN) Coast. Although it has been postulated that predator abundance may regulate the speed of movement up the coast (Armstrong *et al.* op. cit.), fine-scale aerial surveys along the Eastern Cape 'Wild Coast' (Fig. 1A), have indicated that it is principally environmental conditions that affect the movement of sardines and that predators primarily follow them as they move up within suitable conditions (O'Donoghue and Peddemors op. cit.). However, the manner in which these predators interact with sardines and with each other has not been extensively investigated. This research therefore aims to understand these inter and intra-specific interactions using three species commonly associated with the sardine run (O'Donoghue *et al*. op. cit., b): the Cape gannet, *Morus capensis* (Lichtenstein 1823), the long-beaked common dolphin, *Delphinus capensis* Gray 1828, and the Indo-Pacific bottlenose dolphin, *Tursiops aduncus* (Ehrenberg 1833).

On the east coast of South Africa, the Cape gannet is synonymous with the sardine run and its presence is a very useful indicator of sardine presence (Berruti *et al.* 1993; O'Donoghue *et al.* in press, a; O'Donoghue *et al.* op. cit., b). The nearest colony, consisting of 98 000 breeding pairs (Crawford *et al.* 2007), is on Bird Island in Algoa Bay (Fig 1A). Studies of breeding birds have indicated that pelagic shoaling fish comprise the major part of their diet (Batchelor and Ross 1984; Klages *et al.* 1992) and that, as central-place foragers they tend to stay at sea for less than 24 hours (Ropert-Coudert *et al.* 2004). The sardine run occurs outside of the Cape gannet breeding period and they are therefore freed from the constraint of having to return to their colony daily to feed chicks. During the sardine run there is a significant relationship between gannet abundance and distribution and that of sardines (O'Donoghue *et al.* op. cit., a, b; O'Donoghue *et al.* submitted, c). How gannets detect their prey is not known, but seabirds frequently use feeding aggregations of other seabirds and dolphins to detect patches of available prey (Balance *et al*. 2001). As plunge divers, gannets are primarily considered to be visually-oriented predators (Haney and Stone 1988). The sardine run, however, occurs within the inshore waters of the South African east coast, and as such water clarity may be a limiting factor for gannet prey detection. A direct correlation between gannets and common dolphins has been described by O'Donoghue *et al.* (op. cit., a, b, c); O'Donoghue and Peddemors op. cit.), suggesting that gannets may use common dolphins to locate deeper sardine shoals. Inter-specific foraging reliance has, however, not previously been tested.

Common dolphins, like gannets, are winter visitors to the east coast of South Africa (Broekhuysen *et al.* 1961; Cockcroft and Peddemors 1990), whilst preying heavily upon sardines during this time (Young and Cockcroft 1994). Reported group size varies considerably from small groups of only few individuals to groups of several thousand individuals (Cockcroft & Peddemors op cit; O'Donoghue *et al*. op. cit., a, b, c; O'Donoghue and Peddemors op. cit.). It has been suggested that dolphins specialised in feeding on pelagic shoaling fish require larger group sizes to find their unevenly distributed prey, but that when the prey are found they are abundant and able to sustain large aggregations of predators (Gaskin 1982). The sardine run provides an ideal opportunity to test whether long-beaked common dolphin group size changes in relation to prey abundance and/or other predator activity.

Bottlenose dolphins inhabit the east coast of South Africa year-round (Peddemors 1999), apparently residing in home ranges of a few dozen kilometres along-shore (Cockcroft *et al.* 1990). Although sardines are not a major prey item (Cockcroft and Ross 1990), bottlenose dolphin abundance increases along the KZN coast during the months of the sardine run (O'Donoghue *et al.* op. cit., b). Peddemors *et al.* (submitted) suggest that these increased numbers are a result of the alongshore migration of a genetically distinct stock (Natoli *et al*. 2008) of bottlenose dolphins in close association with the sardine run. The role of sardines in the diet of these dolphins is not known, but a significant relationship between bottlenose dolphins and sardines has been recorded for the Wild Coast (O'Donoghue and Peddemors op. cit.). Gannet and bottlenose dolphin distributions are correlated during the sardine run, but this relationship is weaker than that for gannets and common dolphins (O'Donoghue *et al*. op. cit., a, b). Bottlenose dolphins are primarily found close to shore in water depths less than 30m (O'Donoghue *et al*. op. cit., a, b; Ross *et al*. 1987), whereas common dolphins tend to be distributed further offshore (O'Donoghue *et al*. op. cit., c O'Donoghue and Peddemors op. cit.). The interaction between gannets and the two dolphin species provides a unique opportunity to test whether gannets specifically associate with different dolphins according to environmental conditions, such as water depth, to find sardines.

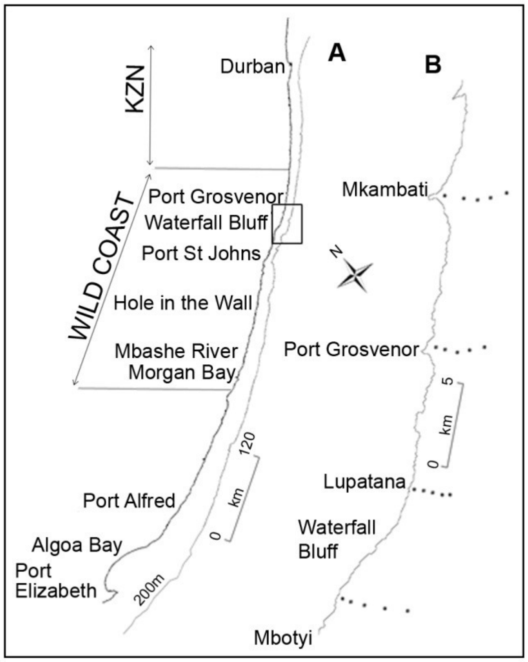

Figure 1. SE Coast of South Africa (A) and continental shelf showing the 200m isobath and the border between the Eastern Cape and KZN (horizontal line). The square box shows the approximate longshore extent of the CTD survey off Waterfall Bluff, which is magnified (B) to indicate the positions of the CTD stations.

Sardines prefer water temperatures between 14 and 20 °C and their spatial distribution is influenced by temperature fronts (Coetzee 1996). There is a significant association between sardine presence along the east coast and water temperature less than 20 °C (Armstrong *et al.* op cit.). This is particularly important along the Eastern Cape Wild Coast where the continental shelf narrows to a minimum of about 9 km (Fig. 1A). Here the warm, southwardly flowing Agulhas Current dominates shelf conditions, which are not suitable for sardine habitation, with little retention of primary production or zooplankton grazers that occur in the oligotrophic water (Carter and Schleyer, 1988). This, combined with their energy expenditure during the sardine run, results in sardines being in poor condition by the time they reach the KZN coastline (van der Lingen *et al.* in press).

However, there are two oceanographic features along the Wild Coast where the influence of the Agulhas Current is reduced. One is a topographically-induced upwelling cell near Port Alfred (Fig. 1A), which usually reaches as far north as the Mbashe River (Lutjeharms *et al.* 2000). Here elevated levels of chlorophyll a (Lutjeharms and Walters 1985) are found in cool, upwelled water providing suitable habitat for sardine occupation. It is believed that this region is the likely conduit for sardine eastward movement each winter (O'Donoghue and Peddemors op cit.). The second location is further north adjacent to the westward inflection of the coastline at Waterfall Bluff (Fig. 1B). The offset between the inflection of the coastline and the bathymetry creates a bight, which provides refuge from the Agulhas Current as it is found further from shore in the lee of the resultant bight (Schumann 1987). Sediment patterns within the bight are suggestive of a northward flowing current (Flemming 1980), and there is some evidence for increased primary production and lower sea surface temperature in this region (O'Donoghue *et al.* op. cit., b; O'Donoghue and Peddemors op cit.). Sardines seem to use the Waterfall Bluff Bight as a holding area until favourable conditions allow northward movement through what is termed the 'Waterfall Bluff gateway' (O'Donoghue *et al.* in press, b). The mechanism of this gateway is, as yet, poorly understood.

Sardine abundance within the above regions varies enormously between years and even days. It follows that this will have important consequences for their predators, such that predators should have developed the ability to efficiently detect and exploit what can be either an ephemeral and elusive resource or a sustained glut. In this study, the abundance, distribution and behaviour of the three predators was recorded during point surveys on cliffs and related to environmental conditions and the presence of sardines. Results are discussed within the context of predator behavioural adaptations on the sardine run.

METHODS

Three sites, Waterfall Bluff, Hole in the Wall and Morgan Bay (Fig. 1a), each with suitably high cliffs were identified for the point surveys. Each site was located within a stretch of coastline that was representative of the regions described in the introduction. Morgan Bay is located within the Port Alfred upwelling region and has 49m high cliffs with a southerly aspect (Fig. 1A). Surveys were conducted here from the 1st – 15th June 2006. Once the sardine run had passed Morgan Bay, the point survey site was moved north to Hole in the Wall. Hole in the Wall is typical of the coastline between the Port Alfred upwelling and Waterfall Bluff. Surveys were conducted for a total of eight days over two years from the 'Whales Back' at Hole in the Wall, which is approximately 20m high and has a south-easterly aspect. From the 20th June 2006 surveys were conducted from the Waterfall Bluff cliffs, where the station was at an altitude of 75m and southerly facing. All counts were conducted weather permitting.

The point surveys were conducted according to standardised methods (Würsig and Würsig 1980). Survey counts, consisting of systematic 10 minute scans of the survey area were conducted every 30 minutes between 06h00 and 16h00 using Pentax XCF 10 x 50 (6.5°) binoculars. The survey area was scanned lengthways parallel to the coast from north to south as this was counter to the dominant direction of movement of animals, which helped to reduce double counting. All animals seen were identified and counted, and their behaviour and direction of movement noted. Any other species within 100 m of the observation with similar behaviour or direction and speed of travel were identified and recorded as being associated with that observation. A theodolite was used to record the horizontal and vertical coordinates of all birds sitting on, flying over or diving into the sea surface, as well as all surfacing marine mammals. Data were directly recorded into a Dictaphone. Environmental conditions, recorded throughout the day, included: air visibility relative to the horizon, glare coordinates, wind direction and approximate strength, Beaufort Sea State (SS) and cloud cover. Measurements were also taken of any interesting physical features e.g. current lines and changes in water visibility or swell conditions.

Intermittently during the day, focal groups of either bottlenose or common dolphins were tracked with changes in behaviour noted. The shape of dolphin pods was also recorded with a minimum of three and a maximum of eight theodolite measurements. These measurements were used to calculate the longitudinal axis of the pod i.e. the distance and orientation of a line drawn between the two most distant members of the pod. This was done in the GIS analysis environment. Longer tracklines were interrupted by survey counts. These tracklines were only resumed if the focus group could be correctly identified. The time elapsed during the survey count was omitted from the trackline analysis.

To estimate the depth of the water column below observations, a digitised bathymetric chart (SAN 1:50 000) was used and the depth ascribed to the centre point of observation polygons. Water depths were classified as follows: 1 – 15 m, 16 – 20 m, 21 – 30 m, 31 – 50 m, 51 – 100 m and 101 – 200 m. Further oceanographic conditions were described using remotely sensed data derived from the Moderate Resolution Imaging Spectroradiometer Aqua Satellite (MODIS). All data were obtained from the Remote

Sensing Server for Marine Sciences website (www.rsmarinesa.org.za) where they are freely available as level 4 products at a 1 km^2 resolution. Daily images depicting sea surface temperature (SST, °C) were used. Due to the problem of coastal "bleed-off" in satellite images, there was an approximately two pixel-width strip, i.e. 2 km, of no-data along the coast. The loss of this data along the coast was mitigated off Waterfall Bluff by data obtained via the deployment of a CTD (Sea-bird electronics sbe 19 seacat profiler) when sea conditions permitted. This allowed verification of the accuracy of remotely sensed SST data. These data also allowed determination of the rate at which nearshore sea surface temperatures cooled shorewards along the sampling transects and detection of the presence of a sub-surface thermocline, which might indicate the presence of the Waterfall Bluff 'gate'.

The horizontal and vertical theodolite coordinates were converted into decimal degrees using *Pythagoras* Version 1.2.15 software and loaded onto a map document using *ESRI* ArcGIS 9. The station height at Waterfall Bluff was three times that of Hole in the Wall. This extra height would have made animals further from shore easier to detect. To reduce bias, the survey area for each site was standardised by calculating the area in a radius equal to one third of the distance from the theodolite out towards the horizon. This distance was 8500, 4500 and 6000 m at the Waterfall Bluff, Hole in the Wall and Morgan Bay sites respectively, which effectively included 87, 84 and 88 % of all recorded observations. Only observations occurring within this survey area were included in calculations of species abundance rates. Because virtually all bottlenose dolphins were within 4 km of the shoreline, this distance was used to calculate the survey area for this species' abundance rate. Only counts made during conditions of $SS \leq 3$ were used in analyses. The survey area at Hole in the Wall was further reduced by glare on cloudless days before 10h00, chiefly because of the greater easterly aspect of this site. The area affected by glare was measured and subtracted from the total surface area of each affected count.

For each species, behaviour was classified as feeding, travelling or milling. The total number of animals counted within each behaviour class was summed for each survey count and divided by the survey area to give an abundance rate per square kilometre (km^{-2}) for each behaviour class. This abundance rate and group size was used to determine whether there was any significant difference in each species' behaviour between the following variables: site, period and wind direction. Each survey count was divided into two hour periods from 06h00 to 16h00. Wind direction was simplified to NE, SE, SW, NW and Calm conditions. The Mann-Whitney U-Test and the Kruskal-Wallis H-test were used to determine if differences were significant.

All survey observations out to 10 km from shore were used to test whether there was any difference in the distance from shore and the depth distribution of species' behaviour classes. The focal group observations were used to elucidate survey count findings. This included differences in speed of movement and changes in pod shape in relation to bathymetric features and remotely sensed oceanographic data.

The frequency occurrence of gannets associated with feeding and travelling common and bottlenose dolphins was calculated for each site. The Chi-square test was used to determine whether there was any difference in the number of observed associations from the number of associations expected if association was random i.e. associations occurring 50 % of the time. The frequency occurrence of associated dolphins (of either species) with feeding, resting and travelling gannets and of associated common dolphins with feeding and travelling bottlenose dolphins was similarly calculated.

RESULTS

A total of 348 survey counts lasting 57 hours and 36 minutes were made over 29 days (Table 1). Each site was surveyed for at least 6 days with a minimum of 51 counts, although at Hole in the Wall these counts were made over two years. Survey counts started later and finished earlier at Waterfall Bluff due to weather conditions affecting the daily two hour hike to get to the survey site. All animals seen during each survey were recorded (Table 2), but analyses in this paper are restricted to the Cape gannet and the common and bottlenose dolphins.

A total of 16 common and 35 bottlenose dolphin focal groups were tracked via theodolite recordings, with total track observations lasting 17 hours and 55 minutes and 19 hours and 55 minutes respectively. Common dolphins were tracked 7, 5 and 4 times at Waterfall Bluff, Hole in the Wall and Morgan Bay respectively, while bottlenose dolphin groups were tracked 7, 13 and 15 times at each respective site.

Mean track duration was 1 hour and 7 minutes for common dolphins and 34 minutes and 10 seconds for bottlenose dolphins.

Table 1. Point survey counts conducted from three cliff sites along the Eastern Cape 'Wild Coast' during June 2006/ 7, showing the earliest and latest count times, the mean and maximum durations of each count (minutes) and the total count duration per site.

Site	**Days**	**Counts**	**Earliest count time**	**Latest count time**	**Mean duration (minutes)**	**Max duration (minutes)**	**Total count duration**
Waterfall Bluff 06	6	51	07h52	15h36	11	22	9 hrs 57 min
Hole in Wall 06	2	29	06h53	15h24	8	14	4 hrs 5 min
Hole in Wall 07	6	75	07h03	16h06	11	20	14 hrs 29 min
Morgan Bay 06	15	193	07h15	17h08	9	23	29 hrs 5 min

At Morgan Bay the sardine run arrived on the 13th June 2006. This followed a period of nearshore cooling, which peaked on the 10th June with a mean survey area SST = 17.9 +/- 0.9 °C with the 20 °C isotherm 12 km from shore. By the 15th June, mean SST within the survey area had warmed to 21.5 +/- 1.2 °C with a minimum temperature of 20.2 °C. At this time, there was a strong thermal gradient with a temperature range of 2.2 °C within the survey area as the warm Agulhas water met the nearshore strip of cool water (Fig. 2). With the arrival of the sardine run, there was a concurrent, significant increase in gannet, common dolphin and bottlenose dolphin group size ($n \geq 22$; $z \geq -2.841$; $p = 0.004$) as well as feeding and travelling abundance ($n \geq 36$; $z \geq -3.186$; $p \leq 0.001$) for all three species, excepting travelling bottlenose dolphins. This intense sardine run activity was, however, not observed again from survey sites further up the coast during 2006.

Gannet abundance and group size (Table 3) was significantly highest at Morgan Bay for all three behavioural classes ($n \geq 30$; $\chi^2 \geq 13.402$; $p \leq 0.004$) while only 102 km to the north, at Hole in the Wall, the lowest abundance of feeding and resting gannets was recorded during 2006 ($n \geq 30$; $\chi^2 \geq 39.866$; $p < 0.001$). Significant daily temporal changes in activity patterns were recorded for gannets. Before 08h00 their feeding rate was significantly higher than resting or travelling rate ($n = 23$; $\chi^2 = 6.483$; $p = 0.039$), however between 10h00 and 14h00 resting rate became significantly higher than feeding or travelling rate ($n \geq 40$; $\chi^2 \geq 18.112$; $p < 0.001$). Analysis of environmental conditions indicated that gannet feeding abundance was higher during SE and SW winds compared with NE and NW winds ($n \geq 18$; $\chi^2 = 26.026$; $p < 0.001$). Gannet travelling abundance was higher during SE and NE winds compared with NW winds or calm conditions ($n \geq 18$; $\chi^2 = 18.361$; $p = 0.001$).

Common dolphins exhibited substantial spatial variation in their behaviour patterns, with abundance and group size of travelling common dolphins significantly larger at Waterfall Bluff and Morgan Bay than at Hole in the Wall ($n \geq 20$; $\chi^2 \geq 10.543$; $p \leq 0.014$). At Waterfall Bluff (Fig. 3D-F; Fig. 4), feeding and travelling common dolphins were further from shore than at the other sites ($n \geq 31$; $\chi^2 \geq 22.839$; $p \leq 0.001$), with feeding dolphins usually further from shore ($n \geq 43$; $z \geq -2.642$; $p \leq 0.008$), but in the same modal depth class (50-100 m), as travelling dolphins. On the 21st June, however, feeding common dolphins at Waterfall Bluff were sighted closer to shore than travelling dolphins ($n \geq 12$; $z = -4.823$; $p < 0.001$) in significantly cooler water ($n \geq 12$; $z = -4.671$; $p < 0.001$) than on the adjacent shelf (Fig. 5).

Table 2. Total number of sightings per survey site during point surveys conducted from cliffs along the Eastern Cape 'Wild Coast' during June 2006 and 2007

Common name	**Species**	**Waterfall Bluff**	**Hole in The Wall 2006**	**Hole in the Wall 2007**	**Morgan Bay**	**Total**
Baitfish	-	1	2	9	1	13
Cape Gannet	*Morus capensis*	1624	337	1627	2964	6552
Subantarctic Skua	*Catharacta antarctica*	-	1	-	4	5
Grey-headed Gull	*Larus cirrocephalus*	3	1	1	15	20
Kelp Gull	*L. dominicanus*	1	3	12	27	43
Gull unidentified	-	-	-	1	-	1
Tern unidentified	-	2	5	15	26	48
Cape Cormorant	*Phalacrocorax capensis*	-	-	1	4	5
White-breasted Cormorant	*P. carbo*	-	4	2	14	20
Bird unidentified	-	-	5	-	1	6
Humpback Whale	*Megaptera novaeangliae*	184	41	33	102	360
Southern Right Whale	*Eubalaena australis*	-	-	-	4	4
Whale unidentified	-	5	1	6	1	13
Indo-Pacific Bottlenose Dolphin	*Tursiops aduncus*	82	66	42	334	524
Long-beaked Common Dolphin	*Delphinus capensis*	111	12	35	121	279
Indo-Pacific Humpback Dolphin	*Sousa chinensis*	-	-	-	1	1
Dolphin unidentified	-	22	13	45	38	118
South African Fur Seal	*Arctocephalus pusillus p.*	-	-	-	9	9

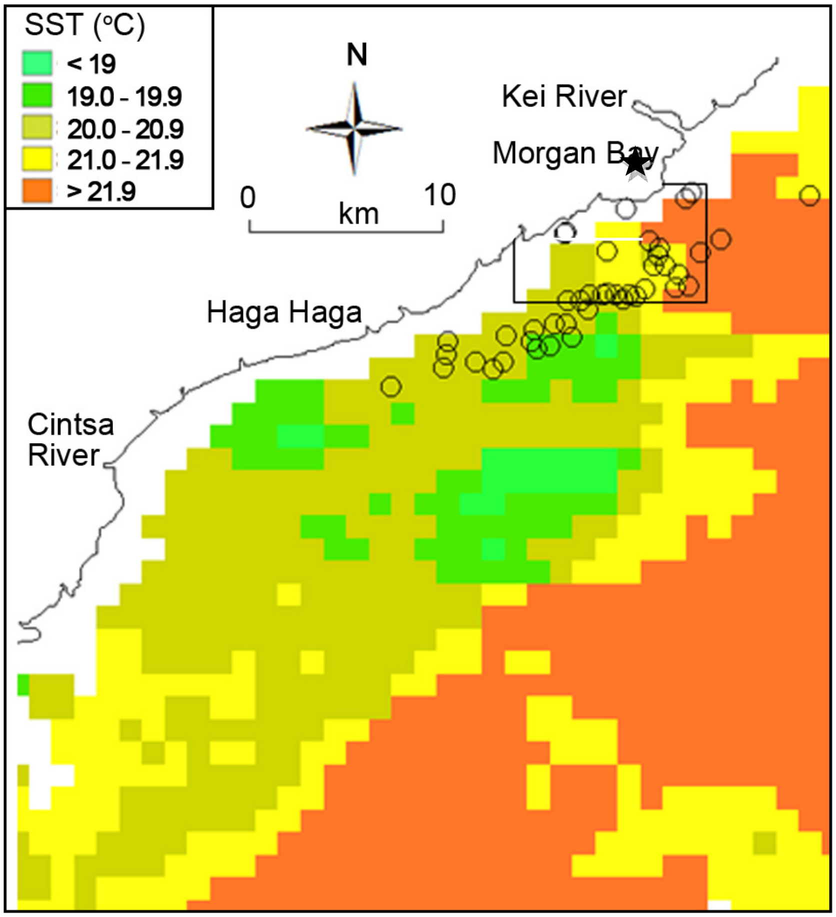

Figure 2. Sea surface temperature (SST – °C) on the 15th June 2006 surrounding Morgan Bay, Eastern Cape. Open circles represent the locations of feeding aggregations measured using a theodolite from the cliffs on the south side of Morgan Bay (indicated by a black star). The open square represents the approximate survey area used in the analyses.

Common dolphins travelled at an average speed = 8.0 km.h^{-1} with a maximum speed = 17.8 km.h^{-1} recorded for non-porpoising dolphins. Dolphin travelling speed at Waterfall Bluff was slower than at the other two sites (Fig. 6). Pod shape of travelling common dolphins changed within the study region ($n \geq 20$; $z = -3.236$; $p = 0.001$); north of Mbotyi dolphins travelled in pods where the longitudinal axis of the pod was significantly more perpendicular to the bathymetric contours compared with pods south of Mbotyi (Fig. 3D-F). No temporal variation in common dolphin abundance, group size or behaviour was observed.

Total bottlenose dolphin abundance did not differ spatially or temporally between the three research sites. Differences were evident, however, in their behaviour. Travelling bottlenose dolphin group size was larger than either feeding or resting group size ($n \geq 24$; $\chi^2 = 13.806$; $p = 0.001$) with larger travelling groups off Waterfall Bluff than at the other two sites ($n \geq 24$; $\chi^2 = 15.801$; $p = 0.001$). Feeding bottlenose dolphin abundance at Hole in the Wall was lower than at the other two sites for both the survey and the focal group data ($n \geq 30$; $\chi^2 \geq 8.531$; $p \leq 0.014$). Feeding bottlenose dolphins were also further from shore and in deeper water than travelling dolphins ($n \geq 19$; $z \geq -4.820$; $p \leq 0.001$), with the latter displaying a clear preference for travel within shallow water (Fig. 3A-C). All travelling groups were shoreward of the 30 m isobath and 81 % were within the 15 m isobath. Prevailing environmental conditions (weather and water) did not appear to effect bottlenose dolphin abundance, distribution or behaviour.

Table 3. Group size per site derived from point surveys along the Eastern Cape Wild Coast. The ‘Sardine Run’ column refers to whether survey counts were conducted before the commencement of, or during, the sardine run.

Species	**Site**	**Behaviour**	**Sardine Run**	**N =**	**Mean**	**Median**	**Standard Deviation**	**Max**
Cape Gannet	Morgan Bay	Feeding	Before	530	62.2	18.0	118.1	1348
			During	193	699.4	155.0	1268.9	6300
		Resting	Before	741	24.0	20.0	82.3	1044
			During	393	175.7	31.0	500.4	5500
		Travel	Before	592	5.8	2.0	15.6	173
			During	233	65.1	5.0	245.4	3000
	Waterfall Bluff	-	During	1097	85.3	11.0	224.7	3100
	Hole in the Wall 2006	-	During	358	8.9	4.0	17.5	153
	Hole in the Wall 2007	-	During	1434	45.9	3.0	154.5	3000
Common Dolphin	Morgan Bay	-	Before	26	111.2	61.0	135.1	530
	Morgan Bay	-	During	26	280.3	197.5	308.9	1400
	Waterfall Bluff	-	During	53	413.1	250.0	336.8	1000
	Hole in the Wall 2006	-	During	15	154.9	125.0	95.3	250
	Hole in the Wall 2007	-	During	41	221.1	200.0	237.6	800
Bottlenose Dolphin	Morgan Bay	-	Before	153	50.5	29.0	59.8	315
	Morgan Bay	-	During	54	111.7	43.5	156.8	750
	Waterfall Bluff	-	During	54	67.6	50.0	74.2	300
	Hole in the Wall 2006	-	During	45	43.7	49.0	26.7	135
	Hole in the Wall 2007	-	During	97	32.1	25.0	20.4	110

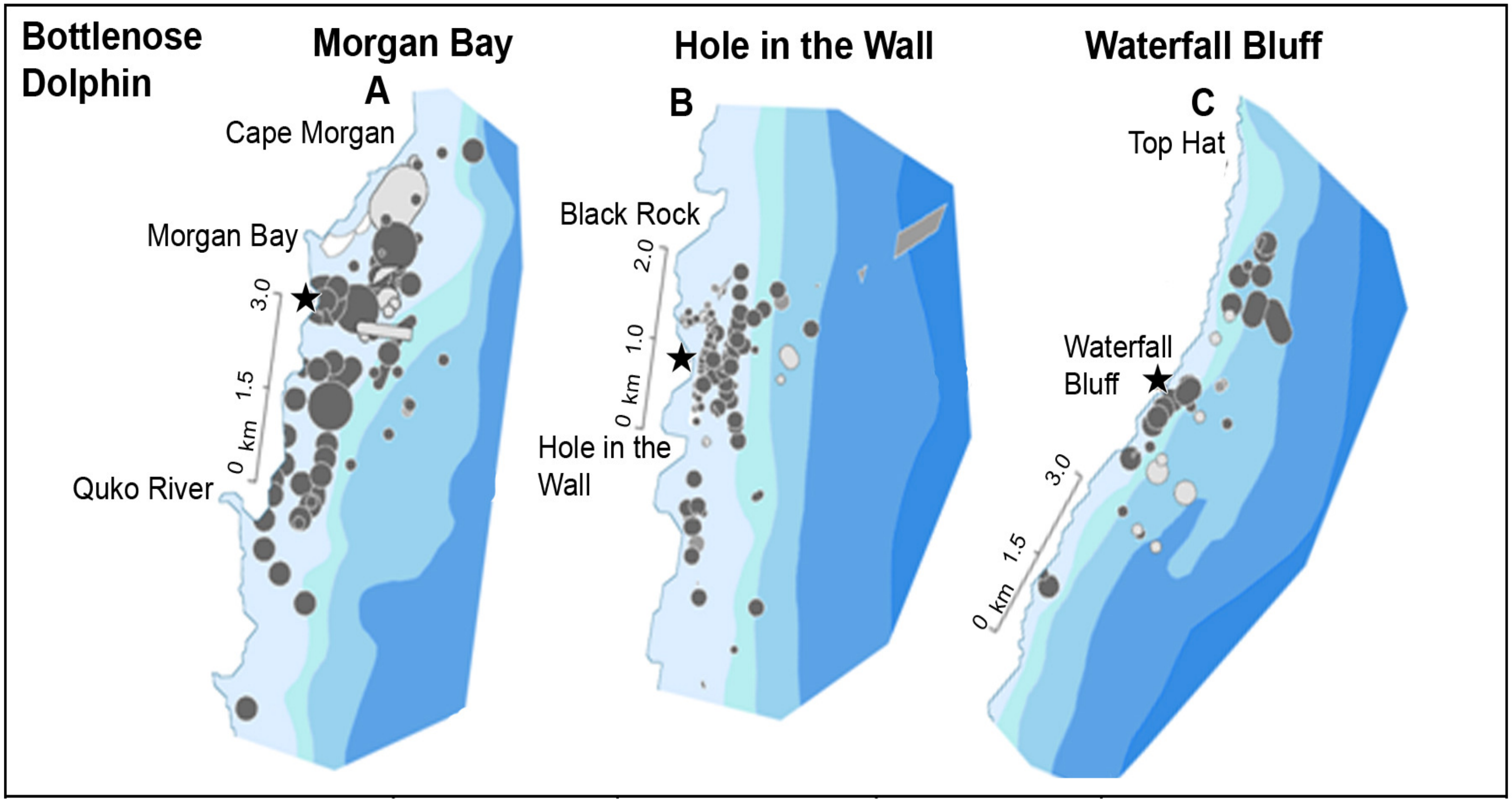

Figure 3A – C. Bottlenose dolphin distribution and behaviour against depth (m), recorded from three survey sites (indicated by a black star) along the 'Wild Coast'. Dolphin behaviour and depth legends are given overleaf.

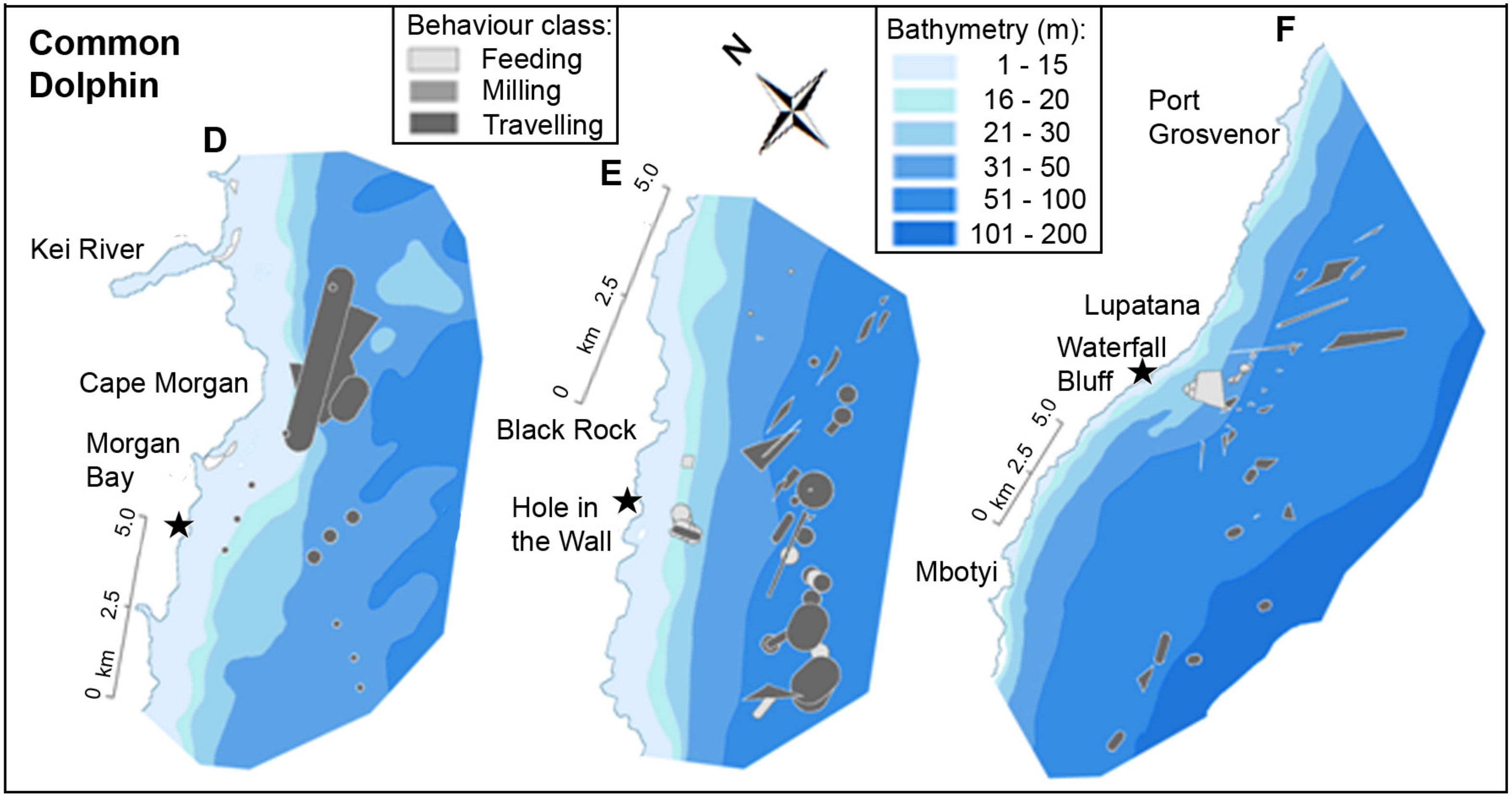

Figure 3D – F. Common dolphin distribution and behaviour against depth (m), recorded from three survey sites (indicated by a black star) along the 'Wild Coast'. Sites: D – Morgan Bay, E – Hole in the Wall, F – Waterfall Bluff

Cape Gannets were strongly associated with feeding common (Fig. 7B) and bottlenose (Fig. 7C) dolphins at all sites ($\chi^2 \geq 8.895$; $p \leq 0.03$). There were significantly fewer than expected gannets associated with observations of travelling common or bottlenose dolphins at any site ($\chi^2 \geq 9.783$; $p \leq 0.002$), excepting gannets associated with travelling common dolphins at Morgan Bay, for which there were more observations of travelling dolphins with associated gannets than expected (Fig. 7B). There were significantly fewer than expected dolphins associated with observations of gannets for any behaviour category at any site ($\chi^2 \geq 52.705$; $p \leq 0.001$), although observations of feeding gannets at Morgan Bay had the highest proportion of associated dolphins (Fig. 7A). There was a significant lack of association between bottlenose and common dolphins (Fig. 7D) across all regions for either behaviour class ($\chi^2 \geq 8.895$; $p \leq 0.003$).

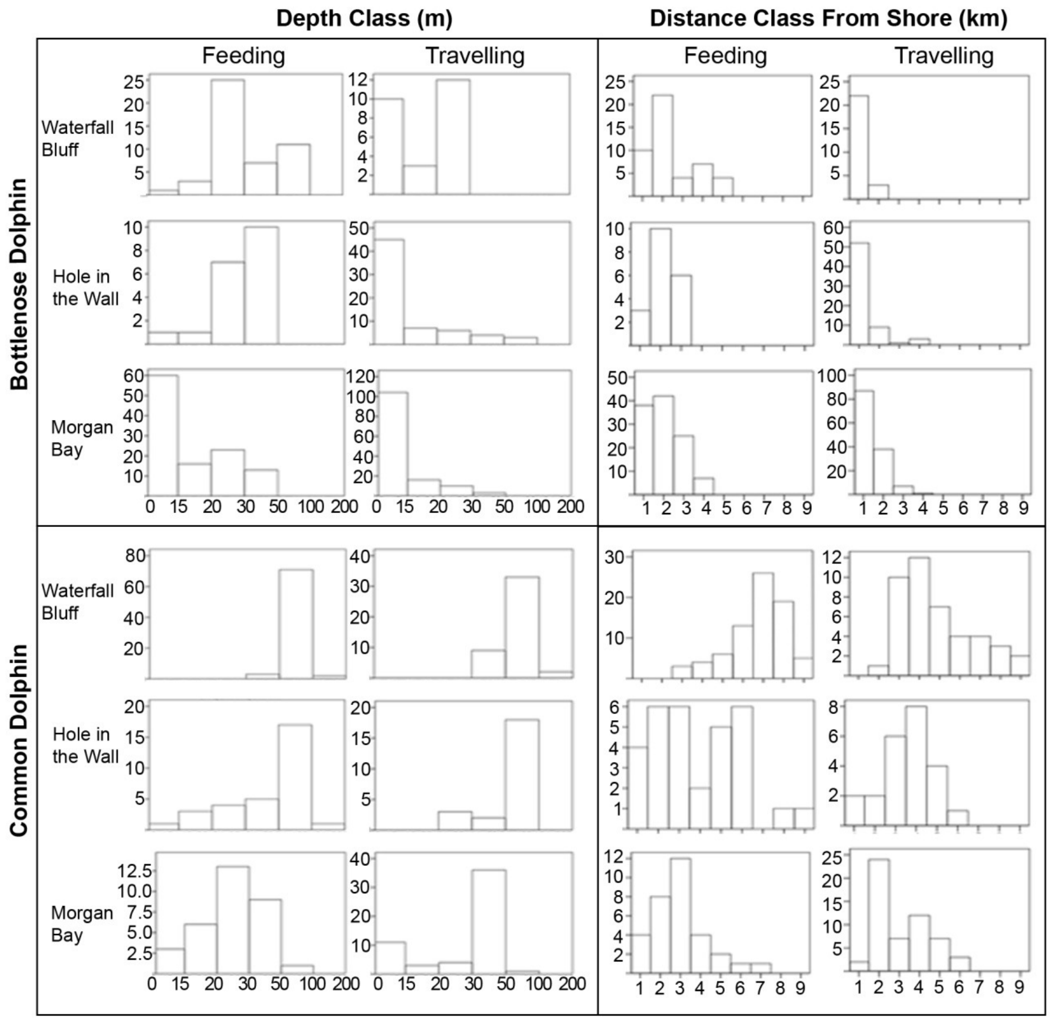

Figure 4. Bottlenose and common dolphin frequency of occurrence per depth class (m) and distance class from shore (km) per behaviour type and per survey site.

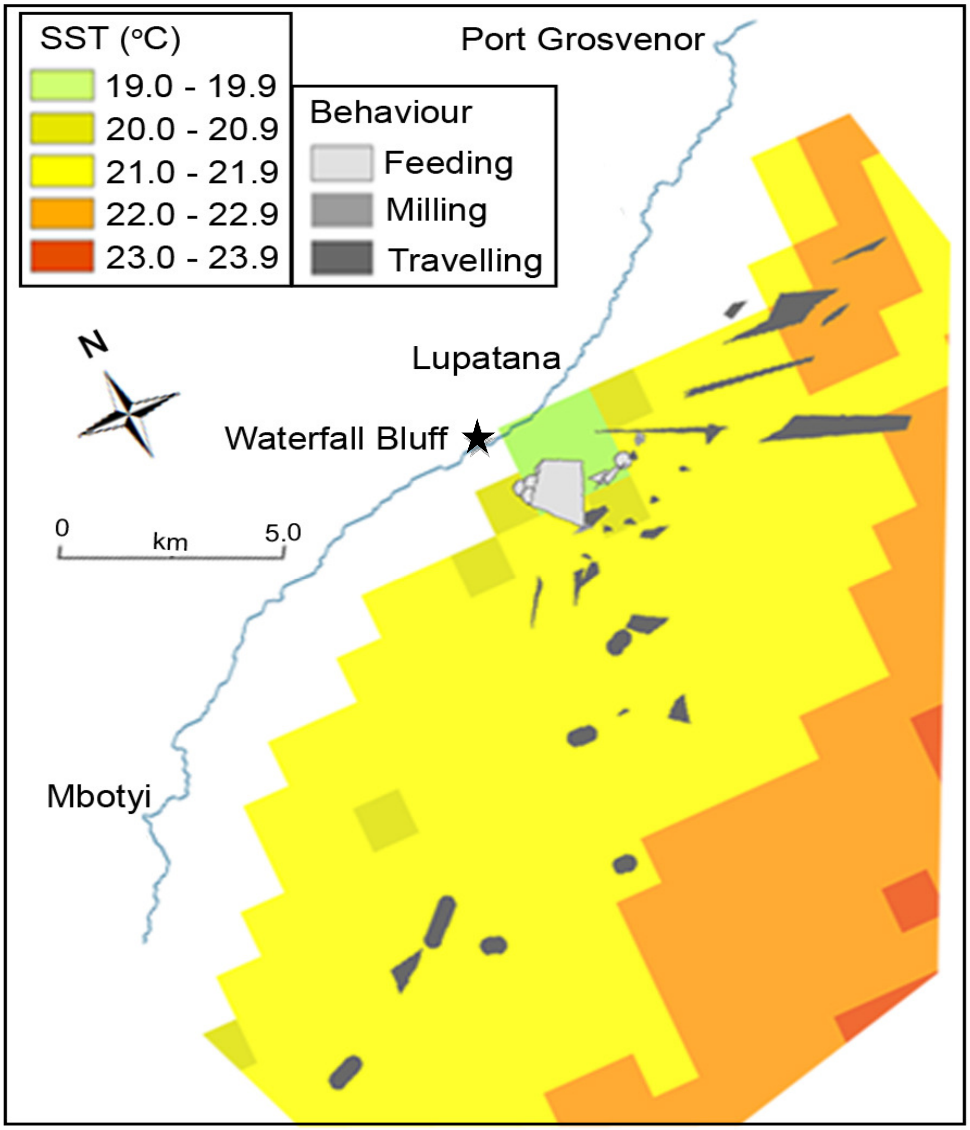

Figure 5. Common dolphin distribution and behaviour, measured using a theodolite (indicated by a black star), in relation to sea surface temperature (°C) on the 21st June 2006 off Waterfall Bluff, Eastern Cape.

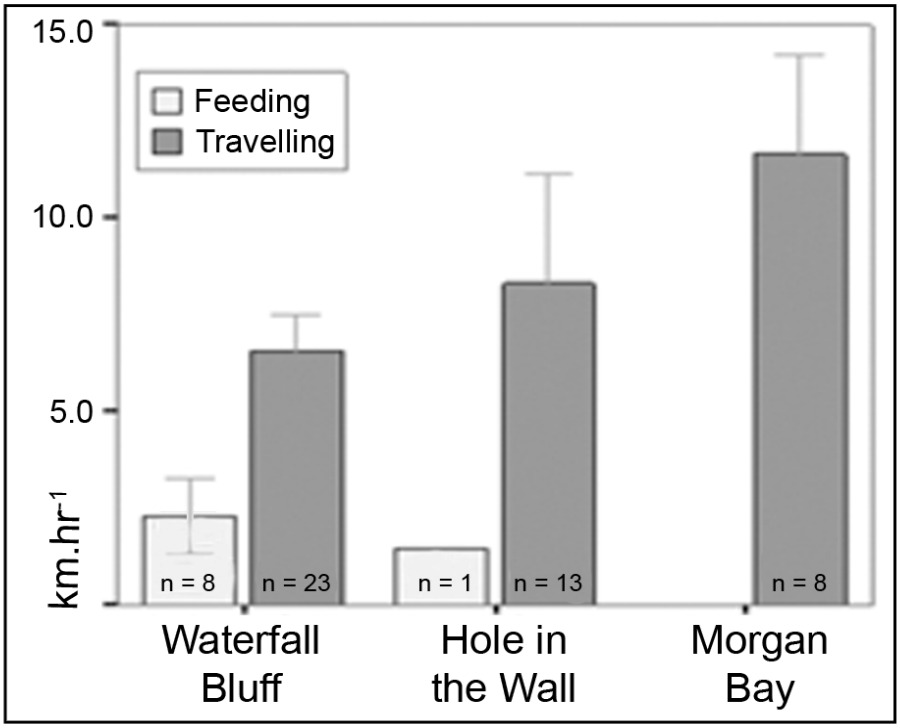

Figure 6. Mean common dolphin travel speed per behaviour class at three survey sites along the Wild Coast. Error bars indicate 95 % confidence intervals.

Remotely sensed SST was on average 0.6 +/- 0.4 °C warmer than CTD temperatures measured within three meters of the surface. CTD and remotely sensed SST measurements were significantly related ($r = 0.548$; $p < 0.001$). Surface temperatures from the 17th to the 30th June remained above 20 °C, with the exception of a small, 4 km^2 patch of water at the north end of Waterfall Bluff Bight on the 21st June (Fig. 5). From the 18th June, there was an intrusion of cool water onto the shelf in the CTD study area. This intrusion strengthened until the 21st; when the depth of the 20 °C isotherm decreased to a minimum of around 10 m, and temperatures below 16 °C were recorded at a minimum depth of around 40 m at the most distant station from shore along the Mbotyi transect line (Fig. 1B). The magnitude of this intrusion of cool water was greatest at this latter station and decreased both northwards to Mkambati and shorewards along the entire survey area. By the 24th June the water column throughout the survey area had warmed to above 20 °C, indicating that the intrusion of cool water had ceased, but by the 27th June, a new intrusion of cool water had started, and had strengthened by the 28th.

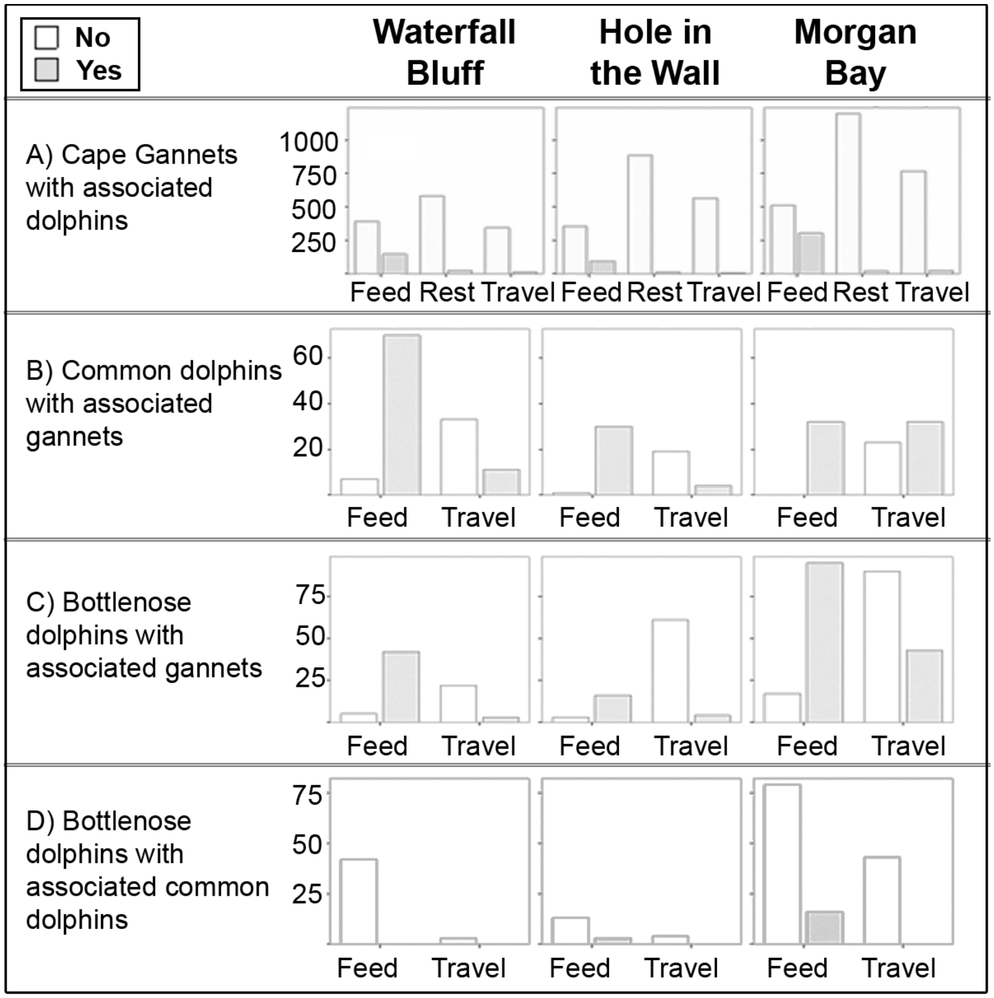

Figure 7. Frequency occurrence of A) observations of gannets per behaviour class and per site with associated dolphins of any species (= yes) or no associated dolphins (= no); and similarly observations of B) common dolphins with associated gannets, C) bottlenose dolphins with associated gannets and D) bottlenose dolphins with associated common dolphins.

DISCUSSION

This study is the first to use land-based observations and tracking to record the abundance, behaviour and movements of a suite of sardine run predators off southern Africa. Elsewhere this methodology has proven to be an effective research technique (Würsig 1986; Würsig and Würsig 1980). Although this technique provides relatively limited spatial coverage, the major advantage of monitoring animals from a fixed station is that, for a relatively low cost, one can generate substantial fine-scale time-series data (Evans and Hammond 2004).

Because of this variability in the sardine run phenomenon, and in an attempt to standardise sighting efficiency between sites, some common dolphin sightings at Hole in the Wall were missed by the abundance calculations. For a species occurring further than 4 km from shore this might have substantially affected abundance calculations. During the survey period at Hole in the Wall, however, sea conditions were very calm with a sea state = 1 and visibility excellent. Dolphins would therefore have been visible far from shore. A perusal of the frequency histogram of common dolphin distance from shore provides no evidence of a sudden increase in sightings beyond the standardised survey area for Hole in the Wall, therefore suggesting suitable representation of the sample. It is assumed, therefore, that the low abundance rate observed in this region was a reasonable representation of common dolphin abundance rather than an artefact of data processing.

The importance of temperature in regulating sardine and predator movement on the east coast of South Africa was particularly evident during 2004 when substantial cooling along the entire east coast was followed by the strongest sardine run in recent years (O'Donoghue *et al.* op. cit., b; O'Donoghue and Peddemors op cit.). Frontal features with strong temperature gradients are often associated with enhanced productivity leading to increased predator abundance (Ballance and Pitman 1998; Davis *et al.* 1998; Pitman and Ballance 1992; Tynan 1997). The arrival of the sardine run on the Wild Coast on the 13th June 2006 followed such a period of nearshore cooling with strong thermal gradients observed in the Morgan Bay region, which probably provided suitable habitat for sardine occupation.

The significant increase in abundance and group size for the three predator species at the start of the sardine run highlights the intense association between predators and prey. All three species are known to be closely associated with the sardine run (O'Donoghue *et al.* op. cit., a, b, c; O'Donoghue and Peddemors op cit.), and their dramatic arrival and passage past Morgan Bay gave every indication that the sardine run had commenced on the Lower Wild Coast. However, two days later and only 102 km up the coast at Hole-in-the-Wall, there was no sign of these predators at all.

Why did the sardine run dissipate? The strong thermal gradients were replaced by homogenously warm water unsuitable for sardine occupation with Hole in the Wall mean SST = 21.3 +/- 0.5 °C. A similar termination of the sardine run occurred along the KZN and Eastern Cape coastlines during 2005 when east coast nearshore temperatures warmed to above 21 °C (O'Donoghue *et al.* op. cit., c) culminating in the end of the sardine run. Intense sardine run activity during late June 2005 was restricted to the narrow strip of cool water south of Mbashe River (O'Donoghue and Peddemors op cit.). Sardine presence is significantly inversely associated with SST along the east coast (Armstrong *et al.* 1991; O'Donoghue *et al.* op. cit., a, b; O'Donoghue and Peddemors op cit.) suggesting that the warm water conditions experienced along the east coast during 2006 probably contributed substantially to the apparent failure of the run during this year. At Morgan Bay it was evident that the majority of the observed feeding aggregations were within cool water, with some concentration at the interface with the warm water.

Gannet abundance off Waterfall Bluff during 2006 was significantly less than off Morgan Bay, and substantially less than abundance off Waterfall Bluff during the previous two years (O'Donoghue and Peddemors op cit.). The low abundance rates and group size can therefore be considered atypical for this stretch of coastline and emphasise the poor strength of the run for this year.

Feeding and travelling common dolphin and gannet groups were significantly further from shore and in deeper water off Waterfall Bluff than off the sites to the south, corroborating findings previously made in this area (O'Donoghue *et al.* op. cit., b; O'Donoghue and Peddemors op cit.). Common dolphin pod shape and speed of travel also differed significantly here, and appeared to be associated with the unique bathymetry. Such association with underwater topographical features has been recorded for common dolphins elsewhere, e.g. southern California (Hui 1979 in Peddemors and Cockcroft 1997; Stevick *et al.* 2002) and the Gulf of California (Gallo 1991) and has been postulated to relate to prey distribution. The change in the shape of common dolphin pods in this area is interesting with dolphins fanning out as they travelled along the depth contour. Travel speed here was also significantly slower than at Morgan Bay, suggesting that dolphins may have been searching for fish. Such changes in common dolphin group shape during foraging have been recorded within the Gulf of California where dolphins appeared to form a parabolic formation apparently to enhance acoustic detection of pelagic shoaling fish (Gallo 1991). Off the Wild Coast, this parabolic formation was not noticed in either this study or previous observations (Peddemors, *pers. Obs.*) and common dolphins appeared to rather swim in a line-abreast formation while sweeping the area during foraging similar to that reported for other Delphinidae (Würsig 1986).

Common dolphins were observed feeding significantly closer to shore on the 21st June in a small patch of water with an SST ≤ 20 °C, whereas SST in the rest of this area was > 21 °C. This suggests the influence of water temperature, especially in the upper part of the water column, in determining the presence of common dolphin prey. This patch of water ≤ 20 °C occurred between CTD stations, and was therefore missed. The CTD data did, during this period, indicate the presence of an intrusion of cool water onto the shelf, the magnitude of which peaked at the most distant CTD stations from shore in the bottom part of the water column, suggesting that the intrusion was probably topographical in origin. The intrusion of water suitable for sardine occupation along the outer part of the continental shelf provides good reason for the increased distance that sardine and predators are normally sighted from shore along this part of the Wild Coast.

The intrusion of cool water was detected off Mkambati. By the 21st June, the first of very few reports of sardines on the KZN south coast were received (O'Donoghue *et al*. op. cit., a). It is probable that the intrusion of cool water enabled the limited amount of sardine present in this region to pass through this stretch of coastline, but that the depth at which this intrusion occurred, and its distance from shore, meant that the sardines were not detected by the shore based observer. This could be the first indication of the how the Waterfall Bluff Gateway may aid sardine movement along this part of the coastline, with the being open from the 18th to the 21st June, and its subsequent closure on the 24th June. The lack of substantial sardine abundance that appeared on the KZN South Coast, having passed through this gateway, was due to the limited amount of sardine that had travelled up from the Lower Wild Coast owing to the warm conditions encountered between the Lower Wild and Waterfall Bluff coasts.

Gannets fed more during the early morning, but feeding declined after 10h00 and lead to resting becoming the primary behaviour between 10h00 am and 14h00. This corroborates the reported temporal variation in gannet behaviour seen during fine-scale aerial surveys along the Wild Coast (O'Donoghue and Peddemors op cit.). This temporal variation between early feeding and midday resting was also recorded for Cape gannets carrying data loggers (Ropert-Coudert *et al.* op cit.) and suggests that the feeding patterns of breeding gannets are sustained during their non-breeding winter period. The significantly higher feeding abundance during SE and SW winds are suggestive of a peak in feeding following the passage of a cold front with the wind swinging around to the SE. Feeding and resting abundance were significantly lower during NE winds, however this was not the case for travelling birds. The high travelling rates recorded during NE and SE winds suggest that gannets use these winds to travel along the continental shelf when looking for prey patches. Gannets did not appear to use SW winds for travel but that may have been because they were being blown northwards as they were feeding or because they were avoiding travelling northwards because of the lack of sardine run activity further up the coast.

Travelling bottlenose dolphins were sighted closer to shore than feeding bottlenose dolphins and they had a clear travelling modal depth preference of less than 15m. Typically, bottlenose dolphins were sighted swimming northwards along the back line of the breakers, and were frequently sighted swimming within the breaking waves. Riding waves has previously been shown to represent a form of energy saving (Williiams *et al.* 1992), but whether this accounts entirely for their strong nearshore presence while travelling is not clear. Feeding bottlenose dolphins were frequently sighted near shallow reefs at both Cape Morgan and Hole in the Wall. On one occasion dolphins were seen to chase their prey into very shallow water in the Hole in the Wall Bay, whereupon they started feeding. During this period of feeding there were no gannets associated with them. The lack of gannets associated with the feeding bottlenose dolphins was unusual and was probably because the plunge-dive feeding gannets were limited by the depth of the water.

The strong association between gannets and feeding dolphins of both species in this study raises the question of whether it is passive accumulation around a shared resource, or whether one or either species in the association actively seeks out the other. The answer to this question was apparent on days of sparse activity. If the passage of either species of dolphin through the study area was accompanied by a change in behaviour from travelling to feeding, nearby flying birds were always attracted and would start circling above the dolphins. The birds would then either circle a few times before moving on, or they would dive onto or in front of the foraging dolphins. Diving birds would frequently precipitate the arrival of more distant birds, with an often rapid accumulation of birds into a feeding aggregation. Presumably, if fish were not available then birds would leave the aggregation and it would dissipate.

Intuitively, birds might benefit from this association as dolphins are better able to find prey below the surface of the water, especially in reduced visibility conditions. It is possible that birds also benefit from common dolphins driving their prey towards the surface and within reach of the diving birds. Würsig (1986) postulated that dolphins used the sea surface as a "wall through which the fish cannot escape" and that this activity allowed seabirds to take advantage of more easily accessible prey. Our data indicate that gannets recognised the change in dolphin behaviour and responded to it. It is therefore likely that the dolphins act as an "information centre" for nearby gannets, much like that described by Ward and Zahavi (1973), and that feeding gannets then act as information centres for more distant foraging gannets.

Whether dolphins benefit from this association is not clear. Occasionally, depredation from gannets may provide a 'free' meal for dolphins, as witnessed when a bottlenose dolphin was observed harassing a Cape gannet that had just surfaced from a dive with prey in its mouth. After approximately five seconds, during which time the sitting bird moved erratically sideways in either direction, the fish was dropped and the dolphin was clearly seen to snatch the fish from the sea surface. However, our observations during many years of working on the sardine run suggest that such interactions are rare.

Inter-specific interactions between common and bottlenose dolphins were unusual and largely limited to feeding dolphins at Morgan Bay. From their depth distribution and theodolite tracklines it seems that these broadly sympatric dolphin species diverge in their habitat preference, particularly when not feeding. It is still not certain whether bottlenose dolphins feed extensively on sardines, but both species do feed opportunistically on locally abundant prey (Peddemors 1999). Although we have witnessed both dolphin species feeding with Cape gannets, sharks, South African fur seals (*Arctocephalus pusillus p.*) and game fish on a single sardine bait-ball, the interaction between the dolphins was minimal and there appeared to be no structured feeding strategy between the two. Some authors have suggested that multi-species feeding around such bait-balls are a 'free-for-all' (Gallo 1991), but our preliminary unpublished observations indicate that there may be more structure and synchrony to multi-species feeding events than previously believed. The current study indicates that gannets and common and bottlenose dolphins do provide each other with opportunities to maximise their foraging through inter-specific observation of behaviour and movements. The sardine run provides an ideal opportunity to conduct an in-depth analysis of inter-specific predator behaviour around bait-balls.

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CHAPTER SEVEN: CONCLUSION

The aim of this doctoral research was to describe sardine and predator distribution along the east coast of South Africa, and to determine how their distributions relate to each other and to environmental variables.

The northward progression of sardine distribution along the South African east coast from May to July was clearly described using coarse scale aerial survey data. Sardines were first sighted along the Waterfall Bluff Coast during May, and reached the KZN Coast by June. Sardine abundance increased substantially during June along the entire South African east coast and remained high during July, but by August had declined significantly along the KZN coastline. This pattern of sardine distribution was confirmed by the spatio-temporal GLM model, where seasonal effects dominated. This confirmed the findings of Baird (1971) and Armstrong *et al.* (1991). These authors suggested that reduced levels of insolation during autumn and the onset of winter storms degrading the summer thermocline and mixing the water column contribute towards the cooling of east coast continental shelf waters to sardines' preferred temperature range, thereby expanding the range available to sardine along the east coast.

Also evident in the spatio-temporal GLM model was the variability in the strength of the sardine run since 2001, with four of the five most recent years in this data set having poor runs. This trend has since continued, with every year from 2006 up to and including 2009 being a weak sardine run. This was supported by sardine egg data off the KZN South Coast by Connell (in press, pers. Comm.[2]), who has reported low sardine egg abundance during these same years, with sardine eggs present for a shorter period of time during the winter/ spring seasons at Park Rynie. Clearly, the sardine runs of the new millennium have been variable and mostly weak. Because of the short time series available for this analysis, it has not been possible to determine whether this variability in the strength of the sardine run is a recent development, or whether it is part of a longer term cycle. However, given the current international concern about global warming and its effect upon sea temperature, and given that the sardine run occurs where the sardine is at the limit of its temperature range, and given the ecological importance of this event to the nutrient impoverished KZN coastline, it becomes evident that further research into the probable effect of the reduction in the occurrence of the sardine run along the east coast of South Africa is critically required.

The decline in sardine run activity northwards along the east coast was apparent in both clupeid and predator abundance during the 2005 FRS *Africana* hydrographic and predator surveys and in the fine scale aerial surveys along the Wild Coast. From 2004 to 2006, the sardine run was observed passing northwards through the Lower Wild Coast every year and during the latter two years predator abundance peaked within this region. During 2006, very little sardine run activity passed beyond the Lower Wild Coast, which contrasted strongly with 2004, where sardine movement up the east coast was extremely rapid with no decline in sardine run activity along the whole Wild Coast. Considering the coastline to the north of the Mbashe River, sardine run activity peaked between Waterfall Bluff and Port St Johns, even during poor sardine run years. This was evident in both the coarse and fine scale surveys. Sardines were sighted significantly further from shore within the Waterfall Bluff Bight, moving closer to shore as they progressed northwards out of the Bight.

Sardine abundance did not decline significantly between the Upper Wild Coast and the KZN Mid South Coast. The coarse scale aerial survey data, however, suggested that it declined from the KZN Upper South Coast. This appeared to contradict the spatio-temporal GLM model, where sardine presence only declined along the KZN North Coast. Both of these data sets, however, found that the percentage of sardine sightings within 100 m of the shoreline peaked along the KZN Upper South Coast, with sardine beach-seine landings also peaking along this stretch of coastline. It is possible that sardines may have been missed in the surf zone along the Upper South Coast during the coarse scale aerial surveys, both because they were beyond the transect strip-width, and because water clarity would have been reduced by the surf action, resulting in fewer sightings. Despite the above discrepancy, it is clear that sardine distribution changes somewhere along the KZN Upper South Coast, and that change involves sardines moving towards shore. Along the KZN North Coast, the substantial decline in sardine presence corresponded with an increase in the distance of sardines from shore, and an increase in the width of the continental shelf.

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Changes in sardine distribution along the east coast were then related to environmental variables using in-situ and remotely sensed oceanographic measurements and historical climate data. Sea surface temperature (SST) was very closely and inversely related to sardine distribution, which confirmed the findings of Armstrong *et al.* (1991). This association was apparent at both the seasonal as well as the coarse and fine spatial scales of sardine movement. The arrival of the sardine run within each zone along the east coast occurred when mean sea temperatures dropped to below 21 °C. Within the fine scale aerial and cliff surveys, the commencement of the sardine run only occurred following a period of cooling of sea surface temperatures, and sardine longshore distribution corresponded very closely with parts of the coastline where mean SST was below 21 °C, namely southwards of the Mbashe River and along the Waterfall Bluff coastline. The similarity in sardine abundance between different regions of the Wild Coast during 2004 coincided with unusually cool conditions, which resulted in rapid sardine movement up the Wild Coast. The controlling effect of temperature was evident in the inverse relationship between sardine abundance and SST during those months, and along those parts of the east coast, where sea temperatures were at the limit of sardine preferred range e.g. during May along the Upper Wild Coast and during June along the KZN Upper South Coast.

Along the KZN Lower South and Wild coasts, continental shelf waters are cooled by the entrainment of South Indian Central Water onto the shelf by Ekman Veering (Schumann 1986). The strength of this upwelling process increases with latitude, and it is visible in the satellite imagery following periods of winds out of the NE, when nearshore surface water is forced away from shore and is replaced by the cool upwelled Central Water. Centred off Port Alfred, but usually extending as far north as the Mbashe River along the Lower Wild Coast, further upwelling occurs. Lutjeharms *et al.* (2000) has described this upwelling as being topographically driven by the westwards widening of the continental shelf at the initiation of the Agulhas Bank. Measurements indicated that this upwelling was permanent, but that it varied in strength and northward extent. It seems as if the amount of upwelling occurring along the east coast of South Africa determines how suitable conditions are for sardine occupation, and this will determine how much sardine moves up the coast. Although only based upon three years of data, this neatly describes the difference in the strength of the sardine runs during the fine scale aerial surveys.

How can we use satellite imagery to predict the strength of the sardine run along the Wild Coast? Lutjeharms *et al.* (2000) found that the upwelling cell off Port Alfred was visible as outcropping at the sea surface in only 35 % of the satellite images that they analysed, and was visible as far north as Port St Johns in 5 % of the images. Although this is a permanent upwelling cell, it is only visible at the surface in just over one third of the satellite images. This is because surface water temperature along the east coast of South Africa is driven by local wind forcing (Pearce *et al.* 1978). As previously described, NE winds cause nearshore cooling of sea surface temperature. The opposite effect occurs with SW winds, where warm Agulhas Current water is pushed shorewards covering the cool, upwelled water below. Given that wind stress is the square of wind speed, the thickness of the warm layer must increase with the strength of SW winds, which would affect the depth at which suitable conditions for sardines occur. In the satellite imagery, following SW winds, temperatures would appear to be warm and not suitable for sardine movement. This would not reflect conditions through the water column, so wind conditions should be considered when using satellite imagery for predictive purposes. Upwelling conditions that are expressed at the sea surface, as in 2004, are indicative of good conditions for sardine occupation, and may be used as an indication of the probability of sardine movement up the east coast, considering a time lag for such a movement to occur.

From the Mid Wild Coast northwards, conditions become warmer and, consequently, less suitable for sardine occupation as the influence of the Port Alfred upwelling cell diminishes. This was evident in the satellite imagery and was reflected in sardine abundance. Why then, was sardine abundance higher along the Waterfall Bluff coastline during 2005 and 2006? Satellite imagery showed that SST was significantly cooler in the lee of Waterfall Bluff compared with shelf waters to the north. During 2005, SST along this part of the coastline was within sardine preferred range, unlike the adjacent coastlines. A similar situation occurred during 2006 when sardine run activity was observed within the Waterfall Bluff Bight, in a small patch of cool water below 21 °C. The temporal occurrence of this patch corresponded with the intrusion of cool water from the shelf break, which was measured using a CTD. This intrusion of cool water was probably topographically driven upwelling in the lee of the bight due to the nature of the bathymetry forcing the divergence of the Agulhas Current from the shoreline at the widening of the continental shelf.

Evidence for slack current conditions within the bight can be found in the sediment bedform patterns (Flemming 1980). The existence of this area of refuge along the east coast must be crucial to the success of the KZN sardine run. Fish that have made it through the Port Alfred upwelling are able to occupy this stretch of coastline until favourable conditions occur for further northward movement. This was apparent during the 2005 aerial surveys, when the Agulhas Current was clearly observed as a current line leaving the coastline from a point immediately north of Waterfall Bluff. Along the inside of this current line there was very concentrated sardine run activity, but very little activity beyond the current line.

The similarity in sardine abundance from the Upper Wild Coast to the KZN Mid South Coast makes sense, given that the coastline is largely straight, therefore there no perturbations of the Agulhas Current, so conditions should not change much along this stretch of coastline and therefore sardine distribution should not affected. The next major change in sardine distribution occurred along the KZN Upper South Coast where sardines moved closer to shore and where the sardine run usually terminates. That this occurs adjacent to the Durban Eddy is of significance. Sea temperature in both the satellite imagery and at the shark nets increases significantly along the Upper South Coast. This is because of the shoreward movement of warm, Agulhas Current water in the Mdoni region, followed by its northward transport past Durban (Pearce *et al.* 1978; Schumann 1982), and it is almost certainly the reason for the demise of the sardine run along the Upper South Coast. This was confirmed by the GLM analysis of environmental variables, where SST emerged as the dominant effect predicting sardine presence along the KZN coastline. In the GLM model, SST declined following periods of easterly winds with current direction at the shark nets running southwards. This corroborated the findings of Schumann (1982) and is consistent with the upwelling process described earlier. The cooling of shelf waters during conditions opposite to those prevailing when the Durban Eddy predominates, and the close association between sardine distribution and SST, provides telling evidence for the deleterious effects of the Durban Eddy upon the sardine run. Further evidence for the constraining effect of temperature comes from the increased sardine abundance that was frequently recorded at the interface between cool water stretching up the coastline, and warm Agulhas Current water pushing up against the coastline. Increased sardine predator abundance was recorded in the cool water at such an interface during the fine scale aerial and cliff surveys and adjacent to the Durban Eddy on the Upper South Coast.

SST measured by satellite imagery was the most useful predictor of sardine presence in this study. Comparisons with in-situ measurements showed a strong correlation between measurements. Advantages of using remotely sensed SST include its spatial and temporal coverage and low cost. There are, however, a number of disadvantages too. Firstly, there is loss of data due to cloud. This problem can be circumvented by using three-day weighted average images. A second problem is the loss of an approximately two pixel width strip of data along the coastline. This is particularly problematic northwards of Waterfall Bluff, where sardines move closer towards shore, which limits the scale at which satellite imagery may be used for the prediction of sardine presence. With advances in remote sensing capability, it may be possible to use finer resolution images, e.g. 300 m resolution, to circumvent this problem. A third problem is that images become available only after a period of approximately 48 hours. This makes real time prediction tricky, but this problem is alleviated by the time lag in the cooling of sea temperature and sardine movement. And, finally, the images are only able to describe conditions at the sea surface, for reasons discussed earlier. Despite these limitations, satellite images do prove useful in identifying suitable conditions for the arrival of sardine along the coast, provided they are augmented with information obtained from aerial or ground-based observations pertaining to the progression of the sardine run.

The second remotely sensed parameter, investigated as a tool to predict sardine presence, was chlorophyll a concentration. Clupeid distribution along the east coast was significantly correlated with this variable, while SST was very strongly and inversely correlated. The pattern of chl a concentration observed along the east coast conformed to those previously reported (Shannon *et al.* 1984; Walters *et al.* 1985), although the actual values in this study were slightly higher. South African east coast continental shelf waters are classified as Case 2 waters, i.e. affected by terrigenous input. Measurements of remotely sensed chl a concentration are inflated by the presence of turbidity and gelbstoff (yellow substance) in the water column. Because of this uncertainty in the accuracy of remotely sensed chl a data, use of this parameter as a tool to predict sardine presence has been deferred. Post-doctoral research is currently being planned to conduct ocean colour validation experiments in order to assess the accuracy of algorithms used to determine chl a concentration in this region. If successful, this parameter will be revisited.

Having described sardine distribution in relation to environmental parameters, I then investigated sardine distribution in relation to other clupeid species and to predators on the sardine run. During the 2005 hydrographic survey, sardine distribution was very closely associated with that of all three other clupeid species recorded, although only sardine was recorded with substantial abundance northwards of Waterfall Bluff. Anchovy and west and east coast roundherring also form an important component of the diet of sardine run predators along the east coast of South Africa. Of these species, it is only the east coast roundherring that is found year round off the east coast, and the presence of this clupeid species must contribute to predator foraging success when sardine are not available. The importance of sardine, however, is evident in the abundance of predators that follow them up into KZN coastal waters. The energetic cost of swimming so far up the east coast must be offset by the easy availability of these fish along the KZN coast.

Predators were included within a suite of sighting cues used to determine sardine presence in the aerial and cliff surveys. This probably inflated the strength of the association reported between sardine and gannet distributions. This close association, however, was also evident during the 2005 hydrographic survey, where sardine abundance was measured independently of predator presence. This highlights the importance of using other sources of data indicating sardine abundance, like catch per unit effort data from the sardine directed fishery in the Eastern Cape, and a more systematic collection of sardine landings data against effort in the KwaZulu-Natal beach-seine fishery. It is evident that the sardine run along the Wild Coast consists of at least four clupeid species, but that sardine are by far the most dominant species along the KZN nearshore coastline, where the majority of sardine run has been conducted. This highlights an important need for research: how much of the Wild Coast sardine run is actually sardine? The sardine run along the Wild Coast during 2005 suggests that the other three clupeid species, east and west coast roundherring and anchovy, are also present in significant numbers. Although ship time is prohibitively expensive for a major hydrographic survey, it may be possible to conduct this research using small boats launched daily from shore, using the same methods as the working boat in Chapter 4.

Predators can, therefore, be used as indicators of the arrival of the sardine run, albeit of the various species of clupeids that make up the sardine run. Of these predators, the principle indicator of the sardine run is the Cape gannet. Although gannets are present along the Wild Coast prior to the arrival of the sardine run, their abundance increases substantially once the sardine run had commences. This increase in gannet abundance was tightly bound temporally and spatially with the arrival of sardines. As with sardine distribution, Cape gannet abundance increased with latitude and during the fine scale surveys also peaked along the Lower Wild Coast. Like sardines, gannet distance from shore was greatest along the Waterfall Bluff coastline, and as they moved northwards up the east coast, they were sighted closer to shore. Less gannet, however, moved into the surf zone along the KZN Upper South Coast, at which point their abundance declined significantly. This may have been related to their method of prey capture; gannets plunge dive from about 30 m height to capture prey up to 10 m in depth (Ropert-Coudert *et al.* 2004b). The shallow depths at which sardines were predominantly found along the Upper South Coast may have increased the risk of serious injury for diving birds, whilst the reduced visibility in the surf zone may have also contributed to difficulty in detecting prey. A similar situation occurring during the fine scale cliff surveys, with gannets diving over feeding bottlenose dolphins, which subsequently chased their prey onto very shallow sandbanks in Hole in the Wall Bay. Some gannets followed, but did not dive onto the feeding dolphins. The remaining gannets continued diving over dolphins beyond the last line of breakers, suggesting that depth may have been a constraint upon the following gannets' feeding.

The close association between gannet and sardine distribution was not surprising, given the importance of sardine to gannet diet (Batchelor and Ross 1984; Berruti *et al.* 1993; Crawford *et al.* 2008). The ability of gannets to travel rapidly over long distances in a foraging range that is effectively very narrow, and their propensity to form highly visible feeding aggregations, make gannets a very useful proxy for determining sardine distribution. Both the fine scale aerial and cliff surveys provided evidence of gannets using the prevailing longshore winds to travel. This must help them to forage over large distances efficiently, and contributes to their close association with sardines both temporally and spatially. Gannets were observed feeding more frequently on the day following the passage of a coastal low. It is likely that strong westerly winds associated with the passage of these weather systems result in unsuitable feeding conditions. Nelson (1978) reported that gannet feeding in large aggregations declines significantly during winds in excess of 15 knots. Such winds occur during the passage of coastal lows, and if these lows occur frequently, they may affect gannet feeding success.

Gannet feeding and resting rates were directly correlated, with gannets frequently observed resting upon the sea surface following feeding. Gannets were observed feeding more frequently early in the morning, whereas during the early afternoon, more gannets were observed sitting upon the water digesting. There was no evidence for an increase in feeding abundance during the afternoon, suggesting that gannets, having fed successfully, rest upon the sea surface. This is in contrast to their feeding behaviour during their breeding season, when a second bout of foraging occurs following a period of digestion (Ropert-Coudert *et al.* 2004a). This second bout of foraging would be to take food back to their chicks. The sardine run occurs outside of the breeding season, so sardine run gannets need not provide food for chicks, and therefore do not need to forage in the afternoon if they feed successfully during the morning.

Gannet fine scale distribution was very closely associated with both common and bottlenose distributions. This association, however, was dependent upon dolphin behaviour. Feeding dolphins were quick to attract foraging birds. This was observed on a number of occasions: if dolphins (of either species) changed their behaviour from travelling to foraging, nearby birds were immediately attracted and started circling over the dolphins. Diving birds were very attractive to more distant foraging and sitting birds, and this frequently and rapidly resulted in the accumulation of a feeding aggregation of gannets over the foraging dolphins. It seems very likely that gannets use dolphins to detect their prey, and initial analysis of underwater feeding dynamics indicate that birds time their plunge dives to correspond with the feeding lunges of common dolphins. It is probable that the dolphins force the fish into an escape response, often towards the surface, making the fish both more accessible and less wary of predation from above. It may also be that as the baitball is scattered by the attacking dolphins, birds are able to focus upon individual fish, and the fish thus lose the safety afforded by their schooling behaviour.

The common dolphin was the most abundant marine mammal during the sardine run. Like gannets, they were sighted along the Wild Coast prior to the arrival of sardines, and their abundance increased substantially upon commencement of the sardine run. Common dolphin abundance and group size peaked between Port St Johns and Waterfall Bluff in both aerial and the cliff surveys where, like gannets and sardines, they were sighted further from shore. The increased abundance along this stretch of coastline persisted even in the absence of clupeids during 2005, implying some significance of this part of the coastline. To the north of Waterfall Bluff, common dolphin abundance and group size decreased significantly, and they were significantly closer to shore, with abundance along the KZN Upper South Coast was very low.

The similarity between common dolphin, sardine and Cape gannet distributions was evident in the correlations recorded in each study. From May to July along the Wild Coast and KZN Lower South Coast, these species' distributions were significantly associated. The lack of association along the KZN Upper South Coast was due to the decline in common dolphin abundance and the divergence in dolphin and sardine distributions in terms of distance from shore. This research underpins the current understanding of common dolphin distribution, whereby they are found across the continental shelf of the South African south east coast throughout most of the year, but are only found inshore along the east coast during the winter months (Peddemors 1999). This research contributes further by showing that common dolphins, unlike bottlenose dolphins, are seldom sighted within the surf zone, and that as they move northwards along the KZN coastline, they break up into smaller groups. This may be for foraging efficiency.

Unlike Cape gannets, common dolphin behaviour did not appear to change during the day as there were no obvious peaks in feeding or travelling behaviour during the day. There was, however, evidence for a change in common dolphin behaviour between different regions of the Wild Coast. Southwards of Mbotyi, common dolphins were sighted travelling in pods where the longitudinal axis of the pod was parallel with the shoreline. Within the Waterfall Bluff Bight, the longitudinal axis was perpendicular to the shoreline, with travel speed slower in this region compared with the rest of the coastline. These changes in behaviour, abundance and distribution within the Waterfall Bluff Bight occur where sardine abundance is highest and where sardine northward movement is frequently constrained due to the Waterfall Bluff Gateway. It is probable that common dolphins have habituated to conditions along this coastline and are therefore encountered here more frequently, and that they have adapted their foraging strategy i.e. pod shape and travel speed to maximise the probability of encountering their prey.

Resident bottlenose dolphin pods inhabit home ranges throughout the study area, and these animals are thought to remain within their home ranges despite the movement of the sardine run along the east coast (Peddemors *et al.* submitted). This, together with the results of stomach contents analysis (Cockcroft *et al.* 1990a), suggests that sardine is not an important prey species to resident bottlenose dolphins. The results presented in this thesis are consistent with the above, whereby the bottlenose dolphin was the marine mammal species least associated with sardine distribution. Reasons for this weak association included the presence of bottlenose dolphin along the east coast outside of the sardine run period, and their strong affinity for water depths of less than 30 m, whereas sardines are widely distributed across the continental shelf to the south of Waterfall Bluff (Armstrong *et al.* 1991).

There were, however, some interesting deviations from the above. During April and May there was no difference in sighting rates of bottlenose dolphin along the east coast of South Africa. This was consistent with their well defined home ranges. However, during June, bottlenose dolphin sighting rate increased significantly along the Wild and KZN Lower South coasts, with sighting rate significantly lower along the KZN Upper South Coast. Along the Lower Wild Coast, bottlenose dolphin abundance and group size increased substantially when both the 2004 and 2006 sardine runs commenced, and was significantly lower during the very weak sardine run of 2006 along the Waterfall Bluff Coast. These differences in alongshore abundance and their relation to the sardine run are of significance. Peddemors *et al.* (submitted) have proposed that there is a migratory stock of bottlenose dolphin that travel up the east coast during the winter months, and have shown that this stock is genetically distinct from the resident stock (Natoli *et al.* 2008). Genetic divergence between resident and migratory animals becomes apparent from the KZN Upper South Coast northwards.

Bottlenose dolphin distribution presented in this thesis corroborates the theory for a migrant stock of dolphins and suggests that the influx of dolphins is from the south. Bottlenose dolphin stomach contents analyses, conducted thus far, found that dolphins do not prey extensively upon sardine, but these studies did not differentiate between resident and migratory stocks. It is not conclusive, therefore, that the migratory stock shares the resident stock's lack of appetite for sardine. The migratory stock will, if not feeding on sardine, be feeding on other fish species that follow the sardines up the east coast e.g. elf, *Pomatomus saltatrix*, and this may be the reason for the association between the migratory bottlenose dolphin stock and the sardine run. A new stomach contents analysis, which differentiates between the two stocks using genetic techniques, is required to resolve the issue of diet of the migratory stock.

Both the coarse and fine scale aerial surveys and the predator survey conducted during the hydrographic cruise, found that bottlenose dolphin distribution was strongly skewed towards shore, and that this distribution was related to water depths of less than 30 m. These findings concur with those previously presented by Cockcroft *et al.* (1990b) and Ross *et al.* (1987). Results from the cliff surveys indicated that depth preference was mostly prevalent when dolphins were travelling, with feeding dolphins significantly further from shore and in deeper water. This probably relates to the distribution and depth of reefs through the study area, which dolphins use to locate their prey (Peddemors 1999). There was some difference in bottlenose dolphin distance from shore along the east coast: off the Waterfall Bluff Coast, 21 % of the coarse scale aerial survey bottlenose dolphin sightings were in water deeper than 30 m, compared with less than 6 % off the Upper Wild Coast. Off Port St Johns, bottlenose dolphins are frequently encountered in a localised area (O'Donoghue pers. obs.) over the shelf break (unpublished data). We suspect that the same pod is being re-sighted, and that their distribution may be related to bathymetric features, like the shelf break or deep reef systems. This suspicion was enforced by the observation of a dolphin with a red fish in its mouth, which was almost certainly a reef fish, although identification of the fish was not possible. Prevailing environmental conditions did not appear to have an effect on bottlenose dolphin distribution or behaviour along the east coast of South Africa.

Humpback whales did not appear to be associated with sardine, despite their frequent proximity to sardine run activity. There have been no confirmed reports of humpback whales feeding during the sardine run, and it may be that these whales do not have an appetite on their northward breeding migration. Humpback whales were not significantly associated with any oceanographic or environmental variables; however their distribution, in terms of distance from shore, changed along the east coast. They were sighted significantly closer to shore between Virginia Beach and Mazeppa Bay, along the stretch of coastline where the continental shelf narrows. This was considered to be a current avoidance response.

In this thesis a number of methodological advances in studying the sardine run phenomenon are presented. Previously published research was based upon the incidental capture and/ or sighting of predators along the KZN coastline and a few hydrographic surveys along the east coast. The main methodological advance presented in this thesis is the use of aerial surveys, at both coarse and fine scales. In these surveys, predator abundance was used to determine the along-shore distribution of the sardine run. The use of micro-light aircraft was a further innovation reducing the cost of aerial surveys, thereby allowing for increased survey hours. Previously, the incidental sightings reported by the KZNSB field staff were published each year in a non peer reviewed report by this organisation. Through comparison with concurrent aerial surveys, these KZNSB data were collated and analysed within a modelling environment, which led to the publication of Chapter 3. Future data collation at the KZNSB will apply the methods used in this thesis. Point surveys, using a theodolite, were conducted for the first time from cliffs along the Wild Coast to investigate fine scale sardine and predator movement in relation to environmental variables. The analysis of these data was conducted in a GIS environment, which was also a novel approach to the study of the sardine run. I intend to extend the findings of the point surveys but using underwater video analysis of predator feeding, which will relate to the association between predators of the run. This too, will involve the application of novel techniques.

The aims of this thesis have been met, with sardine distribution along the east coast of South Africa described at both coarse and fine temporal and spatial scales. The influence of environmental variables upon sardine distribution, particularly that of temperature, have been clearly shown, and in light of the recent spate of poor sardine runs, has highlighted the need for an understanding of how the sardine run will change with an ocean that is warming due to climate change. Given the importance of the sardine run to the ecology of the east coast of South Africa, it is vital that research be conducted upon the probable impact of a diminished sardine run upon the ecology of the KZN coastline.

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