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Abundance and distribution of avian and marine mammal predators of sardine observed during the 2005 KwaZulu-Natal sardine run survey

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Abundance and distribution of avian and marine mammal predators of sardine observed during the 2005 KwaZulu-Natal sardine run survey

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Opportunistic observations to determine the relative abundance and distribution of marine mammal and seabird predators of sardine *Sardinops sagax* were carried out during a dedicated multidisciplinary research survey off the South African east coast in June and July of 2005 that was timed to coincide with the annual sardine run. Associations between different predator species, between predators and clupeoids, and between predators and oceanographic variables, were examined. Species' distributions were primarily separated by latitude and distance from shore. Bryde's whale *Balaenoptera edeni*, African penguin *Spheniscus demersus*, Cape cormorant *Phalacrocorax capensis* and West Coast round herring *Etrumeus whiteheadi* were predominantly found in the cool southern part of the survey region. Peak sardine run activity occurred within 4 km of shore at the northward limit of a strip of cool water (<21 °C) stretching along the East Coast. The principal predators associated with this activity were common dolphins *Delphinus capensis* and Cape gannets *Morus capensis*, and their nearshore distribution was associated with sardine and East Coast round herring *E. teres*. Few clupeoids were encountered along the KwaZulu-Natal continental shelf, although patches of high sardine abundance were recorded near the shore immediately south of Durban. It is clear that during the 2005 survey the sardine run terminated in this region, probably as a result of the nearshore intrusion of warm water from the Agulhas Current.

Keywords: Cape gannet, chlorophyll *a*, common dolphin, hydrographic survey, *Sardinops sagax*, sardine run, SST

Introduction

The annual movement of the South African sardine *Sardinops sagax* up the east coast of South Africa is a spectacular event known locally as the 'sardine run'. The run has been described as arising from an extension of the habitable range of these fish along the East Coast as a result of the cooling of nearshore waters during the austral winter (Armstrong et al. 1991).

The subtropical coastal waters of KwaZulu-Natal (KZN) are considered relatively impoverished owing to low nutrient levels and insignificant upwelling activity (Carter and d'Aubrey 1988, Meyer et al. 2002). Although biodiversity and endemism of fish is highest in this area of South Africa (Turpie et al. 2000), their biomass is low in comparison to the southern and western Cape waters. Sardine provide an important food source for numerous predators, which include piscivorous fish, birds and marine mammals (van der Elst 1981, 1988, Cockcroft and Peddemors 1990, Crawford et al. 1991, 2008). Many predatory fish are associated with the sardine run (Garratt 1988, Fennessy et al. 2010), as are sharks (Dudley and Cliff 2010), seabirds and cetaceans (Peddemors 1999, O'Donoghue 2010a, 2010b). The influx of thousands of tonnes of sardine into the nearshore waters of

KZN is undoubtedly the most important biological phenomenon occurring along this coast, and provides an important annual injection of nutrients (Hutchings et al. 2010).

The sardine run has become an important annual event for regional economies, particularly with respect to tourism focused on the run itself (Dicken 2010), tourism related to swimming at shark-netted beaches in KZN (Dudley and Cliff 2010) and short-term employment opportunities for local communities (Myeza et al. 2010). Human interest in the sardine run is focused as much upon the sardine predators as upon the fish themselves. A better understanding of the distribution of sardine and their predators during the run, and the associations between these species at this time, is crucial in terms of managing human use of this phenomenon.

During May and June, sardine move northward along the Eastern Cape continental shelf towards Port St Johns (Figure 1; Baird 1971). Farther northward, movement towards the KZN coastline appears to be reliant upon suitable oceanographic conditions (O'Donoghue 2009, Roberts et al. 2010) — the presence of sardine along the KZN coast being inversely associated with sea temperatures below 21 °C (Armstrong et al. 1991, O'Donoghue et al. 2010a).
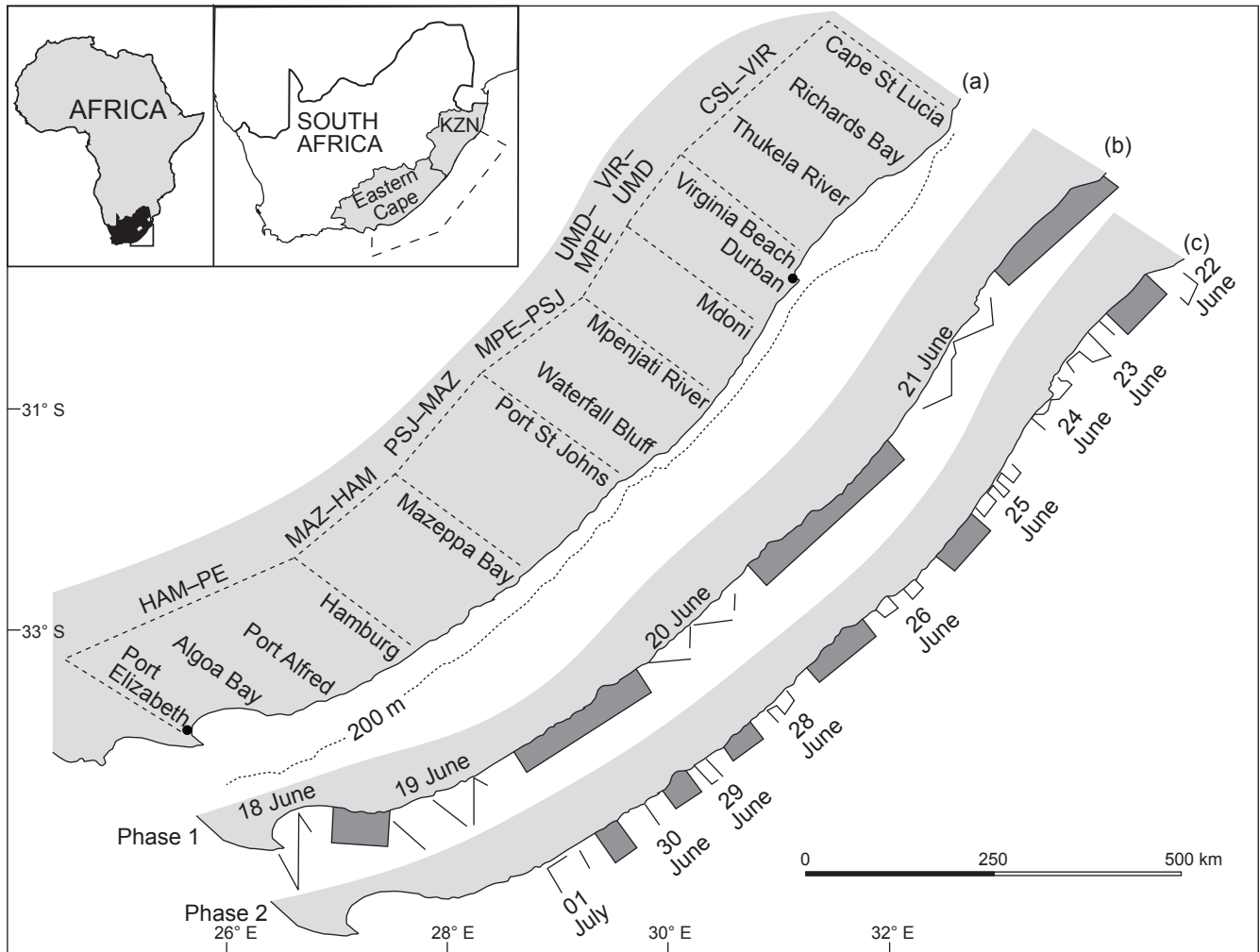
Figure 1: Predator surveys conducted along the KwaZulu-Natal (KZN) and Eastern Cape coastlines during the 2005 sardine run survey: (a) the division of the coast into seven regions and including the 200 m isobath indicating the edge of the continental shelf; and (b) and (c) the transects and survey dates for Phases 1 and 2 respectively. Night-time is depicted as shaded blocks

Current understanding of the occurrence and population structure of sardine off the east coast of South Africa has been derived from three acoustic surveys conducted in August 1986, June 1987 and June 1990 (Armstrong et al. 1991). Further insight into sardine distribution has been gained by using the presence of feeding predators as a proxy for sardine presence during aerial surveys spanning almost 20 years (up to 2005; O'Donoghue et al. 2010b). As aerial surveys have historically been conducted over the coastline only, there is no reliable indication of sardine run activity farther than approximately 4 km from shore. Additionally, although the run is occasionally observed north of Durban and sardine eggs have been sampled off the Thukela River (Figure 1; Beckley and Hewitson 1994), little is known about the northward limit of the run.

In June and July of 2005 a multidisciplinary research survey off the East Coast was undertaken to determine oceanographic conditions, and assess the abundance and distribution of sardine and other small pelagic fish species and some of their predators, during the sardine run. Oceanographic conditions, phytoplankton and zooplankton

distributions, and clupeoid (including sardine) distribution during this survey have been described by Coetzee et al. (2010). This paper investigates the alongshore abundance and offshore distribution of marine mammal and seabird predators during the run, and their association with clupeoid species and the oceanographic conditions prevalent during the survey.

Material and methods

Survey design

The 2005 sardine run survey was conducted from the RS *Africana* and was primarily designed to investigate the abundance, size structure and distribution of sardine and other small pelagic fish species off the East Coast during the sardine run. The survey was split into two phases. Phase 1 was surveyed during 18–21 June in a northerly direction, and consisted of cross-shelf zigzag transects from Port Elizabeth to Richards Bay (Figure 1) designed to determine a suitable spatial grid pattern for the second phase. Phase 2 transects consisted of randomly positioned transects running

perpendicular from the coast out to the continental shelf edge from Richards Bay to Port Alfred during 22 June–1 July. Marine mammal and seabird observations were conducted along transects during both phases, and were terminated at the end of Phase 2 off Port Alfred.

Marine mammal observations

Recordings of marine mammals were made by two dedicated observers searching the sea surface ahead of the ship in a 180° arc to the horizon. Each observer searched a 100° vector from 10° beyond dead ahead to 90° on their respective side of the vessel, following Tynan et al. (2005). Searches were conducted by alternating between using the unaided eye and 10 × 50 binoculars from the flying bridge of the ship (eye height = 17 m) during daylight hours. The following environmental conditions were recorded at the start of each transect: Beaufort sea state, wind direction and strength, and the extent of visibility from the ship. Observations along the transects were only prematurely terminated (i.e. terminated before the end of the transect) if the sea state exceeded six or if visibility was less than two nautical miles. Any observations made while the ship was trawling, returning to a transect after trawling, or at CTD stations spaced every 10 nautical miles along transects, were recorded as incidental. Upon each sighting, the following physical data were recorded: time, vessel location obtained from a GPS, the angle of the sighting relative to the ship's trackline, and the angle of declination determined via a handheld inclinometer. Observations were identified to the lowest possible taxonomic level and, taking into account that individuals could be submersed during counts, the maximum 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 100 m of the primary sighting. Travelling behaviour was defined as all members of a group, or individual animals travelling alone, moving consistently in a single direction. Feeding behaviour consisted of frequent directional changes and burst swimming at the surface (O'Donoghue 2009). No mammal observations were made at night.

Seabird observations

Observations of avian species were made from the flying bridge of the ship by two dedicated and experienced observers. Bird identifications and counts were made in a 180° arc forward of the observation platform during a standard 10-minute period, interspersed with a 20-minute period between counts. All birds estimated by eye to be within 300 m of the ship were identified and 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 count periods but 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 at night (Figure 1).

Data analyses

All non-incidental sightings of marine mammals made while on-transect and during transits between transects were retained for analyses. The location of each sighting was calculated using the ship's location, the angle of declination of the mammal from the ship, and Pythagoras' theorem, 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 1 000 m. The depth class of each sighting was obtained using the spatial join function in the GIS document, 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).

On account of the paucity of the data, sightings from Phases 1 and 2 were pooled. To compare predator, clupeoid 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 our study. To enable spatial analyses, the coastline was divided into alongshore regions, the breaks generally 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). The locations at which the coastline was divided were as follows (Figure 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 by dividing the survey grid into the following classes of distance from shore (km): 0.1–4, 4.1–8, 8.1–16 and >16.0. All sightings, transects and transits, and environmental data were allocated to one of the above blocks using the spatial join function in the GIS document.

The following environmental variables were obtained from the 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. Encounter rates were used as an index of relative abundance. They were calculated for each species within each block of the grid by summing the number of individuals encountered during both phases and dividing this by the total distance surveyed within that block, to give an encounter rate per kilometre (km^{-1}).

Seabird counts were treated similarly with the data from Phases 1 and 2 pooled. Only 10-minute counts that were made when the ship was underway with a mean speed of not less than three nautical miles per hour, and with no directional changes >90°, were retained for analyses. This procedure minimises bias that can arise when counting highly mobile subjects at sea (Tasker et al. 1984). The distance covered in each 10-minute count was computed in the manner described above. The total area surveyed

during each count was then calculated by multiplying the distance covered during the 10-minute count by the survey strip width of 600 m. All 10-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 encounter rate per square kilometre (km^{-2}). Because of the narrow transect strip, the ship's location and depth was used when calculating the depth and Euclidean distance of each seabird sighting from shore.

Clupeoid biomass estimation

Clupeoid abundance and distribution were assessed via continuous acoustic sampling to a depth of 250 m using a Simrad EK60 echosounder, and midwater trawling was used to identify acoustic targets; detailed sampling procedures during the 2005 sardine run survey are given in Coetzee et al. (2010). For this study, clupeoid distribution and density along the East Coast were determined by interpolating the species-specific density point data obtained during the survey using the natural neighbour method with a cell size of 0.019 within the GIS document. In order to compare clupeoid and predator distributions, only those clupeoid data that were obtained within valid predator transects were used. Zonal statistics were used to calculate the mean and maximum density of each clupeoid species per block of the survey grid. Clupeoid distribution during Phases 1 and 2 are presented separately to illustrate the movement of the fish between phases. During Phase 2, a 'small boat' was deployed each day to investigate the nearshore (mostly <2 km from shore, in depths inaccessible to the RS *Africana*) distribution and density of clupeoids by towing a SIMRAD EY500 echosounder (see Coetzee et al. 2010). These data were used for day-scale comparisons with the predator count data.

Environmental data

All remotely sensed SST and chlorophyll a (Chl a) concentration data were downloaded from the Remote Sensing Server for Marine 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 pentad (Chl a) images were used. SST and Chl a concentration along the survey transects were determined by performing a zonal statistics analysis within a 1 000 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 SST data was investigated 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 clupeoid distributions, a

hierarchical cluster analysis (HCA) was performed. The aim of this analysis was to identify species' encounter rates (for seabirds and mammals) or densities (for clupeoids) within the 23 blocks (cases) of the survey grid that were most similar. As these are interval data, the measurement used to determine the similarity between each species within each case was the squared Euclidean distance. Because of the large range in values between species, the data were standardised using Z-values. A dendrogram provided a visual representation of clusters of species; the shorter the distance between joining lines in the dendrogram (fewer cases difference), the closer the association between species' distributions. Only species with at least five encounters were used in this analysis, with the exception of Bryde's whales *Balaenoptera edeni*, which were included despite only being encountered three times.

The dendrogram was then compared with Spearman's rank bivariate correlation coefficients (ρ), obtained between predator encounter rates, clupeoid densities and the following environmental variables: latitude, distance from shore, depth,
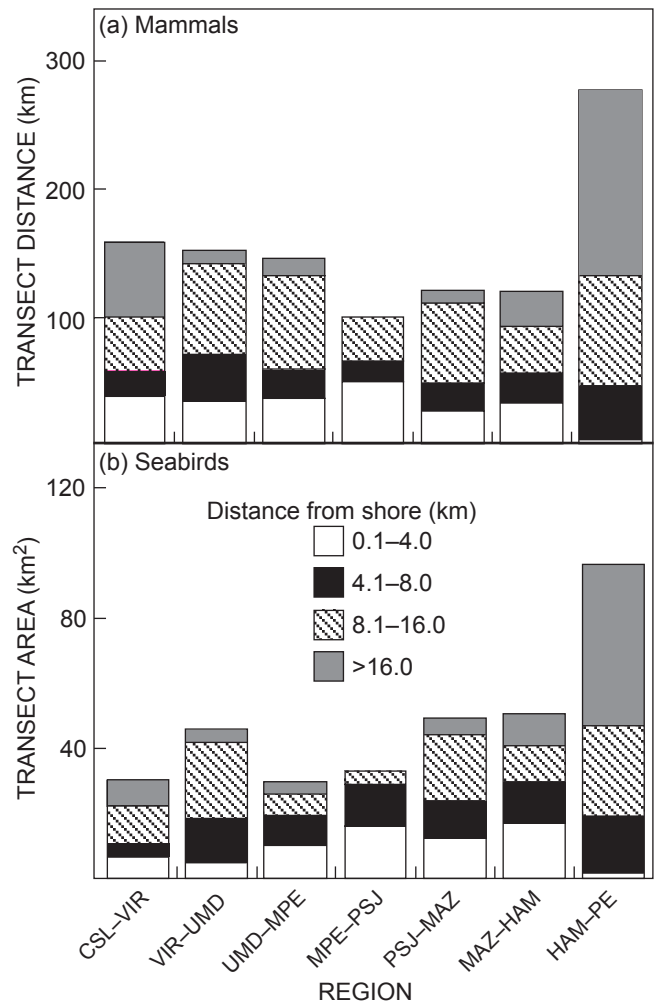
Figure 2: (a) Total mammal survey transect distance and (b) seabird survey transect area covered during the survey per block and distance from shore class. The locations follow the regional divisions shown in Figure 1

mean SST and mean Chl *a* concentration. Similarly, predator encounter rates at the day scale were compared with the clupeoid densities measured by the small boat.

Results

A total distance of 434 and 635 km was surveyed for marine mammals during Phases 1 and 2 respectively. The seabird counts were conducted for 12.7 and 15.6 hours in Phases 1 and 2 respectively, equating to a surveyed area of 149 km^2 and 186 km^2. The total distances and areas surveyed per distance from shore class within each block of the survey grid are shown in Figure 2. Between Virginia Beach and Mazeppa Bay, blocks had a total of <15 km of surveyed transects farther than 16 km from shore, because of the narrowness of the continental shelf in this region. To minimise bias when calculating encounter rates, data from the >16 km from shore class were added to the 8.1–16.0 km classes for those blocks. Similarly, because of a paucity of data for the 0.1–4.0 km distance from shore class between Hamburg and Port Elizabeth, they were combined with the 4.1–8.0 km class. This left a total of 23 depth class/survey block combinations in which distributions were compared.

Mammal distribution

Of the marine mammals encountered, the long-beaked common dolphins *Delphinus capensis* had the highest relative abundance (Table 1). Encounter rates were highest between the Mpenjati River and Mazeppa Bay (Figure 3) with a maximum of 142 km^{-1} sighted within 4 km of the shore between Port St Johns and Mazeppa Bay. Encounter rates of common dolphins were an order of magnitude lower north of the Mpenjati River and there were no sightings north of Virginia Beach. Median distance from shore was 2.9 km, ranging between 0.1 and 12 km. Their encounter rate was

inversely associated with distance from shore (Table 2). Five of the six feeding observations were within 4 km of the shore, four of which were in the presence of feeding Cape gannets *Morus capensis*, with a minimum gannet group size of 350.

The seven Indo-Pacific bottlenose dolphin *Tursiops aduncus* sightings (Table 1) occurred during Phase 2 between Mdoni and Port St Johns (Figure 3). Median and maximum distance from shore was 1.1 km and 2.3 km respectively, with water depth never exceeding 30 m. Their encounter rate was inversely associated with depth and significantly associated with mean Chl *a* concentration (Table 2). Bottlenose dolphins were observed feeding three times, each time in the presence of Cape gannets, the group size of which always exceeded 200.

Humpback whales *Megaptera novaeangliae* were encountered frequently and were the mysticete species with the highest relative abundance (Table 1). They were sighted along the entire coast mainly within 4 km of the shore (Figure 3). Their encounter rate was inversely associated with distance from shore (Table 2). Of the 56 observations of travelling animals, 43 were moving in a northerly direction.

The other mysticete species were encountered less frequently. Four of the six dwarf minke whale *Balaenoptera acutorostrata acutorostrata* sightings were between Cape St Lucia and Virginia Beach. They were recorded between 1.7 km and 16.7 km from shore. Bryde's whales were sighted three times: twice near Port Elizabeth and once off Mazeppa Bay. These sightings were 5.3 km, 13.9 km and 15.1 km from shore respectively. Bryde's whale encounter rate was inversely associated with latitude (Table 2). There was one incidental sighting of a southern right whale *Eubalaena australis* 28 km north of Mazeppa Bay and 1.7 km from shore.

Nine of the 11 Cape fur seal *Arctocephalus pusillus pusillus* sightings (Table 1) occurred between Port Elizabeth

Table 1: Total number of marine mammal and seabird encounters, total count, median group size and range during the survey

Common name	Species name	Number	Count	Median	Range
Long-beaked common dolphin	*Delphinus capensis*	17	9 470	400	50–3 000
Indo-Pacific bottlenose dolphin	*Tursiops aduncus*	7	675	80	20–250
Humpback whale	*Megaptera novaeangliae*	84	160	2	1–8
Dwarf minke whale	*Balaenoptera acutorostrata*	7	8	1	1–2
Bryde's whale	*B. edeni*	3	3	1	1
Cape fur seal	*Arctocephalus pusillus pusillus*	11	36	1	1–12
Cape gannet	*Morus capensis*	96	8 447	9	1–2 875
White-chinned petrel	*Procellaria aequinoctialis*	75	688	3	1–263
Swift tern	*Sterna bergii*	19	36	1	1–30
Antarctic tern	*S. vittata*	5	8	1	1
Indian yellow-nosed albatross	*Thalassarche carteri*	52	173	2	1–12
Black-browed albatross	*T. melanophris*	10	10	1	1
Shy albatross	*T. cauta*	7	8	1	1
Sooty shearwater	*Puffinus griseus*	17	17	1	1–2
Subantarctic skua	*Catharacta antarctica*	15	26	1	1–8
African penguin	*Spheniscus demersus*	6	13	2	1–5
Antarctic prion	*Pachyptila desolata*	8	21	2	1–8
Cape cormorant	*Phalacrocorax capensis*	5	11	3	2–6
Great-winged petrel	*Pterodroma macroptera*	2	2	1	1
Soft-plumaged petrel	*P. mollis*	1	1	1	1
Wilson's storm petrel	*Oceanites oceanicus*	4	6	1	1–3
Unidentified giant petrel	–	1	1	1	1
Feral pigeon	*Columba livia*	2	3	1	1
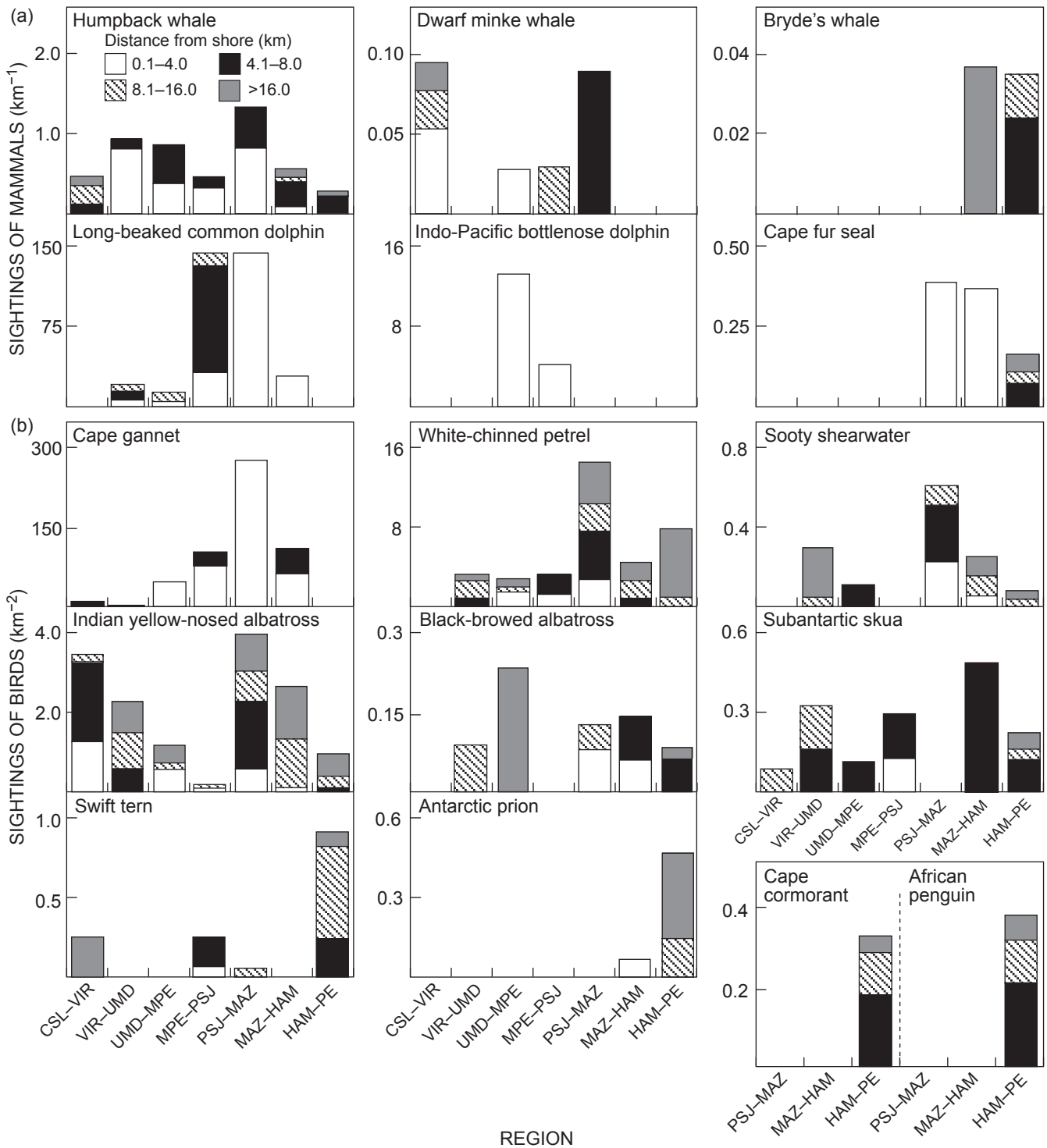
Figure 3: (a) Marine mammal sighting rates and (b) seabird density along the South African east coast during the 2005 sardine run survey per block and distance from shore class. The locations follow the regional divisions shown in Figure 1

and Hamburg. Highest encounter rates were between Port St Johns and Hamburg within 4 km of the shore (Figure 3). There were no sightings of Cape fur seals north of Port St Johns. Median distance from shore was 12.3 km, ranging from 2.8 to 27.4 km, and their encounter rate was inversely associated with mean SST and latitude (Table 2).

Avian distribution

Sixteen species of seabirds were recorded during the 2005 sardine run survey (Table 1). Of the species observed, only three, the Cape gannet, white-chinned petrel *Procellaria aequinoctialis* and swift tern *Sterna bergii*, were recorded regularly in the vicinity of sardine shoals.

Table 2: Spearman's rank correlation coefficients (ρ) between marine mammal and seabird encounter rates, clupeoid densities and environmental conditions within survey grid squares (n = 23) during the surveys. Bold type indicates significant association at either 0.05 (*) or 0.001 (**) level

Variable	Code	CD	BN	HB	MW	BW	CFS	CGAN	WCP	SWFT	IYNA	BBAL	SSH	BSKA	PENG	APRN	CCOM	ANCH	WCRH	ECRH	SARD
Long-beaked common dolphin	CD	—	0.274	0.066	-0.179	-0.321	0.129	**0.567****	0.055	-0.116	-0.361	0.143	-0.133	0.141	-0.315	-0.060	-0.315	-0.221	-0.148	0.222	0.138
Indo-Pacific bottlenose dolphin	BN	0.274	—	0.282	0.181	-0.119	-0.170	**0.423***	0.127	0.048	-0.066	-0.211	-0.272	0.014	-0.125	-0.125	-0.125	-0.238	-0.238	-0.060	-0.048
Humpback whale	HB	0.066	0.282	—	-0.025	-0.055	0.057	0.153	0.231	-0.189	-0.176	-0.041	0.084	0.090	-0.195	-0.365	-0.195	0.151	0.199	0.274	0.245
Dwarf minke whale	MW	-0.179	0.181	-0.025	—	-0.226	-0.324	0.118	-0.157	-0.137	0.200	-0.358	-0.124	-0.327	-0.213	-0.213	-0.213	-0.136	-0.197	-0.057	-0.102
Brydes whale	BW	-0.321	-0.119	-0.055	-0.226	—	-0.170	-0.221	0.030	0.371	0.111	0.000	0.112	0.043	**0.610****	0.192	**0.610****	0.248	0.336	-0.129	0.199
Cape fur seal	CFS	0.129	-0.170	0.057	-0.324	-0.170	—	0.369	0.287	-0.125	-0.082	**0.573****	0.349	-0.051	0.162	**0.589****	0.162	**0.684****	**0.653****	**0.431****	0.368
Cape gannet	CGAN	**0.567****	**0.423***	0.153	0.118	-0.221	0.369	—	-0.058	0.106	-0.379	0.159	-0.200	0.105	-0.193	0.086	-0.193	0.066	0.122	0.320	0.335
White-chinned petrel	WCP	0.055	0.127	0.231	-0.157	0.030	0.287	-0.058	—	0.038	**0.432***	0.349	**0.635****	0.085	0.069	0.062	0.069	0.411	0.250	**0.468****	0.308
Swift tern	SWFT	-0.116	0.048	-0.189	-0.137	0.371	-0.125	0.106	0.038	—	-0.278	0.023	-0.163	0.231	**0.660****	0.363	**0.660****	0.225	0.328	0.064	0.312
Indian yellow-nosed albatross	IYNA	-0.361	-0.066	-0.176	0.200	0.111	-0.082	-0.379	**0.432***	-0.278	—	-0.067	**0.464***	-0.282	-0.024	-0.035	-0.024	0.099	-0.065	-0.010	-0.125
Black-browed albatross	BBAL	0.143	-0.211	-0.041	-0.358	0.000	**0.573****	0.159	0.349	0.023	-0.067	—	0.253	0.280	0.207	0.196	0.207	**0.496****	0.412	0.436	0.355
Sooty shearwater	SSH	-0.133	-0.272	0.084	-0.124	0.112	0.349	-0.200	**0.635****	-0.163	**0.464***	0.253	—	-0.281	-0.016	0.212	-0.016	**0.499***	0.258	0.396	0.247
Subantarctic skua	BSKA	0.141	0.014	0.090	-0.327	0.043	-0.051	0.105	0.085	0.231	-0.282	0.280	-0.281	—	0.235	-0.007	0.235	-0.030	0.173	-0.009	0.184
African penguin	PENG	-0.315	-0.125	-0.195	-0.213	**0.610****	0.162	-0.193	0.069	**0.660****	-0.024	0.207	-0.016	0.235	—	**0.607****	**1.000****	**0.504***	**0.606****	-0.111	0.257
Antarctic prion	APRN	-0.060	-0.125	-0.365	-0.213	0.192	**0.589****	0.086	0.062	0.363	-0.035	0.196	0.212	-0.007	**0.607****	—	**0.607****	**0.458***	**0.500***	-0.103	0.094
Cape cormorant	CCOM	-0.315	-0.125	-0.195	-0.213	**0.610****	0.162	-0.193	0.069	**0.660****	-0.024	0.207	-0.016	0.235	**1.000****	**0.607****	—	**0.504***	**0.606****	-0.111	0.257
Anchovy	ANCH	-0.221	-0.238	0.151	-0.136	0.248	**0.684****	0.066	0.411	0.225	0.099	**0.496****	**0.499***	-0.030	**0.504***	**0.458***	**0.504***	—	**0.887****	**0.614****	**0.738****
West Coast round herring	WCRH	-0.148	-0.238	0.199	-0.197	0.336	**0.653****	0.122	0.250	0.328	-0.065	0.412	0.258	0.173	**0.606****	**0.500***	**0.606****	**0.887****	—	**0.541****	**0.786****
East Coast round herring	ECRH	0.222	-0.060	0.274	-0.057	-0.129	**0.431****	0.320	**0.468****	0.064	-0.010	0.436	0.396	-0.009	-0.111	-0.103	-0.111	**0.614****	**0.541****	—	**0.867****
Sardine	SARD	0.138	-0.048	0.245	-0.102	0.199	0.368	0.335	0.308	0.312	-0.125	0.355	0.247	0.184	0.257	0.094	0.257	**0.738****	**0.786****	**0.867****	—
Mean SST		0.193	-0.064	0.245	-0.102	0.199	**-0.583****	-0.278	-0.277	**-0.559****	0.049	-0.274	-0.165	-0.086	**-0.598****	**-0.545****	**-0.598****	**-0.720****	**-0.832****	**-0.456****	**-0.669****
Mean Chl a		0.219	**0.445****	-0.142	0.229	-0.412	0.327	0.368	0.394	0.055	-0.199	0.148	0.227	-0.007	0.111	0.058	0.111	**0.519****	**0.519****	**0.574****	**0.636****
Depth		-0.180	**-0.420***	-0.372	-0.065	0.090	-0.162	-0.353	-0.306	0.270	0.096	0.053	0.319	0.074	0.063	0.007	0.063	0.031	0.034	0.056	0.038
Latitude		0.097	0.095	0.018	0.387	**-0.500***	**-0.558****	-0.016	**-0.543****	-0.325	-0.081	-0.396	**-0.481***	-0.104	**-0.590****	**-0.578****	**-0.590****	**-0.746****	**-0.773****	**-0.476****	**-0.620****
Distance from shore		**-0.442***	-0.411	**-0.487***	-0.048	0.271	-0.113	**-0.518***	0.141	0.307	0.165	-0.039	0.176	0.048	0.259	0.175	0.259	-0.020	-0.050	-0.265	-0.251

The Cape gannet was the most abundant seabird species encountered (Table 1). The highest encounter rates of 274 km⁻² between Port St Johns and Mazeppa Bay, and 46 km⁻² between Mdoni and the Mpenjati River, were within 4 km of the shore (Figure 3). Median distance from the shore was 2.9 km, ranging from 0.8 to 25.7 km. Gannet encounter rates declined northwards of the Mpenjati River and were inversely associated with distance from shore (Table 2). Cape gannets occurred in large feeding groups of up to 3 000 birds, usually in association with common dolphins. Cape gannets were predominantly in adult plumage, and juveniles comprised between 0% and 6% of birds in feeding groups, averaging 2%.

White-chinned petrels were the second most abundant seabirds recorded. They were present in all but the Virginia Beach to Cape St Lucia block (Figure 3). During Phase 1, 75% of sightings were made between Port Elizabeth and Hamburg, mostly offshore, where water temperatures exceeded 20 °C. In Phase 2, only 5% of sightings were in this area, the majority (68%) being in the Mazeppa Bay to Port St Johns section. White-chinned petrel encounter rate was significantly associated with East Coast round herring *Etrumeus teres* density and inversely associated with latitude (Table 2).

The highest swift tern encounter rate was recorded between Hamburg and Port Elizabeth (Figure 3). Almost all of the encounters were farther than 4 km from shore, and those between Cape St Lucia and Virginia Beach were farther than 16 km from shore. Swift tern encounter rate was inversely associated with mean SST (Table 2).

Indian yellow-nosed albatross *Thalassarche carteri* was the most frequently sighted albatross, with encounter rates approaching 3 ind. km⁻². Although found throughout the region and in all distance classes, they were uncommon between Port St Johns and the Mpenjati River (Figure 3). Their encounter rate was significantly associated with that of white-chinned petrels and sooty shearwaters *Puffinus griseus*. Adult yellow-nosed albatrosses comprised about 60% of those recorded. In Phase 1, most adults were seen between Port Elizabeth and Hamburg, while the highest numbers of immature birds were in the northernmost block between Virginia Beach and Cape St Lucia. During Phase 2, distribution patterns were similar for both age groups. Black-browed albatross *T. melanophris* was comparatively scarce with only immature birds sighted during the survey.

Sooty shearwaters were found in low densities throughout most of the survey area, but were most frequently encountered between Mazeppa Bay and Port St Johns (Figure 3), and were spread within all blocks from inshore to offshore. Their encounter rate was inversely associated with latitude (Table 2). During Phase 2, the distribution of this species was similar to that of sardine, East Coast round herring and anchovy *Engraulis encrasicolus* between Mazeppa Bay and Port St Johns.

Subantarctic skuas *Catharacta antarctica* were recorded in low densities throughout the survey area, usually farther than 4 km from shore (Figure 3). They did not appear to be associated with any clupeoid, avian or marine mammal species.

All encounters with African penguins *Spheniscus demersus* and Cape cormorants *Phalacrocorax capensis* were between Port Elizabeth and Hamburg (Figure 3). They were found where sardine, West Coast round herring *E. whiteheadi* and anchovy densities were high. Antarctic prion *Pachyptila desolata* were only recorded between Port Elizabeth and Mazeppa Bay, mostly between Port Elizabeth and Hamburg. These three species' encounter rates were inversely associated with latitude and mean SST (Table 2).

Clupeoid distribution

During Phase 1, sardine were distributed in two major patches between Port Elizabeth and Mazeppa Bay (Coetzee et al. 2010). Five days later, during Phase 2, sardine distribution was less dense and spread along the coastline between Hamburg and Waterfall Bluff. This distribution was reflected in their mean densities within survey blocks (Figure 4), which was highest between 4 km and 8 km from shore during Phase 1, and within 4 km of the shore by Phase 2. Sardine nearshore distribution measured by the small boat differed from that recorded by the RS *Africana* (Figure 4) with mean density between Mdoni and the Mpenjati River three times higher than within any other nearshore block.

The highest East Coast round herring density was recorded in the block between Port St Johns and Mazeppa Bay, within 4 km of the shore, during both phases of the survey (Figure 4). Whereas West Coast round herring moved northwards between Phase 1 and Phase 2 their highest densities were always between Hamburg and Port Elizabeth. Anchovy density was similarly highest between Hamburg and Port Elizabeth, although they were recorded off Mazeppa Bay during Phase 2. All four clupeoid species' densities were associated with each other and with mean Chl *a* concentration, as well as being inversely associated with latitude and mean SST (Table 2).

Environment

The satellite images clearly show a cool band of water ≤21 °C stretching northwards along the coast to the Mazeppa Bay region during both phases of the survey (Figure 5a). Sea surface temperatures between Mazeppa Bay and Virginia Beach increased during the survey owing to the intrusion of water ≥23 °C. However, small patches of ≤22 °C water were recorded between the Mpenjati River and Port St Johns. Temperature increased with distance offshore and was inversely correlated with maximum Chl *a* concentration ($\rho = -0.711$, $p < 0.001$). During Phase 1, elevated Chl *a* concentrations were recorded in a broad band between Hamburg and Mazeppa Bay, with large patches exceeding 4 mg m⁻³ (Figure 5b). From Mazeppa Bay to Waterfall Bluff concentrations were mostly <2 mg m⁻³. By Phase 2, mean Chl *a* concentration had declined and was restricted to a narrow strip along the coast.

Comparison of distributions

African penguins, Cape cormorants and West Coast round herring formed a tight cluster separated by a distance of less than five cases (Figure 6). This cluster formed part of a larger cluster with progressively increasing distance between swift tern, sardine and Bryde's whales. Most species' encounter rates within this larger cluster were significantly associated with each other and inversely associated with mean SST and latitude (Table 2).

A second cluster consisted of long-beaked common dolphins, Cape gannets and Cape fur seals, separated by
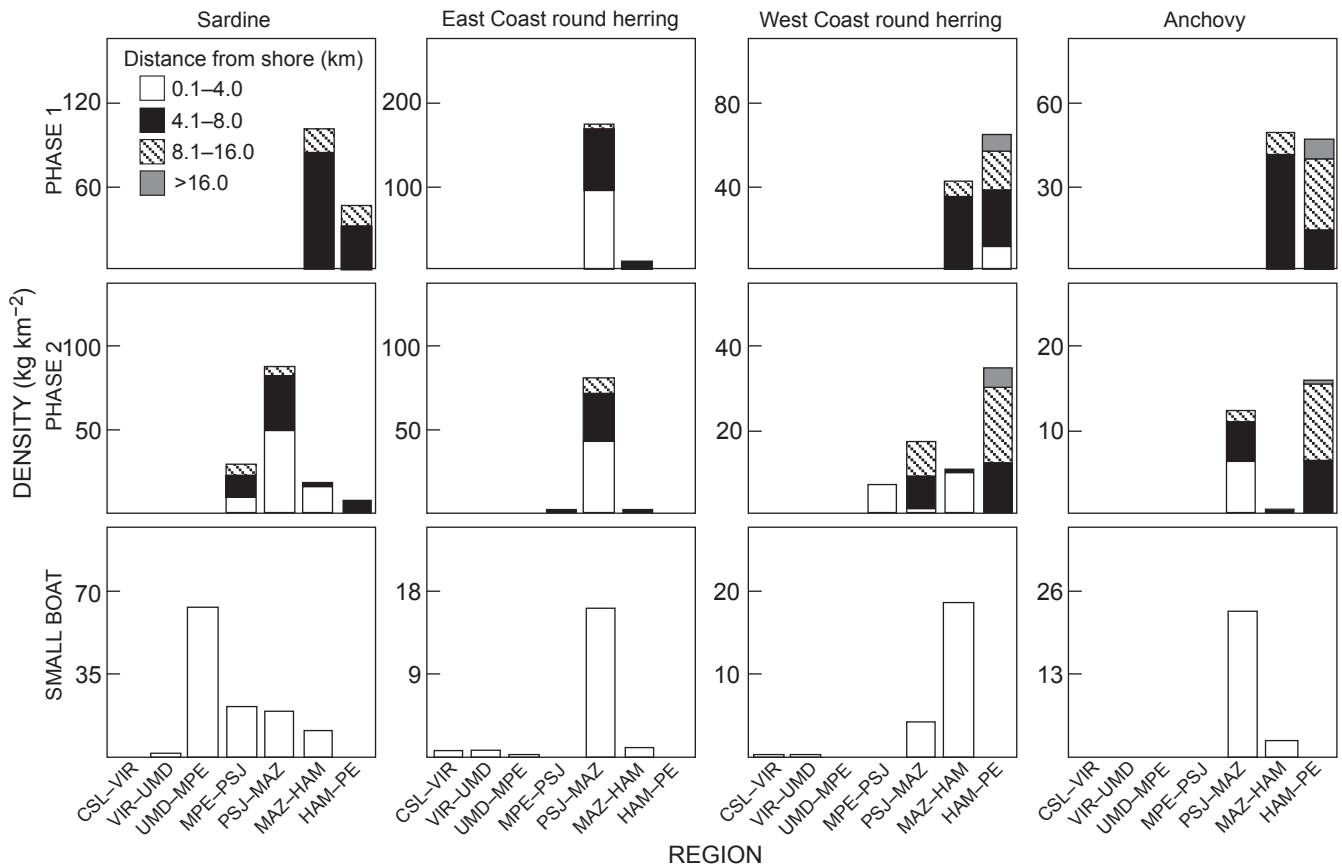
Figure 4: Mean clupeoid density per block and distance from shore class during survey Phases 1 and 2 of the 2005 sardine run survey, and from the small-boat survey during Phase 2
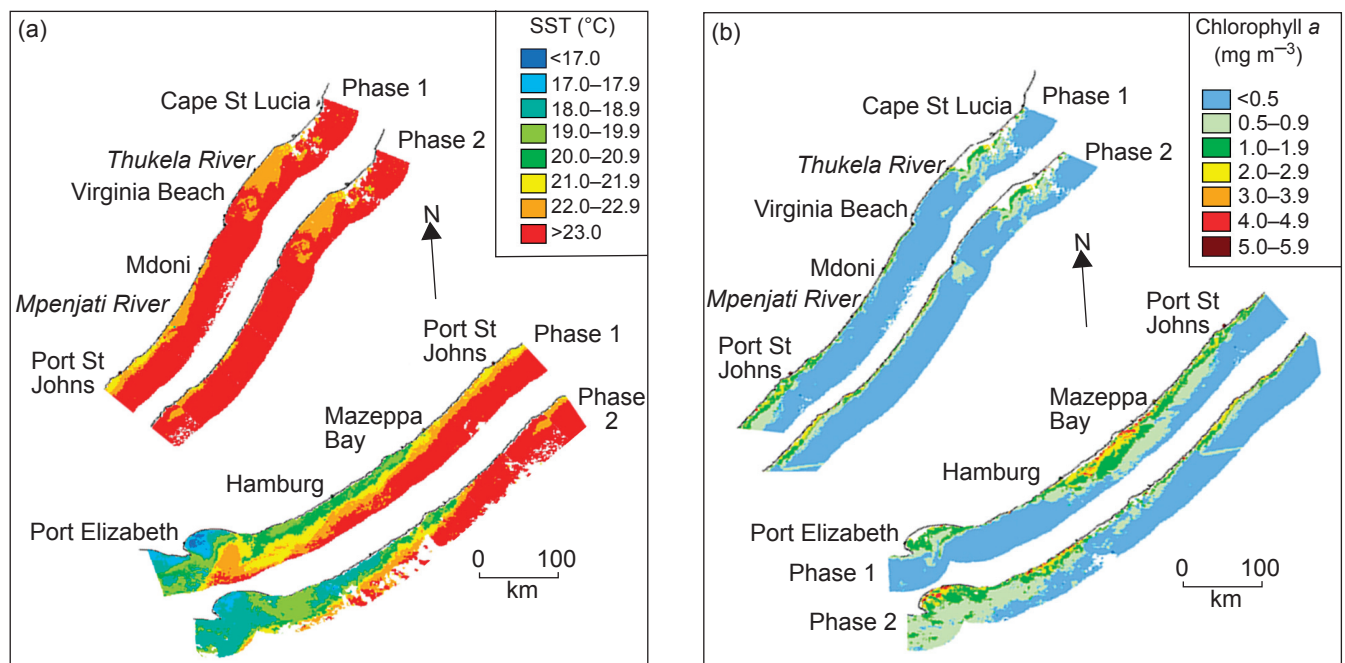
Figure 5: (a) Composite images of remotely sensed SSTs and (b) Chl *a* concentrations derived from images obtained for each stretch of coastline surveyed on the survey day for Phases 1 and 2 of the 2005 sardine run survey over the period 18 June–1 July 2005. White patches within the images indicate no data because of cloud cover
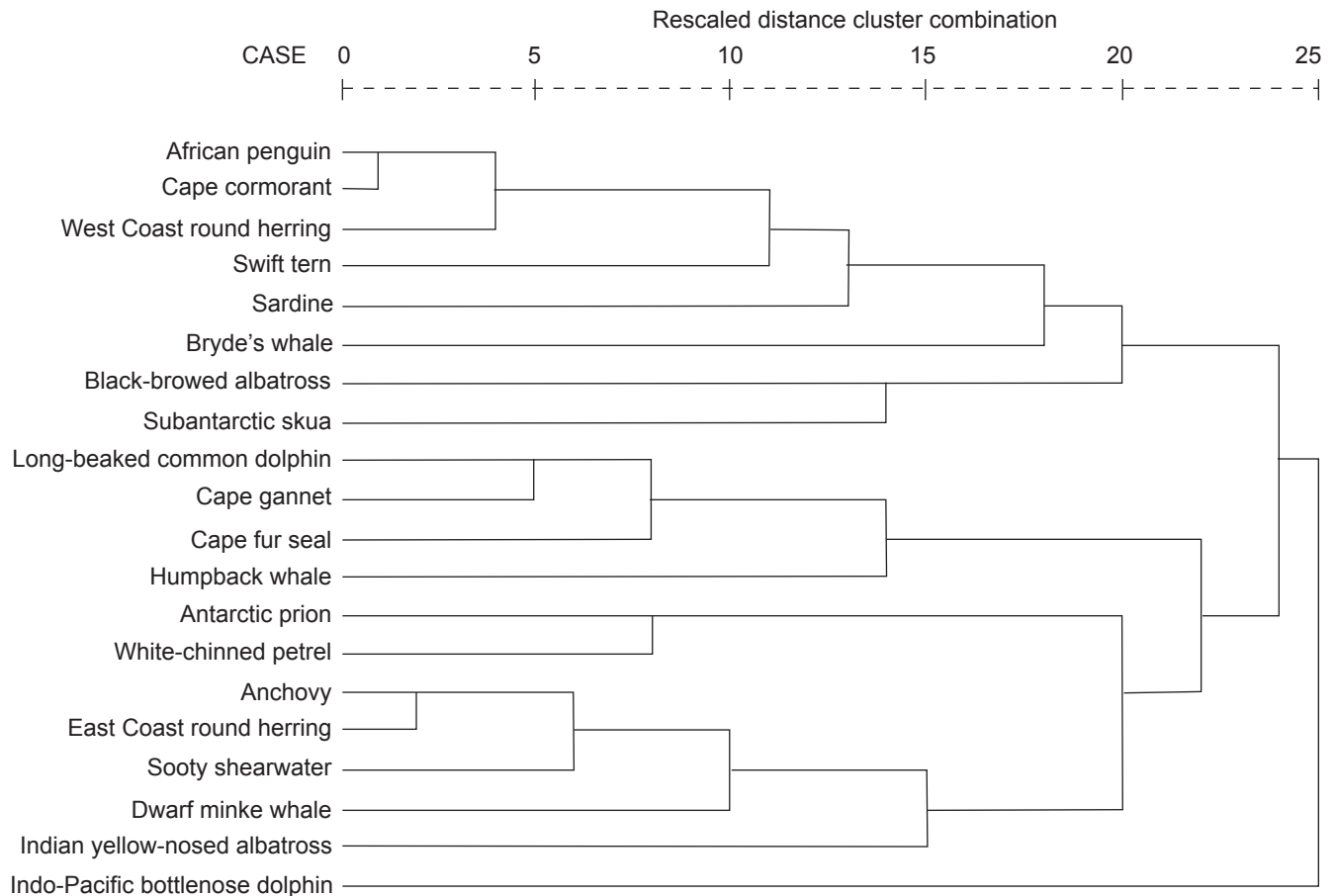
Figure 6: Hierarchical cluster analysis of sardine run-associated predator sighting rates and clupeoid densities per survey block/distance from shore class combination

less than 10 cases (Figure 6), and humpback whales were the most distant member, separated by 14 cases. Of these species, only the Cape fur seal encounter rate was not inversely associated with distance from shore. From the small-boat measurements, common dolphin and Cape gannet encounter rates were significantly associated with sardine and East Coast round herring densities ($\rho \geq 0.880$, $p \leq 0.021$, $n = 6$).

A third tight cluster included anchovy, East Coast round herring and sooty shearwaters, separated by a maximum distance of six cases (Figure 6), with species' encounter rates inversely associated with latitude (Table 2). Dwarf minke whales and Indian yellow-nosed albatrosses completed this cluster. Indo-Pacific bottlenose dolphins were not part of any cluster, but their encounter rate was significantly associated with that of Cape gannets.

Discussion

The data used in this study are based upon a single survey consisting of two passes along the East Coast, of which one (Phase 1) missed out the majority of the coastline north of Port St Johns due to travel during the night. As such, any findings from this study can provide, at best, a 'snapshot'

view of the predators associated with the 2005 sardine run. Nonetheless, given the paucity of data on the offshore extent of the run, we believe that these data do enhance our understanding of this phenomenon.

Mammal distribution

Common dolphins are found inshore off the East Coast only during winter (Peddemors 1999). During this time, their diet is dominated by fish (88.8%), mainly clupeoids (Young and Cockcroft 1994) encountered during the 2005 sardine run survey. In our study, maximum common dolphin and Cape gannet encounter rates occurred within the same region as maximum sardine and East Coast round herring densities, i.e. within 4 km of the shore between Port St Johns and Mazeppa Bay during Phase 2. The decline in common dolphin encounter rates north of the Mpenjati River was also reported by O'Donoghue et al. (2010b), and was coincident with the decline in clupeoid abundance during the present survey.

Despite the similarity in their alongshore distributions, no clupeoids were associated with common dolphins and Cape gannets within the cluster analysis (Figure 6). This was because the common dolphin, and especially Cape gannet, distributions to the south of Port St Johns were skewed shorewards, whereas the clupeoids were recorded across the

continental shelf. When testing only the nearshore 4 km strip of the survey area using the small-boat data for fish, these predators' encounter rates were strongly associated with sardine and East Coast round herring densities. Hence the close association found between sardine, Cape gannet and common dolphin distributions was restricted to within 4 km of the shoreline. It may be that clupeoids distributed across the wider continental shelf to the south of Mazeppa Bay are more difficult for predators to detect. North of Mazeppa Bay, the fish become compressed into the narrow continental shelf, which must make evading predators more difficult, and could explain the peak in common dolphin and Cape gannet relative abundance in this region.

Indo-Pacific bottlenose dolphins are considered to be the most ubiquitous coastal dolphin species on the east coast of southern Africa (Peddemors 1993). However, there were only seven of these dolphins encountered during the survey. Their distribution is known to be highly skewed shoreward, with a preference for water depths <30 m (Ross et al. 1987). During our survey, bottlenose dolphins were never encountered in water depths >30 m, and their distribution was inversely associated with depth. The presence of resident pods of these dolphins along the East Coast during the survey was confirmed by independent aerial surveys (SHO'D pers. obs.) and observations made by field staff from the KZN Sharks Board. The inability of the RS *Africana* to survey in such shallow waters would have led to the paucity of bottlenose dolphin sightings reported here.

Although bottlenose dolphins do not feed extensively on sardine (Cockcroft and Ross 1990), they have been shown to be associated with the sardine run (O'Donoghue 2009, O'Donoghue et al. 2010b). They are thought to feed upon fish species that follow the run northwards (van der Elst 1988, Fennessy et al. 2010), e.g. elf *Pomatomus saltatrix* and pinky *Pomadasys olivaceus* (Cockcroft and Ross 1990). Peak bottlenose dolphin encounter rates corresponded with peak nearshore sardine density, as measured by the small boat. Within this nearshore region, concentrated sardine run activity has been observed by KZN Sharks Board field staff. It is likely that the presence of sardine may have attracted piscivorous predators upon which bottlenose dolphin feed. The association between bottlenose dolphins and sardine was highly localised, and the former were not observed across the continental shelf, hence the lack of association between these species in the cluster analysis (Figure 6).

During their northward reproductive migration, humpback whales are not considered to use the sardine run as a feeding opportunity as there have been no historical, confirmed reports of active feeding during this migration (Best 2007). The lack of association between humpback whale and clupeoid distributions corroborates this apparent lack of feeding during their northward migration.

The predominantly single individual sightings of dwarf minke whales, and their distribution over the continental shelf, concur with previous reports on their behaviour and distribution (Best 1985). In all areas of their range, they have been seen primarily in coastal waters during winter, between June and August (Best 1982, 1985, Zerbini et al. 1997). Minke whale encounter rates were not associated with encounter rates of any other species or environmental condition.

The inverse association found between Bryde's whale encounter rate and latitude confirms its distribution as being primarily south and west of East London (Best 2001). All three sightings were within the offshore range of the so-called 'inshore population' (Best 1977). The association between Bryde's whale, African penguin and Cape cormorant distributions highlights the inter-relationship between these predators. Their normal range is across the Agulhas Bank, but during winter they move eastwards and northwards following prey.

Although fur seals on the south-east coast of South Africa appear to feed predominantly upon benthic and demersal species (Castley et al. 1991), their diet on the South Coast is mainly anchovy and sardine (David 1987). During Phase 2, peak Cape fur seal encounter rates were significantly associated with high densities of anchovy and both species of round herring within 4 km of the coast north of Hamburg. Their relatively high abundance in this region of peak sardine run activity caused them to be included in the same cluster as common dolphins and Cape gannets, despite an inverse association with latitude and mean SST. This emphasises the importance of the run to these animals.

To the south of Hamburg, fur seals were distributed farther from shore and were usually encountered as single individuals. Such distribution is more usual for fur seals from the Bird Island group in Algoa Bay foraging on the Agulhas Bank. The fur seals encountered during the sardine run were approximately 350 km from these islands. This is similar to the average distance travelled by fur seals on the West Coast: 323 km and 519 km for females and males respectively (Oosthuizen 1991).

Avian distribution
Cape gannets are non-breeding winter visitors to KZN waters (Broekhuysen et al. 1961). Gannets of all age groups are known to follow dense fish shoals, including sardine, some as far as the coast of Mozambique (Berruti 1995, Klages et al. 1994). Sardine are important to the diet of these seabirds (Berruti and Colclough 1987, Klages et al. 1992, Crawford et al. 2007) and their close association with the sardine run has been documented by O'Donoghue et al. (2010a, 2010b). The Cape gannet, common dolphin, sardine and East Coast round herring distributions in this study confirm the Cape gannet's close association with the run, and together with their large feeding aggregations, confirms this species' value as the principal predator used to detect sardine activity from shore.

It is noteworthy that juvenile Cape gannets were not commonly encountered, suggesting that they had already dispersed elsewhere. Cape gannets 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 fish shoals by observing movements of other birds and are attracted by other gannets diving (Crawford 2005) and dolphins feeding (O'Donoghue 2009). During the survey, gannets were observed following dolphins, and plunge-dived over both feeding common and bottlenose dolphins.

Although often associated with feeding groups of Cape fur seals, common dolphins and Bryde's whales in the southern Benguela, where its main food is offal and discarded fish

from trawlers (Jackson 1988), there was no obvious correlation between white-chinned petrel distribution and that of the abovementioned marine mammals during the survey. White-chinned petrel encounter rates peaked along the same stretch of coastline as sardine and East Coast round herring, and were significantly associated with east coast round herring density. This petrel was often observed in areas where the water temperature was >20 °C. Of the four clupeoid species, the East Coast round herring, which occurs along the East Coast of southern Africa (Whitehead and Wongratana 1986), is most likely to be found in water warmer than 20 °C, thus its association with white-chinned petrel was understandable.

Swift tern encounter rates were highest south of Hamburg, were farther than 4 km from shore, and were inversely associated with mean SST. The major food of the swift tern is pelagic shoaling fish, principally sardine and anchovy (Crawford and Dyer 1995), and they were frequently sighted in association with these fish. Although included in a cluster with sardine and West Coast round herring, swift terns were encountered as far north as Cape St Lucia, and were therefore not significantly associated with these clupeoid species.

Although clupeoids have been reported to comprise some 20% by mass of the diet of the Indian yellow-nosed albatross in south-western Africa (Crawford et al. 1991), encounter rates of this species was not significantly associated with that of any marine mammal or clupeoids. These albatrosses were encountered regularly throughout the survey area, with a distribution most similar to white-chinned petrels and sooty shearwaters. Encounter rates for these three species were all significantly associated.

Sooty shearwater distribution was not associated with those of any marine mammals, although they have been found to be associated with feeding groups of Cape fur seals, common dolphins and Bryde's whales in the southern Benguela (Jackson 1988, Ryan 2005). In this latter region, the main prey of sooty shearwater are small fish, including anchovy, which comprised 33% by mass (Jackson 1988, Ryan 2005). During this survey, sooty shearwater distribution was significantly associated with anchovy density and they appeared within the same cluster.

Subantarctic skuas are mainly winter visitors to southern Africa. Little is known about their diet in southern Africa (Crawford et al. 1991). They kleptoparasitise other bird species including Cape gannets, white-chinned petrels, gulls and terns (Wanless and Ryan 2005), but there was no evidence for any association with other seabird species observed during the survey.

The main prey items of the African penguin are sardine and anchovy (Crawford 2004), with penguins generally rare east of Algoa Bay (Shelton et al. 1984). During the survey, penguins did not seem to follow their prey north of Hamburg. This could explain the association between penguin encounter rate and West Coast round herring density, which also peaked south of Hamburg.

In the south-western Cape, anchovy and sardine accounted for 87% of the diet of Cape cormorants between 1984 and 1992 (Crawford and Dyer 1995). Cape cormorants are regular visitors, in varying numbers, to KZN waters, mainly

between June and November, when they are associated with the sardine run (Crawford 1997, Cyrus and Robson 1980, Taylor et al. 1999). During our survey, only two birds were recorded east of Algoa Bay. Cape cormorants form large flocks when feeding (Davies 1956) and would have been obvious had they been present. It is not clear why they were not found east of Hamburg. The close association between Cape cormorants, African penguins, swift terns, Antarctic prions, sardine, West Coast round herring and anchovy is likely on account of the inverse association for these species with mean SST and latitude.

Clupeoid distribution

One of the aims of this study was to determine the alongshore and offshore extent of the sardine run. The strong, inverse relationship between clupeoid density, SST and latitude, and the peak in sardine and East Coast round herring densities within 4 km of the shore at the northern limit of the band of cool water, are suggestive of temperature control imposed by the warm Agulhas Current. Nearshore sea temperatures between Algoa and Mazeppa bays are lowered by a persistent upwelling cell in that region (Lutjeharms et al. 2000). The northward extent of this upwelling cell varies, and is thought to regulate the amount of sardine that move up the East Coast (O'Donoghue 2009).

The lack of clupeoids beyond a depth of 30 m to the north of the Mpenjati River, and the high sardine abundance detected by the small boat between the Mpenjati River and Mdoni, indicate that sardine distribution was skewed shorewards along the KZN coastline. This likely constitutes the nearshore movement of sardine typical of the sardine run along the KZN coastline. The nearshore movement was corroborated by KZN Sharks Board field-staff observations that there was sardine run activity in KZN coastal waters during the 2005 sardine run survey, by landings of sardine made by the KZN beach-seine fishery in June and July of 2005 (see van der Lingen et al. 2010), and by the low predator abundance recorded across the KZN continental shelf during the survey. These findings support those of O'Donoghue et al. (2010b), who suggested that sardine 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 constrained.

Comparison of distributions

The first major cluster of the hierarchical cluster analysis was dominated by species (African penguins, Cape cormorants, West Coast round herring, swift tern, sardine and Bryde's whales) with distributions inversely associated with latitude and SST. The second cluster was comprised of species (long-beaked common dolphin, Cape gannets, Cape fur seals and humpback whales) with distributions mostly skewed shorewards. Thus, the distributions clustered according to their positions in the alongshore and across-shore grid of the survey region. Species with distributions not clearly defined by latitude or distance from shore tended to be attached to clusters but separated by a large number of cases. Hence this analysis was successful at grouping the principal sardine run predators into their own cluster.

Conclusion

The study provided the first comprehensive description of clupeoid, mammal and avian distributions during a sardine run along the East Coast. Although a more detailed analysis of the variables underpinning this distribution was not possible, the data provided a basic separation of these species by their spatial occurrence. The survey described the limited offshore extent of the sardine run along the KZN coastline and the lack of sardine across the continental shelf north of Durban, and confirmed the movement of sardine towards shore south of Durban. Thus, future studies investigating sardine biomass along the KZN coastline should include sampling of the nearshore region, especially within 1 km of the shore.

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