THE DIET AND FORAGING ECOLOGY OF CHICK-REARING GANNETS ON THE NAMIBIAN ISLANDS IN RELATION TO ENVIRONMENTAL FEATURES: A STUDY USING TELEMETRY

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Running heads: Cape gannet diet and GPS tracking

ABSTRACT

GPS telemetry in conjunction with a recent diet time series and historical dietary information was used in this study to obtain novel insight into the dietary trends and feeding ecology of Cape gannets *Morus capensis* on the Namibian islands, particularly Ichaboe and Mercury. The gannet diet has changed substantially since the 1950s, reflecting spatio-temporal changes in the availability of commercially important pelagic prey species. The more recent diet time series for Ichaboe Island (Nov 1995 to Feb 2004) showed that trawler scavenged hakes *Merluccius* spp and naturally foraged saury *Scomberesox saurus* dominated the diet by both contribution to mass (35 and 34 %, respectively) and frequency of occurrence (34 and 25 %, respectively). In a significant contrast, juvenile horse mackerel *Trachurus trachurus capensis* (40 % mass, 26 % frequency) and juvenile snoek *Thyrsites atun* (20 % mass, 20 % frequency) were the two main prey species at Mercury Island during Oct 1996 to Feb 2004. Multivariate analysis of data showed significant time and site effects in diet composition between Ichaboe and Mercury for the period Nov 1996 to Mar 1999. Twenty-five and 15 GPS field deployments were made on birds at Ichaboe and Mercury, respectively, during the 2003/4 breeding season. Birds from both locations showed significant differences in their foraging patterns. Birds from Ichaboe had shorter foraging trips (24.3 hrs vs 29.4 hrs), traveled shorter distances away from their island (130 km vs 197 km) and had shorter foraging path lengths (422 km vs 673 km). Birds from Ichaboe foraged in two dominant directions: west, to obtain mainly scavenged fish offal, and north to obtain forage fish. Mercury birds foraged only north, overlapping their foraging zone with birds from Ichaboe in a northerly direction, between 25.8° S and 24.4° S. Birds at all colonies – especially in the south - appear to be constrained by lower quality food and generally poor feeding conditions which seem to be a limiting factor.

Key words: *Morus capensis*, GPS telemetry, diet, foraging ecology, Namibian islands

INTRODUCTION

The Cape gannet *Morus capensis* is endemic to the southern African coast where it currently breeds on six islands, three (Possession, Mercury, Ichaboe) of which are off the Namibian coast (Crawford *et al.* 1983). In terms of The World Conservation Union (IUCN) criteria the species is classified as Vulnerable because of a more than 20% reduction in total population over its range in three generations (BirdLife International 2000). The decline in total gannet population was attributed mainly to a reduction in prey availability after the collapse of the fishery for southern African sardine *Sardinops sagax* (known as pilchard *Sardinops ocellatus* in Namibia) in the late 1960s (Crawford *et al.* 1983, Bianchi *et al.* 1999). The gannet colonies in Namibia especially at Ichaboe Island experienced more dramatic declines, with an estimated 80% reduction in the number of active nests between the 1950s and 1995 (Du Toit *et al.* 2002). Despite a recovery in the South African gannet colonies that were able to switch from sardine to feeding on the relatively abundant anchovy *Engraulis capensis* resource in the 1970s, prey availability for the Namibian gannets remained poor (Crawford *et al.* 1983). In general, foraging conditions for gannets in Namibia remained poor because of increased competition with commercial fisheries for scarce prey resources and marine pollution (Du Toit & Bartlett 2001).

Growing concern over the dramatic and continued decline of the endemic and economically important gannet populations at the three Namibian islands (Fig. 1) has highlighted the need for management and conservation interventions for this species. These interventions would need to be informed by more recent scientific assessments of their diet and foraging ecology in relation to environmental processes that may impact local gannet populations. Recent advances in satellite telemetry and the use of miniaturized GPS data loggers on seabirds (Hamer *et al.* 2000, Weimerskirch *et al.* 2002) has enabled measurements over time of parameters such as feeding location and feeding activity (Garthe *et al.* 1999, Grémillet *et al.* 2004).

The Cape Gannet is a monogamous, monomorphic colonial breeder (Nelson 1978) that normally rears only one chick to optimum fledging mass during the breeding season (Jarvis 1970), generally from September to April the following year. During nestling stage, chicks are attended to by at least one adult, with partners alternating between attending nest and foraging out at sea. But both adults commonly leave nest to forage once chicks are quite large (Adams *et al.* 1992). Gannets forage during the day (Cooper 1978) spending about 40% of their time flying and plunge-diving (Adams & Klages 1999). Foraging bouts are preceded by searches for fish fom air (Davies 1955) and prey is pursued by plunge-diving from heights of 5 – 20 m (Rand 1959), with this activity attracting nearby gannets. Adult mortality is highest during breeding season when - constrained by need to care for chicks and to relief partners at nest – breeding gannets are subjected to amongst other perils occasional extreme ambient temperatures, or predation by seals. Juvenile mortalities peak around post fledging stage (Crawford 2005).

Several studies employing telemetry technology and focusing specifically on gannet foraging ecology and feeding activity were undertaken in the southern Benguela region, in recent years. These studies included the radio-tracking of more than 200 breeding Cape gannets from Malgas (Adams & Navarro, 2005), satellite tracking of birds from Malgas and Bird Island (Lambert's Bay) and GPS tracking with time-depth recorders of 91 Cape gannets from both Malgas and Bird Island (Grémillet *et al.* (2004), citing Crawford *et al.* unpubl data). Cape gannets are fairly large seabirds (body mass 2.6 kg, Crawford 2005) suited to the deployment of small tracking devices to obtain information on their foraging behaviour within areas of the Benguela upwelling ecosystem. Grémillet *et al.* (2004) proposed a maximum theoretical foraging range of 350 km from colonies and observed relatively short foraging trips of 1 - 2 days for breeding Cape gannets.

In this study, GPS technology, together with a historical diet time series, was used to obtain new insight into the dietary trends and foraging ecology of the declining breeding populations of Cape gannet in Namibia in association with key oceanographic features.

MATERIAL AND METHODS

Study area

The wind-driven Benguela Current Upwelling System bordering the southwestern African coastline is a region of high biological productivity, which supports an abundance of fish and top predators such as seabirds and seals (Crawford *et al.* 1987, Shannon & Nelson 1996). The Luderitz Upwelling Cell, a perennial feature located around 27° – 28° S, is the largest and most intense of seven localized upwelling cells in the region (Shannon & Nelson 1996, Shillington 2003). It is thought to act as an environmental barrier, dividing the Benguela into a northern and southern component, with a biological discontinuum in-between (Hocutt & Verheye 2001, and references therein). It is also thought to play a significant role in regulating the fish biomass to the north (off central Namibia) through the supply of nutrients used in plankton production for the higher strata in the energy cycle (Molloy 2003).

This study of the diet and foraging ecology of breeding Cape gannets was conducted at Ichaboe Island (26°17′S, 14°56′E) and Mercury Island (24°43′S, 14°50′E), hosting the two largest of only three gannet breeding sites off Namibia. The physical and biological characteristics of the two islands are described in detail by Rand (1963). Ichaboe Island (6.5 ha) is a flat, low-lying island, 1.3 km off the coast and 40 km north of Luderitz. It continues to support the largest Namibian gannet population, although numbers have decreased dramatically from its pre-1960s position of hosting the world's largest gannet colony. During this study, some 17 000 pairs of gannets nested in sub-groups concentrated mainly near the north-eastern and north-western sides of the island. Mercury Island (3 ha) is a steep, rock island, rising ca. 38 m above sea level. It lies 800 m offshore, 70 km north of Ichaboe and supports the second largest Namibian gannet population (Rand 1963, Crawford 1999). During this study, some 2100 pairs of gannets nested in sub-groups on the south-eastern side of the island.

Investigation of breeding diet

Diet of breeding gannets has been sampled routinely at Ichaboe Island since November 1995 and at Mercury Island since October 1996. Adult gannets returning from foraging trips are caught immediately on arrival at the colony, using a gannet hook. The birds were induced to regurgitate their stomach contents into a bucket or sampling bag by carefully lifting and inverting the bird head down, gently squeezing its stomach. The regurgitations were immediately sorted by species and weighed to the nearest gram, using calibrated Salter 1 kg or 500 g spring balances. Although additional information such as the number of prey species per sample, and individual fish measurements (caudal lengths of whole fish) was taken on occasion at the islands, these data were not available for Mercury Island. Size of prey collected at Ichaboe was recorded from 2001. Prey was identified using FAO species identification guide (Bianchi *et al.* 1999), although hakes were combined because of difficulties in separating species in the diet (Berruti *et al.* 1993). No dietary information was available for the period January 2000 to December 2002 at Ichaboe Island and for the period April 2000 to December 2001 at Mercury Island. Species composition was determined in terms of species proportional contribution to total biomass expressed as percentage of total (% M) and percentage frequency of occurrence (% F = number of stomachs containing fish of a particular species, expressed as percentage of all stomachs during presented time period, following Batchelor & Ross (1984) and Klages *et al.* 1992. All samples collected were given equal weighting and combined to derive mean monthly and seasonal contributions of prey species in the diet. Diet samples taken each year from September to April of next year were combined in derivation of annual indices. This approach minimized "noise" as a result of differences in sampling effort in certain months, and is a viable alternative to the use of monthly averages to derive seasonal indices. In contrasting the seasonal and interannual dietary trends at Mercury and Ichaboe, only the relatively complete data series between October 1996 and March 1999 as well as that of the 2003-4 breeding season were considered for analysis. Multivariate analysis was conducted using PRIMER (Clarke & Gorley 2001) to test for differences in seasonal and interannual variability in gannet diet at the two islands. Specifically, Analysis of Similarity (ANOSIM) tests confirmed a posteriori by a cluster analysis were used to compare differences (similarities) in the assemblage structure of groups of monthly samples collected from Ichaboe and Mercury Islands.

GPS Deployment and Tracking.

Foraging activities of breeding gannets at Ichaboe and Mercury Islands were tracked using GPS electronic data loggers attached to individual breeders using techniques described in Grémillet *et al.* (2004). The deployment of GPS tracking devices seemingly does not cause adverse physical discomfort (Grémillet *et al.* 2004) nor does it impact significantly on the ability of tagged birds to forage as efficiently as non-tagged birds (Grémillet *et al.* 2004, Hamer *et al.* 2000). The GPS data loggers also have a high degree of precision irrespective of weather conditions (Weimerskirch *et al.* 2002). The miniaturized GPS logger units used in this study weighed 67 g in total and consisted of a rigid but lightweight fiberglass casing housing a precision GPS-recorder and a rechargeable $LiMnO_2$ battery.

The fieldwork was conducted within the Cape Gannet breeding season for the period between 9 and 19 December 2003 at Ichaboe Island, and between 29 December 2003 and 9 January 2004 at Mercury Island. At both islands, the study targeted breeders during early to mid chick rearing (i.e. with chicks aged four to eight weeks) for sampling and deployment of tracking devices. This strategy was aimed at ensuring a measure of predictability and consistency in patterns of parental behaviour, and to minimize risks in recovery of equipment and data. At each colony, adult breeders were caught during changeovers at the nest with the aid of a catching pole with a soft noose. Each captured bird was fitted with a GPS logger, attached to the central tail feathers using waterproof tape and epoxy resin (glue); then marked with animal marker paint to aid subsequent recapture. The study nest sites were monitored (every half hour throughout the daytime) for tagged birds from a vantage point nearby the colony. Tagged birds were recaptured upon their return (usually within 24 – 48 hrs later), when the GPS logger was switched off and removed along with any tape attached to feathers. Stomach contents were collected incidentally through voluntary regurgitations. After each retrieval, the GPS logger information was downloaded onto a laptop, the batteries recharged and software reset for next deployment. The study targeted at least 10 pairs (20 individuals) at each colony for GPS deployment. Our methodology and analysis of GPS data closely followed that of Grémillet *et al.* (2004). In the rare instance where more than one trip per bird was recorded, the detail of only one track was included in the analysis, to minimize pseudoreplication. The following parameters were estimated (after Grémillet *et al.* 2004):

i. Foraging trip duration

ii. Foraging path length (the total cumulative distance covered by a bird on a foraging trip)

iii. Maximum distance from the colony

iv. Time spent flying (assuming flying if speed > 10 km.h^{-1})

v. Path sinuosity (the ratio of the recorded flight speed from the GPS to the calculated speed between a set number of fixes, in this case every third positional fix). A Sinuosity index is useful when considering only positional fixes associated with feeding. The method of applying a threshold sinuosity value (i.e. all points with a sinuosity > 3.3) to discriminate between feeding and non-feeding activity, successfully exclude strong wind effects on the flight path and give a reliable representation of activity associated with prey patch exploitation only was followed by Grémillet *et al.* (2004).

Sea Surface Temperature (SST) and Chlorophyll-α (Chl-α) data for the Benguela region between 22° S and 26° S, with an approximate resolution of 1 km x 1 km originate from NOAA's Advanced Very High Resolution Radiometer (AVHRR) and OrbView-2 Sea-viewing Wide Field-of-view Sensor (SeaWiFS) respectively. The images and composites of

SST and Chl-α obtained were generated using algorithms for temperature and chlorophyll-α with the SeaWiFS Data Analysis System (Grémillet *et al.* 2004). The GPS tracks including bathymetry were overlaid onto SST and Chl-α composite satellite images, using a cylindrical equidistant projection with ca 1.1 km (lat) x 1 km (long) grid resolution.

RESULTS

Diet composition

The mean number of monthly regurgitations sampled between November 1995 and February 2004 at Ichaboe Island was 14 ± 9 (n=455, range 2 – 40). The mean number of monthly regurgitations sampled between October 1996 and February 2004 at Mercury Island was 16 ± 8 (n=556, range 4 – 32). The mean mass per regurgitation for Ichaboe was 181 g ± 51 g (range 88 g – 303 g), which was slightly higher than that of Mercury of 165 g ± 37 g (range 76 g – 231 g).

At least 19 teleost species, one cephalopod species, and fragments of unidentified crustaceans and molluscs were recorded in the diet (Table I). By mass, Cape hakes *Merluccius* spp and saury *Scomberesox saurus scombroides* were the most important prey species at Ichaboe Island, followed by juvenile snoek *Thyrsites atun*, horse mackerel *Trachurus trachurus capensis*, anchovy *Engraulis capensis* and roundherring *Etrumeus whiteheadi* (Table I). At Mercury Island, juvenile horse mackerel and snoek were the dominant prey species, followed by anchovy, sardine, saury and Cape hakes (Table I). Prey species of lesser importance such as cubiceps *Cubiceps capensis*, kingklip *Genypterus capensis*, jacopever *Helicoleneus dactylopterus* and tuna *Thunnus* spp were only recorded at Ichaboe Island, and silverside *Atherina breviceps*, mullet *Liza richardsonii* and the crustacean and mollusc fragments only occurred at Mercury Island (Table I). Fish species such as Cape hakes, kingklip, jacopever, and tuna scavenged from trawlers and longliners made an important contribution to the diet of gannets at Ichaboe and this contrasted with mainly forage fish dominating diet at Mercury Island. The available records and reports from resident island supervisors indicated that most of the scavenged diet consisted of hake heads and intestines (offal) obtained from commercial fishing vessels within the foraging ranges of gannets on especially Ichaboe Island.

The length frequency distribution of some of the important prey species from Cape Gannet regurgitations at Ichaboe (sampled intermittently between December 1998 and February 2004) was considered in order to obtain an estimate of the size classes of fish prey selected by gannets within the surrounding foraging areas (Fig. 2) and potentially available to birds from both islands in the regions of overlap of foraging zones. The size distribution for all selected prey species pooled was essentially unimodal with approximately 59% of measured fishes falling within 50 – 100 mm mode. This is because most measures were of anchovy and horse mackerel. There was considerable variation in the mean length of anchovy (n=264, mean 70.9 mm ± 25.8 SD), horse mackerel (n=126, mean 86.6 mm ± 32.1 SD) and saury (n=71, mean 191 mm ± 67.8 SD). Expectedly, the smallest fish measured was an anchovy (32 mm) and the largest a saury (400 mm). Larger-sized fish (above 300 mm length) with the exception of the observed saury was virtually absent from diet at Ichaboe during the above period.

The mean monthly contributions of prey species to the breeding diet of Cape Gannets confirm the overall predominance of Cape hakes and saury at Ichaboe Island and horse mackerel and snoek at Mercury Island (Tables II & III). The data set of mean monthly values, although limited in its wider application to intra-seasonal trends, was useful in highlighting major changes in the availability and mean contribution of prey species to diet around the peak of the breeding cycle.

Trends in the inter-annual percentages of prey species in diet also confirmed the overall predominance of Cape hakes and saury as dominant at Ichaboe Island and horse mackerel and snoek at Mercury Island (Tables IV & V). Pilchard and anchovy were consistently more important in the seasonal diet of Cape Gannets (by %M and %F) at Mercury Island than at Ichaboe.

The composition of diets differed significantly between Ichaboe Island (I) and Mercury Island (M) for the three consecutive breeding seasons between November 1996 and March

1999 (ANOSIM R > 0.3; p = 0.014 or 1.4%; groups I & M). There was also a significant time effect between sampling sites (ANOSIM 2 R = 0.3; p = 0.014) with some overlapping (i.e. partial separation) in monthly composition of diet. Observations on differences between sample groups were confirmed *a posteriori* by a cluster analysis (Fig. 3).

Foraging Ecology

A total of 25 GPS deployments was made on birds at Ichaboe Island and 15 on birds at Mercury Island. These deployments provided 25 complete foraging tracks for Ichaboe Island but only 12 complete tracks for Mercury Island. Birds from Mercury Island stayed out at sea significantly longer, traveled farther distances away from the colony and had longer foraging path lengths than those from Ichaboe Island (Table VI). The average traveling speed of birds from Ichaboe was slightly, but not significantly higher than those from Mercury Island. Not surprisingly, the number of foraging fixes associated with prey patch exploitation was higher on average for birds from Mercury than those from Ichaboe Island, but these differences were once more not significant.

Birds from Ichaboe Island traveled predominantly to feeding locations to the west (12 out of 25 times) and north (11 out of 25 times) of the island (Fig. 4). The western tracks cover a wide offshore area, while the northern tracks cover areas closer inshore to the north and south of Mercury Island. The exploited foraging area for birds from Ichaboe Island comprises an estimated total sea surface of approximately 41 000 km^2 with an available theoretical foraging area of approximately 384 600 km^2 (using 350 km radius, and excluding land areas). Seven incidental diet samples were obtained for tagged birds on recapture. Three samples contained mainly Cape hake offal, and were obtained from birds that foraged to the west of the island. The other four samples obtained from birds that foraged in the inshore regions to the north of Ichaboe (past Mercury Island) contained horse mackerel (n=2), a mix of snoek & squid (n=1) and saury (n=1). In contrast, all tracks for birds from Mercury Island travelled north of the island (Fig. 6), covering an approximate total foraging area used of 69 400 km^2, between Mercury Island and Walvis Bay. Four incidental diet samples contained saury and pilchard in approximately equal measures.

The region of overlap between Ichaboe Island and Mercury Island situated between mainly 25.6° S and 24.4° S latitude comprises an area of approximately 24 400 km^2. This region represents about 60% and 35% of total use area for birds from Ichaboe Island and Mercury Island, respectively. Within this area, birds from the two colonies showed considerable fine-scale overlap in foraging areas (see Figs 8 & 9). The areas associated with foraging for birds from Ichaboe Island (Fig. 8), were mostly between 14°E longitude and the coast (well within 13 °E and the coast) and appeared uniformly distributed. Feeding events seemed to increase in areas north of Ichaboe Island and in the inshore regions. For Mercury Island (Fig. 9) the distribution of feeding events is patchier, and the events seemed to extend further offshore with northward progression away from the island. Birds from both islands commonly foraged in the high chlorophyll α areas and in frontal regions in 13 - 17°C water (Figs 4 – 7). Due to the dynamics of upwelling (Molloy 2003), there is a perceived time lag between intense upwelling activity and plankton production. Nutrients flowing northward out of the Luderitz upwelling cell are retained in areas of higher stratification (commonly at or near frontal zones) where it is used in plankton production, which in turn boosts zooplankton growth, sustaining a higher fish biomass (Molloy 2003).

DISCUSSION

Trends in diet composition and impact of dietary change

Sardine is the preferred prey of Cape gannets because of their high energy density and size (Batchelor & Ross, 1984). Off South Africa, it was the dominant prey until the late 1960s (Rand 1959, Crawford *et al.* 1983), and has on occasion been replaced by other epi-pelagic shoaling fish such as anchovy and saury (Cooper 1984, Batchelor & Ross 1984). Previous studies of seabird diet off Namibia confirmed the predominance of sardine in Cape gannet diet in the late 1950s (Matthews 1961, Matthews & Berruti 1983). During the period 1957-58 sardines constituted 87% by mass of gannet diet off Walvis Bay (n=155, mean length 249 mm) (Matthews 1961) and about 93% by mass during 1958-59 (n =240, mean Lt 207 mm) (Matthews & Berruti 1983). Sardine dominance in diet was also reflected in the percentage frequency of occurrence (76%) and abundance (99%) during 1958-59. Other species, including horse mackerel, snoek, chub mackerel and mullet, each contributed ≤ 1% by mass to the overall diet (Matthews & Berruti 1983).

Anchovy became the dominant prey in the gannet diet off central and southern Namibia by the late 1970s and early 1980s (Crawford *et al.* 1985, Crawford *et al.* 1991). It constituted 52% (n=1083) and 77% (n=345) by mass of gannet diet off central Namibia (Mercury & Ichaboe) and Possession Island respectively, during period 1978-1982. Prey species of lesser importance in the diet of gannets from Ichaboe and Mercury Island (n=1083) during period 1978-82 included pelagic goby *Sufflogobius bibarbatus* (19% by mass), saury (12%), hakes (7%), snoek (4%), horse mackerel (3%), chub mackerel *Scomber japonicus* (1%) and cephalopods (1%) (Crawford *et al.*1991). Interestingly, no sardine was recorded in the diet during this time. The diet from Possession Island (n=345) for the same period contained lesser prey species such as saury (7% by mass), hakes (3%), sardine (1%), and cephalopods (1%) (Crawford *et al.*1991). Again, the sardine contribution to overall diet during 1978-82 was minimal. The increased dominance of anchovy in the gannet diet during 1978-82 seemed to have followed the reported collapse of the commercially exploited Namibian sardine stocks in the late 1960s (Crawford & Shelton 1978, 1981, Crawford *et al.* 1983).

Species composition in the gannet diet from the 1950s through 1980s contrasts sharply with that of the late 1990s through 2000s in this study. Sardine was dominant in the diet during the 1950s and 1960s, followed by anchovy during the late 1970s and early 1980s. According to Crawford (1998) anchovy was plentiful off Namibia until 1983, and with the exception of 1987 has been scarce since 1984. Previously lesser prey in the gannet diet such as demersal hakes, saury, juvenile horse mackerel and snoek now constitute a significant proportion of the diet observed since 1996. Since epi-pelagic shoaling fish are important to the diet of gannets, their presence in the diet is a measure of their relative availability in the feeding ranges of gannets on the islands. Berruti & Colclough 1987 also established that gannet diet is a reliable monitor of the trend in pilchard biomass at low pilchard biomass. Yet, saury and other species such as trawler-scavenged hakes are more important in the diet when pilchard and anchovy are less abundant (Batchelor & Ross 1984).

Another long-term study of the diet of the Cape gannet at Bird Island, Algoa Bay by Klages et al 1992, identified sardine, anchovy and saury as the main prey species. Notably, the relative abundance of the three main species was found to change intra-annually during the period April 1979 to March 1991, with sardine and anchovy more frequent in the diet during the breeding season and saury dominating diet in non-breeding season. This intra-annual trend could not be established in this study because diet sampling effort targeted breeding season only, yet results highlight contrast in composition and variability of breeding diet from the northern and southern Benguela regions.

Catches of the commercially exploited pelagic fish stocks (pilchard, anchovy, juvenile horse mackerel) have fluctuated considerably over the last four decades (Fig. 10), mainly as a result of (over-) fishing and environmental anomalies such as the Benguela Ninos in 1972, 1984 and 1995 (Bianchi *et al.* 1999). In recent years, the sardine stocks in particular (Fig. 11) have fluctuated considerably following years of collapses (1996, 2001) and recoveries (early 1990s) and despite drastic management interventions have not shown any sustained recovery (Bianchi *et al.* 1999, Hampton 2003). The Cape gannet diet off southern Namibia (Ichaboe & Mercury) mirrors the availability of prey species and indicates a shift from a high energy density diet to a lower quality (less energy–rich) diet with increased contributions from scavenged demersal species such as Cape hakes. A similar shift in the longer-term diet of Cape gannets from surface-shoaling prey species such as pilchard and anchovy to other species such as saury and trawler scavenged demersal hake was previously described by Cooper (1984) for gannet populations on the South African west coast. Studies of Cape gannet diet on the west coast have also shown marked differences in the spatial and temporal variation of diet between bird populations on islands (Batchelor & Ross 1984, Berruti 1991). This study confirms these observations and further highlights the similarities and sharp contrasts in the diet composition of gannets on Ichaboe and Mercury Islands, separated by a distance of approximately 70 km and sharing at least some foraging areas. Although many of the (more abundant) prey species such as horse mackerel, snoek, saury, and anchovy were common to the diet at both islands, their order of importance (in terms of percentage contribution by mass and frequency of occurrence) were different between the two islands.

The observed longer term dietary changes have important implications for gannet population dynamics. Batchelor & Ross (1984) showed that gannet chicks fed on a diet of pilchard and / or anchovy fledged more successfully than those fed on a diet of hakes or saury. Gannet chicks have a lesser preference for saury, even though it would provide a better energy return for effort during the breeding season, because of its larger size (Batchelor & Ross 1984). Breeding gannets thus have a preference for smaller fish with a higher energy content to not only meet their own energetic requirements but also provision their young (Berruti 1991). Batchelor & Ross (1984) also linked dramatic increases in the gannet population at Bird Island to the availability of high-energy prey (such as pilchard and anchovy) and an associated decrease in pre-breeding mortality. The general low availability of suitable high-energy prey has been blamed for the poor recruitment of new breeders to the gannet colonies off Namibia (Crawford 1999). It is generally accepted that apart from the decline in prey resource, the population numbers of gannets are affected by amongst others human disturbance, predation by Cape fur seal *Arctocephalus pusillus pusillus*, predation of eggs and chicks by kelp gull *Larus dominicanus*, marine pollution and accidental by-catch in longline fishing (Du Toit & Bartlett 2001). It can now be inferred with some degree of confidence that the decline in the Cape gannet populations off the Namibian coast may be exacerbated by the continued dominance of low quality food items in the breeding diet and overall poor food availability

The high frequency of occurrence and percentage contribution by mass of certain fish species (particularly Cape hakes) scavenged from trawlers and longline vessels have important implications for management of seabird-fisheries interactions, and the longer-term survival of the Cape gannet species. Gannet mortalities as a result of the incidental catch (by-catch) in longline fisheries have been noted (Du Toit & Bartlett 2001), not least because of fishing hooks found in nests of breeders at the colonies at Ichaboe (P. Bartlett pers. comm.). Reports by Namibian fisheries observers as well as local fishermen have also confirmed this alarming trend (MFMR internal report), but the magnitude and scale of this phenomenon and its impact on adult survival and hence gannet population dynamics has yet to be properly quantified. The increased reliance of the Cape Gannet on scavenging from vessels at sea also increases their exposure to a serious and more than often fatal threat of waterlogging from fish oil (Du Toit & Bartlett 2001). Du Toit and Bartlett (2001) observed a total of 719 soaked gannets, mainly adults, over a four-year period between 1996 and 2001 at Ichaboe Island, and considered mortalities as a result of waterlogging an important factor in the decline of local gannet populations.

Impact of Environmental variability on abundance & distribution of prey stocks

Crawford & Shelton (1981) showed that the decrease in the breeding populations of Cape gannet at the three Namibian colonies between 1956 and 1978 coincided with a decrease in the sardine biomass off southern Namibia. Apart from over-fishing and direct competition with commercial fisheries, seabirds are also affected by regime shifts and environmental perturbations on varying time scales with negative impacts on the entire marine food web and ecosystem (Crawford *et al.* 1990, Roux 1998, Hampton 2003). A regime shift took place, after the collapse of the sardine fishery in the 1970s (Crawford 1987), when anchovy and pelagic goby replaced sardine as the dominant pelagic resource off Namibia. This was accompanied by a northward shift (contraction) of the core distribution of sardine, north of the three Namibian gannetries at Mercury, Ichaboe and Possession (Crawford 1999). Boyer & Hampton (2001) also noted a northward shift in distribution of the declining Namibian sardine stock and diminished spawning and migration of mature fish to the south. Similar changes in life history of the declining anchovy stock were thought to occur as well (Boyer & Hampton 2001). Hampton *et al.* (2003) made similar observations comparing patterns of sardine distribution from biomass surveys to historical distribution (Fig. 12). The shift in distribution of sardine (and anchovy) has led to an obvious further reduction in prey available to local seabird populations (Crawford 1999). Regime shifts such as the one described earlier have led to an increase in other species such as pelagic goby, horse mackerel and also jellyfish through effects of environmental change and indirect trophic effects (Roux 2003).

Environmental anomalies in the northern Benguela region have had dramatic impacts on the distribution and abundance of prey stocks over the last ten years or so, putting additional pressure on fish stocks already constrained by over-fishing. Benguela Niños (in 1972, 1984, 1995) and intrusions of low oxygen water from Angola (in 1993 and 1994) caused significant natural mortality and disruption in the ecosystem. The impacts of these perturbations on the diet and foraging behaviour of seabirds especially Cape Gannets off Namibia have not been properly investigated, but a study on another top predator in the region, the Cape fur seal, has shown breeding failure, increased mortality and drastic deterioration in body condition related to the 1995 Benguela Niño on its main prey (Roux 1998). Seabirds including Cape gannets are similarly vulnerable to anomalous oceanographic conditions that will affect the availability and distribution of their prey during the breeding season - when they are constrained in time and space by the need to relieve partners at the nest and to feed chicks regularly (Hull *et al.* 1997). In a study of the impact of an anomalous warm water event on breeding of birds off South Africa, Duffy *et al.* (1984) noted shifts in diet, local breeding failures and increase in mortality of post-fledging young gannets. It is likely that similar localized impacts were experienced by seabirds breeding off the Namibian coast, possibly contributing to delayed breeding and/ or post-fledging mortalities for gannets.

Ecological considerations for observed foraging patterns and strategies

In a study of foraging activity of gannets at Bird Island (Algoa Bay) using activity meters, it was observed that gannets had a mean duration of foraging trips of 15.8 hrs and those birds that returned with sardine (high energy food source) had shorter trips, spent less time flying and had a greater energy intake (Adams & Klages 1999). In another study of foraging activity of gannets at Malgas and Bird Island (Lambert's Bay) using GPS loggers and time-depth recorders, Grémillet *et al.* (2004) showed birds recorded foraging trips of between 1.5 hrs and 2 days, travelled 13 – 242 km away from colony, covering a total of 73 – 956 km, initiated dives of between 9 and 134 per foraging trip, and exploited a limited number of foraging patches. A comparison with foraging characteristics of gannets from the two Namibian islands (foraging trip duration 3.5 hrs – 62.9 hrs, foraging range 25 – 325 km from colony, foraging path length of 130 – 1140 km and number of dives ranging 3 – 375) suggest that on average Namibian gannets, operating in a more depressed environment with regard to food availability, have a higher foraging investment searching for food than birds from colonies in southern Benguela.

The significant differences in foraging patterns between gannets breeding on Mercury and Ichaboe appear to result from different responses to the variability in the abundance and distribution of prey stocks in general and in particular during the breeding season. Birds from Ichaboe seem to use two complementary foraging strategies: making short trips to the shelf edge to scavenge at commercial trawlers and longliners, or north to obtain high-energy forage fish such as pilchard and anchovy, saury and juvenile horse mackerel closer inshore. By comparison, birds from Mercury mainly use the latter strategy. The total foraging area of birds from Ichaboe which has the larger colony (by six-fold) overlapped with that of Mercury by approximately 22%. This contrasts with the very limited overlap between neighbouring South African gannet colonies reported by Gremillet *et al.* (2004). Their study established widely segregated foraging areas and feeding zones between sites, with very limited overlap of 13% and 14%, respectively. This foraging segregation was linked to the distribution of prey resources on the shelf off southern Africa, cultural foraging effects and energy investment of foraging in a variable wind-regime (Grémillet *et al.* 2004).

The areas off central Namibia (south of Walvis Bay) are the traditional spawning and nursery grounds for small pelagic fish such as sardine (in summer within 60 km of the coast, nursing in cool upwelling areas inshore) and anchovy, which has a similar distribution and movement to pilchard and spawns north of Walvis Bay (Hampton 2003). Horse mackerel is spawned off northern Namibia in summer, with the young found further south in areas closer inshore (Hampton 2003). The inshore areas south of Walvis Bay would thus be of particular attraction for Cape Gannets as they sustain a higher biomass of pelagic fish stocks such as sardine (their preferred prey) and anchovy (Hampton 2003).

The availability of higher quality food for birds in the case of Mercury is offset by the higher energy investment made (longer foraging trips) to obtain this food. There is also an apparent potential for increased intra-specific competition for food between the two neighbouring breeding colonies as a result of the existing overlapping foraging zones. This would place additional constraints on breeding gannet populations already burdened by generally poor feeding conditions. The significant differences in foraging between gannets from Mercury and Ichaboe put neither colony at a particular advantage adjudged by the overall decline of both colonies. However, the gannet populations at Mercury Island seem to have stabilized in recent years (Cordes 1998, Maartens 2003) and this is probably attributable to the closer proximity of the island to preferred prey resources and higher contribution to diet of sardine and anchovy. Possession Island (27°10′S, 15°12′E), being the furthest removed from the sardine and anchovy spawning and nursery grounds off central Namibia and located well beyond the southernmost limit of its historical distribution (Fig. 12), appears to be the hardest hit by poor food availability. It is the island with the biggest decline in its gannet breeding population of between 94% and 96% since the 1950s (Maartens 2003). The number of breeding pairs at Possession in 1950s was *ca* 13 400 compared to *ca* 800 in 1995 (Cordes 1998) and 600 - 800 in 2003. Overall, conditions of food availability remain poor for gannets off the Namibian coast and are probably the single biggest limiting factor for gannets during the breeding season.

This study highlights the opportunities for the investigation of top predator interactions with their environment through the use of GPS technology in conjunction with more traditional approaches such as dietary studies. It is particularly useful in providing baseline information for a more detailed and comprehensive study of the mechanisms for the decline of the Namibian gannet colonies focusing on diet and energetics, population dynamics and important environmental influences.

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LITERATURE CITED

ADAMS, N.J. and N.T.W. KLAGES 1999 – Foraging effort and prey choice in Cape gannets. S. Afr. J. mar. Sci. 21: 157 – 163.

ADAMS, N.J. and R.A NAVARRO 2005 – Foraging of a coastal seabird: flight patterns and movements of breeding Cape gannets *Morus capensis*. Afr. J. Mar. Sci. 27: 239 – 248.

ADAMS, N.J., SEDDON, P.J. and Y.M. VAN HEEZIK 1992 – Monitoring of seabirds in the Benguela upwelling system: can seabirds be used as indicators and predictors of change in the marine environment? S. Afr. J. mar. Sci. 12: 959-974.

BATCHELOR, A. L. and G. J. B ROSS 1984 – The diet and implications of dietary change of Cape Gannets on Bird Island, Algoa Bay. Ostrich 55: 45 - 63.

BERRUTI, A. 1991 – Comparison of the diet of breeding and nonbreeding Cape Gannets *Morus capensis*. Ostrich 62: 8 - 12.

BERRUTI, A and J. COLCLOUGH 1987 – Comparison of the abundance of pilchard in Cape gannet diet and commercial catches off the Western Cape, South Africa. S. Afr. J. mar. Sci. 5: 863 – 869.

BERRUTI, A., UNDERHILL, L. G., SHELTON, P. A., MOLONEY, C. L. and R. J. M. CRAWFORD 1993 – Seasonal and interannual variation in the diet of two colonies of the Cape Gannet Morus capensis between 1977-78 and 1989. Colonial Waterbirds 16: 158 – 175.

BIANCHI, G., CARPENTER, K.E., ROUX, J.-P. MOLLOY, F. J., BOYER, D., and H. J. BOYER 1999 – FAO species identification guide for fishery purposes. Field guide to the living marine resources of Namibia. Rome, FAO. 265 pp., 11 colour plates.

BIRDLIFE INTERNATIONAL 2000 – Threatened birds of the world. Barcelona and Cambridge, U.K.; Lynx Edicions and Birdlife International: 852 pp.

BOYER, D. C. and I. HAMPTON 2001 – An overview of the living marine resources of Namibia. S. Afr. J. mar. Sci. 23: 5 - 35.

CLARKE, K. R. and R. N. GORLEY 2001 – PRIMER v5: User manual/ tutorial. Plymouth, UK; Primer - e: 91 pp.

COOPER, J. 1978 – Energetic requirements for growth and maintenance of the Cape Gannet (Aves; Sulidae). Zool. Afr. 13: 305 – 317.

COOPER, J. 1984 – Changes in resource division among four breeding seabirds in the Benguela upwelling system, 1953 -1978. In Proc. 5th Pan-Afr Ornithol Congr. Ledger, J.A. (Ed.). Johannesburg; Southern African Ornithological Society: 217 - 230.

CORDES, I. 1998 – Population trends of seabird on the Namibian offshore islands. In Namibia Brief 20: Focus on Fisheries and Research. Blatt, C. (Ed.). Windhoek; Namibia Foundation: 143 - 145.

CRAWFORD, R. J. M. 1987 – Food and population variability in five regions supporting large stocks of Anchovy, Sardine and Horse Mackerel. S. Afr. J. mar. Sci. 5: 735 - 757.

CRAWFORD, R. J. M. 1988 – Responses of African Penguins to regime changes of sardine and anchovy in the Benguela system. S. Afr. J. mar. Sci. 19: 355 - 364.

CRAWFORD, R. J. M. 1999 – Seabird responses to long-term changes of prey resources off southern Africa. In Proc. 22nd Int. Ornithol. Congr., Durban. Adams N. J. and R. H. Slowtow (Eds.). Johannesburg; Bird life South Africa: 688 - 705.

CRAWFORD, R.J.M. 2005 – Cape Gannet. In Hockey, PAR, Dean, WRJ and PG Ryan (eds). Roberts Birds of Southern Africa, VII ed. John Volker Bird Book Fund, Cape Town: 565 – 567.

CRAWFORD, R. J. M. and P. A. SHELTON 1978 – Pelagic fish and seabird interrelationships off the coasts of South West and South Africa. Biol. Conserv. 14: 85 - 109.

CRAWFORD, R. J. M. and P. A. SHELTON 1981 – Population trends for some southern African seabirds related to fish availability. In Proc. Symp. Birds of the Sea & Shore. Cooper, J. E. (Ed.). Cape Town; African Seabird Group: 15 - 41.

CRAWFORD, R. J. M., SHELTON, P. A., COOPER, J. and R. K. BROOKE 1983 – Distribution, population size and conservation of the Cape Gannet *Morus capensis.* S. Afr. J. mar. Sci. 1: 153 - 174.

CRAWFORD, R. J. M., CRUIKSHANK, R. A., SHELTON, P. A. and I. KRUGER 1985 – Partitioning of a goby resource amongst four avian predators and evidence for altered trophic flow in the pelagic community of an intense, perennial upwelling system. S. Afr. J. mar. Sci. 3: 215 - 228.

CRAWFORD, R. J. M., SHANNON, L. V. and D. E. POLLOCK 1987 – The Benguela Ecosystem Part IV: The major fish and invertebrate resources. Oceanogr. Mar. Biol. Ann. Rev. 25: 353 - 505.

CRAWFORD, R. J. M., SIEGFRIED, W. R., SHANNON, L. V., VILLACASTIN-HERRERO and L. G. UNDERHILL 1990 – Environmental influences on marine biota off Southern Africa. S. Afr. J. Sci. 86: 330 - 339.

CRAWFORD, R. J. M., RYAN, P.G., and A. J. WILLIAMS 1991 – Seabird consumption and production in the Benguela and western Agulhas ecosystems. S. Afr. J. mar. Sci. 11: 357 - 375.

DAVIES, D.H. 1995 – The South African Pilchard (*Sardinops ocellata*) Bird predators, 1953 – 1954. Investl. Rep. Sea Fish. Res. Inst. S. Afr. 18: 1 – 32.

DUFFY, D. C., BERRUTI, A., RANDALL, R. M. and J. COOPER 1984 – Effects of the 1982-3 warm water event on the breeding of South African seabirds. S. Afr.J. Sci. 80: 65 - 69.

DU TOIT, M., and P. A. BARTLETT 2001 – 'Soaked' Cape Gannets at Ichaboe Island, Namibia. Bird Numbers 10 (2): 8 – 9.

DU TOIT, M., BOERE, G. C., UNDERHILL, L.G., COOPER, J., DE VILLIERS, M. S., KEMPER, J., LENTEN, B., PETERSEN, S. L., SIMMONS, R. E., WHITTINGTON, P. A., and O. P. BYERS, (Eds). 2002 – Conservation assessment and management plan for southern African seabirds. Cape Town; Avian Demography Unit and Apple Valley; Conservation Breeding Specialist Group: 194 pp.

GARTHE, S., GRÉMILLET, D. and R.W. FURNESS 1999 – At-sea-activity and foraging efficiency in chick-rearing northern gannets *Sula bassana*: a case study in Shetland. Mar. Ecol. Prog. Ser. 185: 93 - 99.

GRÉMILLET, D., DELL'OMO, G., RYAN, P. G., PETERS, G., ROPERT-COUDERT, Y., and S. J. WEEKS 2004 – Offshore diplomacy, or how seabirds mitigate intra-specific competition; A case study based on GPS tracking of Cape gannets from neighbouring colonies. Mar. Ecol. Prog. Ser. 268: 265 - 279.

HAMER, K.C., PHILLIPS, R. A., WANLESS, S., HARRIS, M. P. and A.G. WOOD 2000 – Foraging ranges, diets and feeding locations of gannets *Morus bassanus* in the North Sea: evidence from satellite telemetry. Mar. Ecol. Prog. Ser. 200: 257 - 264.

HAMPTON, I. 2003 – Harvesting the sea. In Namibia's Marine Environment. Molloy, F. and T. Reinikainen (Eds). Windhoek; Directorate of Environmental Affairs, Ministry of Environment and Tourism: 31 – 69.

HOCUTT, H. and H. M. VERHEYE 2001 – Introduction: BENEFIT marine science in the Benguela Current region during 1999. S. Afr. J. mar. Sci. 97: 195 - 198.

HULL, C. L., HINDELL, M. A. and K. MICHAEL 1997 – Foraging zones of royal penguins during the breeding season and their association with oceanographic features. Mar. Ecol. Prog. Ser. 153: 217 - 228.

JARVIS, M.J.F. 1970 – Interactions between man and the South African Gannet, *Sula capensis*. Ostrich Suppl. 8: 497 – 514.

KLAGES, N.T.W., WILLIS, A.B. and G.J.B. ROSS 1992 – Variability in the diet of the Cape gannet at Bird Island in Algoa Bay. S. Afr. J. mar. Sci. 12: 761 – 771.

MAARTENS, L. 2003 – Biodiversity. In Namibia's Marine Environment. Molloy, F. and T. Reinikainen (Eds). Windhoek; Directorate of Environmental Affairs, Ministry of Environment and Tourism: 103 -135.

MATTHEWS, J. P. 1961 – The Pilchard *Sardinops ocellata* of South West Africa and the Maarsbanker *Trachurus trachurus* - Bird predators, 1957 - 1958. Invest. Rep. S. W. Afr. Mar. Res. Lab. 3: 1-35.

MATTHEWS, J. P. and A. BERRUTI 1983 – Diet of Cape Gannet and Cape Cormorant off Walvis Bay, 1958 - 1959. S. Afr. J. mar. Sci. 1: 61- 63.

MOLLOY, F. 2003 – Biological environment. In Namibia's Marine Environment. Molloy, F. and T. Reinikainen (Eds). Windhoek; Directorate of Environmental Affairs, Ministry of Environment and Tourism: 19 - 22.

NELSON, J.B. 1978 – The Sulidae – Gannets and Boobies. Oxford University Press, Oxford.

RAND, R. W. 1959 – The biology of guano-producing seabirds. The distribution, abundance and feeding habits of the Cape Gannet *Morus capensis*, off the south-western coast of the Cape Province. Invest. Rep. Sea Fish. Res. Inst. S. Afr. 39: 1- 36.

RAND, R. W. 1963 – The biology of guano-producing seabirds. 5. Composition of colonies on the South West African Islands. Invest. Rep. Sea Fish. Res. Inst. S. Afr. 46: 1- 26.

ROUX, J.- P. 1998 – The impact of environmental variability on the seal population. In Namibia Brief 20: Focus on Fisheries and Research. Blatt, C. (Ed.). Windhoek; Namibia Foundation: 138 – 140.

ROUX, J.-.P. 2003 – Risks. In Namibia's Marine Environment. Molloy, F. and T. Reinikainen (Eds). Windhoek; Directorate of Environmental Affairs, Ministry of Environment and Tourism: 137 – 152.

SHANNON, L. V. and G. NELSON 1996 – The Benguela: large scale features and processes and system variability. In The South Atlantic: Present and Past Circulation. Wefer, G., Berger, W. H., Seidel, G. and D. J. Webb (Eds). Berlin, Heidelberg; Springer-Verlag: 163 – 210.

SHANNON, L. V. and M. J. O'TOOLE 1998 – Integrated overview of the oceanography and environmental variability of the Benguela current region. Synthesis and assessment of information on Benguela Current Large Marine Ecosystem: Thematic report 2. 58 pp.

SHILLINGTON, F. 2003 – Oceanography. In Namibia's Marine Environment. Molloy, F. and T. Reinikainen (Eds). Windhoek; Directorate of Environmental Affairs, Ministry of Environment and Tourism: 7 - 18.

WEIMERSKIRCH, H., BONADONNA, F., BAILLEUL, F., MABILLE, G., DELL'OMO, G., and H. - P. LIPP 2002 – GPS tracking of foraging albatrosses. Science 295: 1259.

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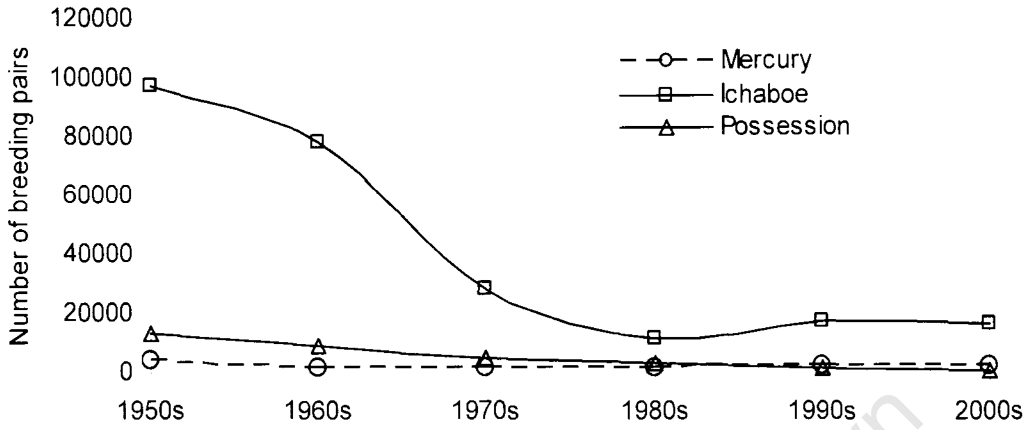
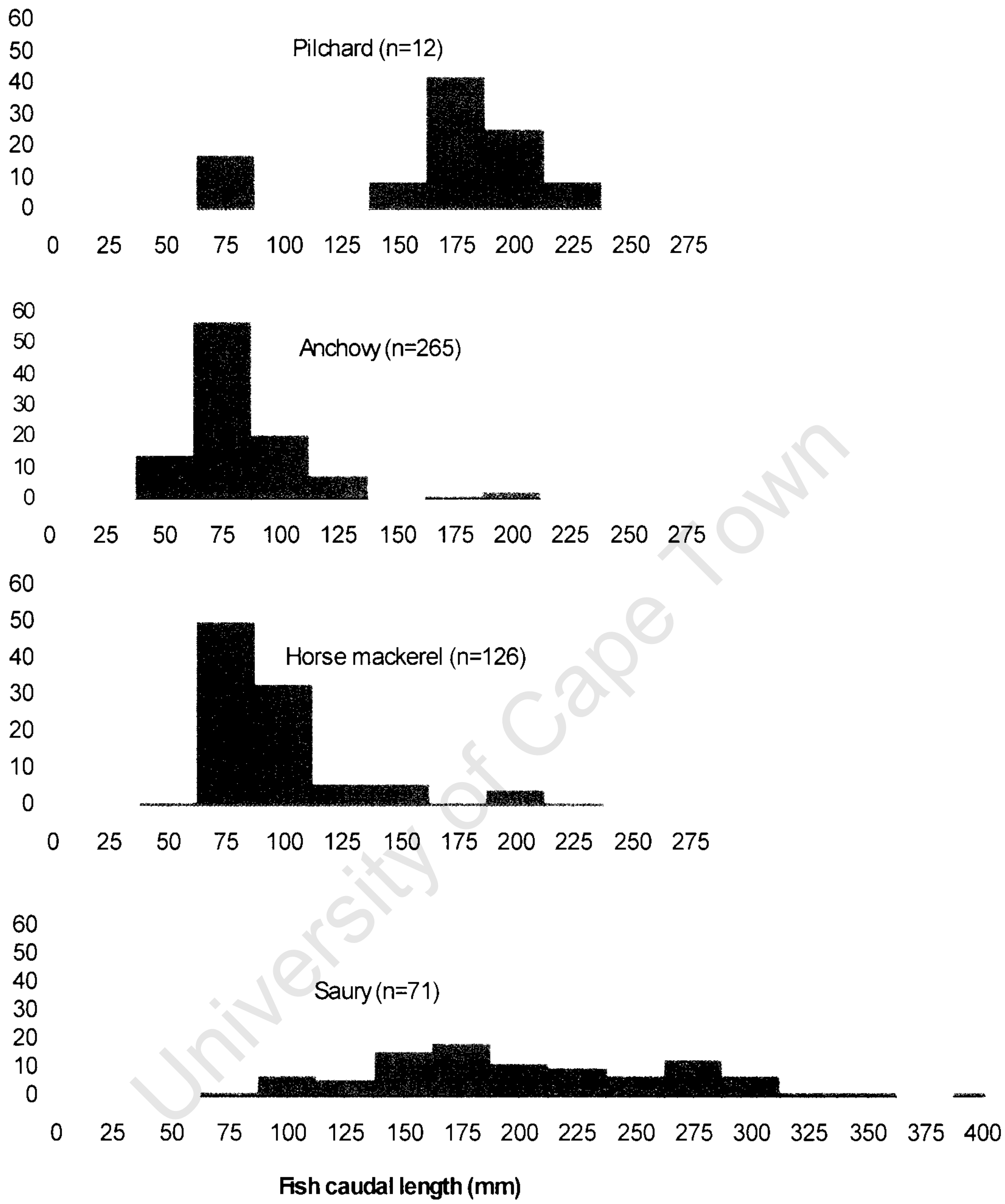


Fig. 1: Population trends of breeding Cape gannets at the Namibian islands (MFMR data, Cordes, 1998). Numbers of breeding pairs represent average decadal values.



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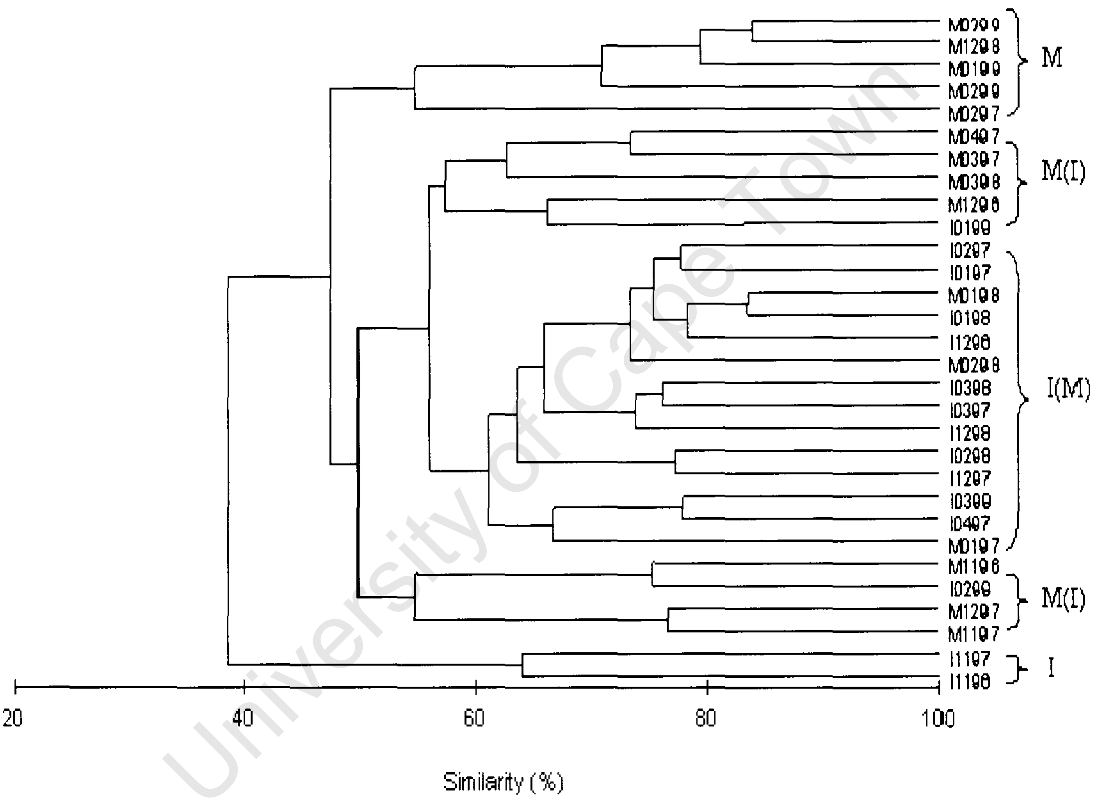

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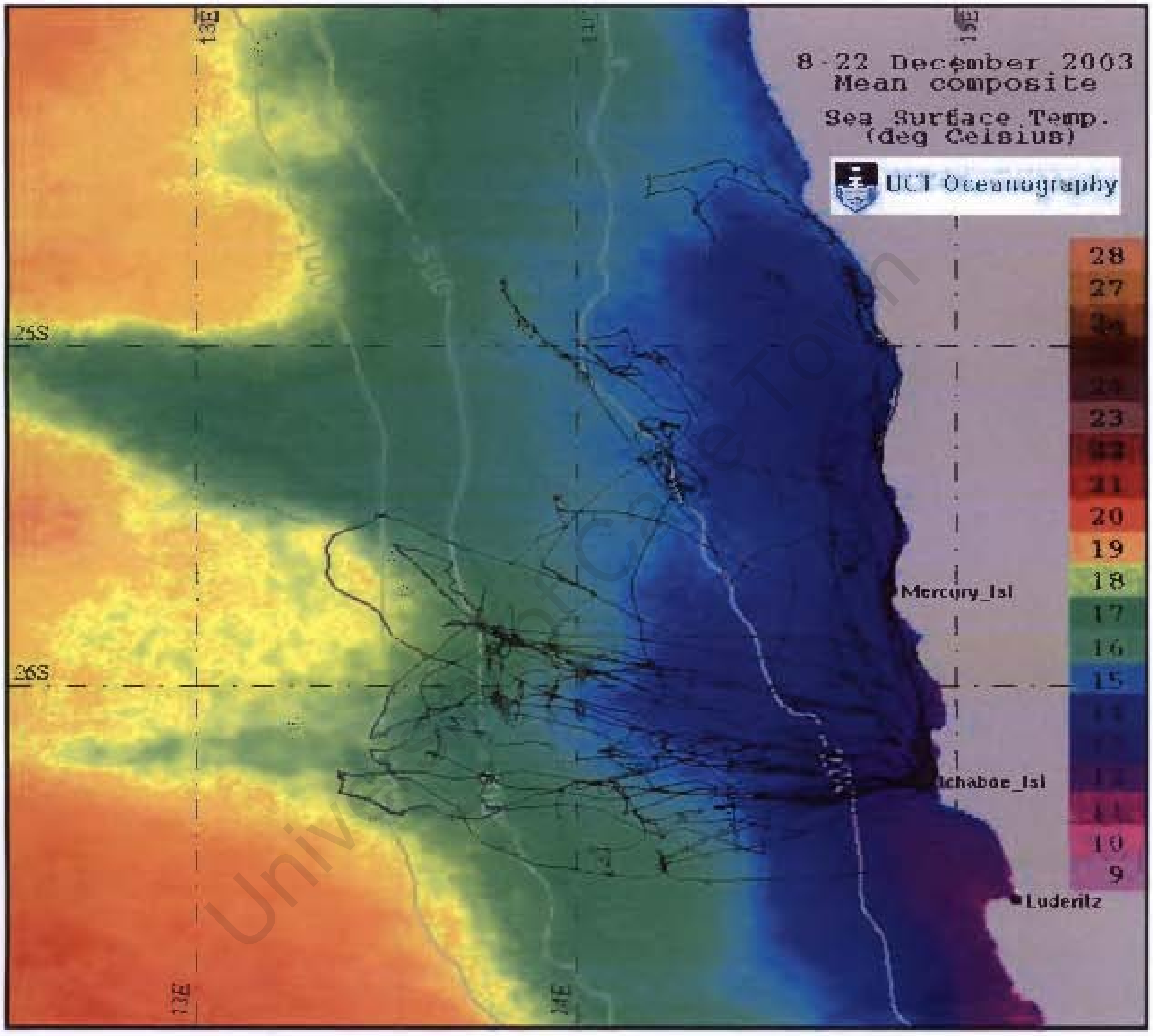
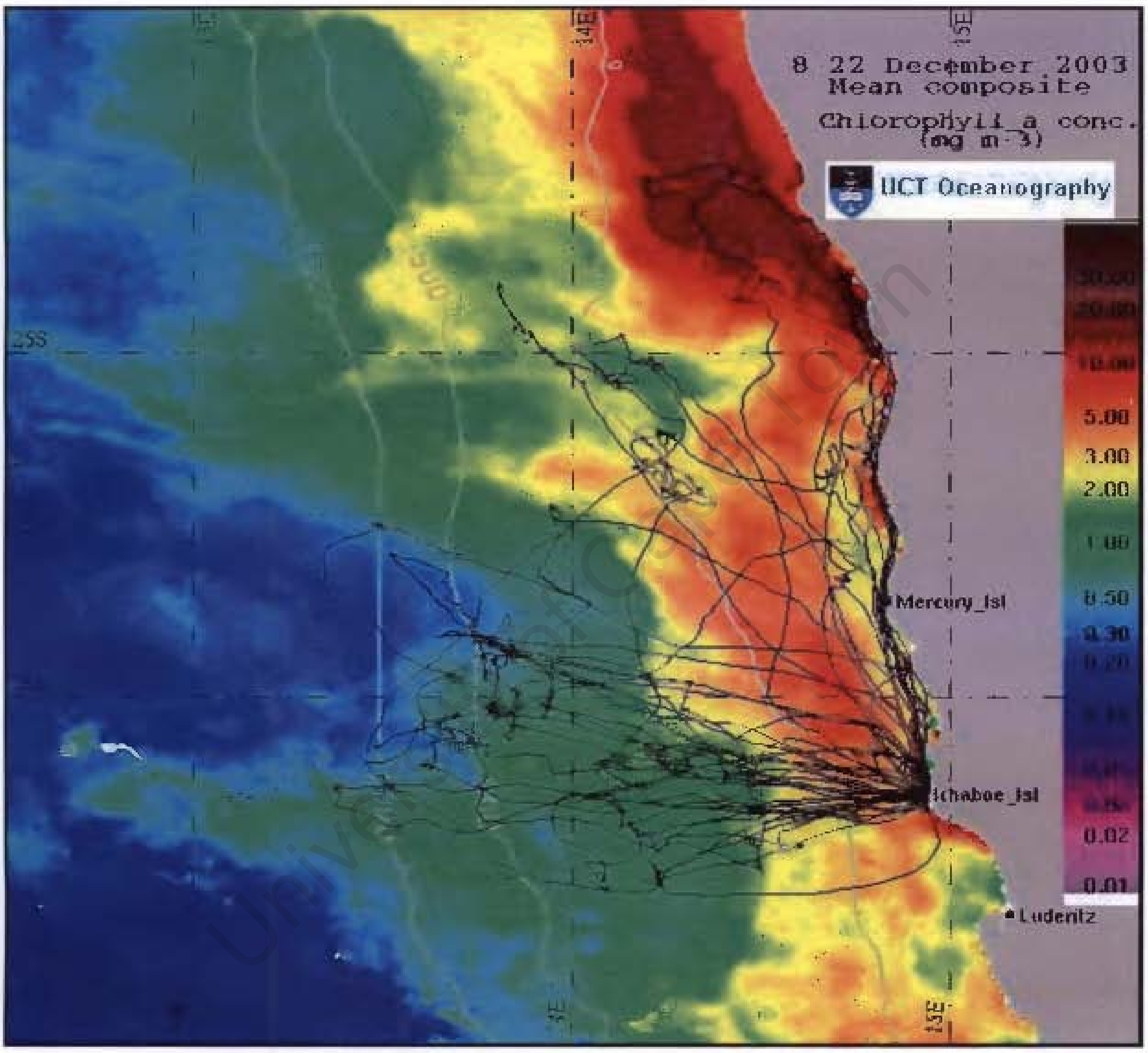


Fig. 4: Foraging tracks of 25 Cape Gannets from Ichaboe Island overlaid on a map showing mean satellite derived sea surface temperature conditions and regional bathymetry during 8 – 22 December 2003.



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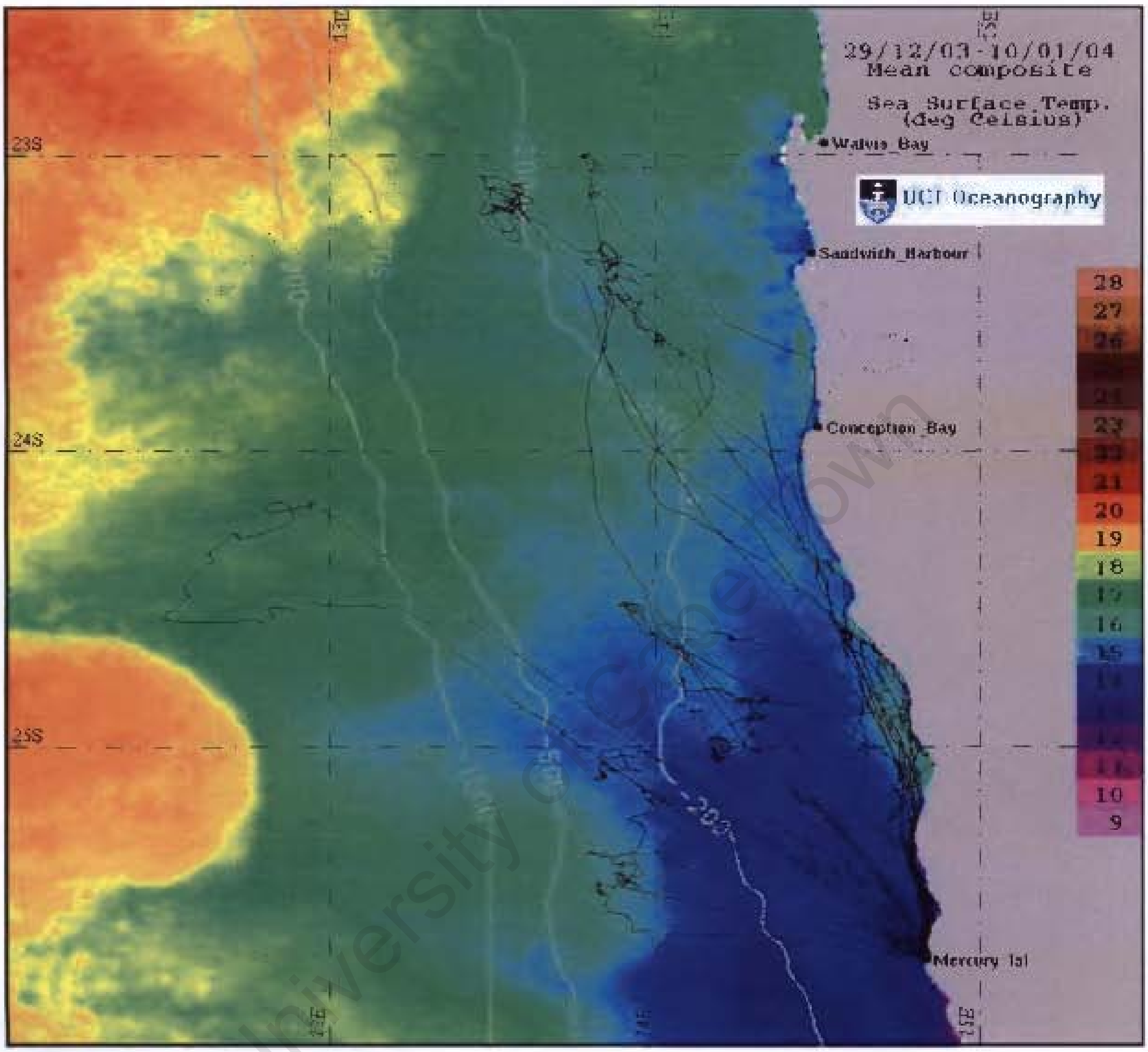


Fig. 6: Foraging tracks of 15 Cape Gannets from Mercury Island overlaid on a map showing mean satellite derived sea surface temperature conditions and regional bathymetry during 29 Dec 2003 – 10 Jan 2004.

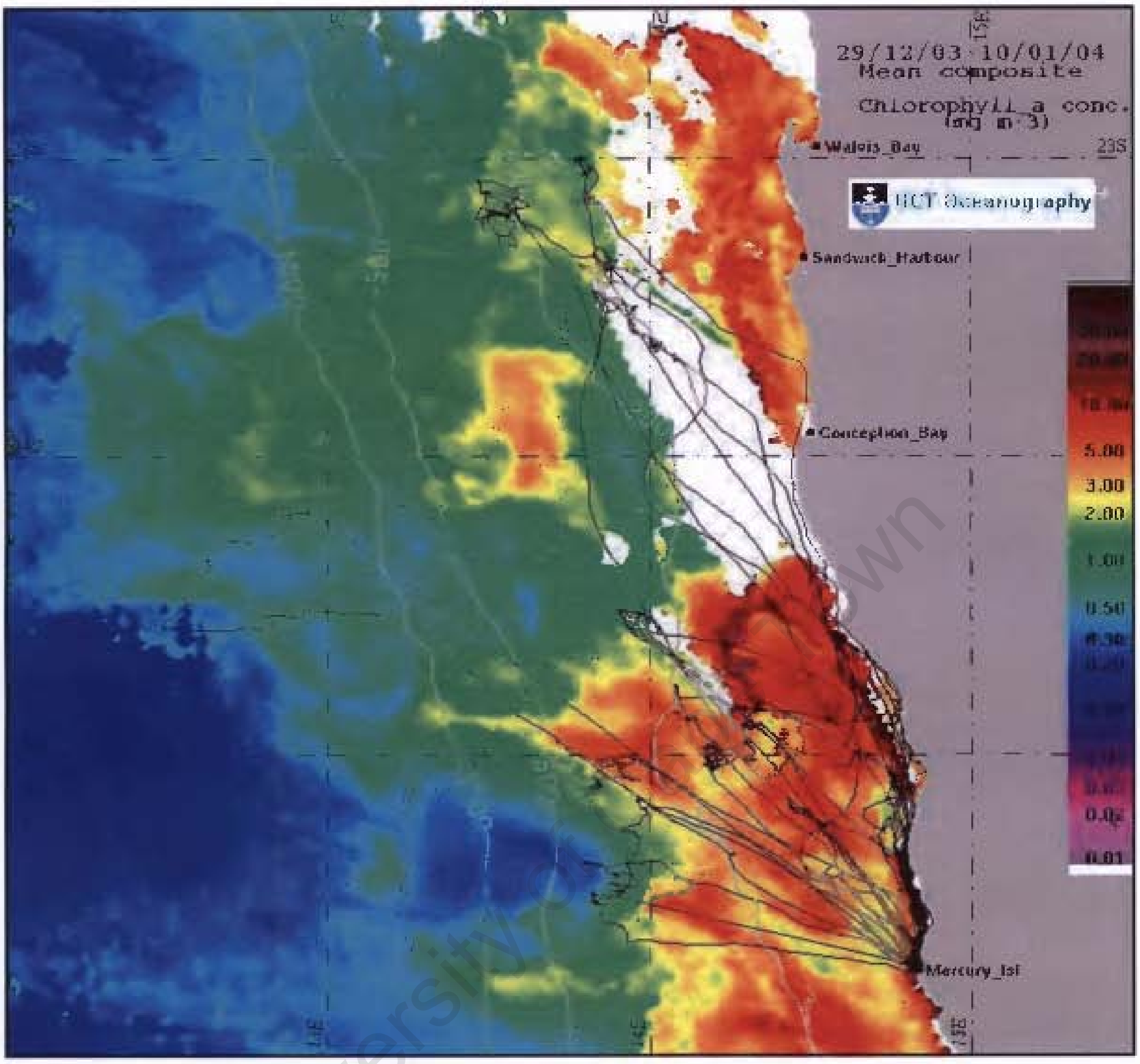


Fig. 7: Foraging tracks of 15 Cape Gannets from Mercury Island overlaid on a map showing mean satellite derived chlorophyll-*a* concentrations and regional bathymetry during 29 Dec 2003 – 10 Jan 2004. White shaded areas indicate regions with poor or no satellite coverage.

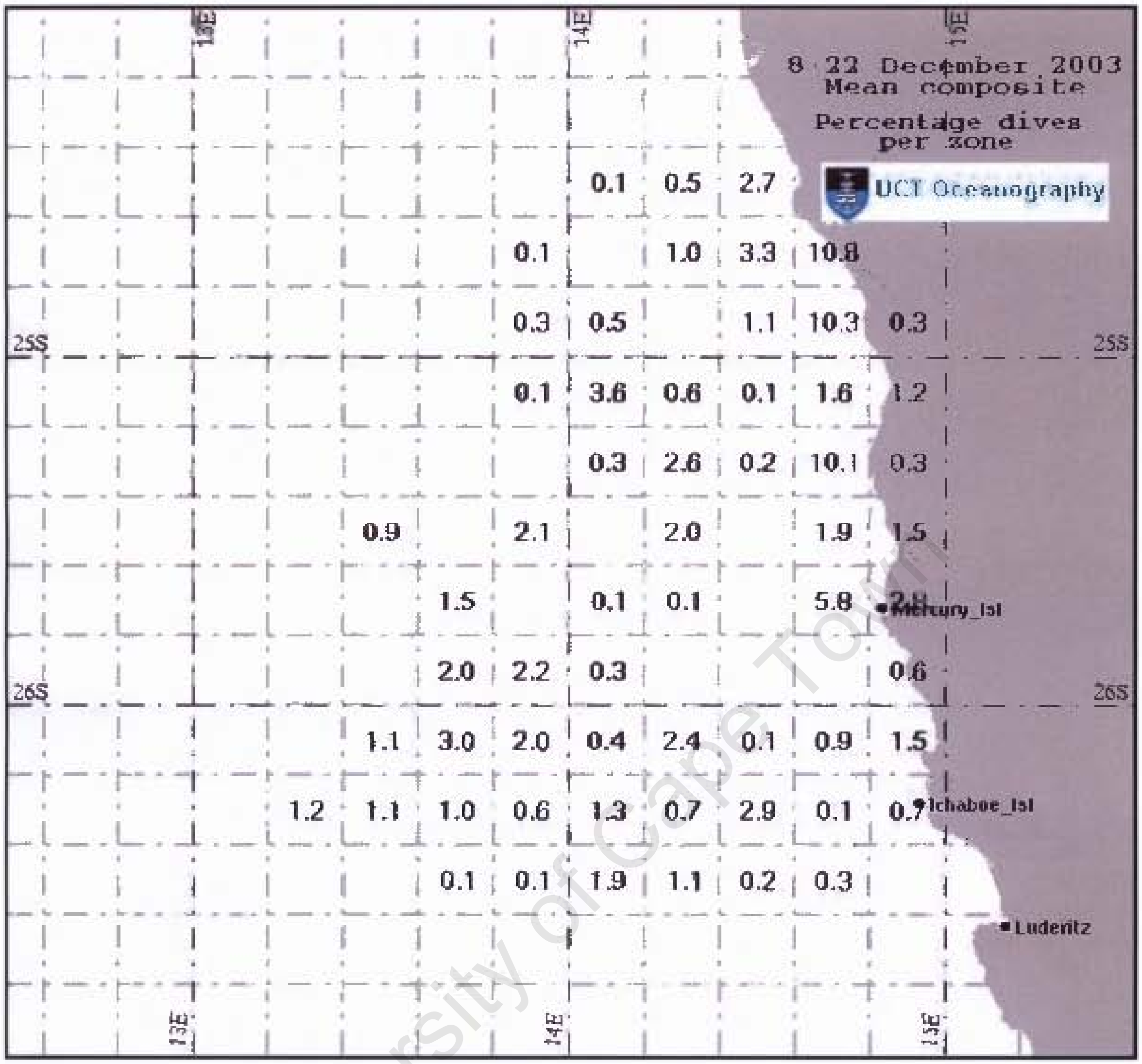
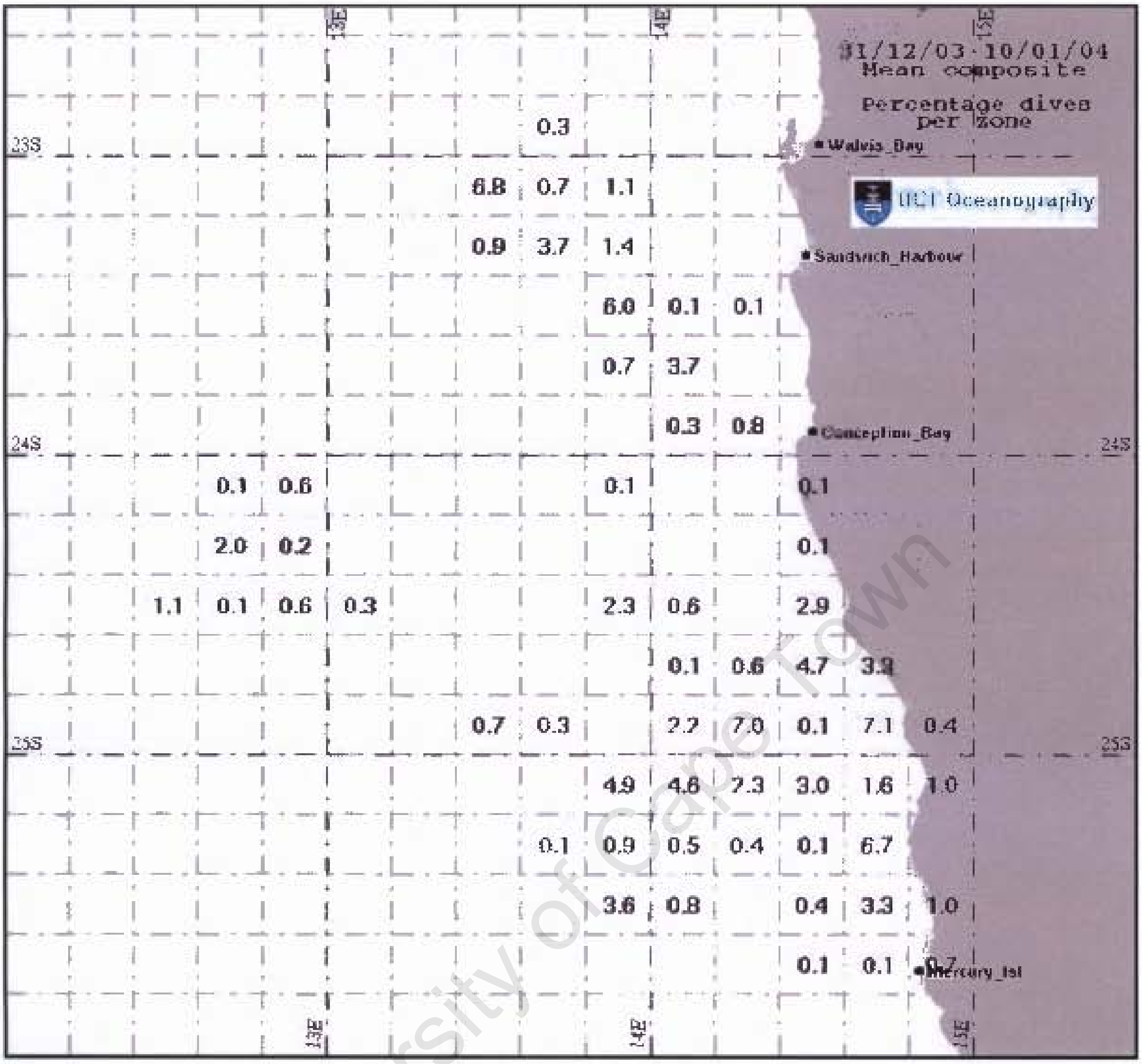


Fig. 8: Feeding density (% positional fixes associated with prey patch exploitation) for 25 birds from Ichaboe Island.



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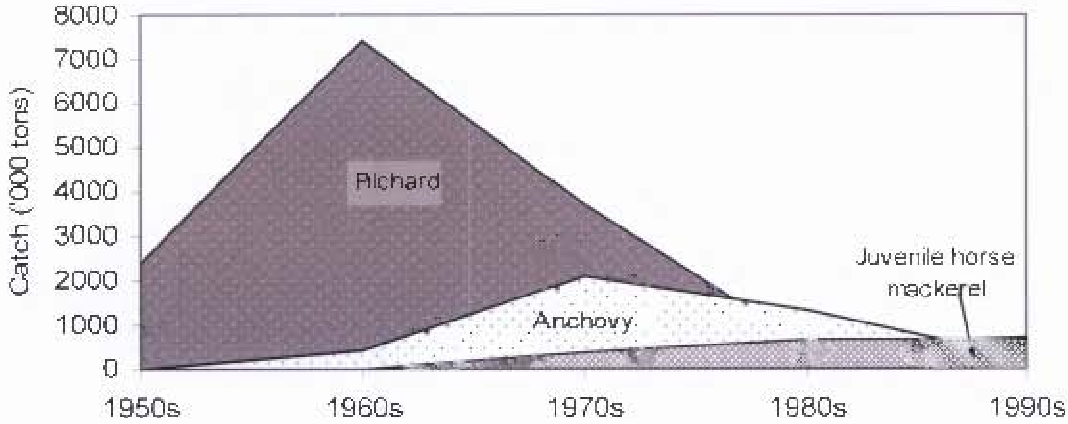

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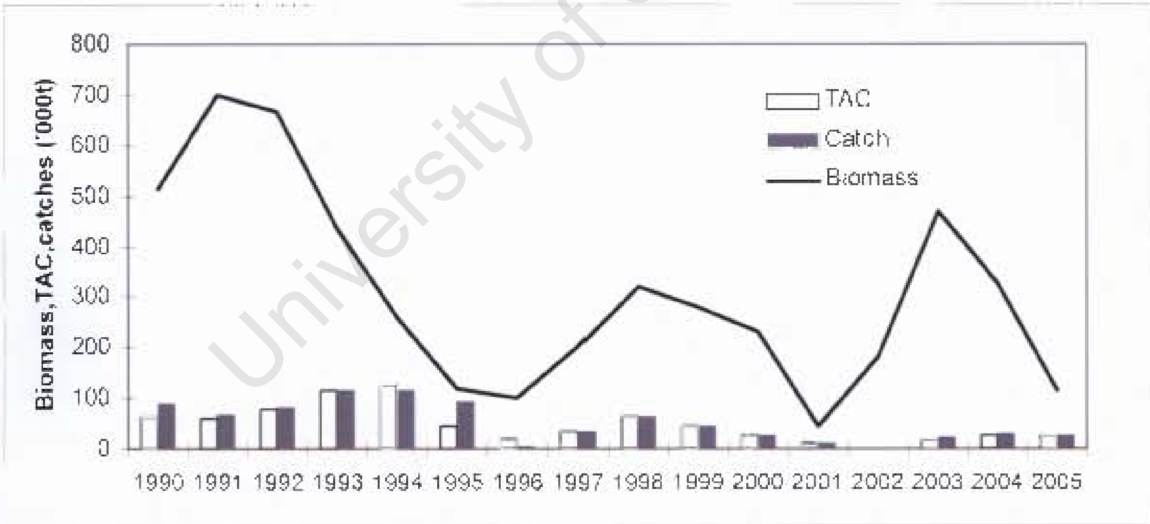

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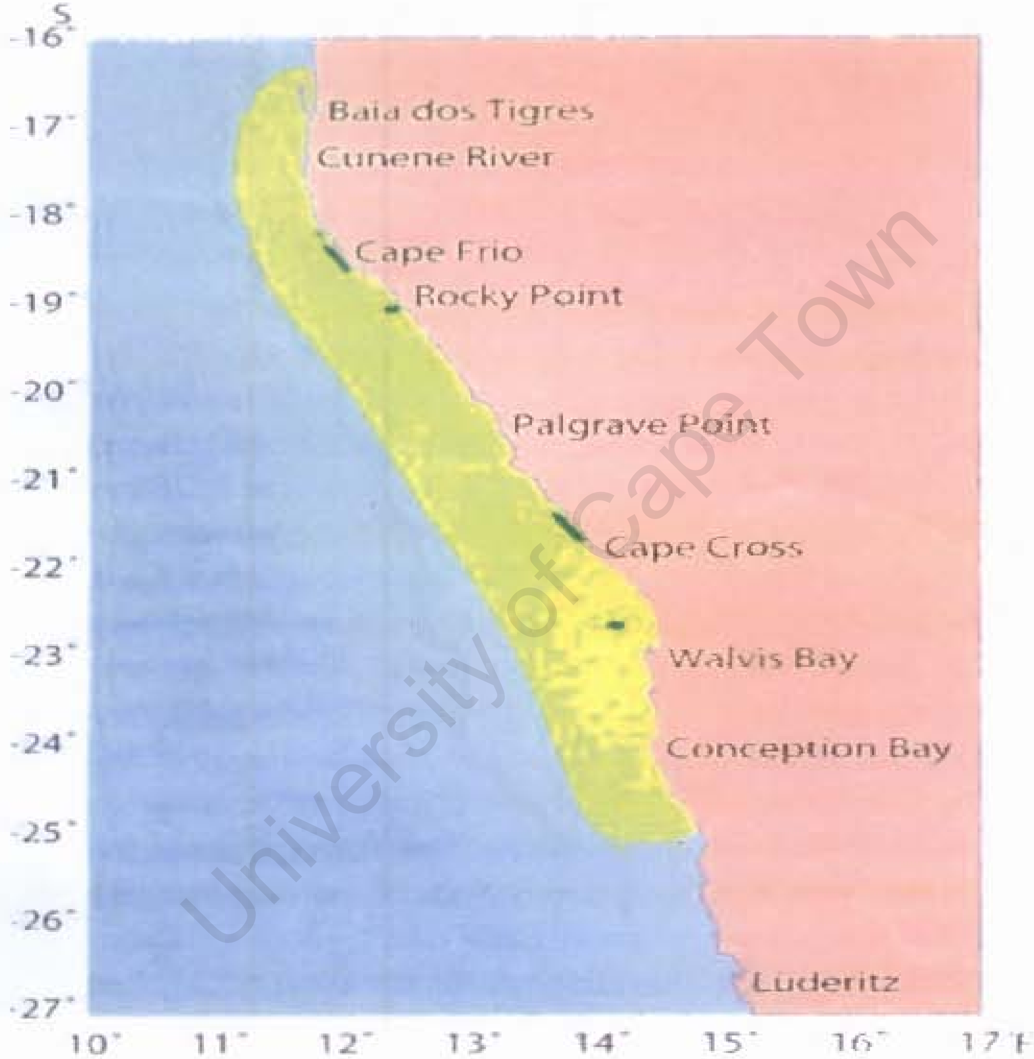

Fig. 12: Sardine distribution (dark green areas) as found during the March 2002 biomass acoustic survey, compared to the historical distribution range (light green area). Map reproduced from Hampton (2003).

Table I: Summary of all prey species recorded and the variation in the composition of the diet of breeding gannets sampled off the Namibian west coast at Ichaboe Island (Nov 95 – Feb 04) and Mercury Island (Oct 96 – Feb 04). All samples collected during the entire sampling period were combined for each island, and prey contribution expressed by percentage mass (% M) and frequency of occurrence (% F).

		Ichaboe		Mercury	
Total Number of samples		455		556	
Total Mass (g)		81 247.5		95 817.8	
Prey species		**%F**	**%M**	**%F**	**%M**
Teleosts					
Etrumeus whiteheadi	Roundherring	9.5	5.9	11.3	4.3
Sardinops ocellatus	Pilchard	5.3	3.0	18.7	12.5
Engraulis capensis	Anchovy	18.7	6.8	27.2	12.0
Merluccius spp †	Cape hakes	35.4	33.7	7.0	5.7
Family Macrouridae †	Rattails	0.4	0.2	0.2	0.0
Genypterus capensis †	Kingklip	0.4	0.1	-	-
Atherina breviceps	Silverside	-	-	0.4	0.0
Scomberesox saurus scombroides	Saury	34.1	25.1	14.4	8.5
Helicoleneus dactylopterus †	Jacopever	0.2	0.1	-	-
Chelidonichthys capensis †	Cape gurnard	0.7	0.0	1.3	0.2
Trachurus trachurus capensis	Horse mackerel	16.5	8.7	39.6	26.0
Chirodactylus brachydactylus	Steenklipvis	0.2	0.0	-	-
Liza richardsonii	Mullet	-	-	2.0	2.1
Sufflogobius bibarbatus	Goby	2.9	0.5	5.6	2.4
Thyrsites atun	Snoek	11.2	10.2	20.1	24.0
Scomber japonicus	Chub mackerel	0.4	0.9	0.4	0.5
Thunnus spp (Family Scombridae)	Tuna †	1.8	2.0	-	-
Cubiceps capensis	Cubiceps	0.2	0.2	-	-
Austroglossus microlepis †	Sole	0.7	0.8	0.5	0.4
Unidentified teleosts		0.9	0.2	2.2	0.7
Unidentified squid		7.7	1.6	5.2	0.6
Unidentified crustaceans		-	-	0.7	0.0
Unidentified molluscs		-	-	0.2	0.0

† Species commonly occurring as offal in the diet.
- Denotes species that are absent from diet.

Table II: The mean monthly contribution of prey species to the breeding diet of Cape Gannets at Ichaboe Island between November 1995 and February 2004.

Prey species	Sep {n=20} (X=2)	Oct {4} (1)	Nov {47} (4)	Dec {92} (6)	Jan {101} (6)	Feb {86} (6)	Mar {85} (5)	Apr {20} (3)
% mass:								
Anchovy	9	0	3	6	14	2	5	18
Hake	52	100	56	37	31	26	26	11
Horse Mackerel	0	0	7	9	7	12	12	0
Saury	26	0	7	38	25	27	16	43
Roundherring	6	0	5	1	6	6	12	0
Snoek	0	0	2	5	6	17	16	20
Other	6	0	20	2	10	10	14	8
% frequency of occurrence:								
Anchovy	40	0	9	15	39	24	24	45
Hake	55	100	51	59	30	35	33	45
Horse Mackerel	0	0	38	23	19	20	49	0
Saury	30	0	21	52	35	39	26	30
Roundherring	10	0	21	7	10	16	32	0
Snoek	0	0	13	8	10	37	24	45

n = number of samples (sample size)
x = number of months sampled

Table III: The mean monthly contribution of prey species to the breeding diet of Cape Gannets at Mercury Island between October 1996 and February 2004.

Prey species	Sep {n=6} (x =1)	Oct {15} (2)	Nov {45} (5)	Dec {108} (6)	Jan {135} (7)	Feb {134} (7)	Mar {85} (5)	Apr {28} (2)
%mass:								
Anchovy	64	46	4	18	11	3	11	38
Pilchard	0	20	19	9	12	9	16	25
Hake	0	0	2	<1	5	13	3	1
Horse Mackerel	0	4	13	38	21	27	35	9
Saury	0	18	6	10	17	5	2	8
Snoek	30	0	51	20	19	26	26	7
Other	6	13	6	5	15	16	7	12
%frequency of occurrence:								
Anchovy	83	60	26	36	24	23	31	57
Pilchard	0	20	56	14	19	16	38	50
Hake	0	0	11	6	17	29	15	7
Horse Mackerel	0	27	31	56	34	41	49	21
Saury	0	40	22	16	34	10	9	36
Snoek	17	0	44	23	19	33	26	7

n = sample size
x = number of months sampled

Table IV: Inter-annual variation in the diet of Cape Gannets at Ichaboe Island between November 1995 and February 2004. Annual indices derived from all samples collected during breeding from September to April.

Prey species	1995/96 n=54	1996/97 n=106	1997/98 n=68	1998/99 n=41	2003/04 n=70
%mass:					
Anchovy	6	4	4	4	6
Hake	50	45	38	11	39
Horse Mackerel	1	4	11	4	8
Saury	22	25	29	39	33
Roundherring	1	3	6	5	5
Snoek	4	14	3	19	2
Other	16	6	9	19	7
%frequency of occurrence:					
Anchovy	17	8	19	12	7
Hake	44	45	41	15	39
Horse Mackerel	4	4	22	5	17
Saury	31	35	43	51	41
Roundherring	4	6	10	7	6
Snoek	9	14	6	20	1

n = number of samples

Table V: Inter-annual variation in the diet of Cape Gannets at Mercury Island between October 1996 and February 2004. Annual indices derived from all samples collected during breeding from September to April.

Prey species	1996/97 n=95	1997/98 n=99	1998/99 n=66	1999/00 n=83	2003/4 n=83
%mass:					
Anchovy	8	19	22	4	1
Pilchard	16	5	24	4	27
Hake	4	17	0	<1	1
Horse Mackerel	9	31	30	18	37
Saury	13	7	<1	6	24
Snoek	29	18	19	47	1
Other	20	3	4	21	8
%frequency of occurrence:					
Anchovy	18	36	44	13	11
Pilchard	24	16	26	10	29
Hake	6	16	0	2	2
Horse Mackerel	21	42	48	33	46
Saury	25	16	2	8	29
Snoek	18	18	18	41	4

n = number of samples

Table VI: Comparative foraging characteristics of Cape Gannets tracked at Ichaboe and Mercury Islands respectively. Median values are given for non-parametric distributions, and average values with standard deviations (S.D.) for normal distributions while minimum and maximum values are indicated in brackets. The sample size (n) is given for each island. The results of relevant statistical tests i.e. parametric Student's t-test and non-parametric Mann-Whitney U-test are provided, with significant values in bold.

Parameters	Ichaboe n=25	Mercury Island n=12	Statistical test results
Foraging trip duration (hrs)	24.3 (3.5 - 52.8)	29.4 (7.2 - 62.9)	U=78, Z = -2.336, **p = 0.0195**
Foraging path length (km)	422 (130 - 783)	673 (214 - 1140)	U=74, Z = -2.466, **p = 0.0137**
Foraging range (km)	130 ± 48 S.D. (25 - 211)	197± 90 S.D. (77 - 325)	t= -3.0042, df = 35 **p = 0.0049**
GPS speed ($km.hr^{-1}$)	23 ± 8 S.D. (15 - 46)	21± 5 S.D. (16 - 33)	t=0.6236, df = 35, p = 0.5369
Number of foraging fixes (feeding events)	60 ± 74 S.D. (3 - 375)	90 ± 58 S.D. (10 - 182)	t= -1.2259, df = 35, p = 0.2284