Comparing body condition and foraging ecology of two populations of Cape gannets on Bird and Malgas Islands

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Abstract

Cape gannets (*Morus capensis)* are one of the dominant seabirds in the Benguela current ecosystem and feed mainly on sardines (*Sardinops sagax)* and anchovy (*Engraulis encrasicolus*). Starting in the late 1990s the distribution of these fish shifted from the west coast of South Africa to the south-east coast. This has resulted in gannets on the west coast feeding extensively on fishery wastes, which slows the growth of chicks and decreases their fledging mass. I compared the foraging ecology, diet and body condition of adult Cape gannets from two colonies, one where individuals have been feeding on fishery wastes (hake) for several years (Malgas Island; west coast) and the other where individuals feed on natural prey (Bird Island; south coast). In October and November 2009, through the use of GPS loggers I compared the foraging behaviour of birds from the two colonies. I compared the diet of gannets at the two colonies, using stomach contents samples and an isotopic mixing model using stable isotope ratios of carbon and nitrogen in blood, feathers and potential prey. I also compared the body condition of adults by measuring pectoral muscle thickness and other morphological parameters. These results were analysed with data from a concurrent hydro-acoustic survey of the distribution and abundance of pelagic fish along the coast of South Africa. The hydro-acoustic survey showed that more than half of the sardine and anchovy stocks were present on the west coast for the first time in several years but that the overall biomass of these two species remained low in the southern Benguela. Stomach samples and isotopic analysis of blood showed that gannets at both colonies fed mainly on sardines during the study period. Long-term diet estimates from feather isotopes suggest that there was little hake in the diet of birds at Malgas Island, despite the direct diet samples showing that hake and saury dominated the diet over the preceding 10 months. This could be due to insufficient prey sampling or the diet samples not being representative of the gannet population as a whole. Gannets from Bird Island made longer foraging trips and flew further from their colony than did those from Malgas Island. Individuals from this colony had slightly greater pectoral muscle thicknesses and body masses (after controlling for size) than those from Bird Island, but

this was not significant. Despite gannets from Malgas Island relying on fishery wastes for a number of years, there has been little effect on body condition among breeding birds when compared with Bird Island gannets feeding on pelagic fish. Two possible reasons for this are that (1) when feeding on fishery wastes, adults decrease their reproductive effort to preserve body condition or (2) gannets on the west coast have regained body mass and pectoral muscle rapidly since the local recovery of sardines. It is likely that the gannets from Bird Island have greater foraging costs due to intra-specific competition for food as the colony has increased five-fold in size over the last 50 years. However, chick growth and adult body condition have been affected only marginally. Despite the presence of sardine and anchovy on the west coast, it is likely that Cape gannets are food limited, especially since there is also a strong spatio-temporal overlap of gannet foraging with the large commercial purse-seine fishery. Better spatial management of this fishery is necessary to ensure the persistence of seabirds and other top predators in the southern Benguela.

Keywords: body condition, fishery waste, intraspecific competition, GPS tracking, pectoral muscle thickness, pelagic fish, stable isotope analysis, southern Benguela

Chapter 1: Introduction

Seabirds and fisheries

Seabirds are one of the most threatened groups of birds (Birdlife International 2004) due to the impacts of fisheries, alien species on their breeding islands and climate change (Tasker et al. 2000; Furness 2003). Commercial fisheries negatively affect seabirds through mortality caused by direct exploitation and interactions with fishing gear, or indirect effects due to the reduction in prey through competition with fisheries (Tasker et al. 2000). Fisheries can also benefit seabirds either by increasing food availability by removing large fish that compete with seabirds for the same forage species (Montevecchi 2002) or discarding large amounts of waste on which seabirds feed (Tasker et al. 2000; Furness 2003). Fishery wastes consist of discards (fish and invertebrates discarded because they are not commercially viable or are caught in excess of the quota) and offal (the heads, livers and intestines of marketable fish; Garthe et al. 1996). It is estimated that between 25 and 30 million tons of waste was discarded worldwide each year in the 1980s and 1990s (Furness et al. 2007). This represents ca. 30% of the marketed harvest of the world's fisheries, creating a food source which may be greater than the amount of food naturally available to seabirds (Furness et al. 2007).

Many seabird populations in Europe have increased due to the availability of fishery wastes (Furness et al. 1992; Garthe et al. 1996; Oro 1996). For example, in the North Sea, the populations of scavenging species, such as great black-backed gulls (*Larus marinus)* and great skuas (*Stercorarius skua*) are maintained at artificially high levels because of fishery wastes (Furness et al. 2007). Most seabirds that benefit from fishery wastes are scavenging species with energetically inexpensive locomotion, such as albatrosses, petrels, shearwaters, gulls and skuas (Furness et al. 2007).

Benguela ecosystem

The Benguela Current Large Marine Ecosystem (BCLME) is one of the four major global upwelling zones, running along the Atlantic coasts of Angola, Namibia and South Africa, between 5-37° S and 0-26° E (Shillington et al.

2006). It is a highly productive system with a large biomass of small pelagic clupeoids, supporting many predatory fish, seabirds and marine mammals (Shannon & O'Toole 2003). However these fish are also exploited intensively by commercial fisheries. The major pelagic fishery in the area targets sardine (*Sardinops sagax)* and anchovy (*Engraulis encrasicolus*), whereas the demersal fishery targets hake (*Merluccius* spp; van der Lingen et al. 2006). The commercial purse-seine fishery for sardine and anchovy began in Namibia and South Africa in the 1940s (van der Lingen et al. 2006). This fishery is commercially very important, catching some 400 000 tons of fish each year for the last 60 years (Roy et al. 2007).

In the southern Benguela, anchovy traditionally spawned over the Agulhas Bank in the austral summer months (December - February), with the eggs and larvae transported by a shelf-edge jet current to nursery grounds along the west coast of South Africa (Roy et al. 2007). The juveniles would then return along the coast to the spawning grounds at one year old (Roy et al. 2007). Since 1996 there has been an eastward shift of both the egg and spawner biomass with two thirds of the biomass found east of Cape Agulhas (Roy et al. 2007). Similarly, most of the sardine spawner biomass was located off the west and south west coasts. However since 1997, there also has been a gradual eastward shift in the sardine biomass. No sardines have been caught west of Cape Point since 2004 (van der Lingen et al. 2005).

Cape gannets

Cape gannets (*Morus capensis*) are one of the three dominant seabird species endemic to the Benguela system that are largely dependent on sardine and anchovy (Crawford 1999). They breed on only six islands along the southern African coast (Crawford 2005), three in Namibia (Mercury, Possession and Ichaboe) and three in South Africa (Bird [Lambert's Bay], Malgas and Bird [Nelson Mandela Bay]). Gannets are visual predators that feed by plunge diving from heights of up to 30 m and reach depths of up to 20 m (Crawford 2005). They feed on epipelagic shoaling fish, mainly sardine and anchovy but also horse mackerel (*Trachurus trachurus*), saury (*Scomberesox saurus*) and redeye (*Etrumeus whiteheadi*). They have a flexible foraging

strategy depending on prey availability and can take a range of prey sizes (Berruti et al. 1993). Cape gannets also forage on fishery waste, mainly from the commercial hake fishery (Abrams 1983; Ryan & Moloney 1988).

Gannets have typical seabird life history traits, they are long-lived, have few offspring, high adult survival and slow chick growth (Stearns 1992). They begin breeding in their third or fourth year of life and lay only one egg (Crawford 2005). The breeding season is in the austral summer (October to February; Crawford 2005). In the non-breeding season birds can disperse widely, some going as far north as the Gulf of Guinea along the west coast and Mozambique along the east coast, although most remain closer to their home sites (Crawford et al. 1983; Klages 1994; Crawford 2005; Grémillet et al. 2008)

Cape gannets are listed as vulnerable by the IUCN (BirdLife International 2008) because of the limited numbers of breeding sites and their decreasing population size (Crawford 2005). The current major threats are from food shortages (through competition with fisheries and the eastward shift in prey distribution; Okes et al. 2009, Pichegru et al. 2009a) and high predation levels by kelp gulls (*Larus domincanus*; Mullers et al. 2009), Cape fur seals (*Arctocephalus pusillus pusillus;* Makhado et al. 2006) and locally by great white pelicans (*Pelecanus onocrotalus;* de Ponte Machado 2007).

The number of gannets breeding in South Africa and Namibia is correlated with the regional biomass of sardine and anchovy (Crawford et al. 2007). Between 1956 and 2006 there was a large decrease in the overall Cape gannet population size (Crawford et al. 2007), mainly due to the rapid decrease of the Namibian populations (a decrease of 90% in 50 years), following the collapse of the Namibian sardine stock due to overfishing (Crawford et al. 2007). The South African sardine stock also experienced a collapse, but gannet numbers were maintained due to an increase in the abundance of anchovy (Crawford et al. 2007). The South African gannet populations have fluctuated in size. The Lambert's Bay colony has varied between 9 000 and 12 000 pairs over the last 50 years (Crawford et al. 2007).

The Malgas Island colony increased from approximately 25 000 pairs in 1956/1957 to more than 56 000 pairs in 1996/1997 but then decreased to about 36 000 pairs by 2005/2006 (Crawford et al. 2007). The Nelson Mandela Bay colony has increased five-fold over the last 50 years and is now the largest Cape gannetry in the world with some 98 500 pairs (Crawford et al. 2007). The recent population trends of gannet colonies on the west and south coasts of South Africa probably result from the eastward shift in the ranges of their main prey species (Crawford et al. 2007).

Gannets and fishery waste

As a result of the shift in their usual prey, Cape gannets on the west coast have been reported to eat a large proportion of fishery waste (at least since 2004; Pichegru et al. 2007, Pichegru et al. 2009a). Even before the shift in sardine and anchovy biomass, large numbers of seabirds and Cape fur seals were attracted to commercial hake trawlers (Abrams 1983; Ryan & Moloney 1988). In one study, Cape gannets were observed at 90% of trawls in winter (Ryan & Moloney 1988). The quantity of waste produced by trawlers is substantial, with 9 000 t of hake discarded annually off the west coast and 2 000 t off the south coast (Walmsley et al. 2007). This industry also discards 30 000 $t.yr^{-1}$ and 13 500 $t.yr^{-1}$ of offal off the west and south coasts, respectively (Walmsley et al. 2007). Hake has only half the calorific value of sardines/anchovies (4.1 $kJ.g^{-1}$ and 8.6 $kJ.g^{-1}$, respectively; Batchelor & Ross 1984). Grémillet et al. (2008) found that gannets that ate a large proportion of fishery wastes, had diets that were 19-37% lower in calorific value than those that fed on natural prey. Despite this reduction in calorific value, a diet of fishery wastes was beneficial to gannets during the non-breeding season as birds decreased their foraging effort (making fewer, shallower dives) and did not disperse as widely as expected for non-breeding colonial birds (Grémillet et al. 2008). However, such a diet does not benefit breeding gannets as parents increased their foraging effort in order to provide chicks with natural prey (Pichegru et al. 2007; Grémillet et al. 2008). In many cases, chicks were fed on a mixed diet with a large proportion of fishery wastes, which probably accounted for their low fledging success (Grémillet et al. 2008).

Gannets have an energetically demanding foraging technique; indeed northern gannets (*Morus bassanus*) have the greatest absolute field metabolic rates of any seabird measured (Birt-Friesen et al. 1989). Cape gannets also have metabolic rates greater than expected for seabirds using gliding or non-gliding flight (Adams et al. 1991). Their energetically demanding foraging strategy probably explains why the three species of gannets are restricted to cold, productive waters, where they can find sufficient food (Furness & Monaghan 1987). Cape gannets have short gut lengths and digest food rapidly, presumably to reduce the food load during their energetically expensive flight (Jackson 1992), but this shorter gut length probably means that they are relatively inefficient at extracting nutrients from food (Hilton et al. 2000a). Their usual prey, sardine and anchovy, are rich in lipids and have a high energy content (Batchelor & Ross 1984), so gannets are able to derive sufficient nutrients and energy despite their rapid digestion. When feeding on energy-poor foods or those that are difficult to digest (e.g. fishery waste), their rapid digestion does not allow the absorption of as many nutrients. Scavengers, such as herring gulls (*Larus argentatus*) have longer guts and slower, more efficient digestive systems (Hilton et al. 2000b). Their high energy requirements and inefficient digestive systems may be part of the reason that the Cape gannet population has not increased while foraging extensively on fishery wastes, as have some species in the North Sea (Furness et al. 2007)

Cape gannet chicks hand-reared on a diet of hake grew more slowly than those fed on sardine and had lower fledging weights (Batchelor & Ross 1984). A high fledging weight is crucial for survival of young gannets as their fat reserves sustain them while learning to hunt (Jarvis 1971). Pichegru et al. (2007) found that a diet of fishery waste would not allow breeding Cape gannets to balance their energy budget. In years when gannet parents had a large proportion of sardine and anchovy in their diets, chicks grew faster than in years where there was a greater proportion of fishery waste in the diet (Mullers et al. 2009). In this context, the junk food hypothesis suggests that animals feeding on lower energy and nutrient content prey have low breeding success (Österblom et al. 2008). This has been demonstrated for a variety of

species when prey abundance has decreased and parents were forced to provision their offspring with lower quality prey (Litzow et al. 2004; Wanless et al. 2005). Red-legged kittiwake (*Rissa brevirostris*) chicks that experienced food scarcity grew more slowly and had higher corticosterone levels than those with normal food levels (Kitaysky et al. 2006). Chronically elevated levels of corticosterone, a hormone that is involved in fat deposition, are thought to affect cognitive and learning ability, an important trait for young seabirds that need to be able to find patchily distributed prey (Kitaysky et al. 2006). The effect of feeding extensively on fishery wastes on the body condition and survival of adult Cape gannets is unknown. The conservative life history traits of gannets (high adult survival, small clutch size and delayed maturity), render them vulnerable to factors that increase adult mortality (Furness & Monaghan 1987). A diet of fishery wastes could result in lower body condition, reduced breeding frequency and possibly lower survival which may also contribute to the overall population decrease.

In this study I investigate the body condition of adult Cape gannets that, in the absence of their natural prey, have been feeding on fishery waste for several years (since 2004, Pichegru et al. 2009a). I compare the foraging ecology and body condition of breeding Cape gannets from two colonies: (1) Malgas island on the west coast of South Africa, where birds have fed predominantly on fishery waste in recent years (Pichegru et al. 2007), and (2) Bird Island (Nelson Mandela Bay) on the south coast where birds still feed predominantly on pelagic fish (Pichegru et al. 2007).

Chapter 2: Study area and methods

Study area

The study was conducted at Malgas Island, at the mouth of Saldanha Bay, Western Cape (33° 03'S, 17° 55'E) and Bird Island in Nelson Mandela Bay, 60 km east of Port Elizabeth, Eastern Cape (33° 50'S 26° 17'E), South Africa (Figure 1). Malgas Island is situated in the Benguela Current upwelling system, between two seasonal upwelling plumes off Cape Columbine and the Cape Peninsula (Shannon 1985). Work was conducted on Malgas Island between the 20 October and 25 November 2009. Bird Island lies within the influence of the Agulhas Current which causes irregular influxes of warm water into Nelson Mandela Bay, but upwelling also occurs in the summer months (Klages et al. 1992). Work was conducted on Bird Island from 18 November to 3 December 2009. All work on gannets was performed under permits issued by South African National Parks.

Foraging behaviour

a) Monitoring foraging trip duration

Gannet nests were chosen within 1 m of the edge of the colony, because selecting nests in the interior of the colony would cause too much disturbance. We assumed that birds at the periphery were of similar age and condition as those in the interior (Klages 1994) and that chick growth was independent of nest location (Mullers & Tinbergen 2009). Thirty-six nests were chosen on Malgas Island and 25 on Bird Island with chicks ranging from approximately 2 to 6 weeks old. Both adults of a pair were captured by their neck using a hooked pole. They were individually marked (on the head or back) with picric acid. The nests were then monitored every hour from before sunrise to after sunset to calculate foraging trip duration (from the first check that the bird was recorded absent to the first check when it returned), attendance bout (from the first check that the bird was recorded present to the first check when it was recorded absent), trip frequency (number of trips per day), nest attendance (the fraction of time each adult was on the nest) and non-attendance (the fraction of time the chick was left unattended). Gannets do not forage at night

(Ropert-Coudert et al. 2004a), therefore if there was a difference in nest attendance between sunset and sunrise, the change was assumed to have occurred shortly after sunset (following Bijleveld & Mullers 2009). Monitoring was undertaken for 22 days on Malgas Island and 8 days on Bird Island. Differences in monitoring time were due to the logistical difficulties in getting to Bird Island.

b) Foraging areas and home ranges

GPS data loggers (Technosmart; 45 g including waterproof housing) were sealed in heat-shrinkable tubing (120 x 55 x 30 mm). The unit represents approximately 1.8% of the body mass of an adult gannet, which is below the 3% limit recommended for deploying loggers on flying birds (Phillips et al. 2003). Birds returning from a foraging trip were observed upon landing. If the bird greeted its partner and the nest contained a chick of at least 2 weeks old, the bird that had been on the nest was captured. A GPS logger was attached to the base of the tail (below the preen gland) on three central tail feathers with waterproof Tesa tape. This attachment method does little damage to the plumage and the tape can be removed entirely upon recapture (Wilson et al. 1997). Handling lasted between 4 to 10 min from capture to release. Nests were then monitored regularly from 6h00 to 19h00 (South African Standard Time) until the bird returned.

Foraging behaviour and habitat was inferred from GPS positions associated with diving behaviour. Previous studies on Cape gannet dives showed that the average dive durations are 2 - 5 s but can exceed 5 s (Ropert-Coudert et al. 2004b, Pichegru et al. 2007). When a GPS transmitter is submerged the signal is lost. In this study, dives were inferred from high-resolution GPS tracks (1 s) because dives correspond to interruptions of the signal received from the satellites. The time difference was computed between each location fix (1 s if the signal is recorded normally). Dives were defined as interruptions >1 s and <30 s; interruptions exceeding 30 s are more likely to be due to satellite signal reception problems. Dives were then assigned to the location fixes preceding the interruption of the signal.

From these data, the average foraging parameters (trip duration, foraging path length and maximum distance from the nest) were extracted. The total foraging area (home range) used by the birds was assessed using Minimum Convex Polygons (MCP - 100%), and the time spent diving per unit area with adaptive kernel analyses with the smoothing factor chosen according to the LCDV method (Girard et al. 2002). Analyses were conducted using Arcview GIS 3.2. Contour levels covering 50, 75 and 90% of foraging locations were estimated.

c) Packed cell volume (PCV)

Packed cell volume (PCV) or haematocrit is a measure of the volume of red blood cells relative to the volume of whole blood. Avian PCVs indicate the extent and efficiency of oxygen uptake (Ots et al. 1998) and can be used as an indicator of aerobic activity (and therefore foraging effort) in the weeks prior to sampling (Carpenter 1975). Low values may also indicate nutritional deficiencies of certain minerals and proteins (Coles 1997). Blood was taken from birds fitted with GPS devices as well as those that were marked for monitoring. Approximately 2 ml of blood was drawn from the tarsal vein, into a syringe rinsed with the anti-coagulant sodium heparin. The blood was transferred to a microtube and stored on ice. Aliquots of this blood were used for determination of PCV, stable isotope analysis, determination of heterophil to lymphocyte ratios and fatty acid analysis. Upon return to the field station, approximately 60 µl of blood was drawn into a capillary tube and sealed with non-absorbent modelling clay. Samples were stored at 4°C for up to 15 hr before spinning in a microhaematocrit centrifuge for 6 min at 18 000 rpm. The PCV was then measured to the nearest 0.1 mm with callipers. Two PCV measurements were taken per individual in order to calculate repeatability (after Lessells & Boag 1987).

d) Pelagic fish abundance

A sardine and anchovy spawner biomass survey was conducted by Marine and Coastal Management (MCM) between 11 October and 19 November 2009. There was a slight temporal mismatch between the timing of the acoustic surveys and the tracking of the gannets (Bird Island- acoustic

surveys 10 - 19 November 2009, tracking: 20 - 29 November; Malgas Island-acoustic surveys 19 - 29 October 2009, tracking: 21 October - 25 November 2009). The survey estimated the abundance of sardine and anchovy using a hydro-acoustic echosounder by conducting transects along the coast from Hondeklip Bay (west coast) to Port Alfred (south coast; Coetzee et al. 2009). Acoustic surveys were logged to a depth of 250 m, except off the shelf where the maximum depth was increased to 500 m. Full details of the survey method are given by Coetzee et al. (2009).

Diet

a) Stomach contents

Randomly selected gannets were captured by MCM staff at the edge of each colony with a hook immediately after returning from the sea. They usually regurgitated their stomach contents once inverted over a bucket. The breeding status of birds sampled was not known, but the diets of breeding and non-breeding birds do not differ (Berruti 1991). The regurgitated prey was identified and proportions by mass in the overall sample were estimated. On Malgas Island, diet samples were collected monthly in 2009 while on Bird Island, stomach contents were only collected in November 2009.

b) Stable Isotopes

Stable isotope analysis increasingly is being used in ecology to determine migration patterns, diet and establish trophic relationships among marine predators (Peterson & Fry 1987; Hobson et al. 1994; Hobson 1999). Conventional methods for determining diet, such as stomach samples or the collection of prey remains or pellets are limited because they reflect short term diet and are biased by the rapid digestion of soft-bodied prey (Hobson et al. 1994). Stable isotope analyses can complement these conventional techniques because the isotopic composition of consumer tissues reflects the diet at the time it was synthesised (Peterson & Fry 1987; Inger & Bearhop 2008). Different tissues are replaced at different rates and by choosing the correct tissue, the diet from different time periods can be estimated. Whole blood has a half-life turnover time ranging from 11 days (Japanese quail *Coturnix japonica*; Hobson & Clark 1992) to 15 days (great skua; Bearhop et

al. 2002). Feathers reflect the diet during the period that they were grown and because keratin is metabolically inert, feathers preserve this isotopic record (Inger & Bearhop 2008). During assimilation of food, biochemical processes favour the incorporation of different proportions of the heavy and light isotopes (Hobson & Clark 1992) causing consumer tissues to differ from their diet by a fractionation factor, which varies between tissues (Tieszen et al. 1983).

Samples of back feathers (5 from each bird) and blood were taken from the birds fitted with GPS devices as well as those for which body condition was measured. Approximately 180 µl of blood was spread thinly on glass slides and air-dried. Once dry, the blood was scraped into individually labelled microtubes. This method has been recommended as an alternative to storage in ethanol or with a NaCl solution, which may affect the $\delta^{13}C$ values (Bugoni et al. 2008). The feathers were washed in distilled water to remove any surface contamination and then cut finely using stainless-steel scissors. The five feathers taken from each bird were analysed together. The feathers and dry powdered blood did not require any further processing as feathers and avian blood generally have low lipid contents (Cherel et al. 2005).

Samples of anchovy, sardine, redeye and hake were collected by MCM during research trawls conducted in the southern Benguela in 2008. The samples were frozen within 30 min of capture. Samples of saury were taken from fresh fish in the diet samples of gannets from Bird and Malgas Islands during this study. Muscle samples from sardine, anchovy, hake, redeye and saury were freeze-dried and finely cut. A mathematical correction was applied, ([$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99$ X C:N]; following Post et al. [2007]) to the sardine samples as the carbon:nitrogen (C:N) ratios were above 3.5 (the lower limit for lipid extraction or mathematical correction suggested by Post et al. 2007).

Stable carbon and nitrogen isotope assays were performed on 0.6 mg subsamples of material, weighed into tin cups to an accuracy of 1 µg on a Sartorius micro balance. The samples were combusted in an NA 1500 NC elemental analyser (Fison's Instruments, Milan, Italy). The gases were passed

to a Finnigan Matt 252 IRMS (isotope ratio mass spectrometer) (Finnigan Matt, Bremen, Germany), via a Conflo III gas control unit (Finnigan Matt, Bremen, Germany). Results are expressed according to the standard delta notation in parts per thousand (‰):

$$\delta X = [(R_{sample}/R_{standard}) - 1) \times 1000]$$

Where X is the heavy isotope of the element in question (here ^{13}C or ^{15}N) and R is the ratio of the heavy to light isotope. $R_{standard}$ values are expressed relative to atmospheric nitrogen for ^{15}N and Pee-Dee Belemnite for ^{13}C. Internal laboratory standards used were Australian National University sucrose, valine (Sigma) and gelatine (Merck) and have been calibrated against the International Atomic Energy Agency standards.

To estimate the proportions of potential prey in the diet based on the isotopic signatures of the gannet tissues, I used a multisource stable isotope mixing model, SIAR (Stable Isotope Analysis in R; Jackson et al. 2009). For blood, a diet-tissue fractionation factor of 2.8 for nitrogen and 1.1 for carbon was applied and for feathers a factor of 4.6 for nitrogen and 2.1 for carbon was applied after Bearhop et al. (2002; data for great skuas). A standard deviation of 1‰ was used to account for differences between gannets and skuas (Votier et al. in press).

c) Fatty acid analysis

Fatty acid (FA) signatures are used as a tool for delineating marine food webs (review in Dalsgaard et al. 2003). Many FAs are readily transferred from prey to predators with little or no modification (e.g. Kirsch et al. 1998); the FA composition of a predator is therefore assumed to reflect, to some extent, a temporal integration of its diet over a longer time frame than stomach contents. Changes in diet can be detected using FA signatures in plasma between 5 and 10 days after a switch (Käkelä et al. 2005).

Aliquots (0.5 to 1.5 ml) of blood for fatty acid analysis were centrifuged at 6000 rpm for 5 min upon return to the field station. The plasma layer of each blood sample was added to test tubes containing 2 ml chloroform + 0.01% butylated hydroxytoluene, covered with nitrogen gas, stored at -4°C and then

at -20°C upon return to the mainland laboratory. Total plasma lipids were extracted using a modified Folch procedure (Folch et al. 1957; Parrish 1999) within a month of collection. Briefly, samples were extracted in 2:1 (v/v) chloroform:methanol solution and 0.9% KCl was added, resulting in the following solvent ratio - 8:4:3 chloroform: methanol: water + KCl. The lipid layers were removed and combined following each of two chloroform washes. Fatty acid methyl esters (FAMEs) were then prepared by heating the total lipid extracts suspended in dried methylene chloride at 100°C for 1 hour in the presence of sulphuric acid in methanol (adapted from Budge et al. 2006).

Gas chromatographic analyses of FAMEs were performed with a gas chromatograph (Hewlett Packard 5890 Series II) equipped with a ZB-WAXplus capillary column (30 m length, 0.25 mm internal diameter, 0.25 µm film thickness; Zebron Corporation) and a flame ionisation detector. Helium was used as carrier gas. The samples (1 µl aliquot each) were manually injected at 250°C with the oven set at 150°C. After 5 min, the oven temperature was raised to 225°C at 2.5°C/min and held for 9 min. The temperature of the detector was set at 260°C. Peaks were integrated using Clarity Lite (version 2.6) and identified by reference to authentic standards (33 components FAMEs standards and marine polyunsaturated FA, Supelco).
Each FA was reported as a proportion of the total FAs identified (%TFAs). FAs are reported in the shorthand form *x:aωb*, where *x* is the number of carbons in the acyl chain, *a* the number of double bonds, and *b* the position of the first double bond from the methyl end of the molecule.

Body condition

a) Morphological measurements

Birds which had been marked for nest monitoring were captured after spending the night on the nest, measured (culmen length to the nearest 0.1 mm and flattened wing cord to the nearest 1 mm) and weighed to the nearest 25 g on a 5 kg spring balance. This weight was assumed to be the weight of the bird with an empty stomach. A ratio body condition index was calculated by dividing body mass by wing length. There are problems with the

use of ratio indices of condition (e.g. they are not always size independent; Hayes & Shonkwiler 2001) but the ratio was calculated for comparison with other studies.

Pectoral muscle thickness varies with body mass in birds and reflects changes due to fasting and fuelling and is a good indicator of condition (Lindström et al. 2000). It is possible that pectoral muscles can be used as energy supplies for flight because birds can consume and replace pectoral muscle tissue rapidly (Lindström et al. 2000). Pectoral muscle thickness was measured using a portable ultrasound machine (SonoSite Titan). A small patch of feathers (approximately 2x2 cm) was removed from the chest, where the clavicle joins the sternum. The probe was placed transversally on the right pectoral muscle at a 90° angle to the sternum. The resulting image showed the curve of the sternum and coracoid joint. Muscle thickness was measured from the lowest point of the curve to the top of the muscle (to the nearest 1 mm). Pectoral muscle thickness of each individual was measured twice to obtain a measure of repeatability, calculated according to Lessells & Boag (1987). The procedure followed was similar to that of Dietz et al. (1999) who demonstrated significant repeatability.

b) Heterophil: Lymphocyte (H:L) ratio

Heterophils and lymphocytes are the most commonly occurring leucocytes in birds (Sturkie 1986). The ratio of heterophils to lymphocytes (H:L ratio) is increasingly being used by ecologists to assess stress in free-living vertebrates (Davis et al. 2008). The first, rapid (on the scale of minutes), response to stress is the release of glucocorticoid hormones (e.g. corticosterone in birds), while a secondary and slower response (0.5 - 2 hr) is a change in the H:L ratio (Gross & Siegel 1983, 1986). Chronic stress causes an increase in the numbers of heterophils and a decrease in the numbers of lymphocytes (Gross & Siegel 1983). H:L ratios have been shown to increase in response to food or water deprivation (Gross & Siegel 1983; Davis et al. 2000; Vleck et al. 2000; Ruiz et al. 2002), temperature extremes (McFarlane & Curtis 1989) and long-distance migrations (Owen & Moore 2006). Some of the advantages of using H:L ratios instead of corticosterone as a measure of

stress is that to accurately determine baseline levels of corticosterone, the blood sample needs to be taken within three minutes of capture. The assay for corticosterone in blood plasma is also expensive and time consuming. H:L ratios are a longer lasting and possibly more reliable indicator of stress than corticosterone (McFarlane & Curtis 1989).

Blood taken for determining PCV ratios was also used for determining the H:L ratio. Thin blood smears were prepared immediately upon return to the field station. These smears were air dried and then fixed in absolute methanol for 10 min and stored until staining 3 weeks later. Slides were stained for 45 min using Giemsa stain. The smears were examined towards the edge of the smear, where the red blood cells formed a monolayer, under oil immersion at 100x magnification. Cells were identified following Lucas and Jamroz (1961). Of the leucocytes, only heterophils and lymphocytes were counted as the other leucocyte types (basophils, eosinophils and monocytes) occur only rarely (Sturkie 1986). The H:L ratio was estimated from a sample of 100 leucocytes. The modified battlement method (*sensu* Bain 2006) was used to examine the smears, in an attempt to minimise bias due to the uneven distribution of leucocytes in the smear (Bain 2006).

c) Chicks

In order to compile growth curves, chicks from the monitored nests were measured (culmen and wing length) and weighed (<2 kg to the nearest 10 g and >2 kg to the nearest 25 g) every 5 days (n = 4 measurements at Malgas Island and 3 at Bird Island). Chicks were measured at approximately the same time of day (between 6h00 and 9h00 South African Standard Time) and in the same sequence at each island.

Statistical analyses

To compare variables between the two islands, I performed t-tests (sometimes on square root or log transformed data) or Mann-Whitney U-tests (where the data were not normally distributed). To compare nest attendance and dive duration, I used a linear mixed model with restricted maximum likelihood estimation. The model used nest attendance/dive duration as the

dependent variable, island as the factor and gannet ID as the subject. To compare body masses, I performed an analysis of covariance with mass as the dependent variable and wing and culmen lengths as covariates. I compared chick growth by calculating the difference in mass between two consecutive measurements and divided this by the number of days between measurements, which gives a growth in grams per day. I then performed a multi-level model with chick ID, chick age, and islands as levels. I compared the stable isotope signatures of carbon and nitrogen between the potential prey species using a Kruskal-Wallis ANOVA.

The plasma FA signatures of birds from Bird and Malgas Islands were compared using a correspondence analysis (CA) on arcsine transformed data. The FAs responsible for the variability between islands were identified using this CA. FAs that contributed a mean of less than 0.5% of total fatty acids to the profile were not included in statistical analyses because the precision of their determination is low.

Statistical programs used were SPSS 18.0, Statistica 8.0 and R 2.10.1 (Ihaka & Gentleman 1996). The threshold for statistical significance was 0.05 and mean values are given ± standard deviation.

Chapter 3: Results

Foraging behaviour

On Bird Island, I equipped 34 birds with GPS loggers and obtained 25 complete tracks (some birds stayed at sea for longer than the battery capacity of the logger). On Malgas Island, I equipped 30 birds with GPS loggers and obtained 21 complete tracks. The loggers were retrieved after a single foraging trip and all birds continued breeding normally. No difference was found in trip duration of the equipped birds and those that were used for behavioural monitoring for both Bird Island (equipped: 22.3 ± 8.1 h, non-equipped: 23.5 ± 18.7 h; U = 2416, p = 0.32) and Malgas Island (equipped: 17.4 ± 9.7 h, non-equipped: 16.4 ± 10.9 h; U = 9461, p = 0.571). Direct observations showed that gannets from both islands spent similar amounts of time at the nest (attendance bout; Table 1) but gannets from Malgas Island had lower nest attendance (fraction of the time spent at the nest; Table 1). This was because chicks at Bird Island were left unattended for a greater proportion of the time. Birds from Malgas Island made a greater number of trips per day (Table 1).

Gannets from Bird Island worked harder than did those from Malgas Island (Table 1). Although the foraging trip duration did not differ between the two islands, birds from Bird Island flew further from the colony and showed a greater foraging path length than birds from Malgas Island. The latter birds performed more dives per hour at sea than those from Bird Island, although the duration of dives was not different. PCV was greater at Bird Island than at Malgas Island (Table 2). The greater proportion of red blood cells in Bird Island gannets suggests that in the weeks prior to capture they were engaged in more aerobic activity (Carpenter 1975). A high repeatability was obtained for estimates of PCV (r = 0.83).

Table 1: Foraging characteristics of adult Cape gannets, from behavioural monitoring (trip frequency, attendance bout, nest attendance and non-attendance) and GPS tracking (trip duration, maximum distance from colony, foraging path length, number of dives per trip hour and mean duration of dives). Significant differences are indicated in bold.

	Bird Island			**Malgas Island**			**Test**	**p**
Parameter	mean ± sd	n	Range	mean ± sd	n	Range	**statistic**	
Trip frequency (number/day)	**0.5 ± 0.1**	**52**	**0.3- 0.8**	**0.7 ± 0.1**	**72**	**0.5 - 0.9**	**2818**	**< 0.001**
Attendance bout (h)	18.2 ± 12.3	52	2 - 74	16.1 ± 10.0	72	1 - 49	91441	0.234
Nest attendance (%)	**41.7 ± 13.8**	**52**	**7 - 66**	**48.6 ± 8.2**	**72**	**25 - 72**	**2483**	**< 0.001**
Non-attendance (%)	**16.6 ± 12.3**	**26**	**0 - 38**	**2.6 ± 4.4**	**36**	**0 - 13**	**137**	**< 0.001**
Trip duration (h)	22.3 ± 8.1	25	7.7 - 45.7	17.4 ± 9.74	21	4.4 - 44.4	3.66	0.062
Max. distance from colony (km)	**149 ± 70**	**25**	**41 - 254**	**86 ± 39**	**21**	**39 - 220**	**8.78**	**0.003**
Foraging path length (km)	**536 ± 236**	**25**	**205 - 923**	**347 ± 140**	**21**	**135 - 776**	**9.93**	**0.003**
Number of dives per trip h	**2.8 ± 1.6**	**25**	**1.0 - 8.9**	**3.8 ± 1.5**	**21**	**1.2 - 7.2**	**5.86**	**0.02**
Mean duration of dives (s)	7.7 ± 4.4	25	3.4 - 12.2	7.1 ± 4.1	21	5.4 - 13.7	0.661	0.509

All tracked gannets from Bird Island travelled south west and foraged in an area of approximately 19 500 km^2 (Figure 1). Several gannets, for which the GPS logger recorded a complete trip, flew approximately 300 km. Tracked birds from Malgas Island foraged over an area of approximately 19 200 km^2, with most foraging to the south west of the island approximately 100 km offshore (Figure 1). Two birds travelled as far as the Cape Peninsula and Danger Point, more than 200 km from Malgas Island (Figure 1) but the other 19 birds remained within 100 km of the island.

The diving behaviour of tracked gannets from Bird Island was associated with the presence of anchovy to the south west of Bird Island (Figure 2), although these fish occurred at lower densities (0.01 - 0.1 g cm^{-2}) than on the west coast. Even though the highest densities of anchovy on the west coast were recorded around Cape Town and the Cape Peninsula, no anchovy were detected where most gannets from Malgas Island concentrated their foraging effort (Figure 2). There were no sardines recorded within the foraging range of gannets from Bird Island at the time of the acoustic surveys (Figure 2). Sardines were recorded off the west coast, but at low densities and gannets did not seem to be targeting these areas (Figure 2).

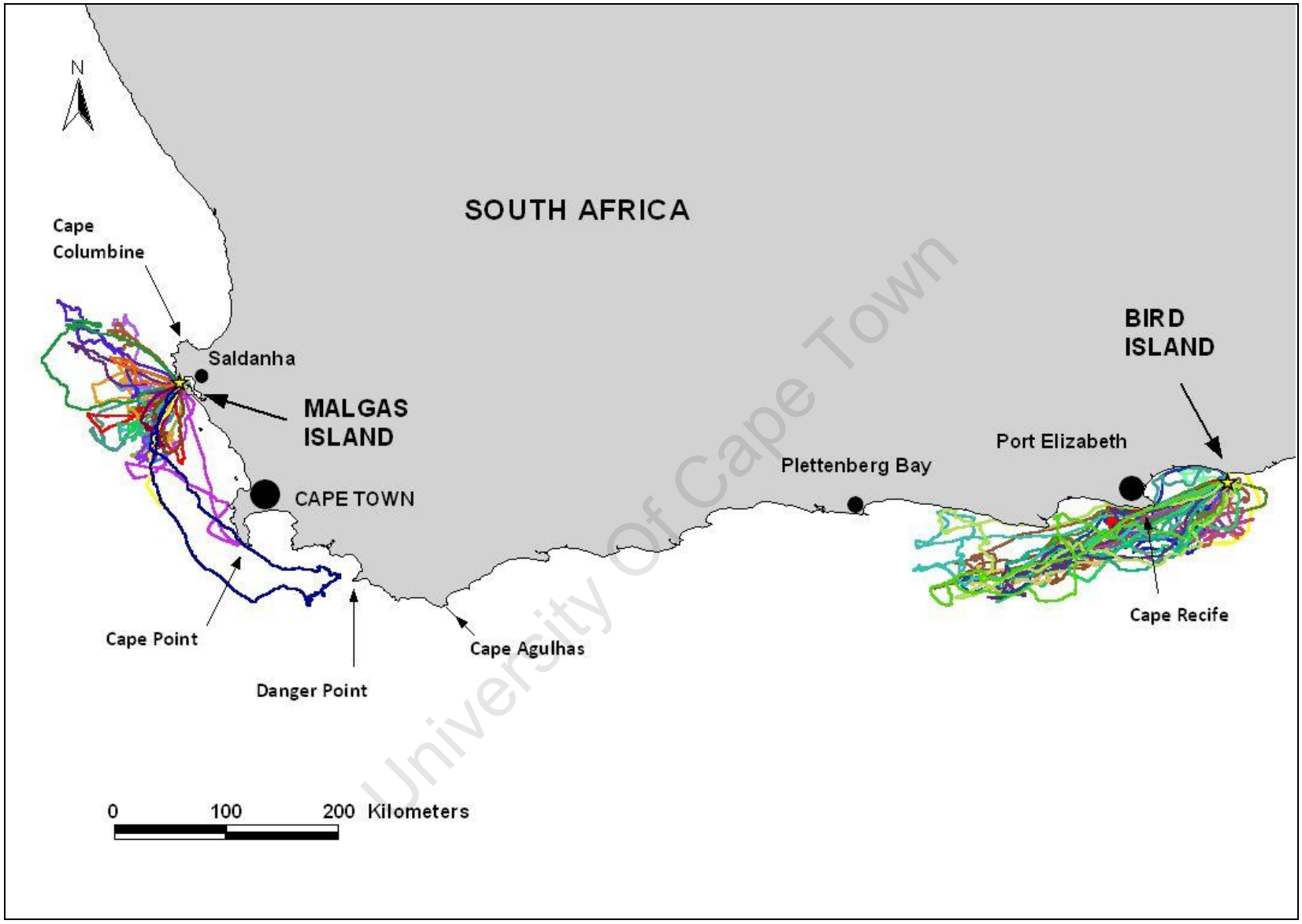

Figure 1: GPS tracks of foraging birds (n= 21 from Malgas Island and 25 from Bird Island). Each line represents the complete track of a single bird. Island colonies shown as yellow stars.

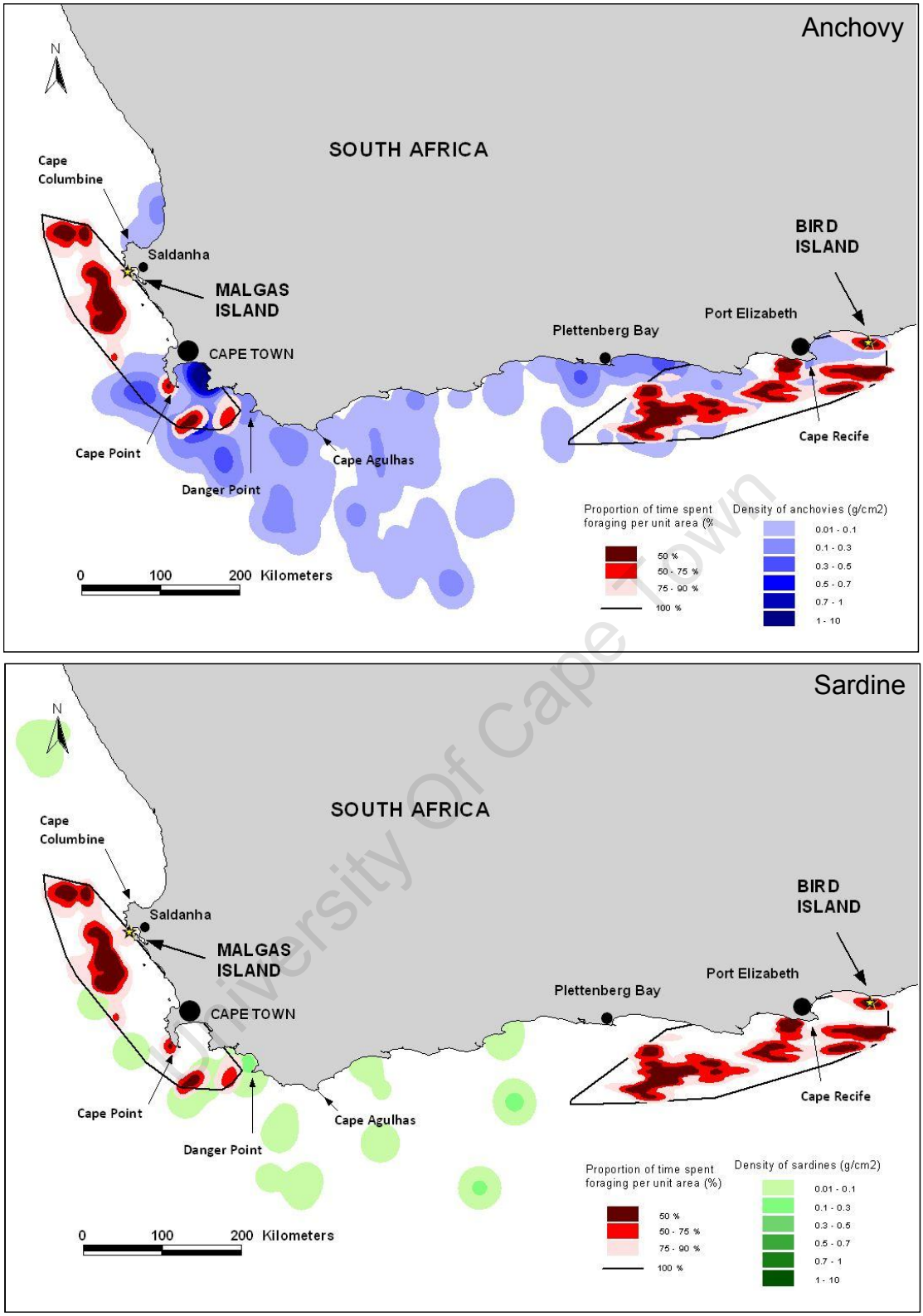

Figure 2: Foraging ranges, calculated from the density of GPS points associated with diving, of birds from Bird and Malgas Islands in relation to the abundance of anchovy (top) and sardine (bottom).

Diet

In November 2009, gannets on Bird Island fed mainly on sardine (48% by mass, n = 28 regurgitates) with anchovy contributing about a quarter to the diet (24%; Figure 3). Hake, redeye and saury contributed relatively little to the diet (14%, 9% and 5%, respectively). Sardine accounted for 76% (by mass, n = 50 regurgitates) of the prey of gannets from Malgas Island (Figure 3). The other two species that contributed significantly to their diet were hake and saury (11% and 10%, respectively). From January to April 2009, saury dominated the diet of gannets at Malgas Island (62-90% by mass), with no hake being consumed (Figure 4). In the non-breeding (winter) months of June to August, gannets ate hake almost exclusively (Figure 4). From September to December, sardines increased in importance to a maximum of 76% in November, while in December sardine and saury made up most of the diet, with no hake being found in the stomach samples (Figure 4).

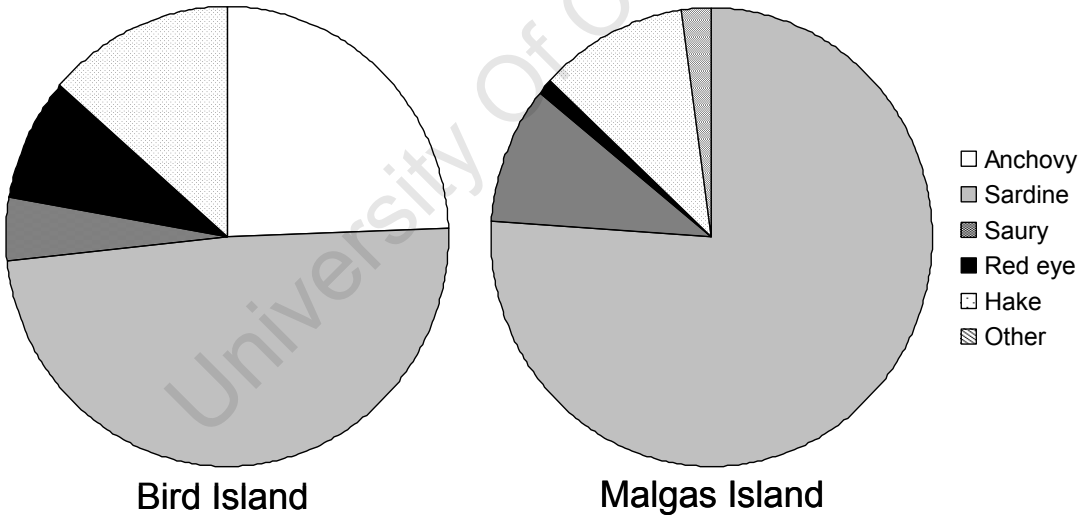

Figure 3: Diet composition (% contribution by mass) of gannets from Bird (n = 28 regurgitations) and Malgas Islands (n = 50 regurgitations) during November 2009.

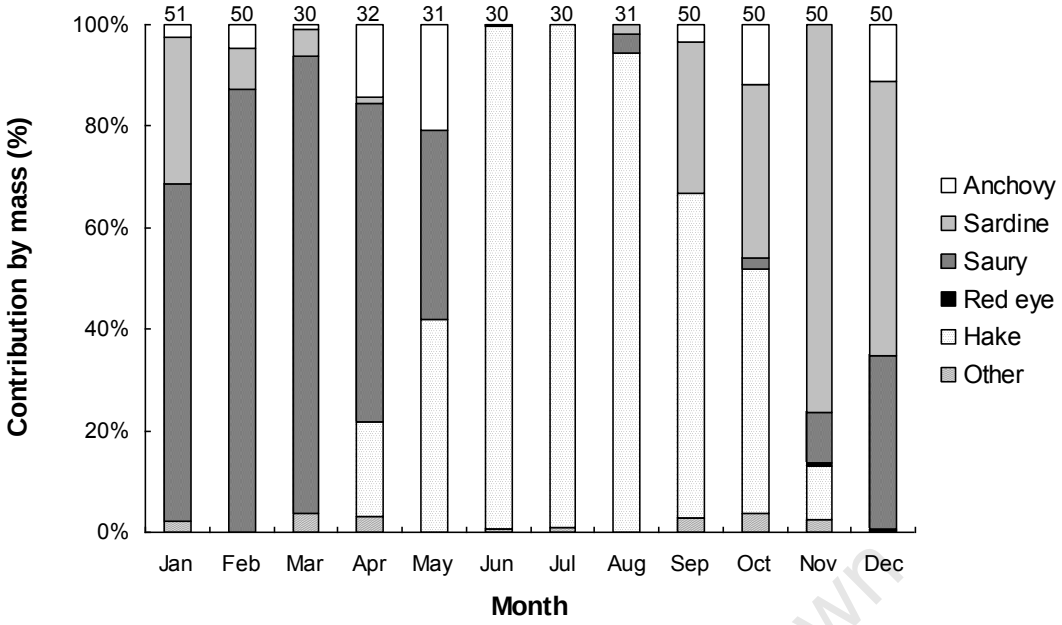

Figure 4: The monthly diet composition of gannets from Malgas Island in 2009 (MCM unpublished data). The numbers at the top of the bars indicate the number of birds sampled.

The isotopic signatures of carbon and nitrogen were significantly different between the two islands for blood and feathers (Figure 5, Table 3). Tissues from gannets from Bird Island were consistently more depleted in ^{13}C and ^{15}N than those from Malgas Island. The mean carbon to nitrogen (C:N) ratios in the blood were less than 3.5 (Bird Island: 3.32 ± 0.04, Malgas Island 3.31 ± 0.06) indicating that the lipid content was low and hence lipid extraction or mathematical correction was not necessary (Post et al. 2007).

Table 3: The mean stable-carbon and stable-nitrogen signatures of blood and feathers from adult gannets from Bird and Malgas Islands.

		Bird Island			Malgas Island			Test	
Isotope	**Tissue**	mean	n	Range	mean	n	Range	**statistic**	**p**
	Blood	-16.1	42	-16.5 - -15.5	-15.8	38	-16.6 - -14.9	-4.599	< 0.001
$\delta^{13}C$	Feathers	-14.5	27	-15.2 - -13.9	-14	31	-14.6 - -13.4	-6.045	< 0.001
	Blood	13.4	42	13.1 - 14.3	13.9	38	13.2 - 15.2	-6.314	< 0.001
$\delta^{15}N$	Feathers	14.1	27	13.5 - 14.6	14.8	31	14.3 - 15.6	-10.213	< 0.001

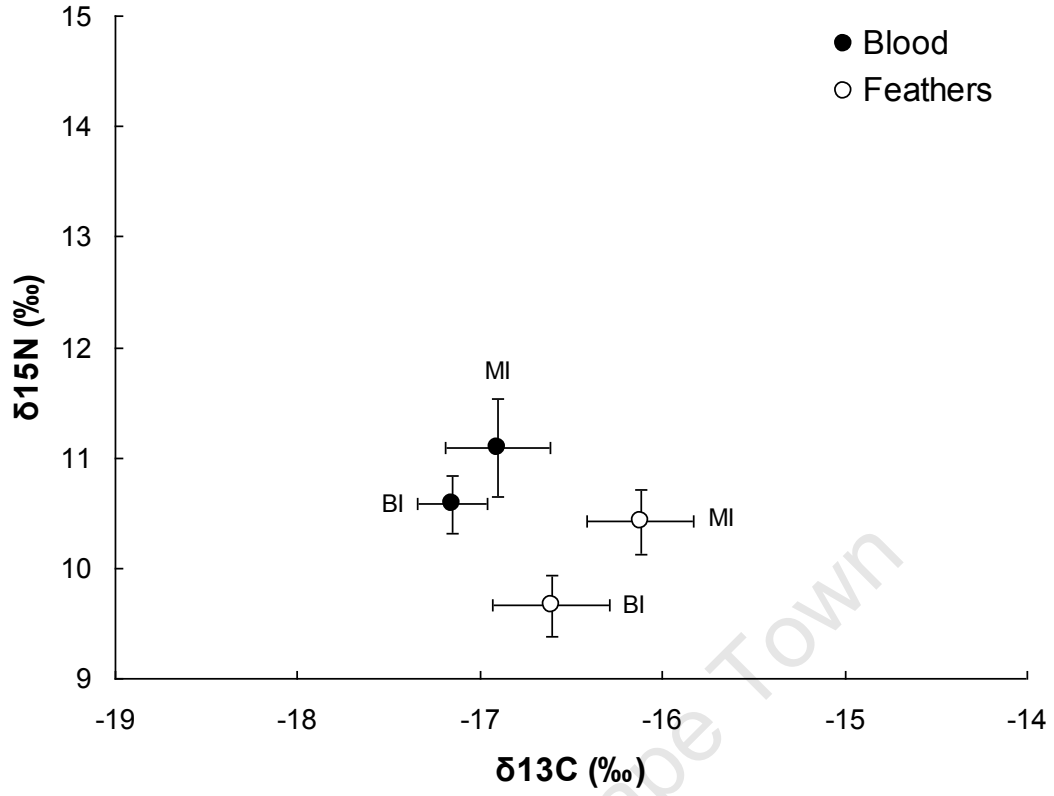

Figure 5: Stable carbon ($\delta^{13}C$) and stable-nitrogen ($\delta^{15}N$) isotope values (mean ± standard deviation) of blood and feathers of adult gannets at Bird (BI) and Malgas Islands (MI).

Hake was significantly more enriched in ^{15}N compared the small pelagic fish (anchovy, redeye, sardine and saury; Figure 6; $H_{4,}$ = 68.49, $p < 0.001$). The carbon signatures of hake and sardine were more depleted in ^{13}C than those of anchovy, redeye and saury (Figure 6; H_4 = 44.50, $p < 0.001$).

Outputs from the SIAR mixing model for blood (i.e. representing diet over 3 – 5 weeks) suggest that gannets at the two islands ate similar proportions of anchovy (29% at Bird Island and 24% at Malgas Island) and sardine (20% at Bird Island and 21% at Malgas Island; Figure 7), although those at Malgas Island took a greater proportion of hake (11% compared to 2% at Bird Island). Saury contributed more to the diet of gannets at Bird Island than those from Malgas Island (31% and 23%, respectively).

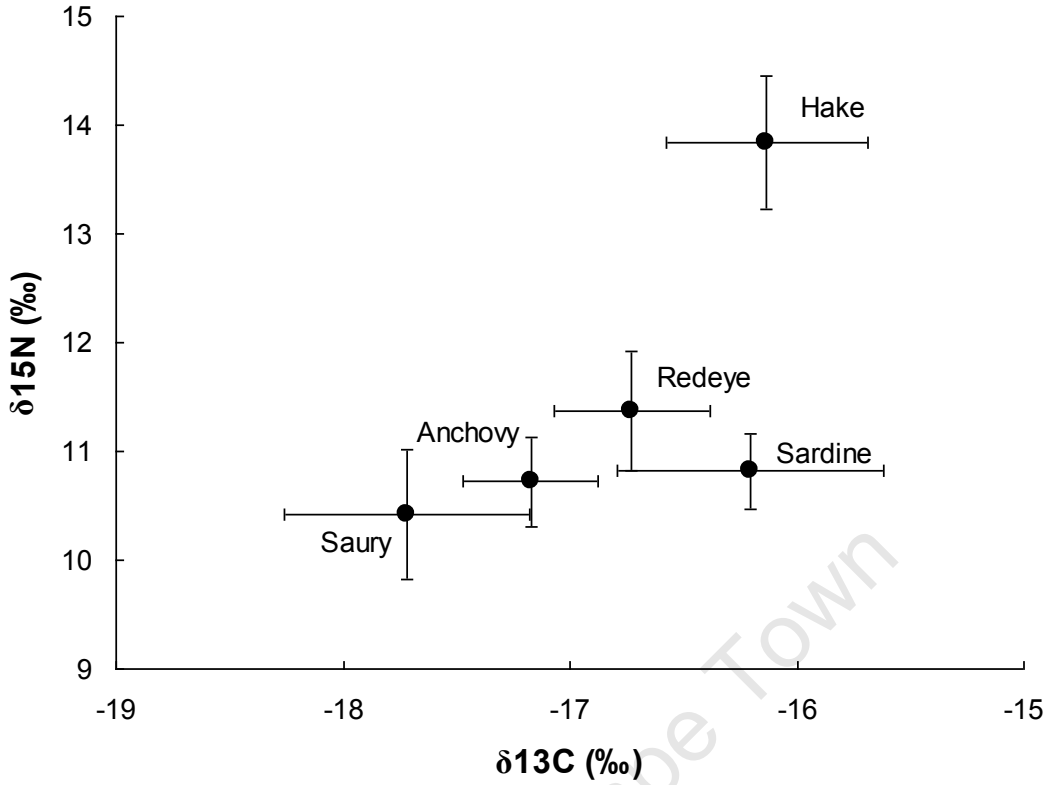

Figure 6: Stable-carbon ($\delta^{13}C$) and stable-nitrogen ($\delta^{15}N$) isotope values (mean ± standard deviation) of potential prey species of Cape gannets (anchovy n = 10, hake n = 45, redeye n = 10, sardine n = 16 and saury n = 7).

The results from the feathers (a signal from the period of feather growth, any time in the previous 10 months) suggest that gannets from Bird Island fed mostly on sardine (35%) and anchovy (24%). Redeye and saury were estimated to contribute equally to the diet while hake was estimated to contribute 4% (Figure 7). Gannets from Malgas Island apparently had fed predominantly on sardine (59%), with very little hake (1%). Anchovy, saury and redeye decreased in proportion compared to the estimates for blood (Figure 7).

Twelve FAs were found at levels exceeding 0.5% of total FAs (Table 4). Saturated fatty acids (SFAs) and polyunsaturated fatty acids (PUFAs) were more common than monounsaturated fatty acids (MUFAs), and no difference was found between birds from different islands, taking into account those FA

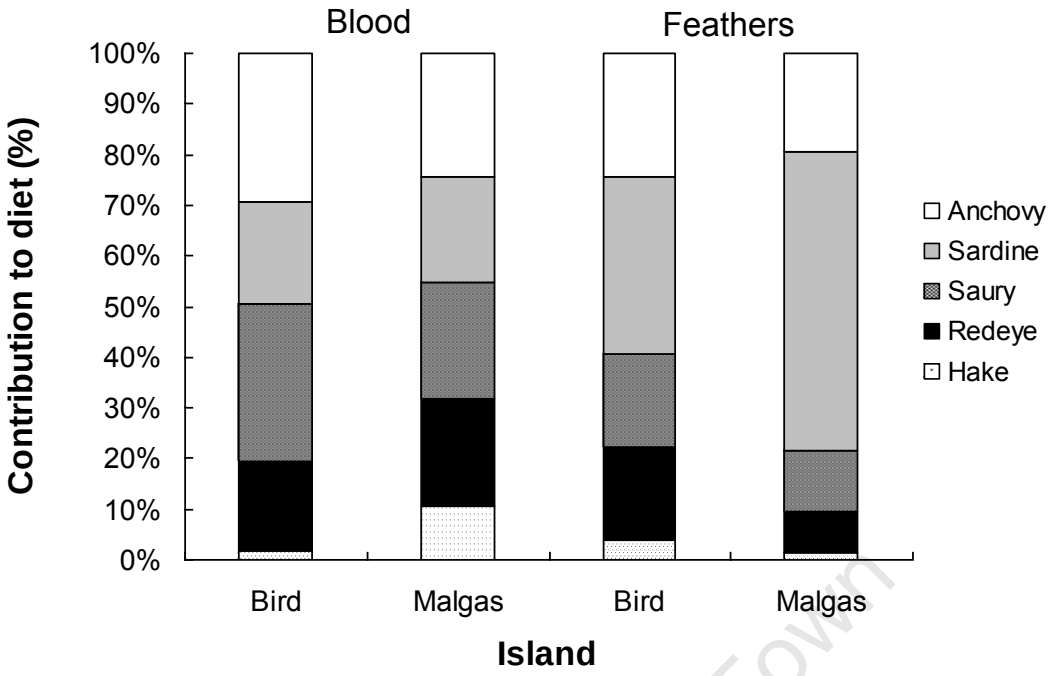

Figure 7: The contribution of potential prey species (anchovy, sardine, saury redeye, and hake) to the diet of Cape gannets, based on an isotope mixing model using isotopic signatures of potential prey and gannet blood and feathers.

classes (SFA: t_{33} = 0.120, p = 0.905); PUFA: t_{33} = -0.587, p = 0.561); MUFA: U = 140.5, p = 0.751). Palmitic acid (16:0; 21% of total FAs) dominated the plasma samples at both islands, followed by 18:0 (18% of total FAs), 20:4ω6, 20:5ω3, 22:6ω3 and 18:1ω9 (all > 10% of total FAs). The FA segregation of the samples is illustrated by a correspondence analysis where the two first axes explained 74 % of the total inertia (Figure 8). The samples from the two islands were mainly separated by their contents in 20:5ω3 (greater in Malgas Island samples t_{33} = -5.16, p < 0.001), 20:4ω6 and 18:2ω6 (greater in Bird Island samples, although the latter FA was only marginally significant, t_{33} = 6.96, p < 0.001 and t_{33} = 1.97, p = 0.057, respectively). Moreover, Malgas Island samples had higher ratios of Σ ω3/Σ ω6 (t_{33} = -5.77, p < 0.001) and 20:5ω3/20:4ω6 (t_{33} = -5.93, p < 0.001) than Bird Island samples. Bird Island had lower proportions of 17:0 (t_{33} = -3.14, p = 0.004) and 16:1ω7 (t_{33} = -2.45, p = 0.02) than Malgas Island, while Malgas Island had lower proportions of

18:1ω7 (t_{33} = 2.07, p = 0.046), although these FAs did not drive the segregation (Table 1; Figure 8).

Table 4: Fatty acid composition (mean ± standard deviation %) in the plasma of Cape gannets from Bird and Malgas Islands (n= 15 and 20, respectively). Only fatty acids that exceeded 0.5 % of the total FAs are listed. FAs are abbreviated as follows- [carbon number]:[number of double bonds] ω[position of the first double bond calculated from the methyl end]. SFAs: saturated fatty acids, MUFAs: monounsaturated fatty acids, PUFAs: polyunsaturated fatty acids. *: p < 0.05, **: p < 0.01, ns: not significant

Fatty acid	Bird Island (n = 15)	Malgas Island (n = 20)	Significance
14:0	1.00 ± 0.45	1.24 ± 0.59	ns
16:0	20.81 ± 3.57	20.36 ± 3.31	ns
17:0	0.45 ± 0.07	0.52 ± 0.07	**
18:0	18.02 ± 1.59	17.93 ± 1.19	ns
SFAs	***41.67 ± 4.21***	***41.50 ± 3.73***	ns
16:1ω7	1.93 ± 0.44	2.29 ± 0.42	*
18:1ω9	11.17 ± 2.12	10.66 ± 1.57	ns
18:1ω7	2.26 ± 0.80	1.87 ± 0.23	*
MUFAs	***16.86 ± 2.24***	***16.15 ± 1.45***	ns
18:2ω6	0.70 ± 0.25	0.58 ± 0.09	ns
20:4ω6	15.34 ± 2.20	10.25 ± 2.10	**
20:5ω3	9.40 ± 3.05	14.88 ± 3.15	**
22:5ω3	2.04 ± 0.56	2.15 ± 0.45	ns
22:6ω3	11.57 ± 2.98	11.20 ± 2.12	ns
PUFAs	***41.47 ± 4.64***	***42.35 ± 4.16***	ns
Others	*5.29 ± 0.98*	*6.03 ± 0.84*	ns
Σ ω3/Σ ω6	***1.39 ± 0.36***	***2.49 ± 0.67***	**
20:5ω3/20:4ω6	***0.63 ± 0.23***	***1.55 ± 0.56***	**

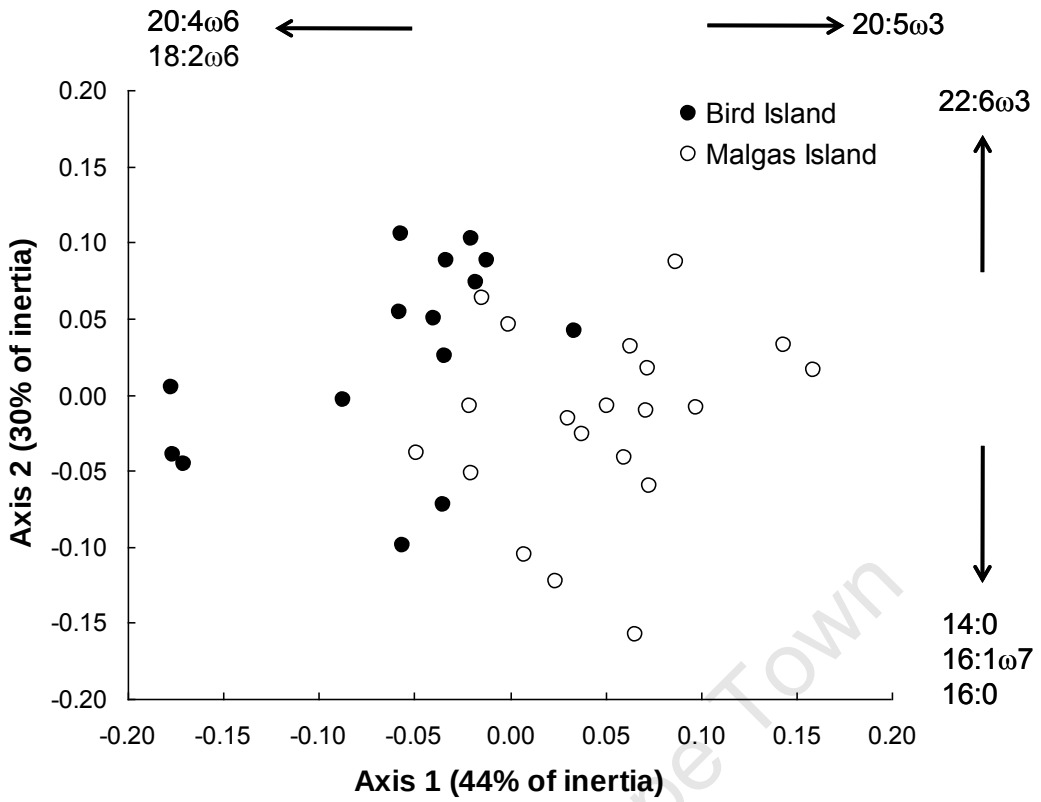

Figure 8: Correspondence analysis of fatty acid compositions of gannet plasma samples. Arrows indicate fatty acids contributing most to the distribution of birds along each axis

Body condition

Repeatability of pectoral muscle thickness measurements was high (r = 0.97). The pectoral muscle thickness of gannets from Malgas Island averaged slightly greater than those from Bird Island, but this was not significant (Table 2). There was no difference in body mass (after controlling for structural size) between the two islands (Table 2). The ratio of body mass to wing size was slightly greater for gannets from Malgas Island, but this was only marginally significant (Table 2). There was no difference in the H:L ratio of gannets on Malgas and Bird Islands (Table 2), suggesting that there is no difference in the stress levels or body condition of gannets between the two islands. However the H:L data were highly variable (coefficient of variation 43 - 44%). Other studies have found a high degree of repeatability and low variability

using this method (Moreno et al. 1998; Plischke et al. 2009), which suggests that the method used in the present study needs to be refined.

The chicks measured to estimate growth rates were still in the linear phase of their growth curve (Figure 9). Chicks from Bird Island (60.6 ± 42.4 $g.d^{-1}$) grew more slowly than those from Malgas Island (62.1 ± 30.6 $g.d^{-1}$) but the age-specific growth rates did not differ (χ^2 = 0.837, p =0.360; n = 24 for both islands)

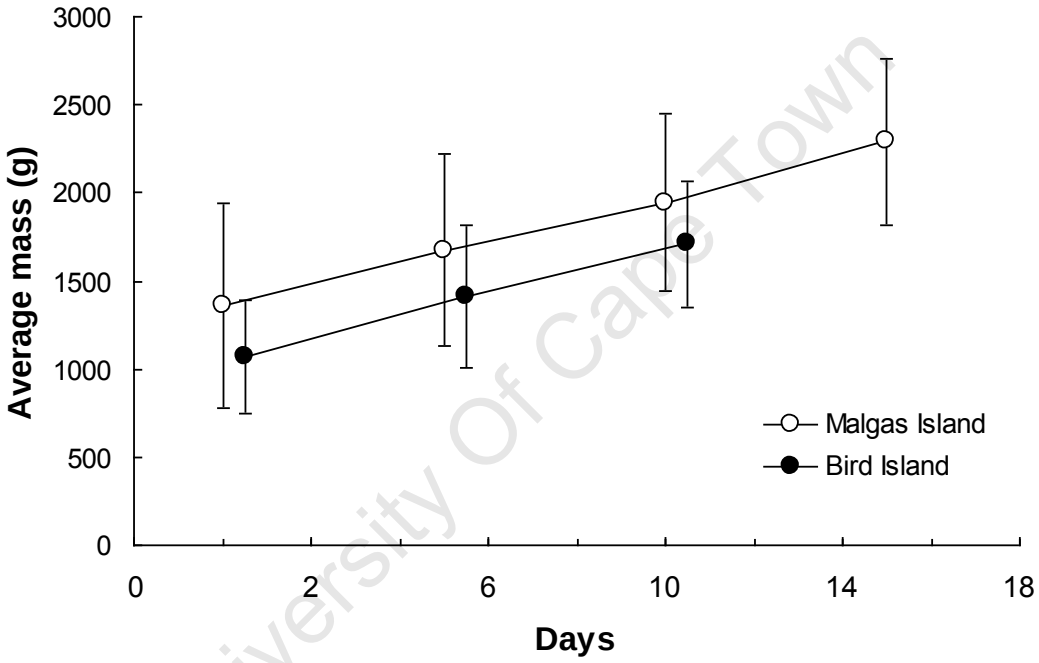

Figure 9: The mean (± standard deviation) change in average mass of chicks from Bird and Malgas Islands (n = 24 for each island) over successive five day intervals.

Table 2: The morphological and body condition parameters of adult Cape gannets. Significant differences are shown in bold.

Parameter	Bird Island			Malgas Island			Test statistic	p
	mean ± sd	n	Range	mean ± sd	n	Range		
Body mass (g)	2556 ± 176	41	2125 - 2950	2590 ± 162	38	2325 - 2900	2.401	0.125
Wing (mm)	480 ± 10.2	41	455 - 505	473 ± 7.2	38	454 - 488		
Culmen (mm)	90.3 ± 4.01	41	83.5 - 99.8	89.2 ± 2.93	38	83.6 - 95.0		
Mass:wing	5.3 ± 0.4	41	4.4 – 6.0	5.5 ± 0.3	38	4.9 – 6.2	-1.87	0.065
Pectoral muscle thickness (cm)	1.6 ± 0.12	25	1.3 - 1.9	1.7 ± 0.16	25	1.4 - 2.1	1.71	0.093
Heterophil: Lymphocyte	3.2 ± 1.40	30	1.1 - 6.7	2.9 ± 1.25	30	1.3 - 8.1	0.844	0.402
Packed cell volume (%)	**55.3 ± 4.75**	**30**	**41.2 - 63.9**	**53.0 ± 3.82**	**29**	**43.3 - 60.0**	**286**	**0.024**

Chapter 4: Discussion

This study assesses adult Cape gannet body condition in relation to their diet. There are however some limitations to the body condition measures used. Body condition is determined by a number of factors including nutritional state, prevalence of parasites and the presence of stressors (for example extreme climatic conditions or reproductive effort; Quillfeldt et al. 2004). Measures of body condition usually are based on morphological indices, either ratios of body mass to some measure of size (e.g. wing or culmen length) or analysis of residuals (e.g. residuals from the regression of mass on length; Hayes & Shonkwiler 2001). The ratio method has been criticised because many of these ratios are not independent of size (Hayes & Shonkwiler 2001). The analysis of residuals has been criticised for violating the assumptions underlying the use of this method (i.e. independence of body size and mass, no correlation between size relative to shape and the parameter against which the residuals are analysed; Green 2001) and because of statistical problems with performing further tests (e.g. analysis of variance) on these residuals (Garcia-Berthou 2001). Comparing body mass through an analysis of covariance (ANCOVA) (i.e. controlling for structural size) is another common method and one that avoids the above pitfalls (Garcia-Berthou 2001). Body mass was compared using ANCOVA in this study, although a ratio index was also calculated for comparison with other studies.

Body condition is also measured through various physiological and health-state indices, such as blood plasma biochemistry and haematology (Quillfeldt et al. 2004). Heterophil to lymphocyte ratios have been used extensively to measure chronic stress in domestic poultry (Gross & Siegel 1983, 1986) but this ratio also has been used in free-living birds as an indicator of stress and body condition as there is a negative relationship between body condition and H:L ratio (Quillfeldt et al. 2008, Plischke et al. 2009). Avian H:L ratios are generally less than one (Sturkie 1986), indicating a greater number of lymphocytes. In this study H:L ratios were all greater than one (range 1.1 – 8.1). Work (1996) and Newman et al. (1997) report reference values >1 for

pelecaniform species: great frigatebird *Fregata minor*, pelagic cormorant *Phalacrocorax pelagicus* and red-footed booby *Sula sula* (range: 1.8 – 5.9; Work 1996, Newman et al. 1997). Because the H:L values reported here are highly variable, more blood cell counts should be performed on Cape gannets in both the breeding and non-breeding seasons and comparisons should be made between the sexes to determine the normal range of values for this species.

This was the first attempt to quantify adult body condition using pectoral muscle thickness in Cape gannets or any sulid. The difference in average pectoral muscle thickness between the two islands was small (Table 2) and it is not known whether this difference has any significance in terms of flight capabilities. Birds can use muscle tissue as an energy source during flight and replace the tissue rapidly (Lindström et al. 2000) thus it is possible that gannets from Bird Island have thinner pectoral muscles than those from Malgas Island as a result of their greater foraging effort (Table 1). More research needs to be conducted into the effects changes in muscle thickness have on the health and condition of gannets.

Availability of gannet food resources

For the first time in several years gannets on the west coast of South Africa were not feeding primarily on fishery wastes during the 2009 breeding season (Mullers et al. 2009; Pichegru et al. 2009a). Sardine and anchovy stocks do not seem to have been more abundant in 2009 than the previous seasons but 2009 was the first year since 1996 that more than half of the sardine and anchovy biomass occurred west of Cape Agulhas (Coetzee et al. 2009). Support for this inference comes from isotopic signatures of blood and regurgitated diet samples.

The overall abundance of sardine and anchovy in 2009 (4.3 million t; Coetzee et al. 2009) was similar to the abundance in 2005 (4.1 million t; Coetzee et al. 2009), when Pichegru et al. (2007) found that gannets from Malgas Island fed on a large proportion of fishery waste (92% by mass). Yet the distribution of sardine and anchovy was different. In 2005 there were patches of sardine and

anchovy within 50 km of Bird Island (Pichegru et al. 2007), while the closest patches of these species were over 200 km away from Malgas Island. In 2009, there were several low density patches of sardine within approximately 50 km and anchovy within 100 km of Malgas Island (Figure 2). In 2009, the availability of sardine near Bird Island was low (no sardine within approximately 400 km), although there were some anchovy patches at low density. The large proportion of sardine found in the diet samples of gannets from Malgas Island suggests that despite the scarcity prey, gannets are highly successful predators that can find fish when humans cannot. Great cormorants (*Phalacrocorax carbo)* are also highly successful at finding prey when human prey abundance estimates are low (Grémillet et al. 2004a). Seabird abundance, breeding success and diet can be used to monitor fish abundance (Furness & Camphuysen 1997) and previous studies have suggested that the abundance of anchovy or sardine in the diet of Cape gannets reflects the trend in the size of the stock, especially when the biomass is low and acoustic surveys are least reliable (Berruti & Colclough 1987; Adams & Klages 1999). The large proportion of sardines in the diet of gannets on the west coast in November may also mean that sardines are more abundant than acoustic surveys suggest. The acoustic survey represents a limited view of fish distribution as it is conducted over a one month period and the surveys around the two colonies did not overlap entirely with the periods of tracking at the colonies (see Methods).

Gannet diet

Stable isotope analyses can provide estimates of the diet and distribution of seabirds that would otherwise be difficult to determine (Peterson & Fry 1987; Hobson 1999) but there are potential problems with the use of this method. The gannet isotopic values for blood and feathers are similar to those of Jaquemet & McQuaid (2008), in that Bird Island samples are more depleted in both ^{13}C and ^{15}N. These differences in $\delta^{13}C$ and $\delta^{13}N$ could be attributed to differences in diet or differences in biogeographic regions along the coast of South Africa (Hill et al. 2006; Jaquemet & McQuaid 2008). Malgas Island is in the productive Benguela ecosystem, which is influenced by seasonal upwelling, whereas the marine environment around Bird Island is influenced

by the warm, less productive Agulhas Current (McQuaid & Payne 1998). Enrichment in stable carbon and nitrogen isotopes has been linked to upwelling activity (Naidu & Niitsuma 2004; Hill et al. 2006), which could explain why Malgas Island samples were more enriched in both ^{13}C and ^{15}N. The results from isotopic mixing model SIAR (Jackson et al. 2009), used to estimate the proportional contribution of possible gannet prey items may have been confounded by the differences in biogeographic regions, as the potential prey were not sampled extensively enough from different locations along the coast. Another factor influencing the SIAR analysis could be the diet-tissue fractionation factors used. Previously published tissue-specific fractionation factors vary widely among species (Cherel et al. 2005; Becker et al. 2007) and especially for $\delta^{13}C$ (Becker et al. 2007). Additional research is needed to establish fractionation factors specifically for Cape gannets. The factors used in this study were based on captive great skuas fed on a diet of sprat (*Sprattus sprattus*; Bearhop et al. 2002) and although a measure of variation was included in the analysis a difference between the two species could have affected the results.

Despite these problems, the diet estimates from blood isotopic signatures were similar to the stomach samples taken in November 2009. Gannets from the two islands had similar diets over the short term, although hake made a greater contribution to the diet of gannets from Malgas Island (Figure 7). However, the diet estimates based on feather isotopic values, do not match the stomach samples for Malgas Island (stomach samples from Bird Island could not be collected for much of the year). Cape gannets do not have a clear moult pattern, with body feathers being replaced gradually from about October to June or July (Rand 1959). All the feathers taken from one individual in this study were pooled because of the difficulty of assigning feathers to a specific growth period. This means that the isotopic signature of the feathers could indicate the diet at any time from November 2008 to July 2009. The results from the isotope mixing model suggest that sardine made up approximately 60% of the diet of gannets from Malgas Island. This is a surprising result as the diet samples from most months in 2009 contained mostly saury (January to April) or hake (May to October; Figure 4). One

potential problem with the diet sampling is that regurgitations collected during the non-breeding season (winter) are taken from birds roosting ashore. Gannets can disperse widely during the non-breeding season and diet samples from birds that are moulting may not necessarily be collected, which could explain the mismatch between diet samples and estimates from feather isotopic composition. Primary feathers may offer a better source of dietary information as they display a more predictable moult pattern (Crawford 2005).

Differences also were detected in fatty acid (FA) signatures between the two islands. There are several hypotheses to explain the observed differences: (1) differences in the diet (different prey species targeted) or (2) birds from both islands forage on the same prey species but these species have different signatures on south and west coasts. The diet hypothesis could be supported by the ratio 20:5ω3/20:4ω6, in addition to statistical difference in the proportions of individual FAs. Fish that feed on detritus or are top predators are normally rich in 20:4ω6 (Kuusipalo & Käkelä 2000). For example, captive herring gulls (*Larus argentatus*) fed on a diet of demersal fish had a greater ratio of 20:4ω6/20:5ω3 than those fed on pelagic species (Käkelä et al. 2005). In this study, gannets from Bird Island had greater levels of 20:4ω6 (and therefore a lower ratio of 20:5ω3/20:4ω6), which is counter-intuitive, as these birds are not expected to feed on fishery wastes (which consist of demersal, predatory fish). FA signatures of fish species depend on their prey and their environment (Dalsgaard et al. 2003) so differences in the FA signatures within species between south and west coasts cannot be excluded as the two coastlines are influenced by different currents (McQuaid & Payne 1998) and organisms on the south and west coasts may have biogeographically distinct food sources available to them (Hill et al. 2006). The FA signatures of the potential prey of Cape gannets have not yet been determined. More lipid studies of fish are necessary to provide support for one of the above hypotheses.

Gannet body condition

The diet of breeding gannets on the west coast was dominated by fishery waste (hake) and saury from 2004/2005 to at least 2007/2008 (Mullers et al. 2009; Okes et al. 2009; Pichegru et al. 2009a). The diet of gannets on the west coast in 2008 is not known but the abundance of pelagic fish was lower in 2008 than in 2009 (Coetzee et al. 2009) so it is probable that gannets were feeding on fishery waste in 2008 as well. Thus gannets from Malgas Island probably have been feeding on a mixture of hake and saury during the breeding season for about 5 years. Hake and saury have lower mass specific energy contents than sardine (25% and 14%, respectively; Pichegru et al. 2009a) so feeding extensively on these species over several years may be expected to have affected the body condition of gannets on the west coast. However, the average pectoral muscle thickness, body mass and condition index of gannets from Malgas Island was not lower than gannets from Bird Island, which primarily feed on natural prey.

It is possible that the presence of saury in the diet, despite being lower in energy content than sardine and anchovy (Pichegru et al. 2009a), helped adults maintain their body condition in the absence of sardine and anchovy. It also may be that there is no long term effect of fishery wastes on adult Cape gannet body condition. There are two potential reasons for this. Firstly, adults probably vary their reproductive investment in relation to foraging conditions. When food is scarce they may defer breeding to enhance their own condition and survival. Life history theory predicts a trade-off between the current reproductive effort and costs to survival (Williams 1966, Stearns 1992). Seabirds are generally long-lived, have high survival and low annual reproductive output (Stearns 1992). It is likely that in years with low prey availability, adult Cape gannets decrease their reproductive effort if their body condition becomes too low. It is likely also however that there is a body condition threshold, below which birds do not attempt to breed (Drent & Daan 1980; Chastel et al. 1995). An unavoidable weakness in the experimental design of this study was that I was obliged to compare the body conditions of breeding birds, which are presumably greater than birds that failed to breed.

Thus there could be a difference in body condition of birds from the two islands at a population level, which would not be detected among the subset of breeding adults. Another complicating factor is that body condition may be high at the start of the breeding season (Nelson 2005) and decline as the season progresses (Mullers & Tinbergen 2009).

The second possibility is that body condition of gannets on Malgas Island was lower in previous years but the recent increase in sardine and anchovy abundance has allowed adult gannets to regain body condition rapidly. Mullers & Tinbergen (2009) calculated a ratio index of body condition for adult Cape gannets using wing length and body mass, resulting in similar values as calculated in the current study. The average condition index for Malgas Island ranged from 5.3 to 5.5 over two breeding seasons (2005/2006 and 2006/2007; Mullers & Tinbergen 2009) while the same condition index averaged 5.5. There are problems with the use of ratio indices of body condition (Hayes & Shonkwiler 2001), but the fact there is little difference in the ratio in this study and that of Mullers and Tinbergen (2009) suggests that adult body condition of gannets from Malgas Island has not changed substantially over the past five years.

Intraspecific competition

Population growth rates are regulated by density dependent (e.g. competition for food or space) and density independent factors (e.g. environmental factors; Turchin 1999). There is increasing evidence that some seabird populations are regulated through density dependent factors especially during the breeding season (Hunt et al. 1986; Birt et al. 1987; Ainley et al. 2003; Ballance et al. 2009) because they are central place foragers (Orians and Pearson 1979). Density dependent population regulation is thought to occur through intraspecific competition for food. Ashmole (1963) proposed that seabirds deplete the prey in the waters surrounding the colony, increasing competition for food. Prey depletion was demonstrated around large colonies of double-crested cormorants (*Phalacrocorax auritus*), but this species feeds on sedentary benthic fish (Birt et al. 1987). Cape gannets feed on highly mobile pelagic fish so prey depletion is difficult to demonstrate. Lewis et al.

(2001) showed that northern gannets from larger colonies travel further to find food, possibly through the disturbance of fish shoals rather than prey depletion.

Birds from large colonies often have longer foraging trip durations (both distance and time) and foraging area is larger than for birds from smaller colonies (Lewis et al. 2001; Ainley et al. 2003; Ballance et al. 2009). In this study gannets from Bird Island flew further from the colony and had longer path lengths than those from Malgas Island. The greater foraging effort on Bird Island is supported by the PCV results, which indicated that gannets from Bird Island performed more aerobic exercise (Carpenter 1975). The sizes of the foraging areas of gannets from the two islands were similar (approximately 19 000 km^2), although most birds from Malgas Island did not use the entire estimated foraging range (Figures 1 and 2). The Bird Island colony increased from 19 000 pairs in 1956/1957 to 98 500 pairs in 2005/2006 (Crawford et al. 2007), whereas the Malgas Island population has decreased by about 25% since 1998/1999 and is one third the size of Bird Island (36 000 pairs in 2005/2006; Crawford et al. 2007). Assuming the current foraging ranges, the foraging density of gannets from Bird Island (10 birds.km^2) is approximately 2.5 times that of gannets from Malgas Island (4 birds.km^2). Thus it is possible that intraspecific competition plays a role in influencing the foraging effort of gannets from Bird Island.

Grémillet et al. (2004b) also found that Cape gannets from a larger colony (Malgas Island) worked harder than those from a smaller colony (Bird Island, Lambert's Bay). However, Pichegru et al. (2007) found the opposite trend when comparing Malgas Island to Bird Island (Nelson Mandela Bay). The difference between these two studies could be due to environmentally reduced prey levels. Grémillet et al. (2004b) compared the two west coast colonies in a year (2002) when the overall abundance of sardine and anchovy was twice as high as in 2005 (the year of the Pichegru et al. [2007] study; Coetzee et al. 2009). Another factor contributing to the difference between the two studies is that Grémillet et al. (2004b) compared two colonies on the west

coast which probably have similar prey bases, whereas Pichegru et al. (2007) compared west and south coast colonies with very different prey bases.

Previous studies have found that reproductive performance (clutch size, breeding success, chick growth and fledgling weight) is lower at larger colonies than smaller ones (Hunt et al. 1986). It was not possible to follow breeding attempts throughout the breeding season in this study so measures of breeding success are not available. Chick growth (at least during the early phases of growth) was not different between the two islands, which suggests that the effects of intraspecific competition on reproduction are not strong. Intraspecific competition also has been implicated in the low body condition of great skuas at large colonies (Votier et al. 2007). The pectoral muscle thickness and the ratio of body mass:wing length of gannets from Bird Island was slightly lower than the gannets from Malgas Island (although these results were only marginally statistically significant), which further suggests that the effects of intraspecific competition may not be highly pronounced.

Conclusions

Gannets on the west coast did not feed extensively on fishery wastes during the 2009/2010 breeding season as they have done for several years. Thus it was not possible to directly investigate the effects of a diet of fishery wastes on adult gannet body condition. However, it appears that a long term diet of fishery wastes has not affected the body condition of gannets. The colony at Bird Island shows signs of increasing intraspecific competition for food, although there are little effects on chick growth or adult body condition.

The presence of sardine and anchovy on the west coast is a positive sign for the gannets that breed there because breeding success of gannets is directly related to the abundance of sardine and anchovy within their foraging ranges (Underhill & Crawford 2007). It is essential that gannets have access to sufficient sardine and anchovy to provision their chicks during the breeding season in order to successfully fledge chicks. Yet it is likely that gannets from both colonies are food limited. Although the foraging conditions for the gannets from Malgas Island probably improved in 2009, the density of pelagic

fish is still low. It is likely that gannets from Bird Island are more food limited than in previous years due to enhanced intraspecific competition and low fish densities on the south coast. There is also a strong spatio-temporal overlap between foraging gannets and the purse-seine fishery which has probably contributed to the decline in Cape gannet population (Pichegru et al. 2009b). Better spatial management of the exploitation of pelagic fish resources is necessary to ensure the persistence of seabirds and other top predators that have fixed breeding sites.

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