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Increased foraging effort of breeding Cape Gannets fails to compensate for reduced prey availability

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January 2013

Submitted in partial fulfilment of the requirements for the degree of
Masters of Science in Conservation Biology

DST/NRF Centre of Excellence at the
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Acknowledgements

I am infinitely grateful to everyone who helped make this project, thesis and year possible. I would firstly like to thank my supervisors, David Grémillet, Lorien Pichegru and Peter Ryan for their patience and availability these past few months, while tirelessly helping me with data analyses, editing my writing, and giving me advice regarding both the project and life in general. And especially thanks to Lorien and David for the amazing time on Malgas Island; I will never forget the adventures we had those few weeks, in addition to the many skills you both taught me.

Next, thank you to Pierre Nel and SanParks for making our stay on Malgas Island possible, and for replenishing our water and supplies on the island. I may not have made it to the island if it were not for the Percy FitzPatrick Institute staff, including Chris Tobler, Anthea Links, Tania Jansen, Margaret Koopman and Hilary Buchanan. Their amazing logistical support throughout the year included helping me track down crucial equipment the day before leaving for the field, driving me to Malgas Island, and printing and submitting the final version of this thesis.

As this was a long-term project, I would like to thank everyone who contributed to the large dataset I was privileged to use, including Emilie Tew Kai, Christina Moseley, Tim Reid and Nicola Okes. Thank you to Janet Coetzee for making the pelagic fish survey data available to me and for advice regarding its usage. Thank you to Bruce Dyer and Leshia Upfold for allowing me access to the data on gannet diet composition. Thanks to Tim Reid and Rowen van Eeden for advice on statistical analyses, and to Clara Péron for the time-saving analyses for the gannet foraging GPS data.

Thank you to the 2012-2013 Conservation Biology MSc class for the support, never-ending entertainment, and fun adventures throughout the year. Finally, thank you to my parents for allowing me to pursue an MSc on the other side of the world and to follow my passion for birds and wildlife. They have always supported me. And, thank you to my pet ducks, Nicky and Gracie, for sparking my interest in birds all those years ago.

This study was funded by the Percy FitzPatrick Institute of African Ornithology (University of Cape Town, South Africa) and by the Centre National de la Recherche Scientifique (Montpellier, France).

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Abstract

Seabirds respond to various forms of environmental change by adjusting breeding and foraging strategies, but these forms of behavioural flexibility have limits. Cape Gannets *Morus capensis* breeding on Malgas Island off the west coast of South Africa and foraging in the surrounding waters of the southern Benguela have been subjected to large fluctuations in natural prey availability over the past decade. The distributions and abundances of pelagic fish in their foraging range have changed due to climate change, overfishing and/or natural variability. When their preferred prey (sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*) is unavailable, gannets consume other food items, including low-quality discards from the hake (*Merluccius* spp.) fishery. In order to determine the limits of flexibility in foraging effort of breeding gannets under contrasting environmental conditions, chick growth, nest attendance, adult body condition and foraging behaviour (trip duration, path length, and maximum distance foraged) were measured over the past decade, along with diet composition and hydroacoustic assessments of prey abundance and distribution. Pelagic fish biomass varied tenfold across the study period and was positively correlated with the proportion of sardine and anchovy in the gannets' diet, which ranged from 17-90%. All measures of foraging effort increased significantly with decreasing sardine and anchovy in the gannets' diet, while patterns of nest attendance (e.g. duration when both parents attended chicks, regularity of attendance bouts) improved significantly with increasing proportions of sardine and anchovy in the diet. Adult body condition was negatively impacted by increasing proportions of hake in the diet, while chick growth rates improved as the proportion of sardine and anchovy in the diet increased. Chick growth was dependent on a combination of diet composition, adult foraging effort (indicated by trip duration, which influences provisioning rates), and the regularity of parental shifts at the nest. Crucially, chick growth was lowest in years when gannet diet comprised < 50% sardine and anchovy and adults were forced to increase their foraging effort (likely due to the location and abundance of the fish), suggesting a limit to behavioural compensation for food shortages. This long-term study across varying environmental conditions has improved our knowledge of the responses of Cape Gannets to a changing oceanic environment. Such information can help predict potential population changes and better inform management strategies, such as the implementation of no-take fishing zones during years when gannet prey abundance is low. Furthermore, an understanding of the sensitivity of various life history traits to the severity of environmental conditions enhances the value of seabirds as indicators of ecosystem health.

Chapter 1: Seabird responses to environmental change

Species adaptations to ongoing environmental change

Global environmental changes are large-scale fluctuations in the earth's climate, atmosphere and ecosystems, and may be driven by either natural events (such as climate patterns reflecting glacial and inter-glacial periods) or anthropogenic influences (such as increased emissions of harmful pollutants; Vitousek 1992). Throughout the earth's history, ecosystems have undergone extreme fluctuations in climate and structure (Vitousek 1992), and it is the strategies and adaptations that organisms undertake in response to these changes, and the life history traits that enable or prevent this evolutionary flexibility, that determine the success of a species under stress. An alteration in a system as a result of human induced global change or natural environmental variability can lead to similar results (e.g. overfishing and algal blooms both negatively impact local marine ecosystems; Vasas et al. 2007). By understanding the drivers and consequences of these reactions, we can better predict the adjusted ecosystems and implement appropriate conservation actions.

Individuals generally respond to a change in their natural conditions in one or more ways: physiological responses, morphological responses and/or behavioural responses (Ricklefs 1990). Behavioural responses include adjustments in foraging strategies and prey preferences (Abraham and Sydeman 2006), adjustments in incubating and brooding behaviour (Gladbach et al. 2009), and changes in decisions to reproduce (as predicted by evolutionary life history theory; Williams 1966, Cairns 1987). These individual-level responses may eventually lead to a population change, such as the abandonment of a breeding site, the inclusion of new food items (e.g. African Oystercatchers *Haematopus moquini* adding the alien mussel *Mytilus galloprovincialis* to their

diet, Coleman and Hockey 2008), or changes in local or global population sizes (e.g. crow and gull populations increasing due to urbanization, Marzluff and Neatherlin 2006).

Changing conditions in the oceans

The oceanic environment is shaped by several parameters such as sea surface temperature, upwelling activity and chlorophyll concentrations (Grémillet et al. 2004a). Oceanic landscapes are generally unpredictable and global changes (both natural and anthropogenic) may affect several aspects of the marine environment. It has been suggested that anthropogenic climate change will likely increase the breadth and frequency of occurrence of marine oscillations, but the effects of such changes on most marine organisms remain poorly understood (Simmonds and Isaac 2007). Changes in ocean acidity levels, temperature, and water currents have been recorded in many of the earth's major oceans, and these changes, sometimes driven by temporary events such as El Niño or by long-term ecosystem changes such as more frequent melting of ice shelves, have been shown to affect several marine organisms including fish distributions and consequently breeding seabirds (Schreiber and Burger 2002).

Flexibility and limits of seabirds facing environmental change

Oceanic conditions contribute to the availability of food to seabirds (Lewison et al. 2012), and condition their foraging strategies (Grémillet et al. 2004a), diet composition (Abraham and Sydeman 2006) and survival (Distiller et al. 2012). The fact that offshore-feeding seabirds face cycles of irregular food supplies likely led to the evolution of a series of life history characteristics such as small-size clutches, slow chick growth rates, delayed sexual maturity, large body sizes, long-life spans (high adult survival) and relatively long foraging trips (Lack 1968). As a result, seabird populations are sensitive to changes in adult survival rates, favouring

adults investing more in their own survival than in reproductive effort (Furness 2003).

Fluctuating environmental conditions throughout the breeding season result in some individuals attempting to breed despite poor conditions, at which point the slow growth rate of chicks helps to buffer against short-term food shortages by reducing the likelihood of starvation (Lack 1968). In addition, a slow chick growth rate may be important for nidicolous species where juveniles must build up fat deposits before fledging, especially if they are still incompetent foragers and fliers at the time of fledging (Lack 1968).

The fact that many offshore-feeding seabirds undertake long foraging trips and concentrate their efforts on a single chick may allow for flexible foraging strategies under adverse environmental conditions (Lack 1968). However, this flexibility is limited by central-place foraging: seabirds breed on islands and need to find their food within a reasonable foraging range (Lack 1968). Changing distributions of food due to climate change or other factors may force parents to feed chicks less and/or more irregularly while in search of prey, or switch to poor-quality food items that may negatively impact their own health and that of their chicks (Grémillet et al. 2008a). In many species of seabirds, food availability and food quality have been shown to influence breeding success, adult body condition, chick growth, nest attendance and juvenile and adult survival (Österblom et al. 2008).

A few seabirds successfully display high behavioural flexibility, adjusting foraging strategy in light of varying or unfavourable conditions (Cairns 1987, Grémillet and Charmantier 2010). Great Cormorants *Phalacrocorax carbo* in West Greenland forage just as successfully (with even higher catch per unit effort rates) as those in mainland Europe, despite significantly lower densities of prey and much colder water temperatures in West Greenland (Grémillet et al. 2004b). Little Auks *Alle alle* also are able to adapt their foraging strategies to various environmental conditions (differing sea surface temperatures), suggesting they may be able to

cope with some degree of predicted climate change (Grémillet et al. 2012). Conversely, Great *Catharacta skua* and Arctic Skuas *Stercorarius parasiticus* apparently struggle to increase foraging effort while guarding chicks in years of reduced food availability (Caldow and Furness 2000). Many seabird species, however, require a certain threshold of food availability within their foraging range, below which breeding success is greatly reduced (Cury et al. 2011). This suggests that behavioural flexibility may be limited at both ends – failure to obtain adequate food due to very low levels of prey as well as failure to compensate for resultant poorer nest attendance and provisioning rates.

Other seabird species display plasticity in dietary repertoire and take advantage of alternate food sources such as fishery discards (Furness et al. 2007, Lewison et al. 2012). The ability to benefit from fishery discards may depend on a species' digestive efficiency and ability to carry prey loads (Österblom et al. 2008), and scavengers such as gulls, albatrosses and skuas may benefit more than fast-digesting species such as Cape Gannets (Jackson 1992). Some seabirds such as gulls intentionally utilize discards in the breeding season (Walter and Becker 1997), while others avoid them due to their low nutritional value (Grémillet et al. 2008a). The long-term consequences of feeding on fishery wastes are not completely understood for many seabird species (Furness 2003, Lewison et al. 2012), and fishery discard management practices differ both spatially and temporally, as do consumption patterns by seabirds (Furness et al. 2007). Collisions with vessel equipment pose a risk of death or injury for seabirds attempting to obtain discards from fishing vessels (Furness 2003, Furness et al. 2007, Gonzalez-Zevallos and Yorio 2006, Watkins et al. 2008), which could be a problem since seabird populations are sensitive to decreases in adult survival (Furness 2003). Furthermore, changes in breeding success in discard-exploiting generalists may have detrimental effects on other nearby seabird species (Furness 2003, Votier et al. 2004, Lewison et al. 2012).

When preferred, high-quality prey is scarce during the breeding season, some species may be forced to turn to discards, and this may lead to poor chick survival rates and high mortality (Grémillet et al. 2008a). The hypothesis that low-quality food has a negative effect on the body condition, breeding success and survival rates of individuals or species that usually consume high-quality food is known as the junk-food hypothesis (Jodice et al. 2006), and has been demonstrated on sea lions (Rosen and Trites 2000), as well as on many species of seabirds (Batchelor and Ross 1984, Jodice et al. 2006, Kitaysky et al. 2006, Grémillet et al. 2008a, Österblom et al. 2008). In seabirds, results indicate that the consumption of “junk-food” can be particularly detrimental to juveniles (Batchelor and Ross 1984, Kitaysky et al. 2006, Grémillet et al. 2008a, Österblom et al. 2008, Mullers et al. 2009), while adults usually (but not always) show higher dietary flexibility and retain their body condition (Moseley et al. 2012). Experimental hand-rearing of chicks on poor-quality food has shown that poor-quality diets can negatively impact the cognitive capacity of chicks, which may lead to higher mortality (Kitaysky et al. 2006). There is also concern that the consumption of fishery discards by seabirds that usually consume high-quality prey may lead to ecological traps, i.e., species become accustomed to habits (such as feeding on discards) that are not beneficial to their survival or reproductive success (Grémillet and Boulinier 2009). Fishery discard management must therefore consider both the positive and negative affects of discards across species, as well as the spatio-temporal patterns of their consumption.

Flexibility in breeding Cape Gannets

One of southern Africa’s seven endemic seabirds, the Cape Gannet breeds colonially on six small islands off the coasts of Namibia and South Africa and feeds by plunge-diving for small pelagic fish in the productive Benguela upwelling system (Crawford et al. 1983).

Monogamous pairs typically return to the same island each year and share parental duties in raising one chick during the September to February breeding season (Jarvis 1971). Chicks are born featherless and grow slowly, fledging only after 3-4 months (Jarvis 1971). In optimal conditions, parents provide chicks with a diet of lipid-rich pelagic fish, dominated by sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* (Batchelor and Ross 1984). Juveniles reach sexual maturity after 3-4 years (Jarvis 1971), so poor conditions may only affect population sizes several years later. The fact that gannets typically lay a single egg is a life history trait common amongst offshore-feeding seabirds that likely evolved in response to difficult environmental conditions (Lack 1968), but experimental twinning studies have shown that Cape Gannets may raise two chicks in good conditions (Navarro 1991), suggesting flexibility in parental foraging strategies and provisioning abilities.

Historically gannets were affected by disturbance from guano-scrappers (Crawford et al. 1983). Today, predation of gannet eggs, chicks and fledglings by Kelp Gulls *Larus dominicanus* (Mullers et al. 2009), Great White Pelicans *Pelecanus onocrotalus* (de Ponte Machado 2007) and Cape Fur Seals *Arctocephalus pusillus pusillus* (Makhado et al. 2006) and shifting distributions of natural prey are the two main threats to Cape Gannets (Crawford et al. 2007). The abundance of pelagic fish off the west coast of South Africa has fluctuated substantially over the past decade (Coetzee et al. 2008). This may be due to competition with fisheries (Okes et al. 2009), natural shifts in the geographic distribution of pelagic fish (Coetzee et al. 2008), or both. Crawford et al. (2007) found significant positive correlations between the biomass of sardine and anchovy in an area and the population size of the Cape Gannet colony that feeds in that area. In the 1950s, Namibia held 80% of the Cape Gannet population and a similar proportion of the sardine and anchovy biomass. Overfishing in Namibia caused the crash of the Namibian gannet population, and the vast majority of Cape Gannets now breed in South Africa (Crawford et al. 2007). The

gannet population on Malgas Island in the Western Cape has gradually declined since the 1998 population of ca. 50,000 breeding pairs (Crawford et al. 2007) and is now estimated at approximately 30,000 breeding pairs (Department of Environmental Affairs (DEA), unpubl. data). As the biomass of sardine and anchovy in South Africa shifted eastward (Coetzee et al. 2008), the Bird Island, Algoa Bay Cape Gannet colony, the easternmost colony, has increased in size, probably due to increased juvenile immigration (Distiller et al. 2012). Bird Island, Algoa Bay, is now the largest gannetry in the world, but this trend may be problematic if the Bird Island colony reaches carrying capacity, as there are few other suitable breeding sites off the south coast of South Africa. Dyer Island has been suggested as a possible breeding site, but past records suggest that Cape Gannets have never bred there (Crawford et al. 1983).

To understand the effects of environmental variability and global change on a seabird such as the Cape Gannet, it is important to analyze individual-level responses over the long-term (Grémillet and Charmantier 2010, Lewison et al. 2012). At the individual level, the abundance of preferred prey species in the gannet foraging area likely has a greater effect on the behavioural and physical responses of breeding Cape Gannets than does any other factor. Previous studies showed that breeding Cape Gannets react to local environmental changes by adjusting their foraging strategy (Pichegru et al. 2010). Some seabirds can cope with reduced prey availability by prey-switching (Abraham and Sydeman 2006), and Cape Gannets indeed feed on multiple species of prey, including squid, hake discards and other low-quality prey items, especially in the non-breeding season (Berrutti et al 1993, DEA, unpubl. data).

Changes in natural prey abundance likely affect many aspects of Cape Gannet behaviour and health, such as nest attendance, foraging effort and adult body condition. Cairns (1987) suggested curvilinear relationships between these factors and food supply across the breeding season; variables will be influenced differently depending on the severity of conditions. Such

patterns highlight the need for long-term studies to identify the effects of prey availability on seabird life history and behavioural characteristics across varying conditions. Well-documented recent variability in the Benguela system, in combination with the fact that Cape Gannets are relatively accessible study subjects, makes the Cape Gannet a valuable tool for understanding the effects of global change on seabirds and other organisms.

This study identified relationships between diet composition, nest attendance, chick growth, adult body condition and foraging strategy in contrasting feeding conditions to develop a better understanding of how breeding gannets adjust their foraging strategy in response to changing prey abundances, and how this adjustment affects their production and survival. I predicted that gannets show a high level of flexibility in foraging, and adjust their foraging effort in response to changes in preferred prey abundance. However, an increase in foraging effort may not be able to buffer consequently poorer nest attendance and provisioning rates, which may lead to lower chick growth rates and overall higher brood mortality. I also predicted that adult gannets should be less sensitive to changes in diet composition than chicks, which require lipid-rich pelagic fish for adequate growth and survival (Batchelor and Ross 1984, Grémillet et al. 2008a). An understanding of the strategies gannets adopt and the consequences of reproducing in sub-optimal conditions may potentially help inform decisions regarding the conservation of this iconic southern African seabird.

Chapter 2: The effects of environmental changes on the foraging behaviour and reproductive performance of Cape Gannets

Introduction

Cape Gannets are currently listed as Vulnerable by the IUCN due to their limited breeding range and competition with fisheries for prey (Birdlife International 2012a). This status may change to Endangered if the global population continues to decline, and if breeding sites exploiting the most depleted prey stocks are eventually abandoned. Chapter 1 discussed several of the threats that gannets on Malgas Island currently face – reduced prey availability following pelagic fish range shifts due to climate change or overfishing, and predation of chicks by Kelp Gulls, Great White Pelicans and Cape Fur Seals. This study examines the behavioural flexibility and reproductive consequences of Cape Gannets attempting to breed on Malgas Island in light of varying abundances of preferred natural prey.

The foraging behaviour and reproductive performance of Cape Gannets have been studied and compared across most of the islands on which they breed, but many studies have been based on only 1-3 years of data (e.g. Grémillet et al. 2008a, Moseley et al. 2012). Seabirds have been shown to react quickly to fluctuations in prey availability (Grémillet and Boulinier 2009), but the strength of relationships between prey availability and seabird parameters may vary depending on the severity of conditions, and conclusions from a short-term study during atypical conditions may be biased (Grémillet and Charmantier 2010). Chick growth rates, adult body condition and nest attendance have been recorded for Cape Gannets on Malgas Island every October and/or November since 2005, and multiple measures of foraging effort have been recorded with GPS loggers every year since 2002 (Grémillet et al. 2004a, 2008a, Pichegru et al. 2010, Moseley et al. 2012, PFIAO unpubl. data). In addition, diet samples have been collected

monthly and pelagic fish abundance has been monitored with acoustic surveys annually since the late 1980s (DEA). This study incorporated and analyzed all of these long-term datasets in order to understand the complex reactions of gannets to changing prey availability during the past 11 years (2002-2012). It also attempted to understand how the life history traits of seabirds such as Cape Gannets may limit the behavioural flexibility of adults attempting to breed in sub-optimal conditions.

Methods

Study site

All data were collected on Malgas Island, West Coast National Park, South Africa (Figure 1; 33°03'S, 17°55'E). Malgas Island is a small (c. 1 km²), rocky island at the mouth of Saldanha Bay and is home to tens of thousands of breeding seabirds. The island experiences a mild Mediterranean climate and the gannets breed during the austral spring and summer when rainfall is low. The island is managed by South Africa National Parks (SANParks) and is not open to the public, in order to reduce disturbance to the breeding birds.

Data were collected on Malgas Island every year from 2002-2012, and nearly all data used in analyses were collected during October and November to facilitate comparisons of variables across years.

Abundance of pelagic fish

The abundance of pelagic fish across the southern Benguela region was determined by acoustic surveys conducted annually by DEA. The availability of pelagic fish to foraging Cape Gannets is in part dependent on the spatial distribution of the fish (Pichegru et al. 2010), so for purposes of this study I was interested in an index of overall pelagic fish abundance in the main gannet foraging area (Figure 1) that could be compared across years. The acoustic survey conducts transects from Hondeklip Bay to Port Alfred generally during October-December, but I only considered pelagic fish abundance from Hondeklip Bay to Cape Agulhas (Figure 1; zones A-C), which is surveyed during October-November. This geographic range is used because it includes the entire area in which gannets breeding on Malgas have foraged over the past decade (see results; also: Grémillet et al. 2008b, Okes et al. 2009, Pichegru et al. 2007). Although Zone A extends further north than most gannets usually forage, it is well within the distance they are capable of foraging and is indeed an area heavily utilized in some years (see results). This study utilizes acoustic survey data from 2002-2011, because the acoustic survey results for 2012 were not yet available.

Diet composition

Diet samples of up to 50 Cape Gannets on Malgas Island were collected over 1-3 days every month by DEA staff. Gannets returning to the colony were captured at random with a hooked pole and inverted over a bucket to promote regurgitation. This study utilizes diet sample data from 2002-2012, collected in October-November (2012 only includes diet samples from October). Diet samples were analyzed to the species level where possible and prey proportions were calculated by wet mass. Each month, the masses of all 50 diet samples were combined so

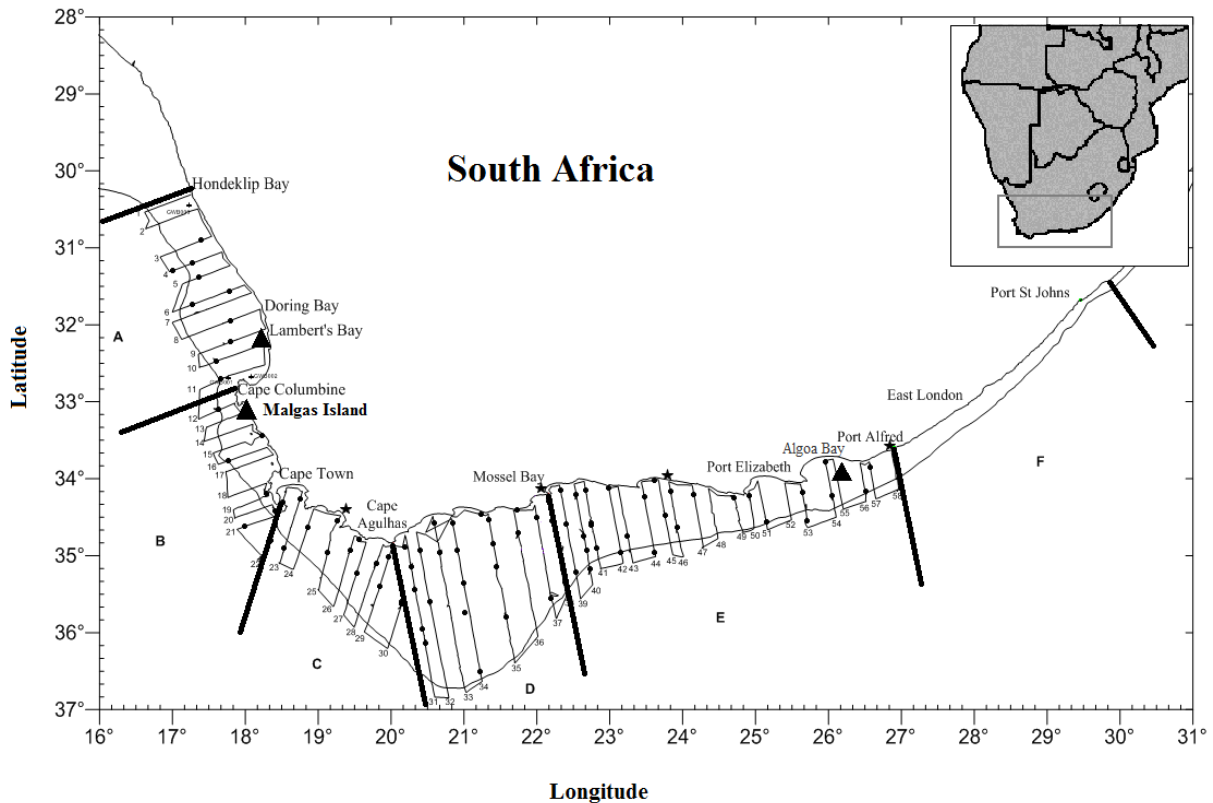


Figure 1. Map showing the zones and transect lines of the annual pelagic fish acoustic surveys conducted by DEA. The black triangles show the locations of the three Cape Gannet colonies in South Africa: Lambert's Bay, Malgas Island and Algoa Bay. Cape Gannets breeding on Malgas Island forage predominantly in zones A, B and C. Map redrawn from DEA unpubl. documents.

the total mass of a prey species divided by the total mass of the diet samples would yield the monthly percent composition per weight of that prey species for the colony. This was done with all prey species in order to calculate a monthly index of diet composition. Besides sardine and anchovy, the diet of Cape Gannets from Malgas Island often contains other natural prey species such as saury (*Scomberesox saurus*), horse mackerel (*Trachurus trachurus capensis*), squid (various species), chub mackerel (*Scomber japonicus*), red-eye (*Etrumeus whiteheadii*) and snoek (*Thyrsites atun*). The main form of unnatural prey consumed by Cape Gannets are hake offal and other discards from the hake trawl industry.

When 50% or less of the gannets' diet is composed of sardine and anchovy, I consider the feeding conditions to be poor (as in 2005, 2006, 2007, and 2011; see statistical methods).

Conversely, the diet of Cape Gannets on Malgas Island contained over 61% sardine and anchovy in 2008, 2009, 2010, and 2012, and these years are considered good years for breeding Cape Gannets.

Foraging behaviour

The foraging strategies of adult gannets provisioning small chicks were determined by deploying GPS loggers on approximately 25-50 adults per year from 2002-2012, during October-November (exact dates given in Appendix A). When an adult gannet returned to a nest with a 1-5 week old chick and performed a greeting display with the partner, the partner on the nest was captured with a hooked pole, as it was assumed that this individual would soon leave for a foraging trip. The individual was weighed (to the nearest 25 g with a 5-kg spring balance) and a GPS logger was attached to the three central rectrices with waterproof Tesa tape (Wilson et al. 1997). Individuals were marked with a wax crayon for easy identification upon the gannet's return from foraging. The tape and logger were removed when the gannet returned to the nest, usually approximately 24 hours after deployment. The individual was weighed again so that pre-trip and post-trip masses could be compared, and wing (flattened chord to the nearest 1 mm with a stopped wing rule) and culmen length (to the nearest 0.1 mm with Vernier callipers) measured. Handling time for GPS logger deployment was generally under 10 minutes, while handling time for GPS logger removal was approximately five minutes. The chicks were not monitored and measured, in order to reduce disturbance to these study nests.

GPS loggers used throughout the study recorded time, position, and speed of the gannets. Loggers and their waterproof housing were always less than 3% of the body mass of an adult Cape Gannet. GPS loggers used from 2002 to 2008 weighed 37 g (see Grémillet et al. 2004a for details) and did not have any negative effects on the behaviour of foraging gannets (Pichegru et al. 2007). All loggers used subsequently were either the same size or smaller. Loggers used in 2009 and 2010 are described by Moseley et al. (2012). Loggers used in 2011 and 2012 weighed 18 g and were designed by Perthold Engineering, LLC (Anderson, SC, USA). The loggers recorded the GPS location and speed of the adult approximately every ten seconds (range: 1 sec to 1 min, depending on year). Information on the total foraging trip duration, the maximum distance from the colony reached, and the total path length of the foraging trip was extracted (see Grémillet et al. 2004a for method). ArcGIS 10 (ESRI 2011) was used to display the GPS foraging tracks, which allowed us to determine if a track was incomplete (due to logger malfunction or battery failure), or if an individual went on more than one foraging trip. To avoid pseudo-replication, each individual was only tracked once. When an individual undertook a second foraging trip before we could catch it and remove the GPS device, the second trip was discarded from the data set.

Adult body condition

Adult body condition was measured from 2005 to 2012, for approximately 25-50 pairs of adults with chicks aged 1-5 weeks, in order to be comparable with adults tracked using GPS loggers. To reduce colony disturbance, nests were selected in the first 1-4 rows of the colony edge, and adults were weighed, measured (wing and culmen) and individually marked. Both parents were measured and weighed on a morning after they had spent the night on the nest when

possible. A simple index of adult body condition was calculated as body mass divided by wing chord, in grams per millimetre (Lewis et al. 2006, Grémillet et al. 2012). The body condition values of the two parents of a single nest were averaged to determine an overall index of parent health for that nest.

There are limitations in using a mass-to-wing ratio as an index of adult body condition, because it ignores other components of body condition such as parasite levels or physiological condition (such as nutrient levels). Furthermore, each parent was only weighed and measured once, so our measurement does not represent long-term body condition (which may be more accurately determined by physiological measurements). However, because the methodology of determining adult body condition has been the same throughout the study period, I assumed it allows comparison of conditions among years and with other variables. It is important to note, however, that the adult body condition index only represents breeding adults with chicks aged 1-5 weeks, and that poor environmental conditions likely cause some breeding attempts to fail prior to the chick stage and some Cape Gannets to refrain from breeding entirely (as predicted by life history theory, Williams 1966, Cairns 1987).

Nest attendance

The 25 to 50 nests where parents were captured to assess adult body condition were monitored every hour from dawn until dusk (usually 06:00 until 19:00 during the study period) from a lookout point, with binoculars. I recorded whether the chick was alone, both parents were present, or only one parent was present. Parents were individually marked with picric acid or Porcimar[©] animal dye in order to distinguish between the two parents, so that it could be noted which parent was attending the nest and how frequently they alternated nest duties.

To analyse nest attendance patterns from 2005-2012, I calculated the average percent of time each chick spent alone on the nest, as well as the time each chick was attended by both parents, during the entire period the chick was monitored. I also calculated the average attendance bout of each parent, and averaged the values from each parent to determine the average duration of the parental nest attendance bouts for the nest. This parameter represents the amount of time between chick feedings, and one would expect this parameter to increase as feeding conditions deteriorate. The variability (standard deviation) in the duration of parental attendance bouts was used as a measure of the regularity of food provisioning for the chick (see Schreiber and Burger 2002). Thus it was assumed that nests with a large standard deviation around the attendance bout duration were more likely subjected to sporadic provisioning rates, which may negatively influence chick growth rates, or at least correlate with poor conditions.

Chick growth

Chick growth rates were determined for the same 25 to 50 nests that were monitored annually from 2005-2012. Chicks were measured every 3-5 days for approximately 3-4 weeks during October-November. Wing chord and culmen length were measured as described above, and mass was recorded with a spring balance to the nearest 10 g with a 2.5-kg balance or to the nearest 25 g with a 5-kg balance (for chicks weighing over 2.5 kg). Growth rate of a chick's culmen and wing length are not dependent on the quality of food the chick receives (Batchelor and Ross (1984), so I considered changes in mass as a useful measure of the chicks' response to varying food availability. In order to standardize chick growth rates for age, I only included measurements of chicks in the linear growth phase, when they weighed 400-2500 g. The linear growth phase of chicks was determined by plotting the mass against the culmen (Figure 2), and

comparing the results of a linear regression with varying minimum and maximum cut-off masses (see Appendix C for details).

An ANOVA performed on the first wing length measurement of chicks (400-2500 g) monitored each year revealed that chicks selected for monitoring were not the same size each year (One-way ANOVA, $F_{7,210} = 11.95$, $p < 0.001$). However, there was no correlation between length of first wing measurement and chick growth rates (Appendix B, $r_s = -0.035$, $p > 0.05$), suggesting that growth rates do not vary with chick age for chicks 400-2500 g (Figure 2).

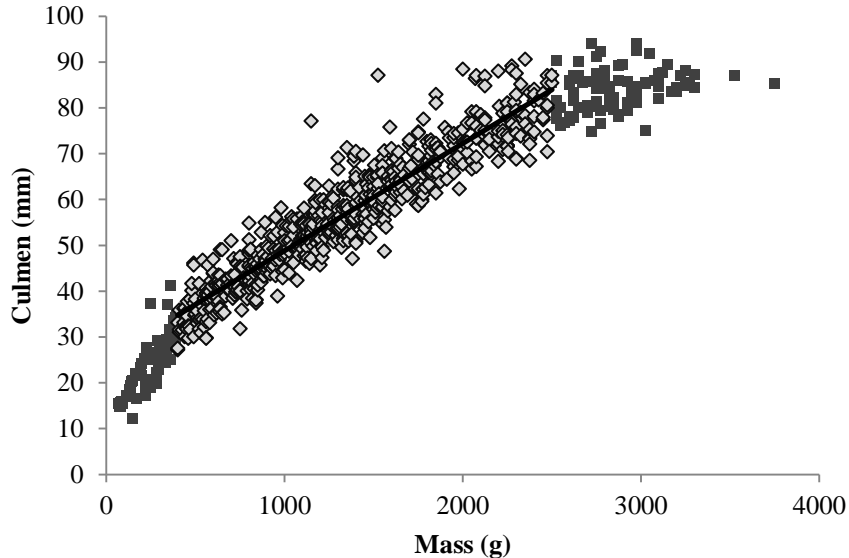


Figure 2. Mass as a function of culmen length of Cape Gannet chicks on Malgas Island 2005-2012 ($n=664$). Grey diamonds show chicks 400-2500 g; linear best fit: $y = 0.0234x + 25.41$ ($r^2 = 0.881$).

Daily growth rates ($\text{g}\cdot\text{day}^{-1}$) were calculated as the difference in a chick's mass between two consecutive measurements divided by the number of days between those two measurements. The growth rate of a chick was calculated for each measurement period, and these were averaged to determine the overall average chick growth rate per individual over the study period.

Statistical methods

Statistical analyses were conducted in R (R Core Team 2012) and Minitab (Minitab Release 13.32, 2000). Significance levels were taken as $p < 0.05$. All variables were tested for normality with Komogorov-Smirnov tests. All measured parameters (prey abundance, diet composition, chick growth rates, nest attendance patterns, adult body condition, and foraging trip duration, path length and maximum distance) were compared between years of poor versus good feeding conditions. Feeding conditions were defined based on the bimodal distribution of the proportion of sardine and anchovy in the diet, with four of the study years where diet contained $< 50\%$ sardine and anchovy by wet mass and the other four years where the diet contained $> 60\%$ of sardine and anchovy (Appendix D). Student's t-tests were used to compare variables with normal distributions between years with low versus high levels of sardine and anchovy in the diet, while Mann-Whitney U-tests were used to compare variables that were not normally distributed. These comparisons were done to determine the sensitivity of each parameter to prey abundance and diet composition, to see, for example, if certain variables remained constant despite changing feeding conditions. Data from 2002-2004 were excluded from the above t-tests because chick growth, adult body condition and nest attendance were not measured. I chose to split the study years by the proportion of sardine and anchovy in the diet instead of by the proportion of hake in the diet following linear regressions that yielded a stronger relationship between chick growth and sardine and anchovy than between chick growth and hake, and I was particularly interested in the effects of diet on chick growth rates.

Because the Kolmogorov-Smirnov tests indicated that the majority of variables (chick growth, % of time chicks spent alone, % of time chicks spent with both parents, foraging trip duration, foraging trip path length, foraging trip maximum distance, parental nest attendance

bouts, standard deviation of attendance bouts) were not normally distributed even after various transformations, Spearman's rank correlations were used to determine correlative relationships between all variables across all years. This analysis was used because one of my main goals was to determine which variables change as prey availability and diet composition change.

Furthermore, it allowed me to determine other patterns, such as which variables alter with changing foraging effort. Finally, knowing which variables were correlated with one another helped to identify multicollinearity when attempting more complex models. Linear regressions were used to determine the effects of diet composition on parent body condition. A stepwise multiple linear regression was used to determine which variables best predicted chick growth.

I predicted that chick growth would be determined by multiple parameters, so I ran a multiple linear regression on chick growth versus the following variables: time chick spent alone at nest, time chick spent with both parents, average parental nest attendance bout, standard deviation in parental nest attendance bouts (average for nest), percentage of diet composed of sardine/anchovy, percentage of diet composed of hake discards, foraging trip duration, foraging trip maximum distance, foraging trip path length, biomass of sardine and anchovy in the foraging area. I then removed variables with insignificant p values (from highest to lowest) and performed Variance Inflation Factor tests to eliminate variables affected by multicollinearity (correlation tables were examined as well). Finally, I added each previously removed variable back into the model, one by one, to determine if they significantly contributed to the model (checking for a significant p value and an increase in the adjusted r^2 value).

Results

Feeding conditions for Cape Gannets on Malgas Island have varied throughout the past decade (Table 1), and I found significant differences between the two categories of poor and good feeding years for nearly all gannet foraging and breeding parameters measured throughout this study (Table 2). On average, poor feeding years were characterized by slow chick growth rates, poorer parental nest attendance, and more infrequent, irregular chick provisioning. In addition, in poor years adults had worse body conditions and significantly increased their foraging trip durations, path lengths, and maximum trip distances (Table 2).

Pelagic fish variability in the Benguela and Cape Gannet diet composition

Most gannets breeding on Malgas Island forage in the Hondeklip Bay to Cape Agulhas section of the coastline (Figure 1, Zones A-C; Pichegru et al. 2010), where the estimated biomass of sardine and anchovy fluctuated between 356,000 tonnes in 2011 and 3,203,000 tonnes in 2002 (Table 1, Figure 3). The average percent composition of sardine and anchovy in the gannets' diet has fluctuated substantially, ranging from 17% in 2005 to 90% in 2012 (Table 1, Figure 3). The biomass of sardine and anchovy in the gannet foraging area was positively correlated with the amount of sardine and anchovy in the diet (Appendix E, $r_s = 0.552$, $p < 0.001$). A linear regression of sardine and anchovy biomass with sardine and anchovy in the gannets' diet for 2002-2011 yielded an adjusted r^2 of 0.31 (Figure 4). The proportion of hake in the gannets' diet has ranged from 2.1% in 2011 to 52.5% in 2007 (Table 1). This pattern is not necessarily synchronous with the proportion of sardine and anchovy in the diet, because when sardine and anchovy are unavailable gannets may consume other pelagic fish, such as horse mackerel (i.e. in 2005 and 2011, see Figure 5), before resorting to hake consumption.

Table 1. Summary of diet composition, prey biomass, foraging behaviour, chick growth rates, nest attendance patterns, and adult body condition, recorded for Cape Gannets breeding on Malgas Island during 11 breeding seasons from 2002-2012. Most data were collected in October-November, except 2002 (December) and 2004 (January 2005). Data are based on nests with chicks aged 1-5 weeks.

	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	Mean ± SD
Prey Availability:												
% hake in diet	17.8	19.5	34.5	28.6	35.1	52.5	21.3	29.5	3.6	2.1	2.6	22.5 ± 15.8
% sardine & anchovy in diet	78.6	77.4	24.6	17.0	50.0	39.9	74.5	61.1	74.4	45.6	90.1	57.6 ± 23.9
sardine & anchovy biomass (x10 ³ tonnes)	3203	2524	1029	746	1205	947	1633	2360	664	356	NA	1467 ± 936
Foraging behaviour:												
trip duration (h)	23.0	18.3	31.3	29.2	22.8	20.4	22.2	14.9	18.5	19.2	19.2	21.8 ± 11.9
SD (n)	9.6 (25)	13.2 (20)	14.2 (15)	12.7 (36)	11.2 (43)	16.2 (31)	8.3 (24)	8.2 (13)	9.1 (43)	9.4 (31)	10.5 (31)	
trip path length (km)	368.6	412.7	476.8	514.4	397.6	347.7	314.4	343.5	371.8	374.3	298.3	383.5 ± 200.7
SD (n)	200.3 (25)	323.1 (20)	199.5 (15)	234.8 (36)	199.6 (43)	190.2 (31)	111.0 (23)	147.0 (20)	153.3 (43)	162.6 (31)	175.0 (31)	
maximum trip distance (km)	106.0	114.5	122.9	132.6	104.0	93.7	72.3	84.3	103.3	110.7	86.7	103.2 ± 53.3
SD (n)	59.1 (25)	82.8 (20)	55.9 (15)	62.8 (36)	55.7 (43)	45.8 (31)	18.8 (24)	40.1 (20)	38.2 (43)	48.3 (31)	45.7 (31)	
Behaviour at nest:												
chick growth rate (g.day ⁻¹)				27.2	38.0	58.8	63.3	63.3	64.6	67.3	62.7	51.1 ± 25.5
SD (n)				28.5 (51)	15.2 (28)	10.4 (30)	21.9 (28)	11.5 (22)	16.8 (23)	27.3 (12)	15.8 (20)	
% time chick was left alone at nest				3.6	1.1	1.9	1.7	2.3	0.4	0.0	0.1	1.7 ± 4.5
SD (n)				7.0 (50)	4.0 (31)	2.6 (33)	5.7 (39)	4.0 (39)	1.3 (25)	0.0 (19)	0.4 (26)	
% time both parents were at nest				2.1	3.6	0.8	4.5	4.0	2.0	4.6	8.1	3.5 ± 4.5
SD (n)				3.6 (50)	3.5 (31)	1.0 (33)	4.5 (39)	3.0 (39)	2.5 (25)	7.8 (19)	5.6 (26)	
parent nest attendance bout (fraction of day)				1.0	0.8	0.5	0.7	0.8	0.5	0.7	0.6	0.7 ± 0.3
SD (n)				0.3 (50)	0.2 (31)	0.1 (33)	0.1 (37)	0.5 (39)	0.2 (25)	0.2 (19)	0.1 (25)	
SD of parent nest attendance bout (fraction of day)				0.6	0.4	0.4	0.3	0.5	0.4	0.5	0.4	0.4 ± 0.3
SD (n)				0.2 (50)	0.1 (30)	0.0 (33)	0.1 (37)	0.7 (39)	0.2 (25)	0.2 (19)	0.1 (25)	
parent body condition (g.mm ⁻¹), nest avg.				6.2	5.7	5.8	6.1	5.6	6.1	6.5	6.2	6.0 ± 0.5
SD (n)				0.5 (51)	0.3 (31)	0.5 (33)	0.4 (39)	0.3 (39)	0.3 (25)	0.3 (19)	0.5 (26)	

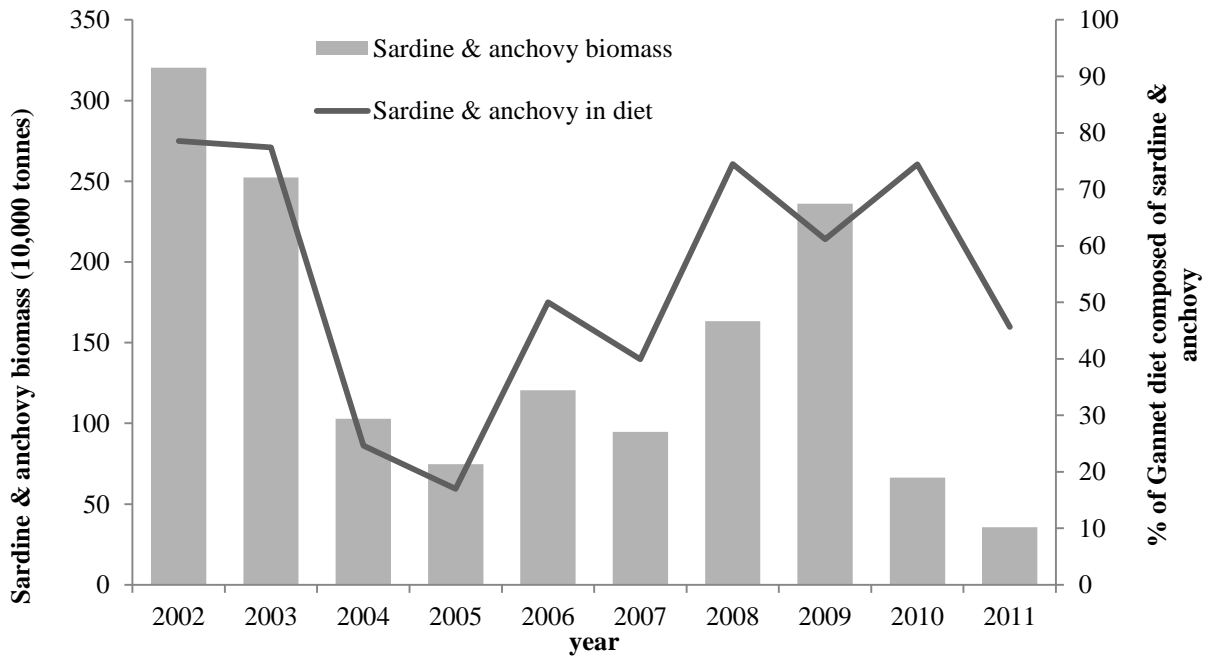


Figure 3. 2002-2011 trend in biomass of sardine and anchovy in the southern Benguela (between Hondeklip Bay and Cape Agulhas) and proportion of sardine and anchovy in the diet (2002-2012) of Cape Gannets breeding on Malgas Island and foraging in the same area. Both variables were sampled in October-November of each year.

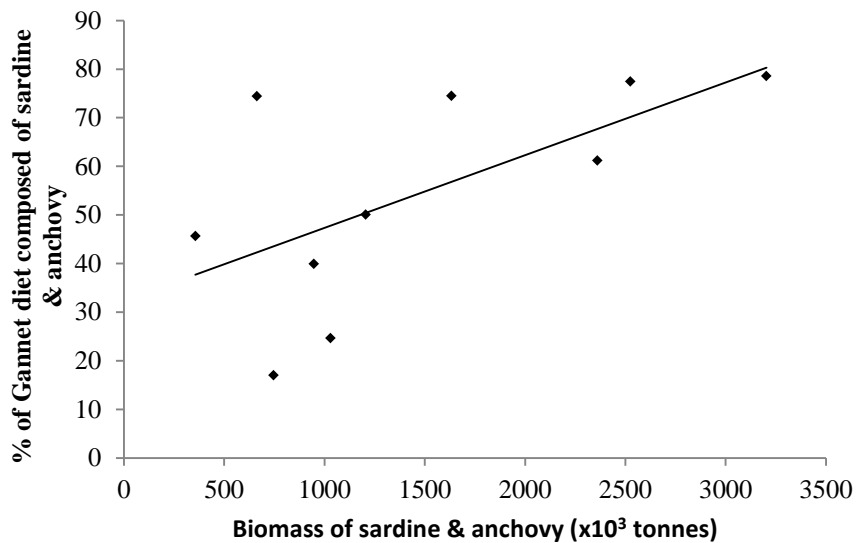


Figure 4. Linear regression between the biomass of sardine and anchovy in the Cape Gannet foraging area and the proportion of sardine and anchovy in the diet, based on annual means for gannets breeding on Malgas Island, 2002-2011.

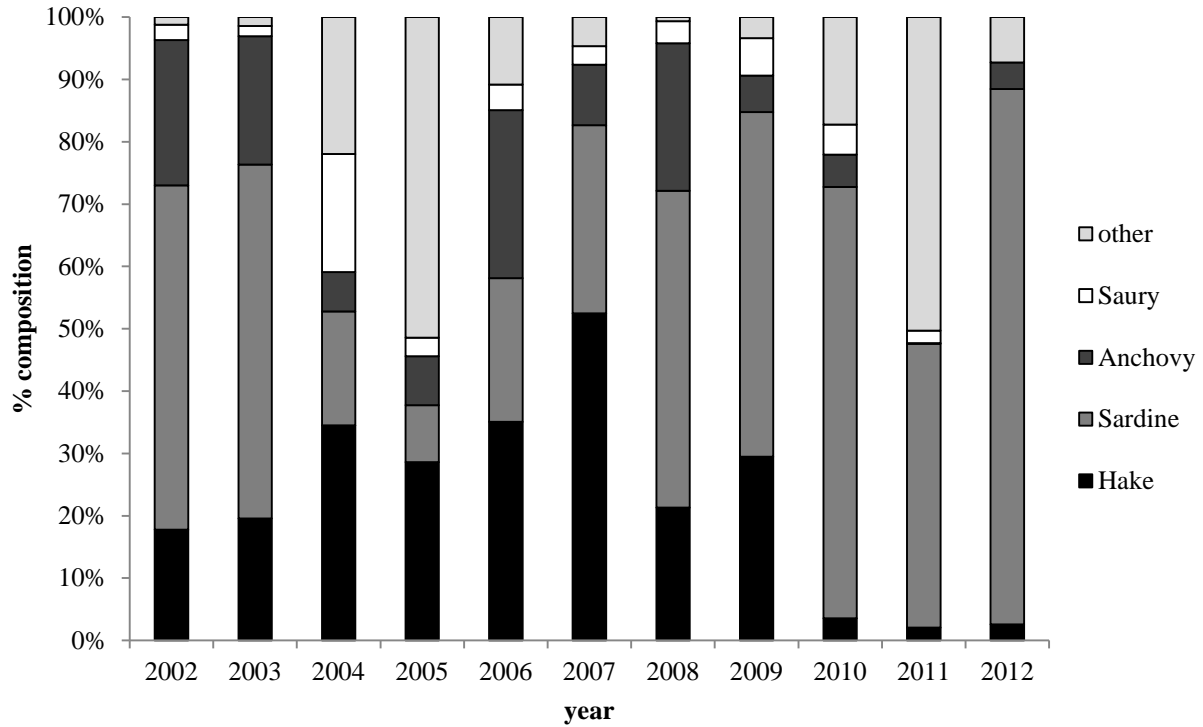


Figure 5. The diet composition (by proportion of wet mass) of adult Cape Gannets breeding on Malgas Island, determined from diet samples collected from 2002-2012 in October-November. The vast majority of the 'other' prey in 2005 and 2011 was horse mackerel.

Table 2. Comparison of variables between years of low (2005, 2006, 2007, 2011; 50% or less) and high (2008, 2009, 2010, 2012; over 60%) proportion of sardine and anchovy in diet of Cape Gannets on Malgas Island. Mann-Whitney U tests or *Student's t-tests.

Parameter	Low level of sardine & anchovy in diet		High level of sardine & anchovy in diet		p
	mean \pm SD	range, n	mean \pm SD	range, n	
% sardine & anchovy in diet*	38.1 \pm 14.7	range: 17.0-50.0, n = 4	75.0 \pm 11.9	range: 61.1-90.1, n = 4	0.011
biomass of sardine & anchovy*	814 \pm 358	range: 356-1205, n = 4	1552 \pm 851	range: 664-2360, n = 3	0.293
% hake in diet*	29.6 \pm 20.9	range: 2.1-52.5, n = 4	14.3 \pm 13.3	range: 2.6-29.5, n = 4	0.271
chick growth rate (g.day ⁻¹)	41.5 \pm 26.8	range: -77.0-123.3, n = 120	63.5 \pm 17.0	range: 20.0-120.0, n = 93	< 0.001
% time chick spent alone	2.1 \pm 5.0	range: 0.0-32.0, n = 133	1.3 \pm 3.9	range: 0.0-29.0, n = 129	0.026
% time chick w/both parents	2.5 \pm 4.2	range: 0.0-19.5, n = 133	4.6 \pm 4.5	range: 0.0-17.1, n = 129	< 0.001
parental attendance bout (fraction of day)	0.8 \pm 0.3	range: 0.4-1.7, n = 133	0.7 \pm 0.3	range: 0.3-3.5, n = 126	0.002
standard deviation of attendance bouts	0.5 \pm 0.2	range: 0.1-1.3, n = 132	0.4 \pm 0.4	range: 0.1-4.5, n = 126	< 0.001
parent body condition, avg. for nest*	6.0 \pm 0.5	range: 4.9-7.4, n = 185	6.0 \pm 0.4	range: 5.0-7.3, n = 73	< 0.001
foraging trip duration (h)	23.1 \pm 12.9	range: 0.48-75.8, n = 141	19.1 \pm 9.3	range: 3.4-49.2, n = 111	0.010
foraging trip path length (km)	411.3 \pm 207.7	range: 25.0-1085.5, n = 141	336.2 \pm 152.5	range: 93.3-890.0, n = 117	0.003
foraging trip maximum distance (km)	110.5 \pm 55.3	range: 12.0-319.6, n = 141	89.4 \pm 39.1	range: 31.6-235.8, n = 118	< 0.001

Foraging behaviour

Cape Gannets breeding on Malgas Island showed flexibility in their foraging trip duration, foraging trip path length and maximum distance travelled from the colony on foraging trips (Figure 6). Trip duration, path length and maximum distance from colony were correlated with each other and varied with diet composition (Appendix E, Table 1). Cape Gannets increased their foraging effort during years when they fed on lower proportions of sardine and anchovy (Appendix E, trip duration: $r_s = -0.190$, $p = 0.01$; path length: $r_s = -0.242$, $p < 0.001$; maximum distance foraged: $r_s = -0.223$, $p < 0.001$), but their foraging effort was not related to the proportion of hake in the diet (Appendix E, $r_s = -0.081$, $p = 0.149$). The maximum distances travelled increased when acoustic estimates of sardine and anchovy biomass were low (Appendix E, $r_s = -0.172$, $p = 0.003$), but there was no significant pattern between these biomass estimates and the duration of foraging trips (Appendix E, $r_s = -0.003$, $p > 0.05$). Sardine and anchovy biomass estimates were nearly significantly correlated with foraging trip path length (see Figure 7, and Appendix E, $r_s = -0.115$, $p = 0.053$).

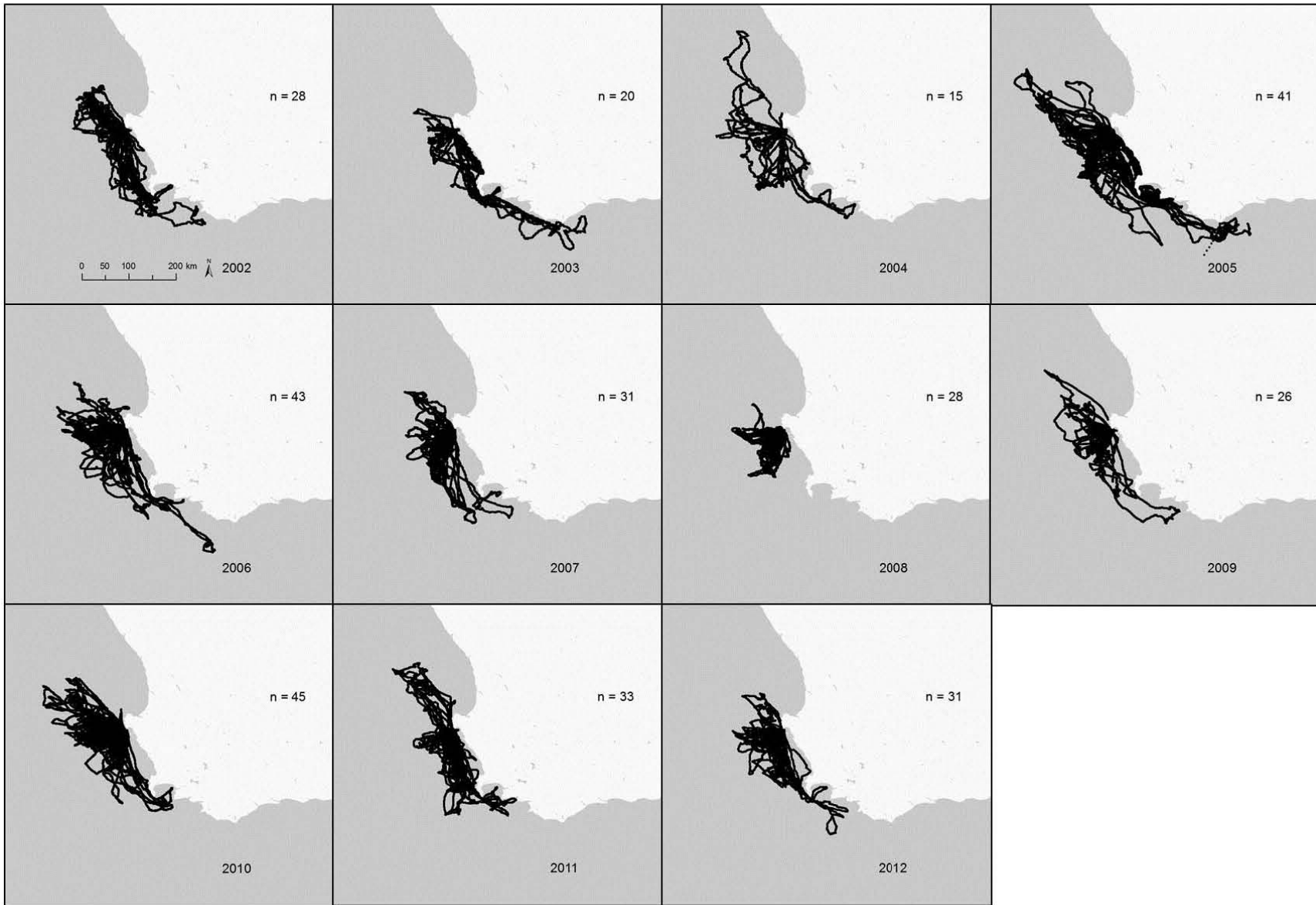


Figure 6. Foraging trips of Cape Gannets provisioning small chicks on Malgas Island recorded with GPS loggers, 2002-2012 (n = 13-45 tracks per year).

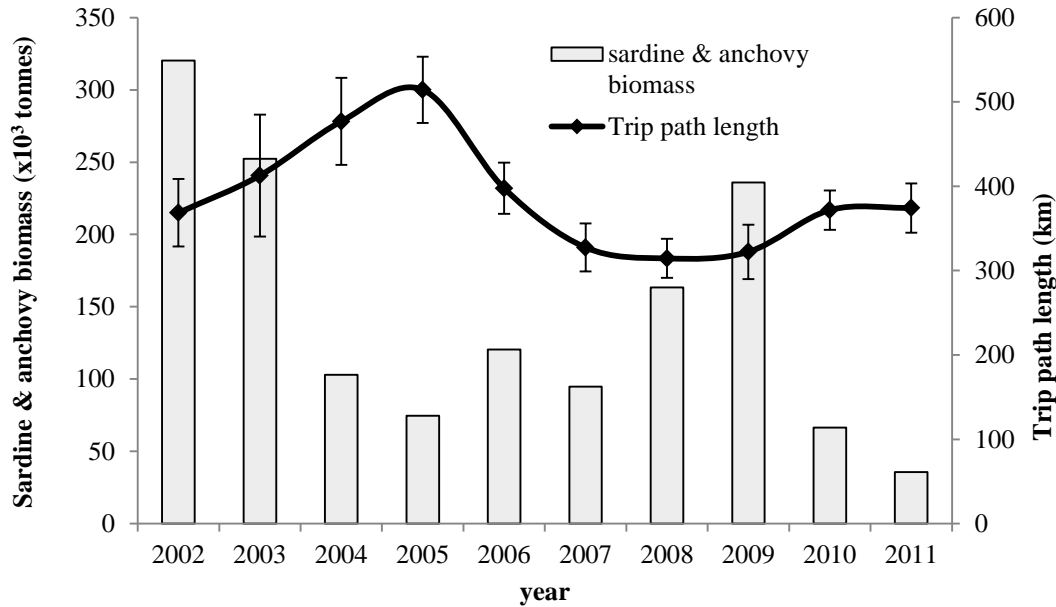


Figure 7. Biomass estimate of sardine and anchovy between Hondeklip Bay and Cape Agulhas, and average foraging trip path length of Cape Gannets breeding on Malgas Island (bars show ± 1 SE).

Body condition and chick growth rate

The body condition of adult gannets (averaged for each pair) was significantly negatively correlated with proportion of hake in their diet (Appendix B, $r_s = 0.470$, $p < 0.001$), but was not correlated with the percent of sardine and anchovy in their diet (Appendix B, $r_s = -0.013$, $p > 0.05$). Linear regressions yielded a negative relationship between adult body condition and hake consumption (Figure 8, adjusted $r^2 = 0.14$, $p < 0.001$). By comparison, chick growth rates were more strongly related to the proportion of sardine and anchovy in the diet than to the proportion of hake in the diet (Figure 8, adjusted r^2 values of 0.25 ($p < 0.001$) and 0.04 ($p = 0.002$), respectively).

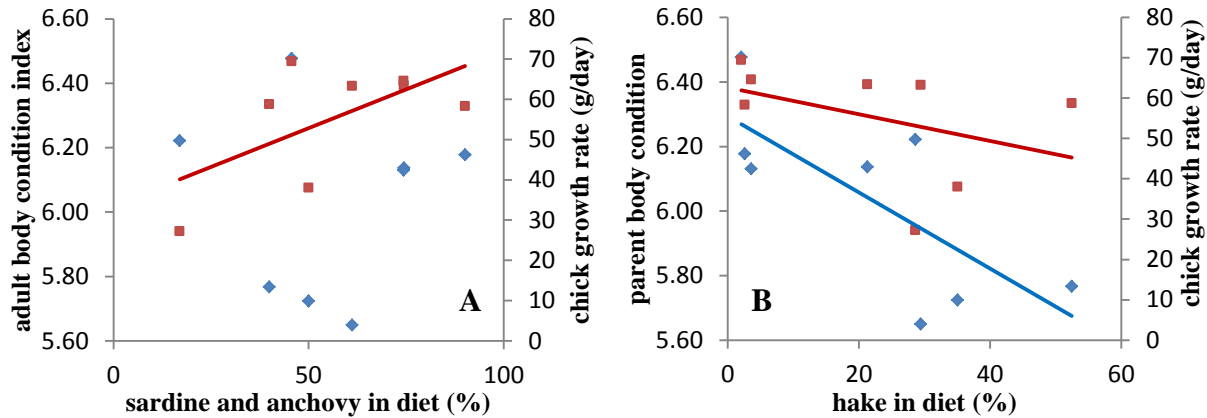


Figure 8. Relationship between Cape Gannet adult body condition (blue) and chick growth rate (red) and (A) % of sardine and anchovy in the diet and (B) % of hake in the diet. Adult body condition versus: % sardine/anchovy in diet: adjusted $r^2 = 0.00$, $p > 0.05$; % hake in diet: adjusted $r^2 = 0.14$, $p < 0.001$. Chick growth rate vs: % sardine/anchovy in diet: adjusted $r^2 = 0.25$, $p < 0.001$; % hake in diet: adjusted $r^2 = 0.04$, $p = 0.002$

Across all years (2005-2012), chick growth rates decreased as all measures of foraging effort increased, most notably as foraging trip duration increased (Appendix F, $r_s = -0.560$, $p < 0.001$). Chick growth decreased with the amount of hake in the diet and increased as sardine and anchovy consumption increased (Appendix B, chick growth vs. hake in diet: $r_s = -0.207$, $p = 0.002$, chick growth vs. sardine and anchovy in diet: $r_s = 0.460$, $p < 0.001$), but chick growth was independent of adult body condition (Appendix F, $r_s = -0.041$, $p > 0.05$). A multiple linear regression indicated that chick growth is best predicted by a combination of factors. I found that chick growth increased as hake consumption, foraging trip duration and irregularity of parental attendance bouts all decreased:

$$\text{Chick growth} = 118 - 0.25 * (\% \text{ of diet composed of hake discards}) - 2.30 * (\text{foraging trip duration}) - 20.90 * (\text{standard deviation in parental nest attendance bouts})$$

with an adjusted $r^2 = 0.32$ ($p < 0.001$; $F_{3,202} = 33.30$).

Nest attendance

Of all chicks monitored from 2002-2012, 70.4% were never observed alone at the nest. Chick growth rates decreased with increasing time spent alone (Appendix B; $r_s = -0.145$, $p = 0.038$), and the amount of time chicks spent alone was higher when the proportion of sardine and anchovy in the diet was lower (Appendix B; $r_s = -0.264$, $p < 0.001$). Parents were more likely to spend more time together at the nest, i.e. they had longer changeover periods between foraging trips, when the biomass of sardine and anchovy in the foraging area and in the gannets' diet were high (Appendix B). When parents fed mostly on hake, chicks spent more time alone (Appendix B; $r_s = 0.326$, $p < 0.001$), parents spent less time together at the nest (Appendix B; $r_s = -0.132$, $p = 0.033$) and chicks grew more slowly (Appendix B; $r_s = -0.207$, $p = 0.002$). The amount of time both parents spent together at the nest was correlated with the growth rate of the chick, albeit not strongly (Appendix B; $r_s = 0.139$, $p = 0.047$).

Parental nest attendance bouts were significantly correlated with foraging trip duration, maximum distance and path length, as recorded by GPS loggers (Appendix F), and I considered the duration of attendance bouts to be a proxy for foraging trip duration and therefore chick provisioning rates. When parents consumed less sardine and anchovy, nest attendance bouts were longer (Appendix B; adjusted $r^2 = -0.257$, $p < 0.001$), but attendance bouts were independent of hake consumption (Appendix B; adjusted $r^2 = 0.002$, $p > 0.05$). Irregular nest attendance patterns (i.e. high standard deviation in attendance bouts), hence irregular provisioning rates, were associated with low levels of sardine and anchovy in diet (Appendix B; $r_s = -0.383$, $p < 0.001$) and in the foraging area (Appendix B; $r_s = -0.244$, $p < 0.001$), as well as with increases in all measures of foraging effort (see Appendix F). Irregular provisioning was associated with lower chick growth rates and chicks being left alone more often (Appendix B).

Discussion

Gannet behavioural flexibility in response to changing prey availability

The abundance of sardine and anchovy in the part of the southern Benguela in which Cape Gannets breeding on Malgas Island forage has fluctuated substantially over the past decade (Table 1). While the exact causes of the changes in pelagic fish abundance and distribution in the Benguela are not completely understood (Coetzee et al. 2008), they definitely affect the breeding success of Cape Gannets and other seabirds in the Benguela (Crawford et al. 2008).

Cape Gannets consume a variety of prey species (Figure 5), but breeding gannets depend on high quality natural prey to rear chicks, and exploiting alternative prey items, especially fishery discards, may lead to reduced breeding success (Grémillet et al. 2008a). Berruti et al. (1993) found that despite the year-round availability of trawler discards in the waters surrounding Malgas Island, Cape Gannets avoid consuming this low-quality food during the breeding season. This is likely due to the fact that hake and other fishery discards have a much lower energetic value than sardine and anchovy (Appendix G), resulting in slow chick growth rates and high mortality (Batchelor and Ross 1984). Pichegru et al. (2010) found that Cape Gannets increase their foraging effort to compensate for reduced availability of natural prey, but they reach a point when they are forced to supplement their diet with fishery discards. Grémillet et al. (2008a) found that when breeding Cape Gannets are forced to feed their chicks hake discards due to low levels of natural prey, overall breeding success is low. Thus reduced abundance of natural prey can cause poor breeding success, affecting colony recruitment and ultimately driving local and global population declines should the availability of natural prey remain low (Cury et al. 2011).

Because this was a long-term study, I was able to assess the effects of diet composition on the foraging strategies of adults, their body condition and the growth rates of chicks across varying conditions. During years when gannets fed largely on hake, chicks spent more time unattended at the nest, had slower growth, and adult body conditions decreased (Appendix B). These results provide evidence for the junk-food hypothesis (see Grémillet et al. 2008a). Even if Cape Gannets can successfully find food by increasing their foraging effort in poor conditions, they are forced to switch to more easily accessible hake discards that lack adequate nutrition for chicks (Grémillet et al. 2008a, Pichegru et al. 2010) because increased foraging effort results in lower chick provisioning rates and longer periods when chicks are left alone at the nest, increasing predation and starvation risks. Thus the spatial distribution of natural prey is important, because when natural prey occurs far from the colony, gannets are forced to make very long foraging trips which decreases their chances of breeding successfully.

Most seabirds show flexibility in foraging behaviour linked to varying environmental conditions (Cairns 1987, Grémillet and Charmantier 2010), and my results clearly show the variability in the foraging strategy of breeding Cape Gannets over the past decade (Table 1, Figure 6). Cape Gannets show high spatial variability in foraging trips, covering a large area off the west coast and occasionally reaching east of Cape Agulhas (Figure 6). Seabirds are successful top predators and this wide spatial distribution of foraging trips appears to be a direct response to changing food availability (abundance and distribution) – a circumstance that likely shaped the evolution of seabird foraging strategies. Foraging trip duration, path length and maximum distance foraged from the colony were all significantly higher in years with low levels of sardine and anchovy in the diet (Table 2). Because the amount of sardine and anchovy in the diet is correlated with the biomass of those species in the gannets' foraging area (Appendix E), it

is likely that the increase in foraging effort was a result of reduced availability of preferred prey. This supports the idea of using the foraging effort of gannets as indicators of prey abundance and overall ecosystem health (Lewis et al. 2006). The fact that foraging trip path length, trip duration and maximum distance are all highly correlated (Appendix E) suggests that any of these measurements may serve as a good index of foraging effort. Interestingly, however, there was no strong correlation between foraging effort and the percentage of hake in the diet. This indicates that hake-related foraging trips could be associated with both long and short foraging trips, or, perhaps, the hake was consumed after a certain amount of time was spent searching for natural prey.

Adults and chicks are affected differently by diet composition

Although previous studies showed that adult Cape Gannets can live off of poor-quality prey (Grémillet et al. 2008a, Moseley et al. 2012), I found that breeding adults have poor body conditions in years with high proportions of hake in their diets. These results are contrary to life history theory, which predicts that adults should not prioritize reproductive effort over their own health and survival (Williams 1966, Cairns 1987, Furness 2003). However, it is possible that adults that choose to breed despite potentially poor conditions are willing to jeopardize their own health to a certain extent. The fact that chick growth was not related to parental body condition (Table 4, Appendix F) further suggests that adult Cape Gannets that attempt to breed put the needs of their chicks ahead of their own.

Fishery discards such as hake have a low energetic value relative to sardine or anchovy (Appendix G), meaning parents may return to the colony with less food due to inefficient energy expenditure during the foraging trip. Furthermore, the anatomy of gannets makes it more

difficult for them to digest discards (Jackson 1992). There was a stronger relationship between adult body condition and the proportion of hake in the diet than with the proportion of sardine and anchovy in the diet (Figure 8). This suggests that, although sardine and anchovy have the highest nutritional value amongst the pelagic fish upon which Cape Gannets feed (Appendix G), adults can still maintain their health on alternate fish species of slightly lower energetic quality, such as horse mackerel and saury.

The degree of sensitivity displayed by gannets to diet composition and the geographic location of pelagic fish is demonstrated by a comparison of 2005 and 2011, two years in which extremely low records of sardine and anchovy (Table 1) caused gannets to consume high levels of an alternate prey species, horse mackerel. In 2005, the diet of Cape Gannets on Malgas Island was 29% hake and 17% sardine and anchovy. Despite the fact that hake consumption was even higher in 2006 (35%), 2007 (53%) and 2009 (30%), 2005 saw the lowest chick growth rates. By comparison, adult body condition was above average in 2005 (Table 1), but below average in 2006, 2007 and 2009. This suggests that adults can consume alternate natural prey but are negatively impacted by hake, while chicks require sardine and anchovy and may be negatively impacted by prey of lower quality, including horse mackerel. However, the situation is further complicated by the spatial distribution of pelagic fish, which in turn affects foraging trips and provisioning rates. In 2011, gannet diet contained 2.1% hake and 46% sardine and anchovy (Table 1), as well as large amounts of horse mackerel. Interestingly, 2011 recorded the highest chick growth rates and adult body condition index (Table 1). The difference between 2005 and 2011 lies in the foraging strategies of adults. In 2005, gannets had the longest foraging trips in terms of both duration (29.2 h) and distance (514 km) and left their chicks alone for the greatest amount of time (Table 1). By comparison, birds in 2011 only foraged for an average 19.2 hours

(below average), travelling 374 km (below average), and no study chicks were left alone at the nest (Table 1). Thus it appears that breeding gannets may be able to compensate for a reduction in sardine and anchovy by consuming alternate natural prey, but only if the alternate prey is close enough to avoid extended foraging trips, which cause a reduction in provisioning rates to chicks as well as poorer nest attendance (and thus higher predation and overall mortality). These findings highlight the need for spatial management considerations and the fact that the behavioural flexibility of foraging gannets is constrained by the demands of their chicks.

Regular nest attendance patterns and provisioning rates are necessary for better chick growth

Predation is a serious problem for chicks and fledglings on Malgas Island (Chapter 1). To prevent predation on their chicks (as well as prevent death by hostile weather conditions), Cape Gannets avoid leaving chicks under one month old unattended and usually wait for the partner to return before embarking on a foraging trip, if the partner is not gone for too long (Jarvis 1971). Poor nest attendance generally occurs when environmental conditions are unfavourable, because if the foraging parent has been gone for an extended period of time, the attending parent may leave for his/her own foraging trip, leaving the chick unattended. This likely occurs because young chicks can only survive for a few days without food (Navarro 1992). In 2012, when the average foraging trip duration was 19.3 hours (Table 1), a parent with a 2-week old chick was observed waiting over three days for its partner to return, at which point it was forced to leave the chick alone in order to forage. This decision to leave such a young chick unattended increased the risk of predation by Kelp Gulls, but was a decision in line with those of most long-lived seabird species who prioritize adult survival (Williams 1966).

The significant positive correlation between the percentage of time both parents spend at the nest together and prey abundance suggests that when both parents can spend more time at the nest together they are not struggling to find food and have more “spare time”. Thus there is a potential for nest attendance parameters to be used as indices of environmental conditions, though nest attendance is a time-intensive measurement to obtain. Good feeding conditions are usually coupled with regularity in nest attendance bouts, and therefore provisioning rates. The variability of nest attendance bouts was negatively correlated with both the amount of sardine and anchovy in the diet as well as in the foraging area (Appendix B), suggesting that when more sardine and anchovy is accessible, parents can undertake foraging trips at regular intervals, and of consistent durations. Chick growth rates were lowest in 2005 (Table 1), a year in which gannets also had the longest nest attendance bouts (1.0 days, Table 1) and highest variability in attendance bouts (SD of 0.6 days, Table 1).

The lack of relationship between chick growth and the percentage of time a chick was left alone may be because being left alone does not cause poor chick growth rates (non-attendance is more likely to cause death due to predation or harsh weather exposure), but instead is another symptom of overall poor breeding conditions. The amount of time a chick was left alone decreased as prey quality increased and adult body condition increased (Appendix B), further supporting the notion that unattended chicks are a clear sign on poor environmental conditions.

Chapter 3: Conclusions and Conservation Implications

Limits of seabird behavioural flexibility vary depending on the species' life history traits and its geographic constraints (Grémillet and Charmantier 2010). In addition, seabird plasticity may vary substantially at the individual level before evolutionary adaptation takes place, thus it is preferable to study responses to change at the individual, rather than population level (Grémillet and Charmantier 2010). Chapter 2 demonstrated that adult Cape Gannets are less sensitive to prey quality (body condition only declines at high levels of hake consumption) than are their chicks (which depend predominantly on lipid-rich sardine and anchovy). Chapter 2 also showed that Cape Gannets raising young chicks can significantly increase their foraging effort in years with poor food availability. However, an increase in foraging effort may not compensate for the resultant low provisioning rates and poor parental nest attendance, or for a lack of high-quality prey such as sardine and anchovy. Thus, despite flexibility in adult foraging strategy, poor feeding conditions are likely to cause low chick growth and survival rates, eventually leading to low breeding success, recruitment and colony-level population declines. If poor conditions persist for prolonged periods, colony-level population declines may lead to global population declines, as some breeding sites may be abandoned while others reach carrying capacity. Because juvenile gannets do not breed until their third or fourth year, the effects of poor breeding conditions may not arise until several years later. Hence longitudinal monitoring of both seabird and prey populations is essential.

Long-term studies across varying environmental conditions are essential to improve our knowledge of the complex responses of Cape Gannets, and possibly other seabirds, to global change. Information on threshold relationships between environmental conditions, breeding

parameters, and breeding success can help to predict population declines and understand which aspects of the breeding cycle are most affected by sub-optimal conditions. The persistence of a population depends on the ability of individuals to cope with changes in their environment, so a clearer understanding of the limits of the behavioural flexibility of Cape Gannets should lead to more effective management strategies in light of inevitable continued global change. At present, Malgas Island is protected within the West Coast National Park Marine Protected Area (Birdlife International 2012b). However, the foraging trips of breeding Cape Gannets extend hundreds of kilometres from Malgas Island (Chapter 2), overlapping extensively with South Africa's pelagic fisheries (Okes et al. 2009). The implementation of no-take fishing zones or reduced Total Allowable Catches during years where the abundance of sardine and anchovy falls below a certain threshold or is located relatively far from Malgas Island may help relieve gannets of having to significantly increase their foraging effort in search of quality prey for their young chicks. These management actions should improve the breeding success of Cape Gannets and restore the population on Malgas Island to recent historic levels.

An understanding of the dynamics of Cape Gannets breeding in poor conditions will not only help to conserve gannets and other seabirds, but may reveal ways in which data on seabirds can be used to monitor the status of the Benguela and its pelagic fish populations, thus improving fisheries management of some of South Africa's economically key fish species. Using seabirds as indicators of ecosystem change has been suggested as a cheaper, potentially more effective method of monitoring than current survey methods (Cairns 1992, Berruti et al. 1993, Monaghan 1996). However, since seabirds generally exhibit some degree of behavioural flexibility, understanding that life history traits are affected differently depending on the severity of conditions is important when using seabirds as indicators of ecosystem health (Grémillet and

Charmantier 2010). Cape Gannets should be valued as both functional components (as top predators) of the Benguela ecosystem and as potentially useful environmental sentinels. It is critical that long-term monitoring and anti-predator control continue and that appropriate conservation action in response to changing environmental conditions is taken to prevent further population declines among west coast Cape Gannet populations.

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Appendix A: Dates of gannet foraging trip sampling (GPS)

Breeding season	GPS logger deployment dates
2002-03	11-16 December 2002
2003-04	13-19 November 2003
2004-05	9-28 January 2005
2005-06	3 October - 6 November 2005
2006-07	9-29 October 2006
2007-08	10-28 October 2007
2008-09	8-19 October 2008
2009-10	12-27 October 2009
2010-11	27 September - 23 October 2010
2011-12	12-31 October 2011
2012-13	10-19 October 2012

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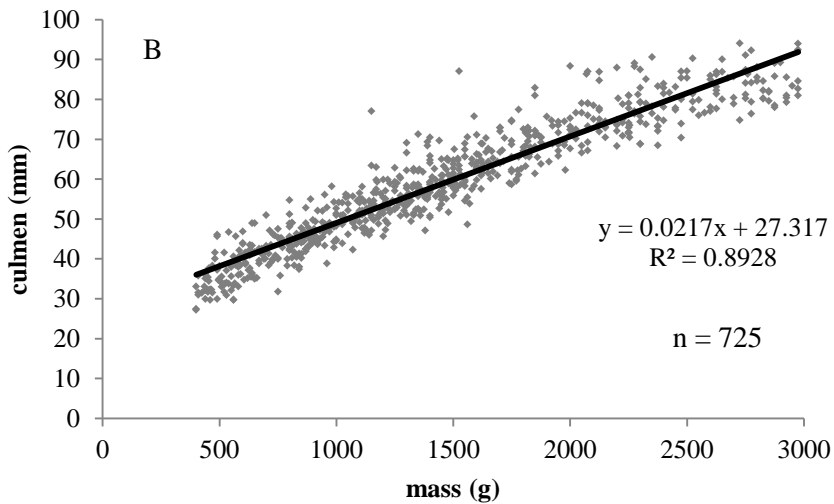
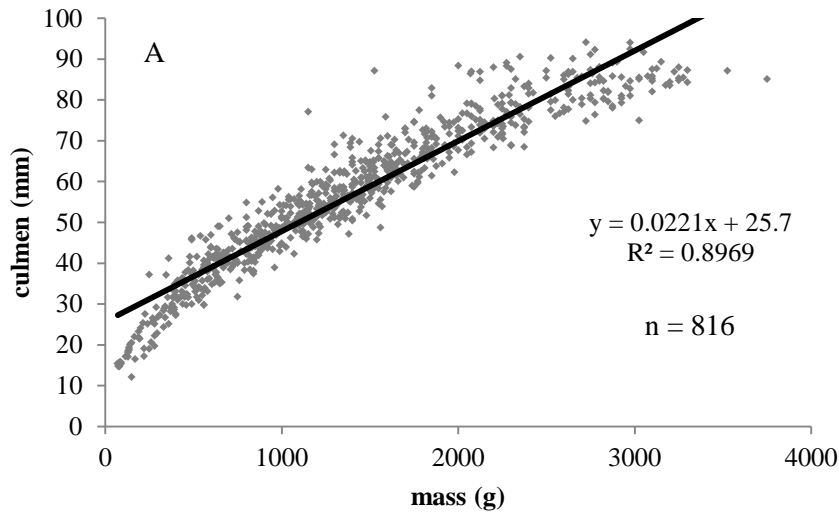
Appendix B: Correlations between Cape Gannet chick growth, attendance, and diet

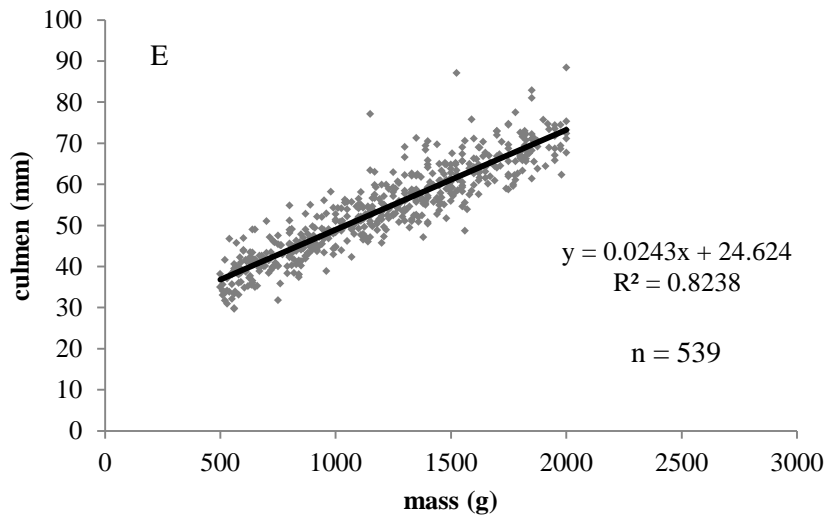
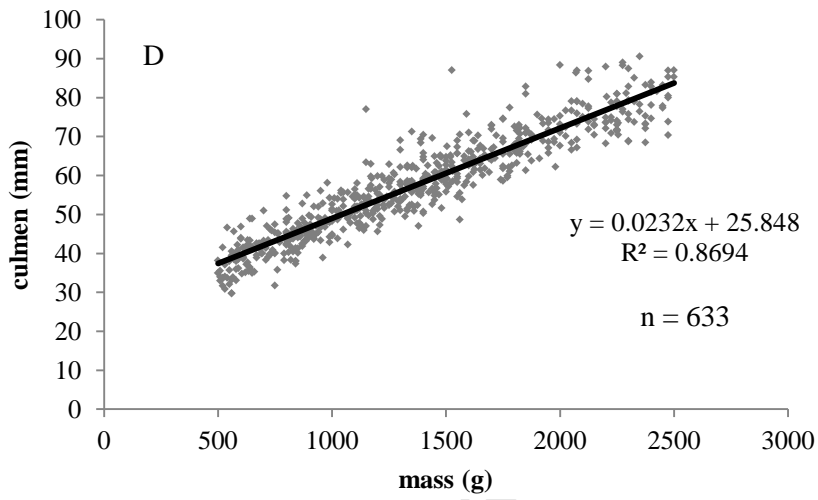
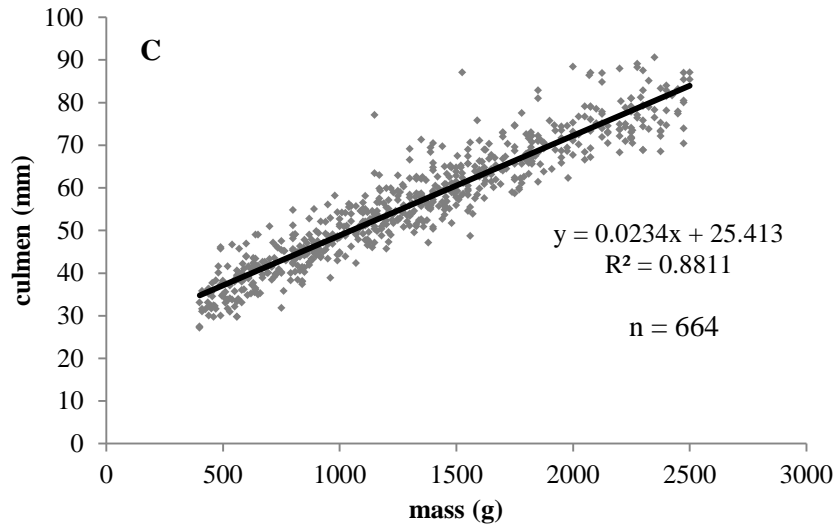
Spearman's rank correlations (with Spearman's rho (r_s) and p value given) for comparisons of chick growth rates, nest attendance patterns, and diet composition of Cape Gannets breeding on Malgas Island from 2005-2012. c.growth = chick growth rate; wing_1 = 1st chick wing measurement (at mass of 400g+); alone = % of time chick alone at nest; 2parents = % of time chick attended by both parents; condition = average parent body condition; SDattend = average (of both parents) standard deviation in duration of nest attendance bouts; att.bout = average (of both parents) duration of nest attendance bouts; diet(S/A) = % of diet composed of sardine and anchovy, diet(hake) = % of diet composed of hake; biomass = biomass of sardine and anchovy from acoustic surveys. Significant correlations are in bold. Nest attendance parameters, wing measurements, and chick growth are analyzed at the individual level (n = 15-51 nests per year), while diet composition is based on colony-wide averages (from a sample of 35-100 individuals per year). The biomass of sardine and anchovy is based on annual acoustic surveys off the coast of South Africa from Hondeklip Bay to Cape Agulhas.

	c.growth	wing_1	alone	2parents	condition	SDattend	att.bout	diet(S/A)	diet(hake)
wing_1	-0.035 0.620								
alone	-0.145 0.038	0.440 0.000							
2parents	0.139 0.047	0.108 0.122	-0.066 0.285						
condition	-0.041 0.561	-0.226 0.001	-0.194 0.002	-0.018 0.778					
SDattend	-0.263 0.000	0.023 0.746	0.160 0.010	-0.138 0.027	-0.053 0.399				
att.bout	-0.383 0.000	-0.105 0.135	-0.074 0.235	-0.289 0.000	-0.021 0.732	0.354 0.000			
diet(S/A)	0.460 0.000	-0.150 0.029	-0.264 0.000	0.380 0.000	-0.013 0.839	-0.383 0.000	-0.257 0.000		
diet(hake)	-0.207 0.002	0.410 0.000	0.326 0.000	-0.132 0.033	-0.470 0.000	0.004 0.951	0.002 0.978	-0.469 0.000	
biomass	0.136 0.059	0.402 0.000	0.101 0.123	0.307 0.000	-0.417 0.000	-0.244 0.000	0.077 0.240	0.485 0.000	0.464 0.000

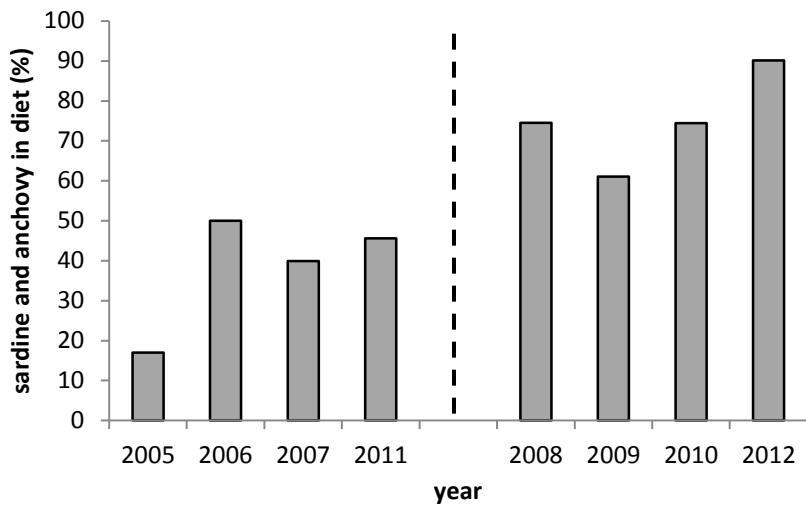
Appendix C: The linear phase of gannet chick growth

Process used to determine the linear phase of chick growth. Mass plotted against culmen of all chicks measured from 2002-2009 and 2012, with varying cut-off points (by mass) and r^2 value, sample size, and linear equation shown. Line slopes, r^2 values, and sample sizes were taken into consideration, and Figure C was deemed the most representative model of the linear phase of chick growth. A. chicks of all masses; B. chicks weighing 400-3000 g; C. chicks 400-2500 g; D. chicks 500-2500 g; E. chicks 500-2000 g





Appendix D: Low versus high proportion of sardine and anchovy in Cape Gannet diet



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Appendix E: Correlations between measures of Cape Gannet diet and foraging behaviour

Spearman's rank correlations (with Spearman's rho (r_s) and p value given) for comparisons of the diet and foraging behaviour of Cape Gannets breeding on Malgas Island from 2002-2012. Duration = foraging trip duration; path length = foraging trip path length, max.dist. = maximum distance from colony foraged; diet(hake) = % of diet composed of hake; diet(S/A) = % of diet composed of sardine and anchovy; biomass = average biomass of sardine and anchovy from acoustic surveys in foraging area. Significant correlations are in bold. Foraging trip parameters are analyzed at the individual level (n=13-43 trips per year), while diet composition is based on colony-wide averages (from a sample of 35-100 individuals per year). The biomass of sardine and anchovy between Hondeklip Bay to Cape Agulhas (Zones A-C) is estimated from annual acoustic surveys conducted during Oct-Nov.

	duration	path length	max.dist.	diet(hake)	diet(S/A)
path length	0.804 0.000				
max.dist.	0.635 0.000	0.875 0.000			
diet(hake)	0.112 0.047	0.081 0.149	0.014 0.801		
diet(S/A)	-0.190 0.001	-0.242 0.000	-0.223 0.000	-0.497 0.000	
biomass	-0.003 0.963	-0.115 0.053	-0.172 0.003	0.391 0.000	0.552 0.000

Appendix F: Correlations between Cape Gannet chick growth, attendance, and foraging behaviour

Spearman's rank correlations (with Spearman's rho (r_s) and p value given) for comparisons of chick growth rates, nest attendance patterns, and foraging behaviour of Cape Gannets breeding on Malgas Island from 2005-2012. c.growth = chick growth rate; alone = % of time chick alone at nest; 2parents = % of time chick attended by both parents; condition = average parent body condition; SDattend = average (of both parents) standard error in duration of nest attendance bouts; att.bout = average (of both parents) duration of nest attendance bouts; duration = foraging trip duration; max.dist. = maximum distance from colony foraged; length = foraging trip path length. Significant correlations in bold. Nest attendance parameters, adult body condition, chick wing measurements, and chick growth are analyzed at the individual level (n = 15-51 nests per year), while foraging trip parameters are based on colony-wide averages (from a sample of 13-43 individuals per year).

	c.growth	alone	2parents	condition	SDattend	att.bout	duration	max.dist.
alone	-0.145 0.038							
2parents	0.139 0.047	-0.066 0.285						
condition	-0.041 0.561	-0.194 0.002	-0.018 0.778					
SDattend	-0.263 0.000	0.160 0.010	-0.138 0.027	-0.053 0.399				
att.bout	-0.383 0.000	-0.074 0.235	-0.289 0.000	-0.021 0.732	0.354 0.000			
duration	-0.560 0.000	-0.052 0.400	-0.111 0.073	0.250 0.000	0.230 0.000	0.493 0.000		
max.dist.	-0.496 0.000	0.041 0.508	-0.294 0.000	0.200 0.001	0.394 0.000	0.296 0.000	0.574 0.000	
path length	-0.529 0.000	0.117 0.058	-0.332 0.000	0.092 0.137	0.394 0.000	0.359 0.000	0.560 0.000	0.923 0.000

Appendix G: Energy content of the main prey species of Cape Gannets

From Batchelor and Ross (1984)

Prey item	Energy content (kJ.g ⁻¹)
Sardine	8.59
Anchovy	6.74
Saury	6.20
Horse Mackerel	5.63
Squid	4.55
Fishery discards (i.e. hake)	4.07

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