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Original Article

Dietary change in Cape gannets reflects distributional and demographic shifts in two South African commercial fish stocks

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Seabirds are upper trophic level predators, and are often highly sensitive to changes in the availability of their prey. Altered prey assemblages resulting from fluctuations in oceanographic conditions may be mirrored by shifts in seabird diet. Long-term studies of dietary change in seabirds therefore provide valuable insight into the nature of environmental shifts within the systems in which they forage. In recent decades, the Agulhas region in South Africa has undergone significant oceanographic change related to warming and intensification of the Agulhas current. Concurrent with this change, the population of Cape gannets *Morus capensis* at Bird Island, Algoa Bay, has grown rapidly, probably as a result of an increased availability of its dominant prey items, sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*. Using one of the longest and most complete time-series available on diet of a seabird (spanning 34 years), we tested for changes in composition and the abundance of dominant prey species of this population. These observed changes were also compared with acoustic survey estimates of their biomass, and annual catch data. Since 1979, the prey composition has remained similar, but the dietary contribution of sardine and anchovy, which fluctuated inversely to each other, increased over the study period. These shifts seem to be reflective of fluctuations in the stock size of sardine and anchovy. Conversely, a third species, saury *Scomberesox saurus*, dominant in the non-breeding diet of the 1980s, decreased significantly in dietary abundance over the following two decades. It is likely that dietary shifts of Cape gannets at Bird Island were related to climate-mediated oceanographic change. The implications of such changes are discussed.

Keywords: Climate change, *Morus capensis*, pelagic fish, prey availability, seabirds.

Introduction

Seabirds are important predators within the marine environment, globally consuming an estimated 70 million tons of prey annually (Brooke, 2004), mainly in the form of low- to mid-trophic level species. Reliance on a narrow trophic range leaves seabirds vulnerable to the effects of instability at lower trophic levels. Reductions in prey availability related to declines in stock size have been shown to negatively impact seabird breeding performance (Cury *et al.*, 2011). This is of concern because many prey resources targeted by seabirds are also targeted by a number of other top predators, in particular, man. Overexploitation of fish stocks is well documented, and has led to industrialized fishing being labelled as the single greatest threat to future marine productivity (Jackson *et al.*, 2001; Brander, 2007). These issues are compounded by the impact of global climate change on marine systems (e.g. Edwards and Richardson, 2004; Hays *et al.*, 2005; Pörtner and Knust, 2007), such as the alteration of marine communities through climate-related species distributional shifts (Cheung *et al.*, 2009).

High energetic demands in seabirds make them particularly sensitive to changes in prey abundance and availability (Piatt *et al.*, 2007) and this is often reflected in their diet. For example, a climate-induced regime shift caused a reduction in the availability of lipid-rich prey for Red-legged kittiwakes (*Rissa brevirostris*) on the Pribilof Islands (Kitaysky *et al.*, 2006). Chicks fledged on an alternative diet of lower quality prey suffered high mortality, and recruitment into the colony was low. Similarly, a collapse of the sardine (*Sardinops sagax*) fishery in central California attributable to fishing and environmental change forced Marbled murrelets (*Brachyramphus marmoratus*) to modify their diet to a lower trophic level (Becker and Beissinger, 2006). Similar diet modifications towards lower quality prey have been linked to low breeding success (Wanless *et al.*, 2005). However, there are also cases in which dietary change has had positive influences on seabirds. For example, an oceanographic regime shift in the North Atlantic resulted in an increase in Northern gannet (*Morus bassanus*) population numbers due to the introduction of lipid-rich warm water migratory species into the diet (Montevecchi and Myers, 1997).

Along the Southern African west coast, the highly productive Benguela upwelling system supports purse-seine fisheries directed at sardine and anchovy (*Engraulis encrasicolus*; Fairweather *et al.*, 2006). Historically, the Benguela system supported a large sardine biomass, but overexploitation of sardine contributed to major stock declines of this species off both Namibia and South Africa (Crawford *et al.*, 1987). As the Namibian sardine stock collapsed, its range shifted northwards, away from major seabird breeding localities (Crawford *et al.*, 2007a). In South Africa, the centre of gravity of both the sardine and anchovy stocks shifted progressively southward and, more recently, eastward (Van der Lingen *et al.*, 2005; Fairweather *et al.*, 2006; Roy *et al.*, 2007). These distributional changes have had a significant impact on marine top predators, causing many to suffer substantial population declines (Crawford *et al.*, 2008, 2011).

One such species is the Cape gannet (*Morus capensis*), a large pelagic seabird endemic to the shelf waters of Namibia and South Africa (Crawford *et al.*, 1983). It is a medium-distance forager, capable of covering several hundred kilometres in a single foraging trip (Pichegru *et al.*, 2007). Its natural diet is dominated by three fish species, namely sardine, anchovy, and saury (*Scomberesox saurus*; Batchelor and Ross, 1984; Klages *et al.*, 1992; Berruti *et al.*, 1993), which it catches by plunge diving (Ropert-Coudert *et al.*, 2004). Breeding is restricted to six islands (Namibia: Ichaboe, Possession, Mercury; South Africa: Bird at Lambert's Bay, Malgas, Bird at Algoa Bay; Rand, 1959; Crawford *et al.*, 2007a). In the mid-1950s, the bulk of the gannet population was located in Namibian waters (Rand, 1959), but corresponding to an altered distribution of sardine and anchovy, the centre of gravity of Cape gannets has moved south- and eastwards (Crawford *et al.*, 2007a). Of the six breeding colonies, five are in decline, while the easternmost (Bird at Algoa Bay) has increased (Crawford *et al.*, 2007a). Overall, however, the total population has decreased by ~40% since the mid-1950s (Crawford *et al.*, 2007a).

Considerable dietary change has been noted along the west coast, and of particular concern has been an increased contribution of fishery discards (mostly hake *Merluccius* spp.) to the diet of Cape gannets (Pichegru *et al.*, 2007; Mullers *et al.*, 2009). While discards represent an easily accessible and abundant resource (e.g. 29 619 t of fish were discarded annually between 1995 and 2000, Walmsley *et al.*, 2007), their low lipid content makes them an unsuitable alternative to natural prey (Batchelor and Ross, 1984; Mullers *et al.*, 2009). Gannet chicks reared on discards tend to have relatively low chances of survival (Mullers *et al.*, 2009), which has in all likelihood contributed towards the negative population growth of western Cape gannet colonies.

During the 1970s and 1980s, the diet of Cape gannets at Bird Island (Algoa Bay) consisted predominantly of sardine, anchovy, and saury, with substantial inter- and intra-annual variation in the contributions of these three species (Klages *et al.*, 1992). Subsequently, however, the marine environment off southern South Africa has changed considerably (Rouault *et al.*, 2009), and there has been an eastward shift in the distributions of sardine and anchovy, which probably influenced the rapid and continued growth of the gannet colony at Bird Island, from 56 869 in 1991/1992 to 98 914 breeding pairs in 2005/2006 (Crawford *et al.*, 2007a). The colony has since remained fairly stable, with an estimated 93 224 breeding pairs for 2012/2013 (Oceans and Coasts, unpublished data), suggesting the onset of density-dependent factors.

To better understand marine ecosystem changes along the South African coast, we here explore Cape gannet dietary data collected over the period 1979–2012. We test for long-term and seasonal changes in the diet of Cape gannets at Bird Island, and predict a gradual increase in the dietary contribution of sardine and anchovy resulting from a greater availability of these species within Eastern Cape waters, but a decrease in sardine after 2005 following the rapid decline of South Africa's sardine stock at that time. Lastly, we compare changes in the abundance of sardine and anchovy in the diet of gannets with acoustic survey density estimates and total annual catches of these species.

Material and methods

Diet data collection

Sampling was conducted at Bird Island (33°50′S 26°17′E), situated at the eastern margin of Algoa Bay along the south coast of South Africa, within the Agulhas bioregion (Figure 1). Regular diet sampling commenced in 1979 (Batchelor and Ross, 1984) and has since taken place annually at varying frequencies (Table 1, full table in Supplementary Appendix SA). The study period spans 34 years with the 1980s and 1990s well represented, but with lower sampling frequencies during the 2000s until December 2011 when monthly sampling took place until March 2013.

Typically, diet sampling took place throughout the day, but was focused around mid-morning and late afternoon, coinciding with a peak in gannets returning to the colony (Batchelor and Ross, 1984). Birds that landed heavily along the colony edge were caught using a crooked pole and upended over a bucket to induce regurgitation. Additional samples were collected opportunistically when birds were seen to regurgitate, either due to human disturbance or handling related to other studies.

Each sample was weighed (to the nearest gram) and separated into its constituent species, which were individually weighed. The number of individuals from each species was estimated from counts of whole fish and the number of heads and tails of each species present within the sample. Fork lengths (FL: 1979–2004) or caudal lengths (2004–2012) of all whole fish were measured. For fish in a state of advanced digestion, otolith lengths were used to calculate FL, which was in turn used to calculate mass by species-specific regressions (Smale *et al.*, 1995). Caudal lengths were converted to FL by back-calculating otolith length from regressions for caudal length (Smale *et al.*, 1995). Species that were not immediately identifiable were cross referenced against Smith (2003).

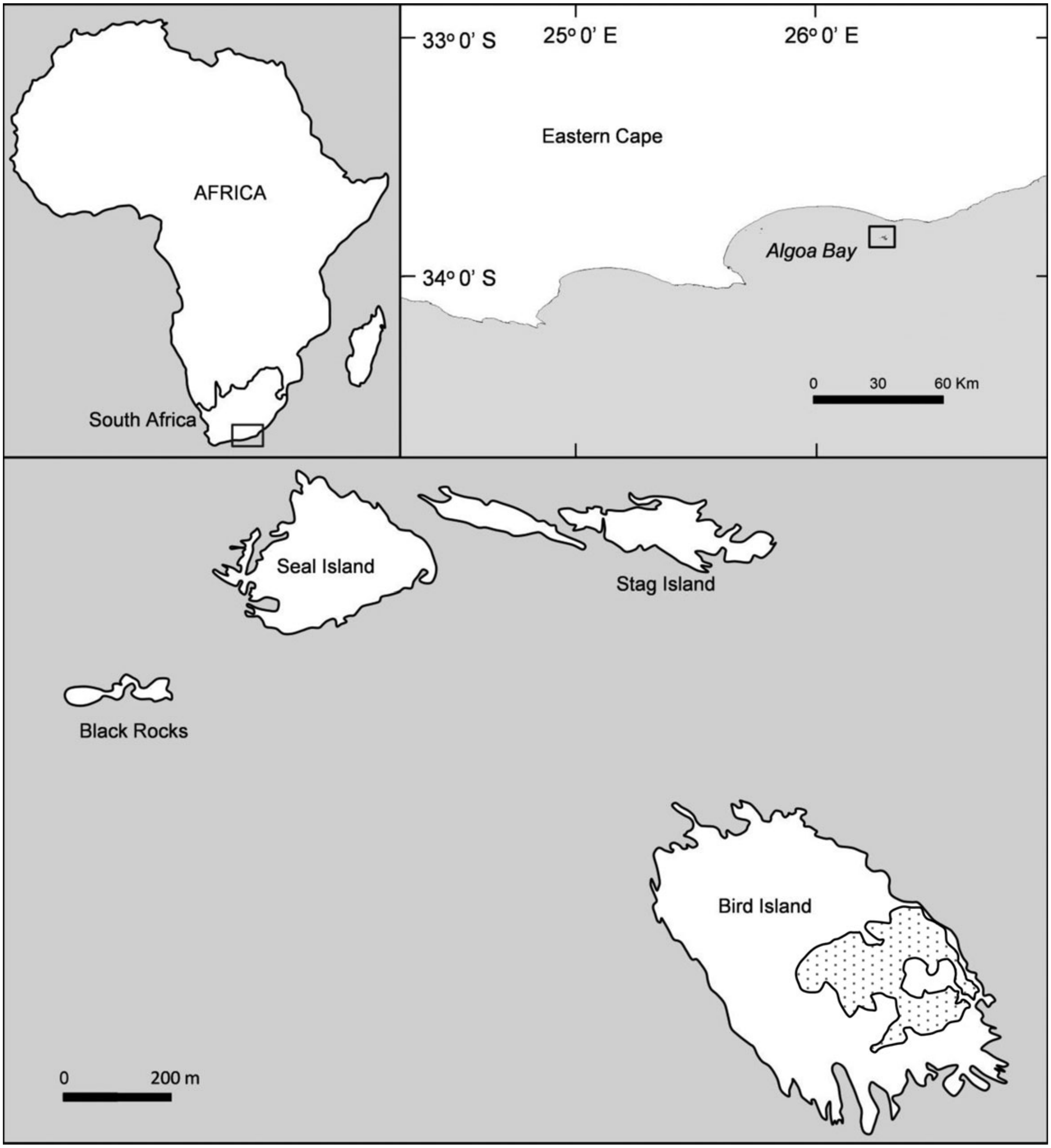

Figure 1. Location of Algoa Bay and the Bird Island group along the south coast of South Africa. The stippled area depicts the extent of the Cape gannet colony at Bird Island in 2013.

Table 1. Number diet samples collected during the Cape gannet breeding and non-breeding seasons at Bird Island over the course of the study.

Years	Breeding	Non-breeding	Total
1979–1989	1399	2498	3897
1990–1999	676	1494	2170
2000–2012	312	1143	1455
		Total	7522

Temporal scale

Adult Cape gannets attend the colony throughout the year, allowing for collection of samples both during and outside of the breeding season. Due to the sporadic nature of sampling, especially during the latter third of the study (2000s), monthly samples were grouped into two seasons: the non-breeding season, centred largely on winter (April–September) and the breeding season (October–March); following Klages *et al.* (1992). The data were then further grouped into three periods (1980s, 1990s, and 2000s) to assess decadal changes in diet composition. To test for annual trends in the diet, only breeding season data were used due to the non-breeding season being undersampled during the 2000s. Across the 34-year period, with the exception of a single year (2000), all breeding seasons were represented. For the purpose of this study, one breeding cycle began at the onset of the non-breeding season (April) and ended following the conclusion of breeding in March the following year (Klages *et al.*, 1992). The diet was divided into five prey groups, namely sardine, anchovy, saury, other live prey (OLP), and fishery discards (discards). Species were classified as discards if they were known contributors to the annual trawl catch, and/or if their habits (e.g. benthic) left them otherwise unavailable to foraging Cape gannets (Klages *et al.*, 1992).

Monthly and seasonal data were analysed according to four criteria: percentage numerical abundance, frequency of occurrence, percentage mass, and FL. Percentage numerical abundance (%NA) represented the proportional number of a particular prey group recorded during that month or season, in relation to the total number of prey items recorded over the same period. The frequency of occurrence (FO) was calculated as the percentage of the total number of samples within each month, and season in which a particular prey group was found. Percentage mass (%Mass) referred to the mass of a prey group as a proportion of the total monthly and seasonal mass of all prey in the diet. From 1979 to 2004, mass data were obtained in the form of reconstituted mass. As such, %Mass of each prey group during this period represents the reconstituted mass of that prey group relative to the overall reconstituted mass of prey. However, following 2004, mass data were recorded as wet mass. Thus, over this period, %Mass represented the mass of each prey group relative to the overall wet mass. Owing to these differing protocols, %Mass was used only to support the trends shown by %NA and FO. Owing to almost complete concurrence between these three indices, only %NA was presented within figures in the results.

Comparisons with survey and catch data

For comparison with gannet diet, adult small pelagic fish density data from the annual summer acoustic survey (available since 1984; Coetzee *et al.*, 2008) and catch data for the Eastern Cape purse-seine fleet were obtained from the Department of Agriculture, Forestry and Fisheries (DAFF). The survey covers the entire extent of the shelf area from Hondeklip Bay to Port Alfred between October and December each year and is conducted along randomly spaced, parallel transects (perpendicular to the coastline), which have been pre-stratified to increase precision of the estimates (Barange *et al.*, 1999). Density estimates (g m^{-2}), for all transects that fell east of Robberg Peninsula, which represents the western extremity of the Bird Island gannet foraging range (Moseley *et al.*, 2012), were extracted for the estimation of average annual density of sardine and anchovy within the gannet foraging range. As the survey is always conducted at the same time of year (October to December), these density estimates were compared against the average contributions of species to the diet during the breeding season (samples collected from October to March) only. Although catch (t) data for sardine and anchovy are available from the late 1940s, they have only been spatially disaggregated since 1987 (Fairweather *et al.*, 2006). Comparisons between sardine and anchovy catches and the proportions of sardine and anchovy in the diet were therefore performed for the period 1987–2012.

Statistical analyses

To test for changes in diet composition between seasons and across years, a permutational multivariate analysis of variance (adonis, method = "bray", permutations = 5000) was performed, using package "vegan" (v. 2.0–8) in R (v. 3.0.1 for Windows). Using the "strata" function within Adonis, we tested for seasonal differences independently between decades, within a single analysis. Likewise, we tested for decadal changes in the composition of the diet for both seasons. Differences were illustrated using non-multidimensional scaling (n-MDS) with a maximum of 20 iterations. Seasonal changes in the contribution to the diet and mean FL of the three dominant prey species were tested independently between decades using Student's *t*-tests, while long-term change was assessed using regression analyses. Piecewise regressions (segmented, package "segmented") were used to assess long-term change where abrupt changes in trends were evident. The "segmented" function statistically determined the true breakpoint in the linear relationship using as its start point, a given breakpoint, which was estimated through inspection of the scatterplot. Pearson's correlations were used to investigate relationships between the contribution of anchovy and sardine to the diet, and their densities in the surveys and their catch data. The survey data were cube-root transformed, while the catch data, and anchovy % Mass were square-root transformed to meet the assumption of normality

Results

Diet composition

In total, 57 729 prey items representing 55 types (of which, 49 were identified to species level) were recorded in the diet of Cape gannets over the course of this study (Supplementary Appendix SA). However, many prey species were recorded infrequently and contributed little to the overall diet. As a result, diet diversity was generally low and dominated by a few species. The three predominant species (sardine, anchovy, and saury) constituted 93.5% of the overall diet by %NA. A further 5.7% was made up by OLP species, predominantly chub mackerel (*Scomber japonicus*), horse mackerel (*Trachurus trachurus*), red-eye round herring (*Etrumeus whiteheadi*), and chokka squid (*Loligo vulgaris*), whereas discards, mainly hake (*Merluccius* spp.), constituted the remainder (0.8%) of the diet.

Seasonal differences in diet

The five main prey groups (sardine, anchovy, saury, OLP, and discards) were all present in both seasons, resulting in considerable dietary overlap between breeding and non-breeding seasons. Composition of the diet, however, changed significantly between seasons over the three decades (%NA: $F = 14.19$, $p < 0.001$; FO: $F = 19.54$, $p < 0.001$; %Mass: $F = 21.41$, $p < 0.001$; Figure 2). During the breeding season, the diet was almost exclusively composed of sardine and anchovy. In contrast, outside of the breeding season, a broader range of species, characterized by a larger proportion of saury, OLP, and fishery discards, was consumed. These differences were most evident during the 1980s and 1990s. During the 2000s, greater dietary overlap between seasons resulted from an increase in the contribution of sardine and anchovy to the non-breeding diet of Cape gannets.

Of the three dominant species, sardine and anchovy contributed a larger proportion to the breeding diet than to the non-breeding diet, whereas saury was most prevalent in the non-breeding diet (Figure 3). For both sardine and anchovy, these differences were most noticeable during the second decade (1990s) when their

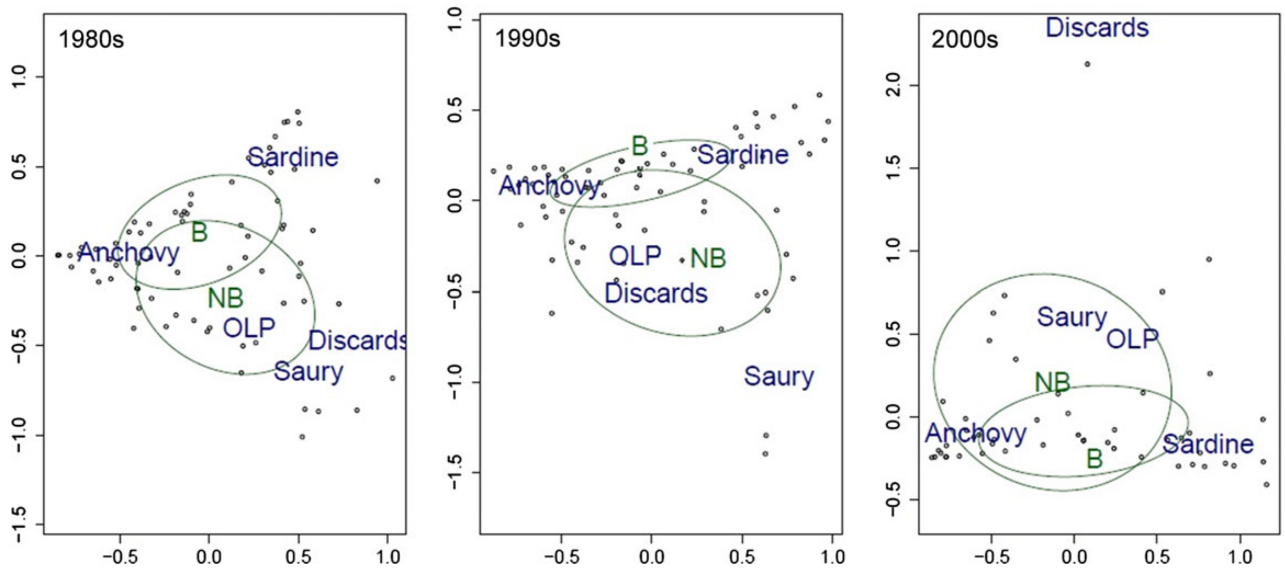

Figure 2. Non-metric multidimensional scaling plots of monthly numerical abundance showing seasonal differences in prey composition of Cape gannet diet across three decades. Sample points represent each sampled month, and their position is related to the relative monthly contribution of each of the five major prey groups. Green ellipses were used to highlight the centre of gravity of months within the breeding (B) and non-breeding (NB) seasons. OLP, other live prey.

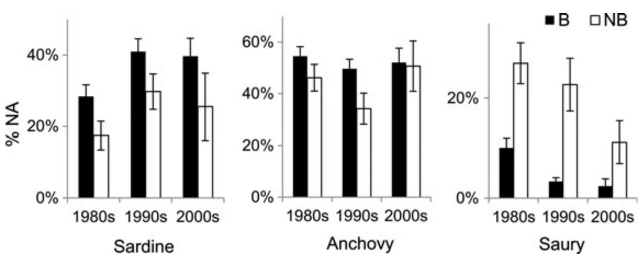

Figure 3. Comparison between the breeding (B) and non-breeding (NB) diet of Cape gannets in terms of the mean (± SE) numerical abundance (%NA) of sardine, anchovy, and saury, across three decades.

dietary contribution was significantly higher during the breeding season (%NA, FO, and %Mass; Table 2). During the 1980s and 2000s, differences in sardine contribution between the breeding and non-breeding seasons were only weakly significant, and were non-significant for anchovy (Table 2). The contribution of saury was significantly higher during the non-breeding seasons of the 1980s and 1990s, but during the 2000s, these differences were only weakly significant (Table 2).

Long-term dietary changes

There was a significant difference in dietary composition between decades (%NA: $F = 6.27$, $p = 0.002$; FO: $F = 10.57$, $p < 0.001$; %Mass: $F = 8.98$, $p < 0.001$). During the 1980s, the diet appeared more evenly distributed across the five major prey groups, but shifted towards an increased contribution of sardine and anchovy by the 2000s (Figure 4). Over the duration of this study, the contribution to the diet of the three dominant species was highly variable, but segmented regressions showed significant trends. The contribution of sardine during the breeding season increased significantly from 1979 until 2005, and decreased thereafter (%NA: $p < 0.001$, $n = 33$, $r^2 = 0.46$; FO: $p < 0.001$, $n = 33$, $r^2 = 0.58$; %Mass: $p = 0.005$, $n = 33$, $r^2 = 0.76$). Anchovy showed an inverse trend, with a significant decrease in abundance from 1979 until 2005 and a consequent increase until 2012 (%NA: $p = 0.002$, $n = 33$, $r^2 = 0.30$; FO: $p = 0.009$, $n = 33$, $r^2 = 0.34$; %Mass: $p = 0.009$, $n = 33$, $r^2 = 0.70$). The relative abundance of anchovy in the diet was strongly negatively correlated with that of sardine (%NA: $p < 0.001$, $n = 33$, $r^2 = 0.62$; FO: $p < 0.001$, $n = 33$, $r^2 = 0.64$; %Mass: $p < 0.001$, $n = 33$, $r^2 = 0.64$). The dietary contribution of saury showed a similar trend to anchovy, decreasing until 2002 and increasing slightly until 2012 (%NA: $p = 0.002$, $n = 33$, $r^2 = 0.28$; FO: $p < 0.001$, $n = 33$, $r^2 = 0.46$; %Mass: $p = 0.003$, $n = 33$, $r^2 = 0.26$). Dietary abundance of OLP and fishery discards showed no significant trends, remaining relatively low throughout the study. In addition, there were no significant trends in the combined contribution of sardine and anchovy.

Fork length

Seasonal differences

Except anchovy in the 2000s, there were significant seasonal differences in the mean FL for all three dominant species in the diet across all three decades (Table 3). For sardine and anchovy, these seasonal differences were not uniform across the three decades. During the 1980s, sardine caught during the breeding season were significantly shorter than those caught during the non-breeding season, whereas anchovy caught during both seasons were of the same mean size. Over the following two decades, the mean FL for both species were significantly longer during the breeding season than during the non-breeding season (Figure 5). In contrast to sardine and anchovy, saury maintained a distinct seasonal size pattern across the three decades of this study, with the mean size of individuals caught during the breeding season being invariably significantly shorter than those taken during the non-breeding season (Figure 5).

Long-term differences

The mean FL of prey species taken by Cape gannets showed considerable variation over the duration of the study. The mean annual FL

Table 2. Seasonal differences in contribution of the three dominant prey species in Cape gannet diet within each of the three decades of the study.

		Sardine			Anchovy			Saury		
Abundance criterion	**Test parameter**	**1980s**	**1990s**	**2000s**	**1980s**	**1990s**	**2000s**	**1980s**	**1990s**	**2000s**
%NA	*p*-value	**0.04**	0.07	0.2	0.19	**0.03**	0.9	**<0.001**	**0.001**	0.07
	t-value	2.12	1.83	1.33	1.32	2.19	0.12	−3.72	−3.62	−1.95
	d.f.	56	47	21	50	41	22	37	24	16
FO	*p*-value	0.1	**<0.001**	0.06	0.25	**0.01**	0.81	**<0.001**	**<0.001**	0.05
	t-value	1.65	3.79	2	1.16	2.61	0.24	−3.98	−4.06	−2.15
	d.f.	55	45	24	53	43	21	43	25	15
%Mass	*p*-value	**0.04**	**<0.001**	**0.03**	0.2	**0.04**	0.75	**<0.001**	**<0.001**	0.05
	t-value	2.09	5.6	2.36	1.31	46	−0.32	−3.64	−4.05	−2.11
	d.f.	55	49	23	67	2.14	24	42	23	14

%NA, numerical abundance; FO, frequency of occurrence. Bold *p*-values represent significance.

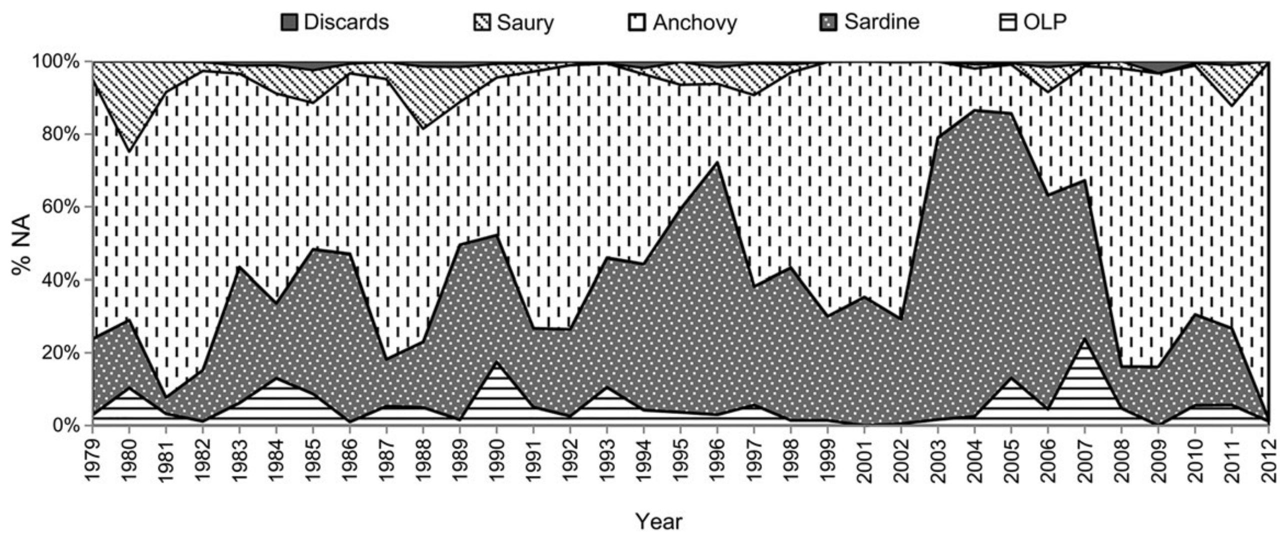

Figure 4. Mean dietary contribution in terms of numerical abundance (%NA) of the five major prey groups (sardine, anchovy, saury, fishery discards, and OLP) during the breeding season across the 34-year study period. Owing to an absence of samples, the year 2000 has been omitted.

of sardines in particular was highly variable, but increased significantly from 1979 to 2003 (Supplementary Appendix SC), and decreased thereafter (segmented regression: $p = 0.03$, $n = 32$, $R^2 = 0.19$). In addition, years of large mean FL generally corresponded to years of high %NA ($p = 0.04$, $n = 32$, $r = 0.38$), FO ($p = 0.02$, $n = 32$, $r = 0.43$), and %Mass ($p = 0.004$, $n = 32$, $r = 0.50$). In contrast to sardine, the mean FL for anchovy decreased significantly from 1979 until 2012 ($p = 0.04$, $n = 33$, $r = -0.36$). Saury FL was grouped into 5-year periods due to relatively small sample sizes. As with anchovy, the mean FL of saury also decreased significantly over the course of the study ($p = 0.04$, $n = 7$, $r = -0.77$). These results were compared against decadal frequency distributions for the three species (Figure 6). The modal length range for sardine remained the same at between 180 and 200 mm over the course of the study. However, across the three decades, there was an increase in the frequency of sardine longer than 180 mm, and there was an increase in the decadal mean length of sardines taken by gannets (1980s: 166 ± 35 s.d. mm; 1990s: 181 ± 34 s.d. mm; 2000s: 186 ± 24 s.d. mm). Anchovy decreased from a modal length of 130–140 mm in the 1980s (mean 126 ± 12 s.d. mm) to 120–130 mm in the 1990s (mean 126 ± 12 s.d. mm), and to between 110 and 120 mm in the 2000s (mean 115 ± 15 s.d. mm). Additionally, in the 2000s, there was an apparent increase in the frequency of anchovies below the length of 100 mm (Figure 6). This was largely due to the size of anchovy within the diet in 2001 and 2002 (Supplementary Appendix SB), which were significantly smaller than those caught during the rest of the study (Wilcoxon test: $p < 0.001$, $w = 238348$). Saury caught during the 1980s and 1990s were mostly between 350 and 400 mm, but this decreased to between 300 and 350 mm by the 2000s (Figure 6) and was also reflected by the means (1980s: 321 ± 60 s.d. mm; 1990s: 322 ± 74 s.d. mm; 2000s: 294 ± 34 s.d. mm).

Comparisons with acoustic survey and catch data

Acoustic surveys

The mean annual %NA of sardine in Cape gannet diet during the breeding season was positively correlated with the annual mean density estimate of the same year as obtained by acoustic surveys within the foraging range of breeding Cape gannets (%NA: $p = 0.002$, $n = 25$, $r = 0.59$; Figure 7). This was also the case for FO ($p = 0.002$, $n = 25$, $r = 0.59$) and %Mass ($p = 0.003$, $n = 25$, $r = 0.56$). A slightly stronger correlation was, however, found between the relative abundance of sardine in the diet and the

Table 3. Seasonal differences in the mean fork length of the three dominant prey species within the Cape gannet diet across the three decades of the study.

	Sardine			Anchovy			Saury		
Test parameter	**1980s**	**1990s**	**2000s**	**1980s**	**1990s**	**2000s**	**1980s**	**1990s**	**2000s**
P	**<0.001**	**<0.001**	**<0.001**	0.09	**<0.001**	**0.004**	**<0.001**	**0.01**	**0.003**
t-value	− 14.41	3.35	10.51	− 1.69	15.86	2.93	− 4.06	− 2.5	− 3.12
d.f.	1 650	291	237	3 325	884	563	539	99	79

Bold *p*-values represent significance.

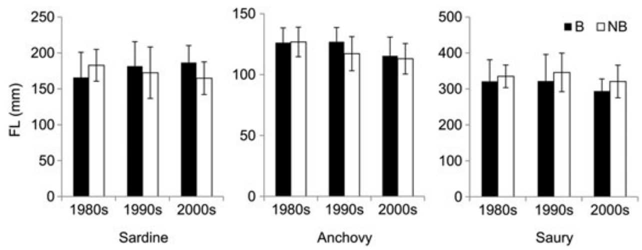

Figure 5. Seasonal differences in the mean fork length (FL; ± s.d.) of sardine, anchovy, and saury within gannet diet, across three decades. B, breeding season, NB, non-breeding season.

survey mean density estimate from the previous year (LAG-1; %NA: $p = 0.001$, $n = 25$, $r = 0.62$; FO: $p = 0.005$, $n = 24$, $r = 0.\ 56$; %Mass: $p = 0.002$, $n = 24$, $r = 0.61$).

Annual dietary abundance (%NA, FO, and %Mass) of anchovy was not significantly correlated with anchovy density during the same or previous year (same year—%NA: $p = 0.19$, $n = 25$, $r = 0.27$; FO: $p = 0.11$, $n = 25$, $r = 0.33$; %Mass: $p = 0.75$, $n = 25$, $r = -\ 0.07$; previous year—%NA $p = 0.15$, $n = 24$, $r = 0.30$; FO: $p = 0.10$, $n = 24$, $r = 0.34$; %Mass: $p = 0.69$, $n = 24$, $r = 0.08$). Interestingly, however, the annual %NA and FO of anchovy was negatively correlated, and %Mass was marginally negatively correlated with the lagged (LAG-1) survey estimate of sardine during the previous year (%NA: $p = 0.01$, $n = 24$, $r = -\ 0.50$; FO: $p = 0.05$, $n = 24$, $r = -\ 0.40$; %Mass: $p = 0.02$, $n = 24$, $r = -\ 0.48$).

Catch data

The mean annual %NA of sardine was positively correlated with the total annual sardine catch for the Eastern Cape (%NA: $p = 0.01$, $n = 24$, $r = 0.49$; FO: $p = 0.04$, $n = 24$, $r = 0.42$; %Mass: $p = 0.04$, $n = 24$, $r = 0.42$; Figure 7). In contrast, the abundance of anchovy in the diet did not show any correlation with total annual anchovy catch (%NA: $p = 0.84$, $n = 23$, $r = 0.04$; FO: $p = 0.84$, $n = 23$, $r = 0.04$; %Mass: $p = 0.78$, $n = 23$, $r = -\ 0.06$), but did show a marginally significant inverse relationship with sardine catch (%NA: $p = 0.07$, $n = 24$, $r = -\ 0.37$; FO: $p = 0.25$, $n = 24$, $r = -\ 0.25$; %Mass: $p = 0.05$, $n = 24$, $r = -\ 0.40$; Figure 7).

Discussion

The diet of Cape gannets breeding at Bird Island has undergone considerable change over the past 34 years. This is apparent in both the seasonal and long-term contribution of their dominant prey species. The prevalence of sardine and anchovy in the diet of Cape gannets has increased with an associated decrease in the abundance of OLP species. This could be reflective of growth in both the sardine and anchovy stocks along the south coast, which is also mirrored by growth of the annual purse-seine catch for the Eastern Cape (Coetzee *et al.*, 2008). Fishery discards, a large contributor to west coast gannet diet, have continued to contribute only a small portion of the diet both between seasons and across years.

Diet composition

Seabirds are known to alter their seasonal foraging effort in response to different energetic requirements during the breeding and non-breeding seasons (Markones *et al.*, 2010). Energetic demands on non-breeding adults are comparatively low, as they need only maintain condition, without the additional constraint of returning to the colony to provision and guard chicks. Thus, outside of the breeding season, adults can maintain body condition on a less selective diet than when breeding. For example, the nutritional deficiency of low quality prey can be balanced through reducing activity (Berruti, 1991). Unlike chicks, adult gannets are capable of swallowing large fish such as saury (Klages *et al.*, 1992), which are often the most cost-effective due to their size and relatively high energy content (Batchelor and Ross, 1984). Outside of the breeding season, gannets are not central place foragers. Therefore, samples collected during the non-breeding season, when birds are able to disperse widely, may represent only a portion of the overall diet. For this reason, the non-breeding diet as recorded in this study may not fully represent the diet of Cape gannets during this time. During the breeding season, chicks require prey that is both rich in energy to maintain growth (Batchelor and Ross, 1984; Mullers *et al.*, 2009) and small enough to swallow, which probably accounts for the greater level of selectivity towards sardine and anchovy during the breeding season. While gannets do increase foraging effort in response to declining prey availability, at very low forage stock abundances, this is not sufficient to maintain high dietary contributions of sardine and anchovy (Cohen *et al.*, 2014). Consequently, the need to be selective during the breeding season leaves gannets highly susceptible to the effects of changing prey availability.

Sardine and anchovy

The positive relationship between the abundance of sardine in the diet and sardine density suggests that when available this species is preferentially taken with its contribution reflecting its relative availability to gannets (Batchelor and Ross, 1984; Adams and Klages, 1999). This is supported by the strong negative correlation between the contribution of sardine and that of anchovy to the diet, although it should be noted that this relationship may be artificially strengthened because estimates of dietary abundance of sardine and anchovy do not represent independent samples. It has also been argued that for the purposes of monitoring sardine biomass, gannet diet would only provide an accurate indication of trends at low sardine biomasses and would not reflect absolute abundance (Berruti and Colclough, 1987). The lack of a significant

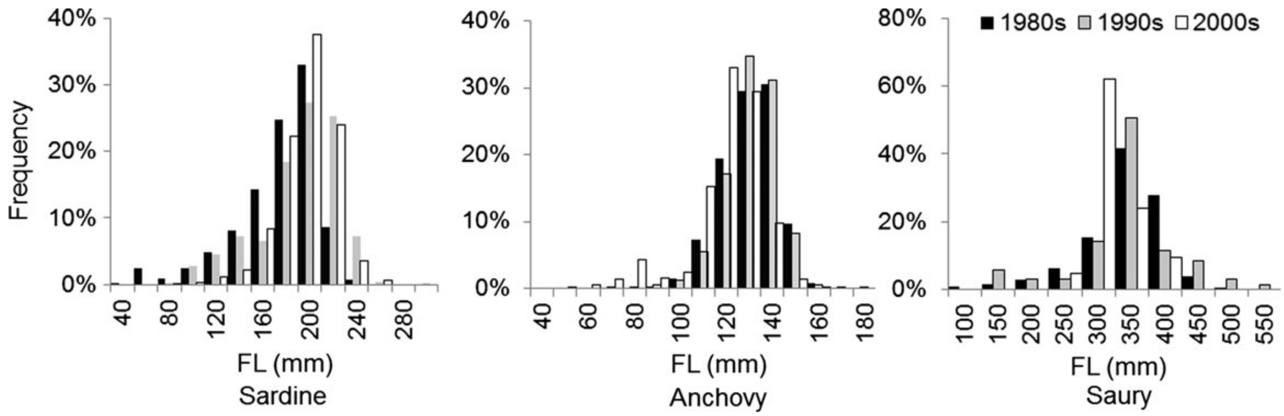

Figure 6. Frequency distributions showing decadal change in the fork length (FL) of sardine, anchovy, and saury caught during the Cape gannet breeding season.

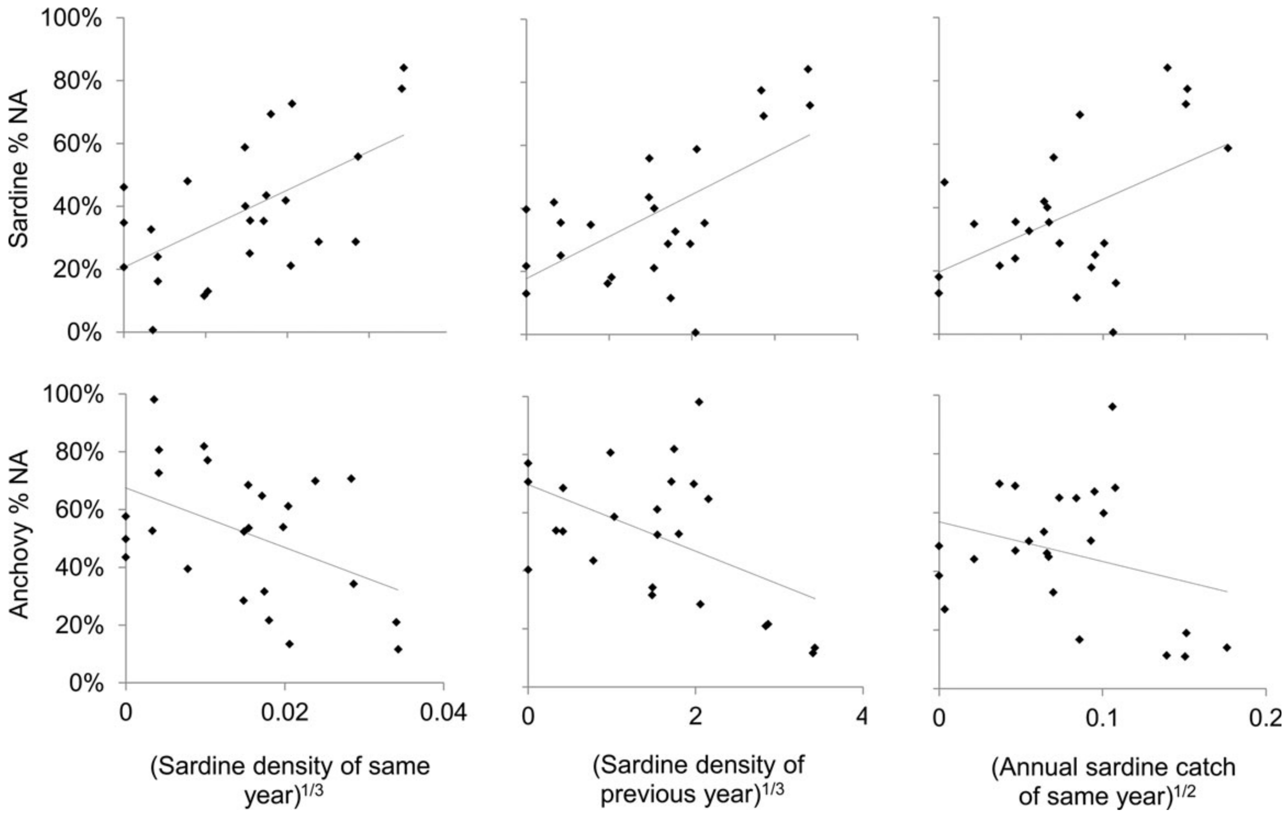

Figure 7. Numerical abundance (%NA) of sardine and anchovy in relation to estimates of sardine density during the same and previous year, and total annual sardine catch for the same year.

correlation between anchovy in the diet and estimates of its abundance could be a result of this species occurring generally further offshore, and at greater depths during the day than sardine (Lawson *et al.*, 2001). This, together with the large individual size of sardine (compared with anchovy), may make sardine more conspicuous and easier to find.

Progressive improvement of diet quality of Cape gannets at Bird Island, particularly through an increase in the contribution of sardine to the diet up until 2005, provides further support that increasing availability of high quality prey has driven population growth at this colony (Crawford *et al.*, 2007a). Sardine also represents an important prey for many other seabird species, including African penguins (*Spheniscus demersus*), Cape cormorants (*Phalacrocorax capensis*) and Swift terns (*Thalasseus bergii*; Crawford *et al.*, 2007b). When prey resources are limited, dietary overlap could lead to interspecific competition for food. This may be partly mediated through foraging segregation within a three-dimensional environment; the large foraging range of Cape gannets allows them to better track changes in prey distribution than other seabird species (Crawford *et al.*, 2008), while penguins and cormorants are able to attain greater depths when searching for prey (Hockey *et al.*, 2005). Nonetheless, the decline in sardine abundance since 2005, evident both in terms of biomass and its contribution to gannet diet, indicates that this species is becoming less available as a primary food source in the Eastern Cape. This has been mediated through a dietary replacement by anchovy, which has recently increased in abundance.

Saury

The presence of saury in the non-breeding diet of Cape gannets at Bird Island has previously been linked to seasonal changes in oceanographic conditions (Klages *et al.*, 1992). Being an oceanic species, saury is mostly found offshore (Dudley *et al.*, 1985), but in autumn and winter, the prevailing westerly winds often drive Agulhas water over the shelf, which brings this species inshore (Klages *et al.*, 1992). Increases in the intensity of the Agulhas Current and the frequency of southeasterly and easterly winds since the 1980s (Rouault *et al.*, 2010) may have reduced the number of Agulhas water intrusions over the shelf and with this decreased the availability of saury during the 2000s. Alternatively, the declining contribution of saury to the diet may be related to a distributional change. Historically, the core of the south coast saury population was located east of 21°E and south of 35° (Berruti, 1988). However, the species, which prefers waters of between 16 and 19°C (Parin, 1968), may have undergone a distributional shift as a result of recent warming of the Agulhas Current (Rouault *et al.*, 2009). The decreasing importance of saury during the third decade, particularly within the non-breeding season, could also be related to an increased prevalence of sardine and anchovy. Both species showed a marked increase in the non-breeding diet across the three decades, and replaced saury as the dominant contributor to winter diet.

Fishery discards

The continued low dietary contribution of fishery discards to the diet of Cape gannets breeding at Bird Island suggests that natural prey stocks remain healthy within the foraging range of this colony. However, it should be noted that although there is a well-developed hake fishery along the south coast, its annual catch is considerably smaller than that of the west coast (Walmsley *et al.*, 2007). During the late 1990s, the annual mean mass of discards for the south coast (5722 t) was 81% lower than that for the west coast (29 619 t; Walmsley *et al.*, 2007). Consequently, fishery discards as an alternative food source are unlikely to be as reliable and readily available as they are on the west coast, and their abundance in the diet may not necessarily reflect the abundance of natural prey.

Fork length

Sardine and anchovy

Differences in the size of sardine and anchovy taken during the breeding and non-breeding seasons of Cape gannets are likely related to the life history of these two species. During winter, the stocks of both species are dominated by recruits, while in summer, there is an increased contribution of adult fish (Barange *et al.*, 1999), and this accounts for the larger mean size of sardine and anchovy taken by gannets during their breeding season. Concurrent increases in the mean FL of sardine, the contribution of sardine to Cape gannet diet and the biomass of sardine in the Eastern Cape until 2004, suggest an increase in the proportion of adult fish within the stock over this period, which is supported in the literature (Coetzee *et al.*, 2008). It follows that the apparent decrease in sardine FL from 2004 represents an increase in the dominance of subadult sardine ($<$180 mm) in the region. It is believed that the south coast sardine stock is derived predominantly from recruitment of 1-year-old fish from the western Agulhas Bank (Coetzee *et al.*, 2008), with little recruitment derived from the south coast itself (Hampton, 1992; Barange *et al.*, 1999). Since 2004, recruitment into the system has remained low resulting in a progressive decline in stock size along the south coast (Coetzee *et al.*, 2008). In addition, high adult mortality has led to a shift in the age-structure of the stock, which is now dominated by young fish (J. Coetzee, pers. obs.). This likely accounts for the decrease in the mean FL of sardine within the gannet diet following 2003. Sardine stocks are not highly dependent on years of strong recruitment to maintain stock size (Barange *et al.*, 1999). However, successive years of high adult mortality and consequent dominance of immature fish would negatively influence reproductive output and likely population numbers, which appears the present situation on the south coast (Coetzee *et al.*, 2008).

Over the course of this investigation, the size of anchovy taken by gannets decreased, suggesting a change in anchovy stock structure towards younger fish. Barange *et al.* (1999) found that anchovy spawning took place within the southern Benguela ecosystem, with the stock dominated ($>$60%) by young recruits ($<$105 mm). From these spawning grounds, anchovy moved eastwards as they grew, attaining mean caudal lengths of $\sim$125 mm by the time they reached the eastern Agulhas Bank. During 1996, an abrupt change in environmental conditions resulted in surface cooling of waters east of Cape Agulhas, which served to strengthen the cross-shelf temperature gradient (Roy *et al.*, 2007). These climate-mediated changes resulted in an eastward shift in the distribution of spawning anchovy (Roy *et al.*, 2007). Although small anchovy still occur predominantly on the west coast, perhaps a portion of the juvenile stock could be retained on the Agulhas Bank due to increased spawning activity on the south coast, which may explain the recent increase in the proportion of young anchovy ($<$105 mm) within the gannet diet (from 4.6% in 1979–1995 to 12.8% in 1996–2012). Good recruitment in 2001, with decreased contribution of older anchovies, and consequently low mean length (mean caudal length of 92 mm) would explain the particularly small size of anchovies caught by gannets during 2001 and 2002 (Barange *et al.*, 2005).

Saury

Although the mean FL of saury showed similar trends to that of anchovy, the absence of reliable stock assessments for this species makes interpretation of such changes difficult. Historically, the size of adult saury was found to increase from the west to the east coast of South Africa (Batchelor, 1982). Berruti (1988) suggested that juvenile saury undergo a south and eastwards migration as they grow. Mature fish are believed to migrate westwards in summer to spawn and to escape temperatures at the upper limit of their thermal range (Christensen, 1980). Therefore, decreasing saury size during the last few years of this study could be related to warming of the Agulhas Current (Rouault *et al.*, 2009), which has forced larger fish to seek cooler waters. The shorter mean FL of saury during the breeding phase, which coincides with mid-late summer, seems to support this.

Implications

Currently, the diet of Bird Island Cape gannets remains dominated by three species of small pelagic prey. Shifts in the relative contribution and size of sardine and anchovy in the diet seem to reflect changes in their densities within the Eastern Cape. For anchovy, this is probably driven by climate-mediated changes in oceanographic conditions (Roy *et al.*, 2007). For sardine, this distributional shift is thought to be related to growth of the eastern stock, and was likely exacerbated by continued heavy fishing on the western stock (Coetzee *et al.*, 2008). Changes in the availability of these two species along the south coast are probably related to expansions and contractions of the stock (Lluch-Belda *et al.*, 1989). Recent declines in the abundance of sardine have been linked to continuous poor recruitment (Coetzee *et al.*, 2008), and a resultant contraction of the sardine stock range could be reducing the availability of this species to gannets. Fishing pressure is also of concern, and is known to increase fish stock variability (Anderson *et al.*, 2008). Although fishing effort in the Eastern Cape remains low, it may be that a high level of exploitation on the west coast has served to exacerbate the current stock decline.

Conclusions

This study highlighted a significant change in the diet of Cape gannets at Bird Island over the past three decades, reflecting shifts in the distributions and abundances of sardine and anchovy stocks along the South African south coast. Under these conditions, this Cape gannet colony has grown rapidly, and now supports the bulk of the world population (Crawford *et al.*, 2007a). However, recent declines in the abundance of sardine (in terms of biomass and diet), together with intraspecific competition, may significantly impact the population trajectory of this colony in the future.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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