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Food habits of an endangered seabird indicate recent poor forage fish availability off western South Africa

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Large recent decreases of Cape gannets *Morus capensis*, Cape cormorants *Phalacrocorax capensis* and African penguins *Spheniscus demersus* in South Africa resulted in their being listed as Endangered. These seabirds, endemic to the Benguela upwelling system (BUS), primarily rely on anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* for food, yet decreased during periods of abundance of these prey species. In order to investigate this dichotomy, we examined long-term dietary characteristics for gannets in the region in relation to acoustically-derived biomass of prey. Principal component (PC) analysis of diet composition indicated an alternation in the use of anchovy and sardine (PC1), as well as a marked decrease, after the early 2000s, in the availability of these preferred forage resources (PC2). PC2, which we term the Forage Availability Index, was positively related to numbers of gannets and cormorants breeding each year and to estimates of survival of adult penguins at their two largest colonies in northwest South Africa. This indicates that recent availability of anchovy and sardine was insufficient to support these bird populations. Our results emphasize the need to account not only for overall abundance but also local availability of forage resources, when applying an ecosystem approach to managing fisheries for seabirds.

Keywords: anchovy, diet composition, forage availability index, principal component analysis, sardine, seabird population dynamics

Introduction

Seabirds are more threatened and their status has deteriorated faster over recent decades than other comparable groups of birds (Croxall *et al.*, 2012). The main at-sea threats are posed by fisheries and climatic impacts on food webs, mortality from fishing gear, and pollution (Croxall *et al.*, 2012). Most marine predators, including cetaceans and large fish species, travel widely and can dive to considerable depths to obtain food (e.g. Leatherwood and Reeves, 1983). However, seabirds are central-place foragers when breeding and most feed in the upper (epipelagic) part of the water

column (Shealer, 2002). Hence, it is important to account for the availability of forage resources when considering impacts of fishing and the environment on the prey of seabirds (Boyd *et al.*, 2017; Sydeman *et al.*, 2017). Yet, assessments of forage fish abundance are often undertaken for the entire water column, as is the case for anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela upwelling system (BUS; e.g. Augustyn *et al.*, 2018). Furthermore, there have been recent large changes in the environments of several marine ecosystems, including the BUS (e.g. Blamey *et al.*, 2015; Lamont *et al.*, 2018),

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Figure 1. Important seabird breeding localities off western South Africa north of Cape Town. Triangles indicate localities where the diet of Cape gannets was studied.

that may have influenced the availability of forage fish to epipelagic predators.

In the BUS, four seabirds subsist mainly on anchovy and sardine (Hockey *et al.*, 2005). Off northwest South Africa, there were recent large decreases in the populations of three of these, all endemic to the BUS: African penguin *Spheniscus demersus* (Crawford *et al.*, 2011), Cape gannet *Morus capensis* (Crawford *et al.*, 2014), and Cape cormorant *Phalacrocorax capensis* (Crawford *et al.*, 2016). Consequently, each species is classified as Endangered by the International Union for Conservation of Nature (Birdlife International, 2017). In contrast, numbers of the fourth seabird, greater crested (swift) tern *Thalasseus bergii*, increased (Crawford, 2009). Unlike the three endangered species, greater crested terns undertake nomadism between breeding localities (Crawford *et al.*, 2002; Crawford, 2003), can fly overland (Underhill *et al.*, 1999) thereby reducing commuting distances, and have lower energy requirements than the larger penguins, gannets, and cormorants (Gaglio *et al.*, 2018b). The population declines of the three endangered seabirds have been attributed mainly to food stress (Crawford *et al.*, 2015, 2018), although recent stock assessments have indicated a concurrent high biomass of anchovy or sardine off western South Africa (west of Cape Agulhas, Figure 1; e.g. van der Sleen *et al.*, 2018). This presents a conundrum for management and suggests that a greater understanding of food availability is required to elucidate the causes of the seabird decreases (cf. Sherley *et al.*, 2013).

In lieu of the apparent abundance of anchovy or sardine, we hypothesized that the *availability* of these nutritious resources for predators feeding in the epipelagic zone recently decreased off northwest South Africa. Monitoring changes in dietary preferences of seabirds can provide insights into the availability of prey resources (Votier *et al.*, 2004). Thus, to test our hypothesis, we

applied multivariate analyses to the long-term composition of the diet of Cape gannets to describe variation in their take of different prey species. Abundances of anchovy and sardine off South Africa have displayed large fluctuations (Augustyn *et al.*, 2018) and previous studies showed that the contributions of both these species to the diet of gannets were linked to their abundance, with the use of anchovy and sardine inversely related (e.g. Berruti *et al.*, 1993; Crawford and Dyer, 1995; Green *et al.*, 2015). We anticipated that the analyses would reflect this contrast between the use of anchovy and sardine. In accord with our hypothesis, we also predicted a decrease over time in the combined contribution of anchovy and sardine to the diet, i.e. in a *Forage Availability Index* (*FAI*) for these preferred prey species. We further envisaged that the index would be better related than biomass estimates to demographic statistics of the three endangered seabirds.

We expected the combined contribution of sardine and anchovy to gannet diet to be a good indicator of the availability of these fishes to the epipelagic community of the BUS because anchovy and sardine undertake extensive movements in this system (e.g. Crawford, 1980) and Cape gannets are wide-ranging animals that are known to switch to feeding on offal discarded by fisheries when their preferred prey is at low availability (Grémillet *et al.*, 2008). In contrast African penguins, Cape cormorants, and greater crested terns have smaller foraging extents when breeding and do not generally utilize offal, so that forage fish may dominate their diet even when scarce (Crawford *et al.*, 2014; Gaglio *et al.*, 2018a).

Methods

Diet composition

From 1978 to 2016, the diet of Cape gannets was sampled monthly throughout their breeding season (September-March; Hockey et al., 2005) at Lambert's Bay and Malgas Island in western South Africa (Figure 1). Gannets returning to the colonies after foraging were caught with a hook on the end of a pole and upturned over an empty bucket, into which many regurgitated (Berruti et al., 1993). The contents of regurgitations were sorted into five categories (sardine, anchovy, saury Scomberesox saury, hakes Meluccius spp., and other species) and the mass of all categories was weighed. For each locality and month, the mass of different categories was summed for all regurgitations and their proportional contribution to the diet was calculated (Berruti et al., 1993). For each of the 38 breeding seasons (1978/1979-2015/2016) that were sampled, the average contribution of a prey category to the diet was obtained for both localities, applying equal weight to each month (Crawford et al., 2014). For the entire period, the average contribution of a prey category to the diet was obtained by applying equal weight to each breeding season. Identification of prey to species was straightforward because nearly all regurgitations comprised easily identified species and were not highly digested (Berruti et al., 1993). Regurgitations provide an indication of the quantity of food returned to colonies rather than the original mass eaten, but for Cape gannets were not thought excessively to influence the proportions by mass of different prey types ingested because often within a regurgitation, the degree of digestion was similar for different prey species. Furthermore, the prey species identified in regurgitations were similar to those found in previous studies that used the stomachs of Cape gannets shot at sea (Hockey et al. 2005). Further details of diet sampling are given in Supplementary data.

Forage indices

We obtained forage indices by applying principal component analysis (PCA) to the contributions of sardine and anchovy to the diet of Cape gannets at each site by month (September through March) from 1978/1979 to 2015/2016, a 7-month × 38-year matrix. We interpreted derived principal components (PCs) having eigenvalues \geq 3 (Jolliffe, 2002) by examining loadings of monthly diet composition on the PC.

One PC reflected prey switching between anchovy and sardine (PC1), whereas the other (PC2) appeared to reflect the combined availability of sardine and anchovy in the diet (see Results). We took PC2 as an Availability Index for sardine and anchovy and compared it to annual estimates of the spawner biomass of sardine and anchovy west of Cape Agulhas (Augustyn et al., 2018, Department of Agriculture, Forestry and Fisheries) by calculating the difference between the z-score normalized PC2 and the zscore normalized combined spawner biomass. We fit a GAM of the form $Y_i = \alpha + S(X_i) + \epsilon_i$, where Y_i is the value for the residual difference of the two z-scores in year i; α is the intercept; $S(X_i)$ is a non-parametric smoothing function, specifying the effect of the year X_i ; and $\epsilon_i \sim N(0, \sigma^2)$ is the residual error. We used thin plate regression splines and allowed the degrees of freedom of the smoothing function to be selected automatically by generalized cross-validation (GCV), with the option for the function to be linear [e.g. $S(X_i) = \beta \times X_i$, where β is the slope].

Relationship of seabird parameters to forage indices

Last, in order to investigate the influence of forage availability on South African seabirds, we related PC2 to nine time-series of population statistics: annual nesting attempts of (1) Cape gannets (1980-2015), (2) African penguins (1997-2015), (3) Cape cormorants (1985-2015) and (4) greater crested terns (1984-2015) (Crawford, 2009; Crawford, et al. 2011, 2014, 2016; Makhado, et al. 2016); (5) breeding success (chicks fledged per pair) of Cape gannets at Malgas Island (1988-2015; Grémillet, et al., 2008; updated); survival of adult African penguins at (6) Dassen and (7) Robben islands (1994–2011; Sherley, et al., 2014); and number of (8) adult and (9) immature African penguins moulting at Dassen Island (1994–2009; Robinson, 2013) [for African penguin, Cape gannet and greater crested tern, the numbers at all colonies in the region were used; for Cape cormorants, the numbers at eight well-monitored colonies in the region were used: Lambert's Bay, Malgas, Jutten, Meeuw, Schaapen, Vondeling, Dassen, and Robben islands (Crawford et al., 2016)]. We selected these timeseries (Supplementary Table S1 and Figure S1) because they reflect seabird abundance (i.e. nesting effort) as well as vital rates that drive population size (i.e. breeding success, survival, and counts of immature birds as a proxy for recruitment). We similarly compared them with estimates of the combined spawner biomass of anchovy and sardine west of Cape Agulhas.

Seabirds often show non-linear responses to the abundance or availability of their prey (e.g. Cury *et al.*, 2011; Sherley *et al.*, 2017). We therefore used generalized additive models (GAMs) to explore the form of the relationships between the seabird response variables and PC2 or biomass. We initially used the "gamm" function from the *mgcv* library (version 1.8-22; Wood, 2017) for R (version 3.4.3) to fit a model of the form $Y_i = \alpha +$ $S(X_i) + \epsilon_i$, where Y_i is the value for a seabird performance measure in year *i*; α is the intercept; $S(X_i)$ is the non-parametric smoothing function, specifying the effect of the PC or biomass on



Figure 2. The contributions of sardine, anchovy, hakes, saury, and other species to the diet of Cape gannets (% mass) at Lambert's Bay and Malgas Island during the breeding season, 1978/1979–2015/2016. The *x*-axis refers to the year in which the breeding season was initiated. Values for Lambert's Bay in 2006 were imputed (see Supplementary data for details).

each seabird performance measure; and other parameters are as described above.

For each model, we assessed residual plots for normality, heterogeneity of variance and an absence of autocorrelation (using the "acf" function in R). In one case (number of Cape cormorant nests), the normality assumption was violated. We thus computed the natural log of the cormorant numbers, refit the models, and re-examined the residual plots. For four data series, the normalized residuals from the initial model demonstrated significant autocorrelation. We therefore refit the models specifying an error structure with first-order autocorrelation using the "corAR1" function from the *nlme* library (version 3.1-131; Pinheiro *et al.*, 2017) for R. We then re-examined the residual plots to ensure an absence of autocorrelation in the normalized residuals of the models used for inference (Supplementary Figure S2).

Results

Diet composition

Across the 38 breeding seasons (1978/1979–2015/2016), totals of 11 197 and 20 422 regurgitations were collected at Lambert's Bay

Table 1. Results of principal component analysis on sardine and anchovy in the diet of Cape gannets at Lambert's Bay and Malgas Island in their September–March breeding season, 1978/1979–2015/2016.

Principle		Proportion of variance explained	
component	Eigenvalue		
1	12.04	0.43	
2	3.97	0.14	
3	2.02	0.07	

and Malgas Island, respectively, or averages of c. 300 and 540 per season. The relative contributions by mass of the main prey categories to the diets of Cape gannets at Lambert's Bay and Malgas Island during the breeding season are shown in Figure 2 and Supplementary Table S2. At both localities, the proportion of sardine in the diet increased substantially after 1983 and then remained high until the end of the twentieth century. However, sardine fell to low levels from 2004–2008 and 2013–2014. The proportion of anchovy was high in most years from 1978 to 1988



Figure 3. The values for PC1 and PC2 (the *FAI*) obtained from analysis of monthly Cape gannet diet at Lambert's Bay and Malgas Island during the breeding season, 1978/1979–2015/2016. The *x*-axis indicates the year in which the breeding season started.

but then decreased and showed substantial fluctuations. The proportion of saury increased after 2002 and hake was important at Malgas Island in the early 1980s and from 2004 to 2009.

Forage indices

The multivariate analysis provided two significant PCs (Table 1). PC1 explained 43% of the variance and increased from negative values in the late 1970s and early 1980s to mostly positive values after the mid-1980s (Figure 3). We interpret PC1 as an alternation between sardine and anchovy in the gannet diet. All 14 sardine loadings had positive values, whereas 13 of the 14 anchovy loadings were negative and the 14th was only marginally positive and less than all sardine loadings (Table 2).

PC2 explained 14% of the variance. It fluctuated around 0 from 1978 to 1985, 2 from 1986 to 2003 and -2 from 2004 to 2015 (Figure 3). For PC2, 24 of the 28 loadings for sardine and anchovy had positive values, 18 of which were >0.1 (Table 2). We therefore considered PC2 as a *FAI*, an index of the availability of anchovy and sardine to seabirds. The GAM used to examine the relationship between the biomass of sardine and anchovy and the *FAI* showed a non-linear trend, with a clear transition from mainly positive residuals before 2000 to mainly negative residuals thereafter [Figure 4; effective degrees of freedom (edf) = 5.33, *F* = 10.2, *p* < 0.001].

Relationship of seabird parameters to forage indices

GAMs provided evidence of non-linear relationships between the *FAI* and the breeding effort of both Cape gannets (edf = 4.40, F = 17.7, p < 0.001) and Cape cormorants (edf = 2.22, F = 3.75, p = 0.025). For gannets, the numbers breeding increased when PC2 (which increases as anchovy and sardine contribute more to the diet) was >c. -1 (Figure 5a) and for cormorants when it was >c. 1 (Figure 5b). Additionally, the survival of adult African penguins showed linear relationships with PC2 at both Dassen (edf = 1, F = 24.7, p < 0.001) and Robben (edf = 1, F = 16.5, p < 0.001) islands, with survival rates generally lower when PC2 was negative than positive and decreasing markedly when PC2 was < c. -1.5 (Figure 5c and d). The remaining five seabird parameters showed non-significant linear relationships with PC2: four showed positive trends, with only the number of breeding greater crested terns having a weak negative trend (Supplementary Figure S3b).

Table 2. Variable loadings for principal components 1 and 2.

Variables	Principle components		
Variables	1	2	
Sardine, Lambert's Bay, September	0.19	0.09	
Sardine, Lambert's Bay, October	0.22	0.11	
Sardine, Lambert's Bay, November	0.20	-0.09	
Sardine, Lambert's Bay, December	0.21	-0.08	
Sardine, Lambert's Bay, January	0.22	0.13	
Sardine, Lambert's Bay, February	0.20	0.16	
Sardine, Lambert's Bay, March	0.16	0.21	
Sardine, Malgas Island, September	0.13	0.31	
Sardine, Malgas Island, October	0.24	0.05	
Sardine, Malgas Island, November	0.23	0.16	
Sardine, Malgas Island, December	0.24	0.11	
Sardine, Malgas Island, January	0.20	0.25	
Sardine, Malgas Island, February	0.17	0.32	
Sardine, Malgas Island, March	0.06	0.40	
Anchovy, Lambert's Bay, September	-0.14	0.08	
Anchovy, Lambert's Bay, October	-0.19	0.03	
Anchovy, Lambert's Bay, November	-0.17	0.26	
Anchovy, Lambert's Bay, December	-0.19	0.29	
Anchovy, Lambert's Bay, January	-0.21	0.17	
Anchovy, Lambert's Bay, February	-0.18	0.11	
Anchovy, Lambert's Bay, March	-0.16	-0.01	
Anchovy, Malgas Island, September	-0.18	0.03	
Anchovy, Malgas Island, October	-0.23	0.15	
Anchovy, Malgas Island, November	-0.24	0.13	
Anchovy, Malgas Island, December	-0.17	0.25	
Anchovy, Malgas Island, January	-0.17	0.25	
Anchovy, Malgas Island, February	-0.18	0.03	
Anchovy, Malgas Island, March	0.04	-0.24	



Figure 4. Results of generalized additive modelling of the change over time in the relationship between PC2, the *FAI*, and the combined spawner biomass of sardine and anchovy west of Cape Agulhas. Diamonds show residual differences between *z*-score normalized PC2 values and *z*-score normalized estimates of forage fish biomass (residual = $Z_{FAI} - Z_{biomass}$). On the *y*-axis, *s*[*x*, *y*] indicates the smoothing term, where *x* is the explanatory variable and *y* is the estimated degrees of freedom of the smoothing term. The grey shading shows pointwise 95% confidence intervals.

However, the breeding success of gannets at Malgas Island was only marginally not significant (p = 0.06) and was much more likely to be poor for negative than for positive values of PC2 (Supplementary Figure S3c). No seabird parameter was



Figure 5. Results of generalized additive modelling of the effects of PC2 on four indicators of seabird performance in South Africa. PC2, the *Forage Availability Index (FAI)*, represents the combined contribution of sardine and anchovy to the diet of Cape gannets. The indicators of seabird performance are (a) number of nests at which Cape gannets were breeding between 1978/1979 and 2015/2016; (b) number of nests at which Cape cormorants were breeding between 1978/1979 and 2015/2016; (c) and (d) apparent survival of adult African penguins at Dassen and Robben islands, respectively, between 1994/1995 and 2011/2012. On the *y*-axis, *s*[*x*, *y*] indicates the smoothing term, where *x* is the explanatory variable and *y* is the estimated degrees of freedom of the smoothing term. The grey shading shows pointwise 95% confidence intervals and diamonds show the partial residuals around the significant covariate effects.

significantly related to the combined biomass of anchovy and sardine (Supplementary Figure S4).

Discussion

The multivariate analysis of gannet diet identified two significant PCs: PC1 appeared to reflect prey switching between the two high-quality forage species, whereas PC2 seemed to contrast good and poor prey regimes for anchovy and sardine combined. Consequently, we took PC2 to be an index of the availability of these fishes to seabirds off northwest South Africa, the *Forage Availability Index (FAI)*. Its use in this manner was corroborated by clear positive relationships between PC2 and five independent measures of seabird performance that contrasted an absence of such relationships with biomass.

Nutritious and "junk" prey

In one study, the energy contents of sardine, anchovy, saury, and hakes, the main food of Cape gannets, were respectively 8.59, 6.74, 6.20 and 4.07 kJ g^{-1} (Batchelor and Ross, 1984). A later study similarly recorded reasonably high values of 6.59 and 6.03 kJ g⁻¹ for sardine and anchovy, respectively (Balmelli and Wickens, 1994). On account of their higher energy content relative to other species, sardine and anchovy have often been regarded as preferred prey for Cape gannets (Berruti et al., 1993; Adams and Klages, 1999; Crawford et al., 2007, 2014; Green et al., 2015). In contrast, hakes eaten by Cape gannets are mostly fishery discards and have been termed "junk food", owing to their lower calorific content (Grémillet et al., 2008). Gannet chicks fed sardine also consumed less food and had higher fledging masses than those fed hakes (Batchelor and Ross, 1984). Foraging effort of Cape gannets increased and nest attendance decreased with reduced consumption of sardine and anchovy, whereas adult body condition was negatively impacted by increases of hakes in their diet (Cohen et al., 2014). During pronounced scarcity of sardine and anchovy in the mid-2000s, hake discards proved inadequate for many gannets to rear chicks (Grémillet et al., 2008), although appeared to be sufficient to maintain adult survival (Distiller et al., 2012). The other main alternate prey species is saury, which off western South Africa occurs outside the oceanic front in waters of 18–22°C roughly 80 km or more from the coast (Dudley et al., 1985). Except from January to March, when both the front and saury move inshore, its distribution requires gannets to expend considerable energy to access it (Berruti et al., 1993). In South Africa, condition of sardine deteriorated in the 2000s (Ndjaula et al., 2013). Elsewhere, a decreased condition of preferred prey species led to poor seabird performance (Wanless et al. 2005).

Forage Availability Index and seabird performance metrics

Whereas significant relationships with the *FAI* were obtained for numbers of Cape gannets and Cape cormorants that bred, this was not the case for African penguins or greater crested terns, or for numbers of adult and immature penguins moulting at Dassen Island, although all three measures of penguin abundance showed positive trends with the *FAI*. Unlike Cape gannets and Cape cormorants, which breed in the austral spring and summer, in South Africa many African penguins and greater crested terns breed in autumn and winter outside the September–March period used to obtain the *FAI* (Crawford *et al.*, 2002, 2013). African penguins may moult at colonies other than those at which they breed and may feed some distance away from their colony when not breeding (Whittington *et al.*, 2005). The different ecology and relatively low energy requirements of greater crested terns have allowed them to sustain high survival (Payo-Payo *et al.*, 2018) and successfully provision chicks on young-of-the-year anchovy and other small fish species (Gaglio *et al.*, 2018a, b).

At both Dassen and Robben islands, survival of adult African penguins was significantly related to the *FAI*. At these localities, penguins mostly moult from September–January (Underhill and Crawford, 1999; Wolfaardt *et al.*, 2009). Moult is a critical time for African penguins as they remain onshore and fast for about 21 days while they replace their entire plumage; they must fatten before and after moult to build up and replenish their energy reserves (Randall *et al.*, 1986). Hence, their survival may be influenced by food availability outside their breeding season (Sherley *et al.*, 2014) but within the spring–summer period used to derive the *FAI*.

The validity of the *FAI* as a measure of epipelagic availability of sardine and anchovy off northwest South Africa is supported by other observations of poor performance by, or unusual behaviour of, seabirds in that region, which followed the marked decrease of this index early in the twenty-first century (see Supplementary data).

Forage availability and ecosystem management of seabirds

The large decrease of the FAI in the early 2000s (Figure 3) followed prior shifts to the southeast of spawning sardine and anchovy, which may have been caused by altered environmental conditions or intense localized fishing (Roy et al., 2007; Coetzee et al., 2008). Although biomass of anchovy off South Africa's west coast remained high after 2003 (van der Sleen et al., 2018), it appears then to have been less available to gannets and other seabirds during spring and summer than previously. In particular, the switch from mainly positive residuals to mostly negative residuals in the difference between the FAI and forage fish biomass indicates that the amount of sardine and anchovy that gannets were able to capture for a given level of biomass dropped abruptly at the turn of the recent century (Figure 4). The decreased availability of these prey species may have been caused by the observed geographic shift in their distribution, by them assuming a deeper position in the water column or a combination of both mechanisms. In a modelling study, depth of prey primarily determined foraging success of Peruvian boobies Sula variegata and guanay cormorants Phalacrocorax bougainvilliorum, which feed mainly on Peruvian anchoveta Engraulis ringens in the Humboldt upwelling system off western South America (Boyd et al., 2017). In that system, Peruvian boobies and guanay cormorants are the ecological equivalents of Cape gannets and Cape cormorants in the BUS (Crawford et al., 2006). Since 2001, South Africa's purse-seine fishery has not taken its allowable catch of anchovy and in recent years, the extent of this under-catch has increased (DAFF, 2016), suggesting that availability of anchovy to the fishery also decreased.

The recent low forage availability meant that, from 2004 to 2015, the *FAI* only once (2008) rose above the level of -1, at which the relevant GAM predicted numbers of Cape gannets breeding north of Cape Town would increase (Figure 5a), whereas between 1978 and 2003, it only fell below that threshold

in 1984 (Figure 3). Cape cormorants had a higher threshold (c. 1, Figure 5b) at which numbers breeding were predicted to increase. This was exceeded in 13 of 17 years between 1986 and 2002 but not before or after that period (Figure 3). The higher threshold for Cape cormorants probably results from the fact that, unlike Cape gannets, they are mostly unable to access alternative food such as saury and hake offal. When the biomass west of Cape Agulhas of sardine spawners fell below c. 25% of its maximum observed value, survival of adult African penguins at Robben Island decreased markedly (Robinson et al., 2015). This was the case at both Dassen and Robben islands in most years when the FAI had a negative value (Figure 5). Similarly to seabirds in other ecosystems, breeding success of Cape gannets and African penguins in the southern BUS became more variable and on average decreased when the combined biomass of sardine and anchovy was less than about one-third of its maximum observed value (Cury et al., 2011). For Cape gannets at Malgas Island, this also happened when the FAI had negative values (Supplementary Figure S3c).

Thresholds provide one means to implement an ecosystem approach to fisheries (EAF) and may relate to allowable by-catch mortality (e.g. Rollinson et al., 2017) or escapement levels for forage resources (e.g. Cury et al., 2011). In addition to linking prey abundance with seabird performance (e.g. Cury et al., 2011; Robinson et al., 2015), the development of indices of food availability will assist in identifying forage thresholds through accounting for portions of food resources that are unavailable to predators. In the southern BUS, an EAF should aim to maintain a positive FAI. Although implementation of an EAF may have short-term costs for forage fisheries, its non-application could disadvantage other users of these resources such as burgeoning marine ecotourism industries (e.g. Lewis et al., 2012) and fisheries exploiting species at higher trophic levels. Furthermore, failure to adopt an EAF may lead to irreversible ecosystem change and longer-term loss of ecosystem services, as was demonstrated for the northern BUS (Roux et al., 2013). In contrast, meaningful ecosystem-based management of forage resources in the California upwelling system has benefitted predators there (Ainley et al., 2018).

In summary, the *FAI* for nutritious forage fishes in the epipelagic zone off northwest South Africa explained several of the trends in seabird populations and demographic parameters observed in this region. Importantly, these included large decreases in the number of breeding Cape gannets and Cape cormorants and in survival of African penguins at their most important colonies. In doing so, the *FAI* highlights the need to understand changes in the availability (as opposed to abundance) of prey species when identifying thresholds to be used in an EAF aimed at ensuring healthy ecosystem functioning. That Cape gannet diet produced such a useful index resulted in large measure from the species' ability to switch between prey types and its wide foraging range.

Supplementary data

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

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