Influence of feeding conditions on breeding of African penguins—importance of adequate local food supplies

Joël M. Durant[1],*, **Robert J. M. Crawford[2,3]**, **Anton C. Wolfaardt[3,4,5,6]**,
Kobus Agenbag[2], **Johan Visagie[4]**, **Leisha Upfold[2]**, **Nils Chr. Stenseth[1,7]**

[1]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo,
PO Box 1066 Blindern, 0316 Oslo, Norway

[2]Oceans & Coasts, Department of Environmental Affairs, Private Bag X2, Rogge Bay 8012, South Africa

[3]Animal Demography Unit, Department of Zoology, University of Cape Town, Rondebosch 7701, South Africa

[4]CapeNature, Private Bag X29, Rondebosch 7701, South Africa

[5]Marine Research Institute, University of Cape Town, Rondebosch 7701, South Africa

[6]Joint Nature Conservation Committee, PO Box 585, Stanley, FIQQ 1ZZ, Falkland Islands

[7]Institute of Marine Research, Flødevigen Marine Research Station, 4817 His, Norway

ABSTRACT: Off the coast of South Africa, the 2 most important prey items for African penguins *Spheniscus demersus* are sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*, species heavily exploited by commercial fisheries. At Dassen Island, the proportion of burrows occupied for breeding by African penguins from 1995 to 2008 was affected positively by the interaction between the overall biomass of sardine and anchovy. However, sardine had a positive effect while anchovy had a negative one. This unexpected negative relationship may result from a reduced local availability of anchovy linked to the fishing effort that continued to be focussed in the vicinity of Dassen Island, while the growing anchovy stock experienced an eastward shift away from Dassen Island in recent years, creating a spatial mismatch between penguin and available anchovy. A decrease of the Southern Oscillation Index tended to advance the onset of penguins' breeding, as did an increase in sea surface temperature (SST) at the sardine and anchovy spawning grounds. An increase in SST at the nursery and spawning areas tended to decrease the penguin per capita growth rate. Earlier breeding resulted in decreased chick production, possibly because it created a temporal mismatch between chick rearing and winter availability of young-of-the-year anchovy and sardine along South Africa's west coast. The local abundance of prey is more important for breeding African penguins than overall fish abundance. Consequently, management of the purse-seine fishery should be adjusted spatially in order to ensure adequate local food supplies for breeding African penguins.

KEY WORDS: Breeding participation · Competition with fisheries · Conservation · Seabirds · Spatial management

INTRODUCTION

Beyond potentially depleting them (Pauly et al. 2002), the exploitation of fish stocks by industrial fisheries has significant repercussions on the whole food chain, including on top predators such as marine mammals and seabirds (e.g. Frederiksen et al. 2004a). A clear understanding of competition between top predators and fisheries is therefore an essential prerequisite for decisions regarding spatial management of the distribution of fishing effort as a conservation measure (Okes et al. 2009). Likewise, it is important to consider the complex

relationships between fish stocks and top predators when setting conservation goals and priorities in fisheries management in an ecosystem context.

Recent climatic changes have been reported to disrupt otherwise tight trophic interactions between predator and prey in many systems at all levels of the food chain (Durant et al. 2004, 2007 and references therein). Large-scale climate variation may also affect life history traits of top predators (Stenseth et al. 2002). For instance, there is evidence that large-scale climate variation has influenced the breeding phenology (Frederiksen et al. 2004b), proportion of the adult population attempting to breed (Jenouvrier et al. 2003), reproductive success (Frederiksen et al. 2004a), and survival (Grosbois & Thompson 2005) of seabirds. Changes in the distribution and/or abundance of their prey species, for instance, may affect the population dynamics and distribution of seabirds (Durant et al. 2009). Where such changes have resulted in a distribution mismatch between seabirds and their prey, local prey abundance around breeding localities may have an important effect on the breeding success of seabirds. In such a case, it is disputable to use general patterns (e.g. abundance estimate given by population survey) to estimate the effects of prey abundance on seabird populations (Grémillet & Boulinier 2009). In addition, not all seabird species respond similarly to changes in food abundance. Seabird species with short foraging ranges and inflexible diet types are more vulnerable to a reduction in the abundance of food in the vicinity of their colonies than species with larger foraging ranges and more generalist diet preferences (Furness & Tasker 2000). Consequently, it is necessary to conduct new studies relating alternative food resources indices (spatial scale, time scale, prey size) to seabird population parameters.

The African penguin *Spheniscus demersus* L. is endemic to southern Africa where it feeds predominantly on small pelagic fish; more than 90% of the diet is composed of sardine *Sardinops sagax* J. and anchovy *Engraulis encrasicolus* L. (Hockey et al. 2005). African penguins are inshore foragers, with a restricted foraging range during the breeding season of 20 to 40 km (Pichegru et al. 2009). These 2 factors, short foraging range and restricted diet type, make its population vulnerable to changes in the distribution and abundance of sardine and anchovy (Crawford 1998), which are targeted by the purse-seine fisheries of Namibia and South Africa (Crawford et al. 2008a). Indeed, the current decrease in its breeding population is mainly a result of a scarcity of food that resulted from large catches of fish by commercial purse-seine fisheries and environmental fluctuations (Crawford 1998, 2007). Recently, numbers of breeders at the western colonies have decreased rapidly, probably due to

food scarcity (Crawford et al. 2008b), whereas eastern colonies in the Western Cape have increased or remained stable, albeit at a low level (Underhill et al. 2006, R. J. M. Crawford unpubl. data). In 2010 the International Union for the Conservation of Nature (IUCN) reclassified the threat (Red List) status of the African penguin from Vulnerable to Endangered (BirdLife International 2010). The ongoing declines in African penguin numbers also led the South African government to investigate the potential usefulness of closing areas to purse-seine fishing around selected breeding colonies.

The aim of the present study was to investigate the influence of the environment (feeding conditions and climate) on the African penguin population breeding at Dassen Island (33° 25′ S, 18° 04′ E; Fig. S1 in the supplement at www.int-res.com/articles/suppl/m420p263_supp.pdf). Data on the occupancy of burrow nests by penguins, and per capita growth rate of the breeding population collected over 14 yr, were compared to information on prey availability and climate.

MATERIALS AND METHODS

Penguin descriptors. A sample of about 1000 burrow nests of African penguins at Dassen Island (33° 25′ S, 18° 04′ E) was checked regularly (about once every 15 d) between 1995 and 2008 for the presence of breeding birds (Wolfaardt et al. 2009). For the purposes of the present study, burrows were considered occupied if they contained a bird incubating one or more eggs (hereafter defined as burrow occupancy). The year was reset to start 1 October (1 October = Day 1, 30 September = Day 365), the beginning of the main moulting period, i.e. annual cycle, for adult penguins in the Western Cape (Wolfaardt et al. 2009).

For each year, the mean burrow occupancy date (Date-O) was estimated on the day coordinate (Day 1 to Day 365) by using circular statistics (weighted cirmean) as implemented in the CircStats library of R.

For each year, the burrow occupancy peak (Max-O) was estimated using the maximum proportion of burrows occupied by incubating birds per month. We similarly estimated the maximum proportion of the sampled burrows that contained chicks of any size (Max-C), regardless of whether they fledged, to use as a proxy for chick production.

The per capita growth rate (PerCap) of penguins at Dassen Island was calculated from the total number of active nests counted for the whole island from 1991 to 2008. PerCap during year$_t$ is thus $\ln(N_{t+1}) - \ln(N_t)$. Whole-island counts of active nests were conducted annually, according to the methods described by Shelton et al. (1984), Crawford et al. (1990), and Underhill

et al. (2006). A nest site was considered active if it contained eggs or chicks, if it was defended by an adult bird, or if there were clear signs of recent nest-building activity.

Environmental descriptors. *Prey abundance: sardine and anchovy biomass (1000 t) estimated by hydroacoustic surveys in November:* Sardine and anchovy surveys covered the known spawning areas of these fish species off South Africa and consisted of a series of pre-stratified, randomly spaced, parallel transects, designed to obtain estimates of stock size with known precision using hydro-acoustic techniques (de Moor et al. 2008). Over the period of 1995 to 2008, the biomasses of sardine and anchovy were positively correlated (r = 0.569, p = 0.034), but they were not when log transformed (Table S1 in the supplement). We used log-transformed values.

Fishery catch (1000 t): Estimates of the annual purse-seine catch of sardine and anchovy within about 20 km of Dassen Island (local catch) were obtained from J. J. van der Westhuizen (Marine and Coastal Management, pers. comm.). The overall annual purse-seine catches of sardine and anchovy off South Africa (sum of the 12 mo fishing activity for January to December) were also obtained. Catches in the vicinity of Dassen Island were used to estimate the local fishery effort. Annual overall catches with a 1 yr lag were used to examine the impact of fisheries on the penguin population at Dassen Island.

Southern Oscillation Index (SOI; yearly average calculated on 12 mo starting 1 October): Large-scale climate indices, such as SOI, are combinations of climate measurements that reduce complex space and time variability into simple measures (Stenseth et al. 2003, Stenseth & Mysterud 2005). These large-scale climate indices, or 'packages of weather', may then give a better explanation of the biological changes than local-scale oceanographic parameters that are well known to affect marine productivity (from phytoplankton to fish). El Nino Southern Oscillation (ENSO) was shown to account for a significant part of the variation in the sea surface temperature (SST; °C) of the west African coastal upwelling region (Roy & Reason 2001). SOI was therefore used as a proxy of remote forcing of the marine environment at Dassen Island. Monthly SOI was obtained from the Climate Analysis Section from the National Center for Atmospheric Research (www. cgd.ucar.edu/cas/catalog/climind/SOI.signal.ascii). A yearly average was calculated on the penguin year starting on 1 October.

SST from satellite imaging: SST influences distribution and spawning habitat of sardine and anchovy in the southern Benguela upwelling system (van der Lingen et al. 2001). Changes of SST may explain recent changes in the distribution of sardine and anchovy.

Monthly AVHRR Pathfinder v5 SST images, obtained from the Physical Oceanography Distributed Active Archive Center at NASA (http://podaac.jpl.nasa.gov/DATA_CATALOG/avhrrinfo.html), were used to compute a time series of spatially averaged SSTs. Data from day- and night-pass images were combined, which yielded a sample size of 204 values per month. Only SSTs for which the data-quality parameter was ≥4 and that were in the range of 10 to 30°C were retained, and an average was only computed when 30% (arbitrary) or more of the 204 values passed this test.

We calculated the SST for the 0 to 200 m shelf over the primary spawning ground at the western Agulhas bank (average from November to April; $SST_{spawning}$) and for the nursery area (from October to March; $SST_{nursery}$) in the north (see Fig. S1). We also calculated the maximum value measured for the same areas and time frame.

Statistical analysis. Penguin biological data (Date-O, Max-O and PerCapita) were related to environmental descriptors using generalized additive model (GAM) formulations with a quasibinomial error distribution in order to handle a binomial distribution of occupancy values, as implemented in the mgcv library of R2.8.1 (Wood & Augustin 2002). Specifically, let Y_t be the burrow occupancy at time t. Let $x_{i,t}$ be a vector of the explanatory variables at time t where i identifies a single component. Let s_i be nonparametric, smoothing functions, specifying the effect of the covariate x_i on the demographic variable Y_t. The formulation is:

$$Y_t = \alpha + \Sigma_i s_i(x_{i,t}) + \varepsilon_t \qquad (1)$$

where α is an intercept and ε is a stochastic noise term. The GAM procedure automatically chooses the degrees of freedom of the smoothing function s_i (i.e. how linear is the curve) based on the generalized cross validation (GCV) score. The function can also be chosen to be linear (i.e. $s_i(x_{i,t}) = b_i \times x_{i,t}$, where b is the slope).

Time series used in the analysis are presented in Figs. S2 & S3 in the supplement. A backward selection strategy for GAM regressions was applied based on minimization of the GCV score, and a measure of the model predictive squared error R^2. A covariate was retained if it caused a decrease of the model GCV score.

We checked 2-way interactions using Bürmann's expansion (Chan et al. 2003). We found no auto-correlation in the residuals of the selected models.

RESULTS

No significant relationship was found between the mean penguin burrow occupancy date (Date-O) and

the maximum occupancy (Max-O) observed (GAM, p > 0.05). Chick production (expressed by the maximum proportion of burrows with chicks Max-C) at Dassen Island was not significantly related to Date-O (GAM, p > 0.05) but was positively related to Max-O (GAM, p < 0.0001, deviance explained [dev] = 78.4%). Table 1 presents the 3 best models for each dependent variable.

The mean date of burrow occupancy (Date-O; ca. 3 June ± 42 d) was positively affected by an increase of SOI_t (Fig. 1A). In other words, African penguins tended to breed earlier at Dassen Island in years of low SOI values (warm SST and more frequent El Niño events). Consistently the second best model showed that an increase of SST recorded at the spawning area (max. $SST_{spawningt}$) led to earlier breeding.

The per capita growth rate (PerCap) was negatively and linearly affected by maximum SST recorded at the nursery area for sardine and anchovy during the months of October to March (max. $SST_{nurseryt}$; Fig. 1B).

The change in burrow occupancy (Max-O) was modelled using fish abundance, as given by the interaction term (ln[sardine], ln[anchovy]), and the SOI_{t-1} (SOI of the 12 mo before the new penguin year (Fig. 1C,D). The second best model used ln(sardine) and SOI_{t-1}, suggesting that an increase in sardine abundance results in increased burrow occupancy (Table 1).

The total catch of sardine and of anchovy in calendar $year_t$ (sum of the 12 mo fishing activity for January to December, the bulk of which is taken by October) negatively influenced the abundances of these fish species measured in November of $year_t$, respectively dev = 35.3%, p < 0.05 and dev = 67.9%, p < 0.01. The November biomass estimates are used to fix the initial total allowable catches (TACs) of the following year

($year_{t+1}$). Local anchovy fishing, within 20 km of Dassen Island, was proportional to the overall catch of anchovy in the same year (dev = 72.4%, p < 0.001), but this was not the case for sardine (Dev = 18.1%, p = 0.17). The proportion of sardine fished around Dassen Island compared to the total catch decreased linearly between 1995 and 2007 (dev = 51.0%, p < 0.01), while for the same period the relationship for anchovy was positive but not significant (dev = 15.9%, p = 0.22). When expanded to the period between 1987 and 2007, the proportion of anchovy fished around Dassen Island compared to the total catch increased significantly (GAM: dev = 28.1%, p < 0.05). Note that the total catch of sardine and anchovy around Dassen Island did not remain constant through time (p = 0.30). The hypothetical chain of mechanisms linking environmental conditions and the reproduction of the African penguin population at Dassen Island resulting from our study is summarized in Fig. 2.

DISCUSSION

Following previous studies on African penguins in South Africa (e.g. Crawford 1980, 1998, Crawford et al. 2006), we expected anchovy abundance to be the main explanatory variable for changes in burrow occupancy of penguins and of their per capita growth rate. This was not the case. However, anchovy abundance was the explanatory variable for the third best model explaining the changes in per capita growth rate (Per-Cap; Table 1). The models that better explained per capita growth rate used only changes in SST at the sardine and anchovy nursery area north of Dassen Island (Figs. 1B & S1) or over their spawning grounds, and not

Table 1. *Spheniscus demersus.* Results of the GAM analysis on the relationship of Dassen Island penguin burrow occupancy (Date-O, Max-O) and per capita growth rate (PerCap) with food abundance or environmental indices. Models can be written $Y_t = \alpha + s_1(x_{1,t}) + s_2(x_{2,t}) + \varepsilon$, with s being a nonparametric smoothing function, specifying the effect of the covariates x_i on the dependent variable Y; α being an intercept; and ε being a stochastic noise term. ln(sardine)$_t$, ln(anchovy)$_t$ corresponds to an interaction term: $s_1(x_{1,t}, x_{2,t})$. p-values for each variable (**p < 0.001, and *p < 0.05) are shown. After each explanatory variable (x_1 or x_2), the general sense of the relationship is indicated with + or – (where both symbols are used, this indicates a non-linear relationship). GCV: generalized cross validation score; SOI: Southern Oscillation Index; SST: sea surface temperature; t: survey year t

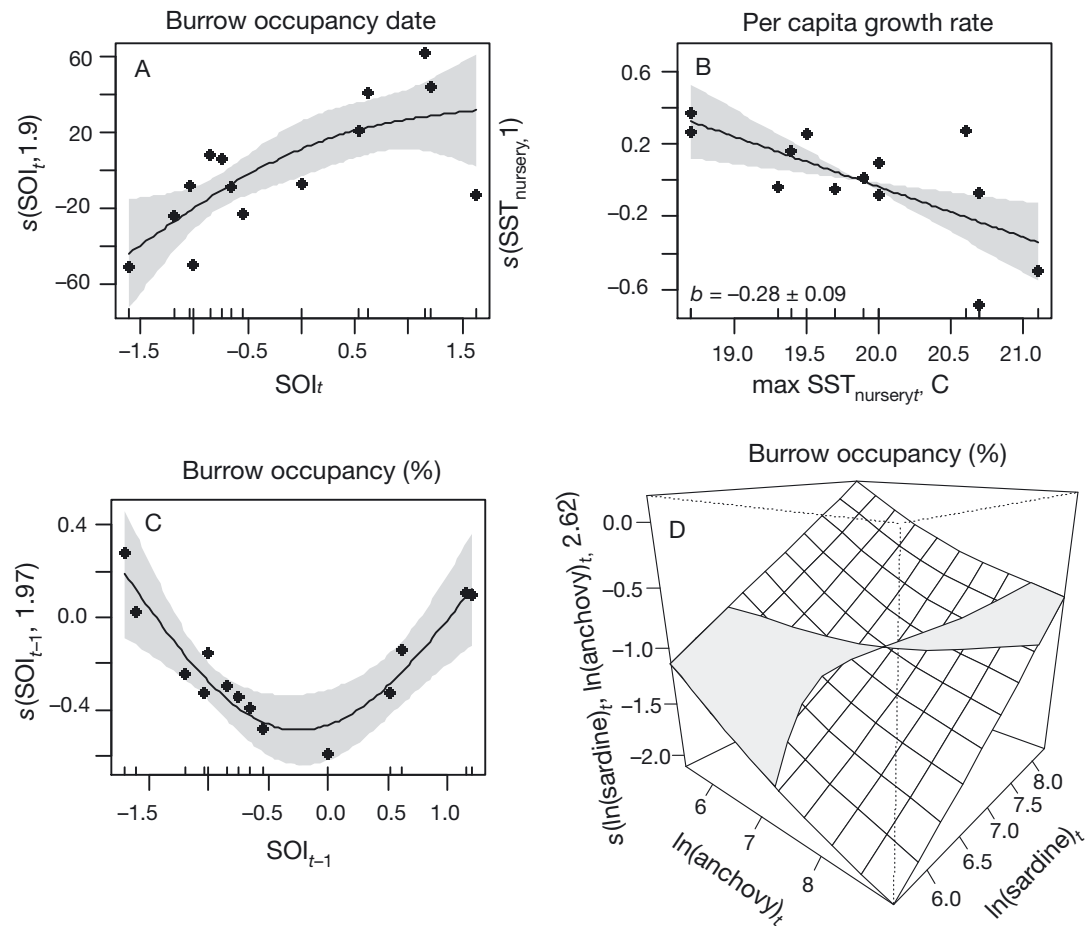| Y	x_1		x_2		n	R^2	Deviance	GCV
Date-O$_t$	SOI$_t$*	+			14	0.479	55	1190
	Max. SST$_{spawningt}$*	–			14	0.342	43	1491
	ln(anchovy)$_{t-1}$	+,–			14	0.342	43	2042
PerCap$_t$	Max. SST$_{nurseryt}$**	–			13	0.433	48	0.062
	Mean SST$_{spawningt}$*	–			13	0.260	32.3	0.080
	ln(anchovy$_{t-1}$)*	–			13	0.138	21.0	0.094
Max-O$_t$	(ln[sardine]$_t$, ln[anchovy]$_t$)**	+,–	SOI$_{t-1}$*	–,+	14	0.777	85.8	0.016
	ln(sardine)$_t$*	+	SOI$_{t-1}$	–,+	14	0.542	63.4	0.028
	ln(sardine)$_t$**	+	ln(anchovy)$_t$*	–	14	0.470	57	0.028

Fig. 1. *Spheniscus demersus.* Results of GAM modelling of effects of fish abundance and climate on per capita growth rate and burrow occupancy of African penguins breeding at Dassen Island. Model predicted values are given by the sum of 1 to 2 covariate effect: $Y_t = \alpha + s_1(x_{1,t}) + \varepsilon$ for (A,B), and $Y_t = \alpha + s_1(x_{1,t}) + s_2(x_{2,t}, x_{3,t}) + \varepsilon$ for (C,D), with s being a nonparametric smoothing function, specifying the effect of the covariates x on the dependent variable Y; α being an intercept; and ε being a stochastic noise term. (A) Mean date of burrow occupancy ($R^2 = 0.48$), (B) per capita growth rate ($R^2 = 0.43$), and (C, D) proportion of burrows occupied ($R^2 = 0.78$). In (B) the slope of the linear relationship is indicated. Sardine and anchovy abundances (expressed in 1000 t) being positively correlated, the whole area described by the grid in (D) is not applicable, there was never low abundance of sardine with high abundance of anchovy. In (D), the grey area represents the more probable sets of sardine/anchovy pairs as defined by the correlation between the 2 variables. For all graphs, $s(x,y)$ is the smoothing term, where x represents the explanatory variable and y is the estimated degrees of freedom of the smoothing term. The shaded areas indicate the pointwise 95% confidence intervals. SOI: Southern Oscillation Index; SST: sea surface temperature; t: survey year t; ●: partial residuals around the significant covariate effects

fish abundance. However, changes in SST may contribute towards a change in the distribution of sardine and anchovy (e.g. by mediating a shift in the spawning area; Roy et al. 2007). Consequently, the positive relationship between SOI (negatively correlated with SST at the spawning grounds; see Table S1) and mean burrow occupancy date (Table 1) suggests that the timing of breeding by penguins may be influenced by the distribution of their main prey.

In the present study, broad-scale environmental parameters such as SST explained variability in penguin breeding parameters better than a direct assessment of their prey. Such a relationship is not surprising

(Durant et al. 2004) as plankton and fish respond strongly (in abundance and in location along the coast of South Africa) to changes in temperature, making it a good proxy for prey availability (but see Grémillet et al. 2008). Temperature is usually measured in the same location(s) several times each year, thus giving a good assessment of seasonal and annual changes in a relatively large area. However, typical prey assessments (as conducted on scientific cruises) provide snapshot information on prey location, and may be poorly correlated with real change in regional stocks. In other words, broad-scale environmental parameters contain information on prey availability (i.e. accessibility for
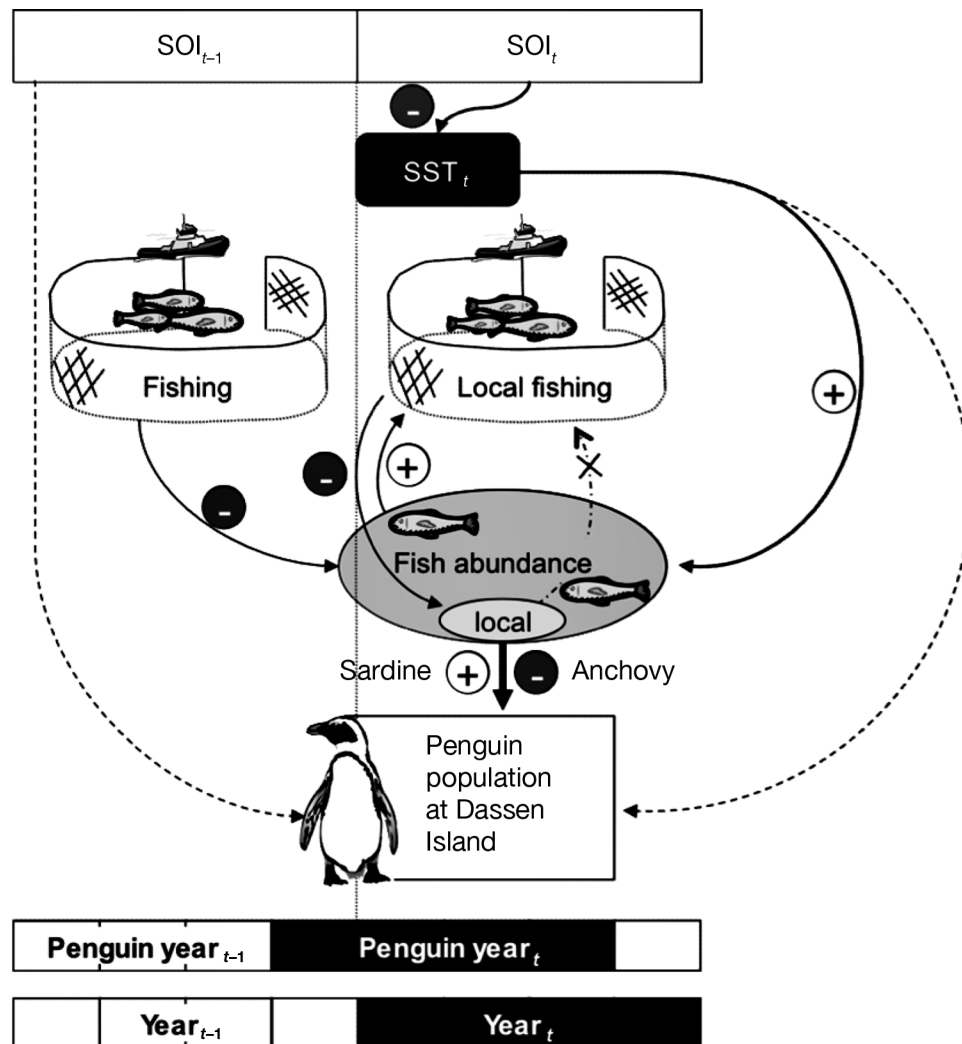
Fig. 2. *Spheniscus demersus.* Hypothetical chain of mechanisms linking environmental conditions and the reproduction of the African penguin population at Dassen Island. Dashed arrows indicate indirect links and solid arrows indicate direct links (see Table 1, Fig. S5 in the supplement). Local fishing, following the quota based on overall rather than local fish abundance, is depleting fish availability for penguins around Dassen Island during breeding, thus negatively affecting the population. During years of high sea temperature in the nursery and spawning area for the sardine and anchovy, reduced food availability created poor conditions for penguin reproduction. + and – on the figure indicate the direction of the relationship coming from the different models

the predator as well as abundance) that is lacking in an overall measurement of prey abundance. Our results also suggest different effects of the 2 species of pelagic fish prey on penguins breeding at Dassen Island. Previous studies, at both Dassen Island and Robben Island, have reported a positive relationship between the combined biomass of sardine and anchovy and breeding success (Crawford et al. 2006, Wolfaardt et al. 2008). In the present study, burrow occupancy at Dassen Island (Max-O) seemed to be influenced primarily by sardine abundance. The dominant response to sardine may mask a relationship between penguins

and anchovy. However the best model included anchovy biomass as a second explanatory variable that had a negative impact on the proportion of burrows occupied (Fig. 1D). A possible explanation for this unexpected relationship is that anchovy became less available to penguins at Dassen Island at the same time that their biomass was increasing.

Analysing fishery data, we found that catches of anchovy around Dassen Island were significantly related to the overall biomass of anchovy measured in November of the previous year. This would have been expected if the distribution of anchovy had not

changed, because the allowable catch in any year is based on the estimate of biomass in the previous November. However, after 1995 a greater proportion of the anchovy biomass occurred farther south and east of Dassen Island (Roy et al. 2007), whereas an increased proportion of the anchovy catch was made in close proximity to the island. All but one of the anchovy processing plants occur within 150 km of Dassen Island. It appears that the south and east displacement of anchovy led to proportionally more intense fishing around the island in an attempt to harvest the allowable catch, which was set at a high level because the overall biomass remained high. This likely led to the depletion of anchovy around Dassen Island. Hence overall fish abundance estimated from large-scale surveys may be an inadequate estimator of local fish abundance around seabird colonies, highlighting the need for spatial management of fish catches (Pichegru et al. 2009). The same pattern was not observed for sardine. This may be due to the fact that, unlike anchovy, sardine catches around Dassen Island were not related to the overall sardine abundance ($F_{1,11} = 0.3708$, $p = 0.555$; see Fig. S4 in the supplement).

There was also an effect of climate on the proportion of burrows occupied by penguins, in this case the average SOI of the previous year. SOI accounts for a significant part of the variability of the coastal SST anomalies measured in the Benguela upwelling region (Schumann et al. 1995). Indeed, SST measured at the spawning ground was negatively affected by SOI during our study period (see Fig. S5 in the supplement). SOI (and ENSO events) is expected to change the environmental conditions encountered by African penguins (e.g. Roy et al. 2001). At Dassen Island, a greater proportion of penguins attempted breeding when the previous year was an extreme SOI (+ or –). Both extremes may thus be positive for penguins. Low temperature linked to high SOI values may increase sardine production due to improved feeding conditions (see Lehodey et al. 2006). High temperature linked to low SOI values may create optimal conditions for sardine spawning in the upper water layer where nutrient enrichment is maintained (Daskalov et al. 2003), thereby also enhancing sardine production. Increased sardine production would lead to an increased availability of young-of-the-year (YOY) sardine recruiting along South Africa's west coast where Dassen Island is situated (e.g. Crawford 1980). This hypothesis is supported by the positive effect of the SOI of the year on the timing of breeding by penguins (low SOI leading penguins to breed earlier). The influence of SOI_{t-1} and SOI_t on the proportion of burrows occupied and the mean burrow occupancy date, respectively, may result from our choice to use penguin years that do not necessarily correspond to the annual cycle of the pelagic fish species.

Outside of the breeding season, African penguins are not constrained by the local availability of prey. Penguins at localities in the Western Cape may travel considerable distances in order to fatten up before and after moult, including to the sardine and anchovy spawning grounds off southern South Africa (Crawford et al. 2008b). This may explain why our models did not incorporate fish abundance of the same year but of the previous year to explain mean burrow occupancy date and per capita growth rate of African penguins at Dassen Island. The penguins' body condition prior to breeding may influence their decision to breed (e.g. Chastel et al. 1995, Gauthier-Clerc et al. 2001). Our results suggest that outside the breeding period, penguins were able to build up reserves by making use of good feeding conditions linked to a general increase of the anchovy stock regardless of where it was located along the South African coast (Table 1).

From 2004 to 2008, breeding at Dassen Island appears to have been initiated about 1 mo earlier than from 1995 to 2001 (respectively Days 146 ± 17 and 185 ± 10 after 1 October, i.e. end of February to beginning of April). This conforms to the trend of an earlier moult for adults at Dassen Island since 1997 (Wolfaardt et al. 2009). Although the time of the peak in burrow occupancy by penguins did not affect the maximum occupancy observed, it was positively related to the proportion of burrows with chicks. In other words, the later the breeding, the greater the proportion of burrows with chicks. This suggests that chick rearing conditions become better as the season progressed, which conforms to the known availability of YOY anchovy and sardine along South Africa's west coast in the austral winter (Crawford 1980). This highlights the dilemma of African penguins breeding at Dassen Island. High anchovy abundance linked to warm conditions may induce earlier breeding (mediated through the body condition of the bird) but at the same time may lead to a lower production of chicks. African penguins at Dassen Island seem then to be confronted with a temporal mismatch due to the reduced availability of sardine, in addition to a spatial mismatch with their main prey (Durant et al. 2007, Grémillet et al. 2008) created by the eastward displacement of fish stocks.

CONCLUSIONS

The conservation of the African penguin relies on an adequate availability of food, so that reproduction is sufficient to offset adult mortality (Crawford et al. 2006). Food availability in the Benguela upwelling system is presently affected by 2 major external forces: (1) an eastward shift of resources, which may be linked to climate change (Crawford et al. 2008a), and (2) fish-

ing pressure. Since nothing can be done to prevent the shift of pelagic resources, conservation measures for penguins are better achieved through managing the other stressor. There is a need to manage the pelagic fishery in a manner that accounts for the needs of top predators such as the African penguin, and which accounts for the fact that, as shown for anchovy, the overall abundance measured by acoustic surveys does not seem to reflect the abundance at particular localities (Grémillet & Boulinier 2009). Therefore, spatial management of such fisheries is recommended. If the interpretation of our results is correct, the local closure of the purse-seine fishery within 20 km of Dassen Island, put in place in 2008 by the South African government, should lead to a stronger relationship between anchovy abundance and African penguin reproduction at the island.

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