



Original Article

Quantifying the projected impact of the South African sardine fishery on the Robben Island penguin colony

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Quantitative methods are needed to evaluate the ecological effects of fishing forage species upon which predators depend. African penguin *Spheniscus demersus* numbers at the Robben Island colony rose during the 1990s co-incident with a marked increase in sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* abundances, but decreased appreciably during the 2000s as sardine suffered a series of poor recruitments. A population dynamics model is developed which relates penguin adult annual mortality to local sardine biomass, and is fit to penguin moult counts and re-sightings of tagged penguins. The predator–prey interaction is best explained by a sardine–penguin mortality relationship with average penguin survival decreasing only when the local sardine biomass is less than approximately one-quarter of the maximum observed. Results suggest that the rapid growth of the colony during the 1990s was driven primarily by immigration. Penguin projections are generated by linking to future sardine abundances predicted under the operational management procedure used to set catch limits for these sardine and anchovy fisheries, and compared with equivalent scenarios without fishing. Results indicate that fishing is likely to have a relatively small impact on penguins, especially when compared with uncertainties that arise from the variable spatial distribution of the sardine population.

Keywords: African penguin, ecosystem approach, fishing impact on predators, forage fish, predator–prey interaction, sardine, *Spheniscus demersus*.

Introduction

Prompted by growing concerns about the broader sustainability of fishing practices, there has been a movement towards the ecosystem approach to fisheries (EAF): fisheries management strategies that consider not only target species but also the impact that fishing may have on other components of the ecosystem (Garcia *et al.*, 2003). Interactions may be expected where fisheries and predators overlap spatially and target the same fish (Plagányi and Butterworth, 2005). This is especially the case if the predators have a foraging range that is restricted, for example, to the vicinity of a land-based breeding colony.

Much recent research has focused on suggested modifications to default harvest level specifications for forage species to safeguard food requirements of dependent predators. For example, Smith *et al.* (2011) report results indicating that at traditional maximum sustainable yield (MSY) related levels, fishing could result in large

impacts on other components of the ecosystem, including marine mammals, seabirds, and predatory fish of high commercial value. Simulations suggested that halving exploitation rates would reduce most impacts on other ecological groups while still producing a yield of ~80% of MSY. Other examples of such studies are Cury *et al.* (2011), Tyrrell *et al.* (2011), and Pikitch *et al.* (2012).

The African penguin *Spheniscus demersus* breeds on several coastal islands and a few mainland colonies. One of the largest colonies is located at Robben Island (33°48'S 18°23'E) near Cape Town (Figure 1). A thriving penguin colony was located at the island when European colonists arrived at the Cape in the 17th century, but hunting and egg collecting had extirpated the colony by the 19th century. Breeding was once again observed there in 1983 (Crawford *et al.*, 2011). The colony grew rapidly, peaking in 2004. However, this was followed by a steep decline in nest counts. Similar declines have been reported at other island colonies. Factors thought to

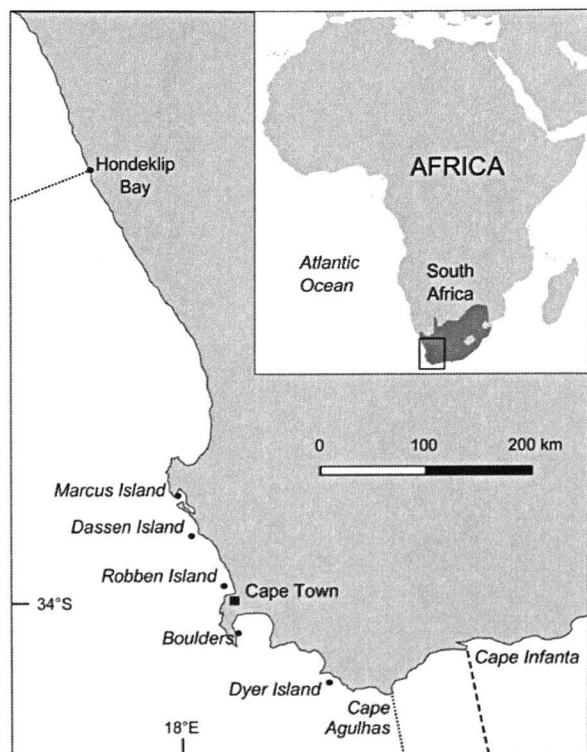


Figure 1. Map of the southwestern part of South Africa showing the location of five penguin colonies. The dotted lines mark the limits of the November biomass survey strata A–C (Hondeklip Bay to Cape Agulhas). The dashed line at Cape Infanta marks the eastern limit of the standard recruit survey area, which extends from the Namibia–South Africa border in the northwest which is defined by the Orange River. The Agulhas Bank is a large shallow area to the south of Cape Agulhas.

contribute to the ongoing decline in penguin numbers include scarcity of food, predation, and oil spills (Koenig, 2007). Two other seabird species abundant in the Benguela ecosystem (off the west coast of South Africa and Namibia) have also declined severely in the last 50 years: Cape gannets *Morus capensis* and Cape cormorants *Phalacrocorax capensis* (Hamann *et al.*, 2012). Crawford (2007) emphasizes the importance of taking the foraging needs of seabirds into account in fisheries management. Sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* make up the bulk of the penguin diet (see Supplementary material, Penguin diet). Of particular concern is the shifting distribution of these forage fish, presumably mediated by environmental factors (e.g. Rouault *et al.*, 2010), which may result in a spatial mismatch between the main penguin breeding colonies and their preferred prey (Crawford, 1998).

The South African fishery for small pelagics exploits primarily sardine and anchovy. The median total annual catch since 1950 is ~360 000 t. The fishery is South Africa's largest in terms of landed mass (De Oliveira and Butterworth, 2004), and is the second most valuable in monetary terms (de Moor *et al.*, 2011). The African penguin is considered a good indicator species of ecosystem impacts of the sardine and anchovy fishery. Reasons for this include the importance of these species in the penguin diet (Crawford *et al.*, 2011), the restricted foraging range of penguins during the breeding season (Pichegru *et al.*, 2009), and the availability of extensive penguin research and data.

A joint operational management procedure (OMP) was first implemented to set catch limits for both sardine and anchovy in 1994 (Cochrane *et al.*, 1998). The procedure has been refined and updated at regular intervals to take account of additional data and understanding of the resources. The latest available OMP, known as "Interim OMP-13" (de Moor and Butterworth, 2012b), has been used in this study.

Although the South African small pelagic fishery has an average escapement that is already similar to the level being advocated by Smith *et al.* (2011), additional management measures are now being considered to ensure that sufficient fish are available to provide for the foraging needs of predator species (Plagányi *et al.*, 2007). This is in line with the South African government policy to implement EAF management, as required by the Marine Living Resources Act No. 18 of 1998 (Cochrane *et al.*, 2004). Evaluating the penguin–pelagic fishery interaction is seen as the flagship project in this regard.

This paper describes a population model for the Robben Island penguin colony. The primary purpose of the model is to provide insight into penguin population dynamics, so that projections of abundance can be effected under different levels of fishing. Key features of the model are attempts to estimate the relationships of penguin reproductive success and adult survival to sardine and anchovy abundance. This enables the evaluation of the influence that future sardine biomass levels may have on the penguin population trend. Expected sardine biomass, in turn, is affected by fishery catches. This enables the evaluation of the performance of the small pelagics (sardine and anchovy) OMP in terms of the effect of fishing on penguin abundance through reduction in the abundance of forage fish. This is a matter of key interest in the Small Pelagic Scientific Working Group of the Department of Agriculture, Forestry and Fisheries, which is responsible for providing scientific advice to government regarding the sardine and anchovy fisheries, and under whose oversight much of this work was conducted.

Data

Three key types of data are used as inputs to the model described below: counts of moulting penguins, re-sightings of banded penguins, and the time-series of hydroacoustic survey estimates of sardine biomass. A brief summary is given here, as well as information about two major oil spills. These data are described in detail in the Supplementary material and in Robinson (2013).

Moult counts

While nest counts taken at the peak of the breeding season are often used as seabird abundance estimates, these do not account for any birds that might abstain from breeding in some years. Also, African penguins breed over an extended period, so that a peak-season count may miss a substantial number of birds (Crawford *et al.*, 1995). As all penguins moult annually on land, regular counts of penguins in the feather-shedding phase of moult can provide a more reliable time-series of abundance. The time-series used in this work (1989–2012) was derived using a new method of interpolation between counts, which is described in the Supplementary material, Moult counts. This method assumes that the sum of two Gaussian functions can provide a good representation of the number of birds moulting each day.

Sardine and anchovy biomass

Detailed knowledge of the magnitude and variation of sardine and anchovy abundance has been greatly enhanced since the inception of

hydroacoustic surveys in 1984 (Hampton, 1992; de Moor *et al.*, 2008). Two surveys are conducted each year: a recruitment survey every May–June, and a 1+ biomass survey in November. (The latter reflects the biomass of fish aged 1 year and older, assumed to be the spawning stock for anchovy; sardine reproduce from age 2—see de Moor *et al.*, 2011.) The survey provides the sardine and anchovy abundance estimates, split by strata. The model described below uses estimates of November 1+ biomass observed west of Cape Agulhas (strata A–C, see Figure 1), because this region corresponds closely to the foraging area for the penguins.

Re-sightings of banded penguins

African penguins have been tagged with individually identifiable flipper bands since 1947. Re-sightings of banded African penguins have been recorded throughout their range, including at Robben Island since 1989 (Whittington *et al.*, 2005b). A few hundred adult penguins in addition to some juvenile birds have been fitted with bands annually. Re-sighting efforts were greatly increased following the MV “Apollo Sea” oil spill in 1994. During the large relocation and cleaning operation following the MV “Treasure” oil spill in 2000, many thousands of penguins were banded. As a result of this large tagged cohort, most of the re-sightings recorded for Robben Island come from that group.

Oil spills

Two major oil spills (in 1994 and 2000) had a severe impact on seabird mortality at Robben Island (Wolfaardt *et al.*, 2009). This is taken into account explicitly in the model so as not to negatively bias estimates of natural mortality in those years.

Model description

Frequently ecosystem models are not fitted to data, being used to draw qualitative inferences only. However, here an approach was needed that enabled both fitting to various types of predator data and an ability to statistically assess the quality of those fits because quantitatively reliable outputs were required. Furthermore, many ecosystem modelling approaches are constrained by a generic framework. However, to adequately address the key management questions in this case, it was helpful to develop a specifically tailored modelling approach. The resulting model is simultaneously rigorous and pragmatic, and the associated analyses also account for a range of uncertainties.

The most important of the various components of the model developed are (i) the relationship between penguin annual adult mortality and sardine biomass in the penguin population dynamics model, and (ii) the estimation of model parameter values through fitting to moult counts and tag–recapture data.

Tables 1 and 2 list the parameters of the model, separating these into those fixed on input and those estimated in the model fitting process (see the Model fitting section).

Basic dynamics

The model considers the number of female penguins $N_{y,a}$ of age a at the start (1 January) of year y at Robben Island. The initial population size (at the start of year $y_0 = 1988$) is N_0 and its age structure is taken to correspond to steady change:

$$N_{1988,a} = \begin{cases} N_0 e^{-a\lambda} & \text{for } 1 \leq a < A \\ \frac{N_0 e^{-a\lambda}}{1 - e^{-\lambda}} & \text{for } a = A \end{cases}, \quad (1)$$

Table 1. Model parameters: parameter values fixed on input to the penguin–fish model.

| Parameter | Description | Value |
|-----------------|---|-------|
| A | Plus group age | 5 |
| p_j | Detectability of juveniles relative to adults in the moult count | 1.0 |
| a^* | Age of first breeding attempt | 4 |
| σ_j | Standard errors of the logarithms of the juvenile proportions | 0.1 |
| σ_{Ht} | Standard deviation of reproductive success | 0.1 |
| H_{\max} | Maximum allowed reproductive success | 2 |
| q_M | Proportion of moulters susceptible to observation | 0.9 |
| M_{\min} | Minimum allowed mortality rate | 0.04 |
| d^* | Parameter of logistic prior on δ in the biomass–mortality relationship | 0.02 |
| σ_δ | Parameter of logistic prior on δ in the biomass–mortality relationship | 0.005 |
| \hat{c} | Overdispersion factor for the tag–recapture likelihood | 5.57 |

where A is the plus-group age, taken here to be $A = 5$. Both N_0 and λ are parameters whose values are estimated in the model fitting process.

The following equations describe the population dynamics:

$$N_{y+1,a} = \begin{cases} \frac{1}{2} H_y \sum_{a=a^*}^A N_{y,a} \exp\left(-\frac{4}{12} M_y\right) (1 - \tilde{p}_y^{\text{oil}}) & \text{if } a = 1 \\ N_{y,a-1}^* \exp(-M_y) & \text{if } a = 2 \\ N_{y,a-1}^* \exp(-M_y) + I_y & \text{if } a = 3 \\ N_{y,a-1}^* \exp(-M_y) & \text{if } 4 \leq a < A \\ (N_{y,a-1}^* + N_{y,a}^*) \exp(-M_y) & \text{if } a = A \end{cases}, \quad (2)$$

where H_y is the annual reproductive success [number of chicks per mature female reaching 1 January of the year following birth, where 50% of these chicks are assumed to be female (at sea, sampling of 237 penguins by Rand (1960) gave a sex ratio close to parity)], M_y the adult (post 1 January of the first year of life) annual mortality rate in year y (note that this parameter subsumes any emigration that might occur. See also the discussion on transients in Supplementary material, Fitting to tag data), multiplied by 4/12 in the equation for $a = 1$ because the peak of the breeding season is assumed to be on 1 May (Figure 2), \tilde{p}_y^{oil} the proportion of chicks estimated to have died as a result of any major oil spill in year y , a^* the age at which the penguins first attempt to breed (taken here to be $a^* = 4$), and I_y the number of penguins (all assumed to be of age 3) immigrating to Robben Island in year y (investigations allowing for more flexible variation over time suggested that it is appropriate, given estimation variance considerations, to estimate this as four constant levels for the periods 1989–1990, 1991–1993, 1994–1996, and 1997–1999, and to set it to zero thereafter). The number of penguins in year y of age a that survive the major oil spills is defined as:

$$N_{y,a}^* = N_{y,a} (1 - \tilde{p}_y^{\text{oil}}), \quad (3)$$

Table 2. Model parameters: parameters estimated within the penguin – fish model.

| Parameter | Description | Prior | Posterior mode |
|-----------------------|--|------------------|----------------|
| $\ln N_0$ | Log of initial population size | $U[1,10]$ | 6.794 (892) |
| λ | Initial population profile parameter | $U[0,3]$ | 0.205 |
| σ_{add} | Additional variance in moult counts | $U[0,1]$ | 0.000 |
| $\bar{\sigma}$ | Parameter related to variability about the assumed biomass – mortality relationship | $U[0.001,0.5]$ | 0.088 |
| η | Reproductive success relationship | $U[0,1]$ | 0.512 |
| X_y | Adult mortality random effects | $U[-4.5,4.5]$ | |
| H_y | Reproductive success | $U[0.001,0.999]$ | |
| p_y | Tag re-sighting probabilities | $U[0,1]$ | |
| α | Parameters of the biomass – mortality relationship | $U[0,1]$ | 0.087 |
| β | | | 0.589 |
| γ | | | 0.173 |
| δ | | | 0.041 |
| $\ln I_{1989-1990}$ | Log of the number of 3-year-old penguins immigrating to Robben Island in the years indicated | $U[-4,10]$ | 6.691 (805) |
| $\ln I_{1991-1993}$ | | | 6.034 (417) |
| $\ln I_{1994-1996}$ | | | -3.999 (0) |
| $\ln I_{1997-1999}$ | | | 5.670 (290) |
| t_1 | 1989, 1993, 1995 – 1999, 2004 – 2009 | $U[0,5]$ | 0.109 |
| t_2 | 1990 | | 1.259 |
| t_3 | 1991 | | 0.633 |
| t_4 | 1992 | | 1.956 |
| t_5 | 1994 | | 0.000 |
| t_6 | 2000 | | 0.000 |
| t_7 | 2001 – 2003 | | 0.684 |

Where the parameter is estimated as the log of an abundance, the corresponding abundance value follows in parentheses. Priors were specified with the intention that they be uninformative.

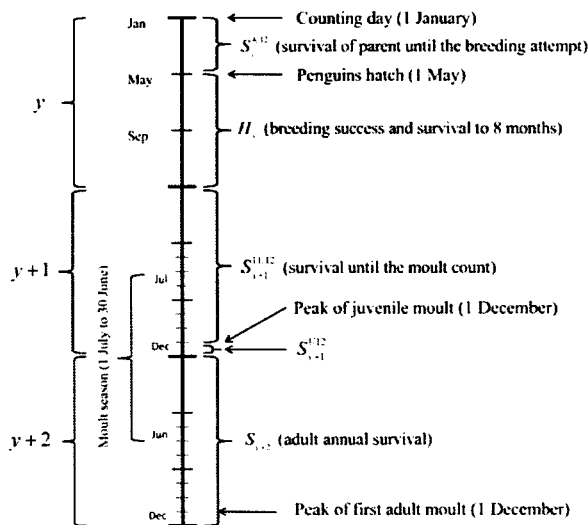


Figure 2. A time-line of the first years of the life of a penguin. As the peak of the breeding season is in the austral autumn, hatching is assumed to take place on 1 April. Most juvenile penguins moult into adult plumage at the end of the following year. The first adult moult usually takes place around the beginning of the following December, in the third year of a penguin’s life. As most penguins moult during spring and summer, the annual moult season is taken to run from 1 July until 30 June the following year.

where

$$\hat{p}_y^{\text{oil}} = \frac{N_y^{\text{oil}}}{\sum_{a=1}^A N_{y,a} \exp(-(m_j/12)M_y)}, \quad (4)$$

N_y^{oil} is the number of juvenile and adult penguins estimated to have died as a result of oiling in year y , and m_y the month in which the oil spill occurred in year y .

The Supplementary material provides model inputs related to the major oil spills as well as the parameter values that are fixed on input to the model. The choice here for the age at which penguins enter the breeding population in the model ($a^* = 4$) reflects the median of the observed ages (Crawford *et al.*, 1999; Whittington *et al.*, 2005a). Note that this is the age at which the penguins become potential breeders in the model, and no explicit assumptions are made about the proportion of pairs that actually attempt breeding each season.

Adult mortality is assumed to be age-independent. Note that the mortality rate M_y does not include loss of penguins as a result of the major oil spills, and the total survival rate S_y , defined as:

$$S_y = \exp(-M_y)S_y^{\text{oil}}, \quad (5)$$

includes both natural mortality and oil-induced mortality.

Population model

Both the rate of natural mortality M_y and the annual reproductive success H_y are assumed to depend on some function of prey biomass (the deterministic effect), but to be influenced also by some noise (random effects). For reproductive success, the estimates are drawn from a β distribution which ensures that biologically plausible bounds are respected. For adult survival, the alternative approach below was developed.

Adult survival depends on the normalized annual biomass levels $B_{S,y}$ determined from surveys, where the time-series I_S is some function of the sardine and anchovy November 1+ biomass and May

recruit biomass survey results for particular spatial regions:

$$B_{S,y} = \frac{I_{S,y}}{\max_y\{I_{S,y}\}} \quad (6)$$

In the same way, reproductive success depends on a similar index of biomass level $B_{H,y}$:

$$B_{H,y} = \frac{I_{H,y}}{\max_y\{I_{H,y}\}} \quad (7)$$

In the base case model implemented here, I_S is taken to be the sardine 1+ biomass west of Cape Agulhas estimated in the November survey. The series I_H is taken to be the anchovy recruit biomass west of Cape Infanta estimated in the May survey. These choices are considered biologically reasonable for the following reasons (Crawford *et al.*, 2011):

- (i) before and after moulting (summer), penguins are thought to fatten on sardine, gaining condition in preparation for breeding, and
- (ii) during the breeding season (winter), the fish caught for provisioning chicks are predominately anchovy.

Furthermore, a correlation analysis (Robinson, 2013) of various pelagic survey time-series with penguin abundance estimates showed that the sardine 1+ biomass survey best reflected the rapid decrease in penguin numbers since 2003. Anchovy biomass remained high during this period. The selection of November survey strata to include only those west of Cape Agulhas is appropriate considering the foraging range of non-breeding penguins which spend several weeks at a time at sea. Although breeding penguins have a limited foraging range as they must return to their nests every day or two, the choice of the anchovy recruit biomass series west of Cape Infanta is appropriate because most of the fish covered by this survey probably migrate past Robben Island from West Coast spawning grounds during autumn and winter (Crawford *et al.*, 2006).

Adult mortality

Annual adult penguin natural mortality M_y is assumed to depend on prey abundance $B_{S,y}$ as follows:

$$M_y = M_{\min} + f_S(B_{S,y})e^{X_y} \quad (8)$$

The M_{\min} term is included to impose a biologically plausible lower bound on the mortality rate, set here to be $M_{\min} = 0.04$. The random effects X_y are distributed as $N(0, \sigma_y^2)$ with:

$$\sigma_y = \sqrt{\exp\left[\frac{\tilde{\sigma}}{f_S(B_{S,y})}\right]^2 - 1} \quad (9)$$

Hence, the (median-unbiased) random effect is lognormal, but because the σ_y depends on the biomass $B_{S,y}$, the M_y distributions will all have exactly the same standard deviation. This is considered appropriate because it then follows that the data related to each year receive roughly equal weighting in the model fitting process, and further, when projecting, high resource biomass does not necessarily lead to low penguin mortality, as would follow (inappropriately so) were σ_y to have been assumed to be constant and independent of $B_{S,y}$.

Biomass – mortality relationship

The choice of an appropriate function for the assumed relationship between pelagic biomass and penguin adult annual survival is complicated by the fact that the survival values are estimated within the model, and thus tend to depend on the relationship itself. Of the functions tested, the following four-parameter logistic curve proved the most suitable:

$$f_S(B_{S,y}) = \alpha + (\beta - \alpha) \frac{1}{1 + \exp[(B_{S,y} - \gamma)/\delta]} \quad (10)$$

A prior for the δ parameter was added with the purpose of excluding very steep gradients of the function, as one would not expect step functions to provide the most realistic models for biological relationships.

Reproductive success

The reproductive parameters H_y^* are estimated for each year on the interval $[0, 1]$ and then transformed to the range $[0, H_{\max}]$ to obtain the annual reproductive success rates H_y as follows:

$$H_y = H_{\max} H_y^* \quad (11)$$

Here, $H_{\max} = 2$ is taken to be the maximum reproductive success rate possible, because this is the largest number of chicks that a pair can produce successfully each year.

The H_y^* parameters are assumed to be β -distributed about their predicted values \bar{H}_y^* . Setting $\kappa_{H,y} = \bar{H}_y^*(1 - \bar{H}_y^*)/\sigma_H^2 - 1$, the parameters of this β distribution $\alpha_{H,y}$ and $\beta_{H,y}$ are:

$$\begin{aligned} \alpha_{H,y} &= \bar{H}_y^* \kappa_{H,y} \\ \beta_{H,y} &= \kappa_{H,y} (1 - \bar{H}_y^*) \end{aligned} \quad (12)$$

The relationship between \bar{H}_y^* and the fish biomass index $B_{H,y}$ is assumed to be constant in expectation for the base case, given that analyses [for example, when allowing for a linear relationship between anchovy recruit biomass and penguin reproductive success, the estimate for the slope parameter came out very close to zero (see Supplementary Figure S9)] did not provide any indication of dependence:

$$\bar{H}_y^* = f_H(B_{H,y}) = \eta \quad (13)$$

though alternative functional forms could be considered.

To obtain β distributions that have a single mode and vanish at the ends of the interval, the estimation procedure ensures that both $\alpha_{H,y}$ and $\beta_{H,y}$ are > 1 .

Immigration

As the Robben Island colony is clearly not a closed population, immigration must be considered. The inclusion of tag–recapture information allows, in principle, for the estimation of immigration in the model as it may resolve the confounding between estimates of natural mortality and of immigration. All immigrants are assumed to be pre-breeders in adult plumage (Whittington *et al.*, 2005b) as reflected by Equation (2). Initially, a separate estimate was made for the number of birds immigrating to Robben Island each year, but there was not support for the addition of so many estimable parameters. Therefore, years were grouped together and an

appropriately parsimonious model was selected using the Akaike information criterion (AIC). There was no support for immigration from the year 2000 onwards.

Model fitting

The model is fitted to counts of adult and juvenile moulters as well as to tag-resighting data by maximizing a likelihood. The standard assumption of distribution lognormality is used for fitting to the moult data. For the tag data, standard capture–mark–recapture modelling techniques are applied (Lebreton *et al.*, 1992; Maunder *et al.*, 2009), but with the inclusion of additional mortality (which may incorporate emigration) in the year that a penguin is banded in the model of the tagged population. For more details, see the Supplementary material, Additional information about model fitting.

The model was fit using AD Model Builder (Fournier *et al.*, 2012).

Parameter estimation

The main results reported in this paper are in the form of joint posterior modes and of posterior medians and probability intervals obtained from a Bayesian approach implemented using the Markov-chain Monte Carlo (MCMC) method. Convergence was checked using the Gelman–Rubin and Heidelberger–Welch diagnostics.

However, a difficulty arises with Bayesian integration over the parameter $\tilde{\sigma}$ which quantifies the degree of spread of survival estimates about the assumed relationship with pelagic fish abundance (i.e. the spread of the X_j random effects). For reasons discussed in the Supplementary material, Objective function minimized, this gives rise to numerical difficulties. Instead, therefore, results were conditioned on a fixed value of $\tilde{\sigma}$ obtained from a maximum likelihood estimation process which used ADMB-RE to integrate out these random effects by the Laplace approximation (Skaug and Fournier, 2006). The resultant estimate of $\tilde{\sigma}$ was 0.088 with an associated Hessian-based standard error of 0.013.

Because as a result, the posterior distributions calculated do not allow for uncertainty in the estimate of $\tilde{\sigma}$, sensitivity to alternative values was tested, with the results summarized in Supplementary material, Additional results.

Certain of the results in the figures following show joint posterior mode values as well as various posterior percentiles. The reason is that during the development of this work, some on the guiding Small Pelagic Scientific Working Group preferred results presented in the form of Maximum (Penalized) Likelihood Estimates (MPLEs). For reasons discussed in Supplementary material, Objective function minimized, these are conditioned on the ADMB-RE estimate of $\tilde{\sigma} = 0.088$.

Linkage with the small pelagics OMP

A key aspect to the penguin–sardine model is the assumed relationship between adult penguin annual mortality and sardine abundance. In the base case model, this mortality is taken to depend on the sardine 1+ biomass west of Cape Agulhas that is estimated in the November survey. Future sardine abundance depends on future fishing mortality. Distributions of plausible future sardine abundances under different candidate MPs (i.e. harvest control rules) are generated with the operating models that underpin the testing of OMPs for sardine and anchovy (de Moor and Butterworth, 2012a).

The management procedure adopted in December 2012 for the South African sardine and anchovy resources, known as Interim OMP-13 (de Moor and Butterworth, 2012b), has been used to generate

a large set of plausible projected sardine survey abundances. The details of the harvest control rule are described in the Supplementary material, Sardine harvest control rule. Note that it is assumed that the link between projected sardine biomass and penguin abundance is unidirectional. Under this assumption (discussed further in Supplementary material, Additional information about projections), a change in penguin abundance does not substantially affect sardine mortality as a result of increased or decreased predation. The set of projected sardine abundances for any particular management option can thus be calculated independently of the penguin population dynamics.

The reason for calculating projected penguin numbers is to evaluate which potential OMPs for sardine and anchovy satisfy the objective of an EAF of not having an excessively negative impact on penguins. In principle, a range of candidate OMPs could be tested, and only those that satisfy this EAF criterion would be considered for implementation as the OMP adopted.

Future sardine biomass spatial distribution

In addition to the total annual abundance of sardine over the projection period, the proportion of sardine located to the west of Cape Agulhas is required for the calculation of future adult penguin annual mortalities. As described above, plausible future sardine biomass trajectories are obtained from the operating model for sardine population dynamics, assuming future catches are generated using Interim OMP-13. The sardine resource is currently managed as a single stock. As such, the operating model used when developing the OMP provides a single overall sardine abundance for each year with no spatial disaggregation. This means that an assumption is required concerning the proportions of sardine biomass located to the west of Cape Agulhas in future years.

The proportion of sardine observed to the west of Cape Agulhas has been variable over the history of the small pelagic hydroacoustic surveys (Coetzee *et al.*, 2008). The mean proportion to the west from 1984 to 1998 was 74%. This dropped to a mean of just 26% over the years 1999–2007, but has since increased to 48% for 2008–2012.

In the simulations that follow, two alternatives regarding the future spatial distribution of sardine biomass are considered. Historical proportions of sardine biomass observed west of Cape Agulhas in the November hydroacoustic surveys are split into two sets: 1984–1998 and 1999–2012. This essentially provides two scenarios for penguin population projections. In the more optimistic scenario, sardine is assumed to return immediately to a spatial distribution similar to that observed before 1999, resulting in a larger proportion of sardine being available to the penguins on average. In the alternative scenario, the sardine distribution is assumed to remain similar to that observed thus far in the twenty-first century.

For each year of each of the simulated projections, a value is chosen at random from the relevant set of proportions observed historically. This value then multiplies the total sardine abundance for that year. The first scenario (1984–1998 proportions) clearly results in a higher biomass of sardine available on average to Robben Island penguins than the second scenario (1999–2012 proportions; Figure 3). The biomass index of $B = 1$ corresponds to the maximum sardine 1+ biomass previously observed to the west of Cape Agulhas (1 343 000 t in 2003).

Projected penguin numbers

A distribution of 10-year penguin population trajectories is calculated from 1000 plausible future sardine abundance trajectories for a particular fishery management option, given an assumption regarding the proportion of sardine to the west of Cape Agulhas

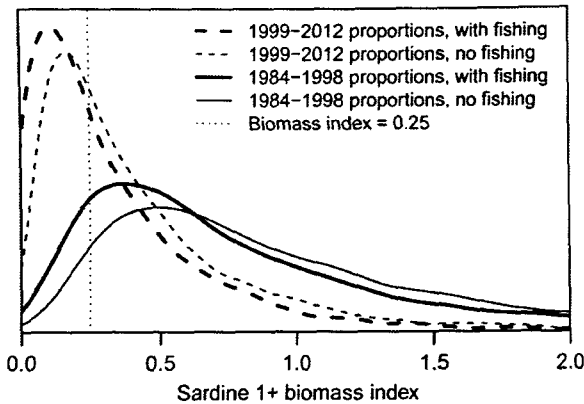


Figure 3. Distributions of 10-year projections of sardine observed 1+ biomass indices west of Cape Agulhas assuming 1984–1998 proportions (solid lines) and assuming 1999–2012 proportions (dashed lines) of the overall 1+ biomass in this region. The thick lines are for projections assuming catches taken as specified by the sardine-anchovy management procedure adopted for use in 2013 (Interim OMP-13), while the thin lines are for projections assuming no future fishing.

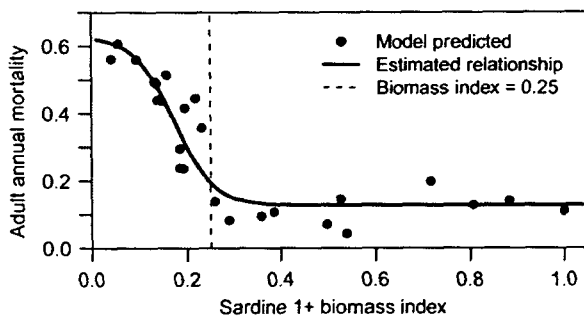


Figure 4. The estimated relationship (posterior mode) between the sardine 1+ biomass index (scaled to the maximum November survey estimate of 1 343 000 t in 2003) and penguin adult mortality. The vertical dashed line is at 25% of the maximum observed biomass.

in the future. From an ecological perspective, the most conservative fishery management decision is when fishing is suspended entirely. Distributions of projected sardine biomass indices indicate that on average, more fish would be available to Robben Island penguins under a “no catch” scenario compared with under Interim OMP-13 (Figure 3).

The calculations for the projected penguin population dynamics are analogous to Equation (2). Major oil spills are not taken into account explicitly in the future, and no immigration term is included in the projection equations. The reproductive success factor H for each year in a projection was resampled with replacement from the posterior mode estimates of H_t values over the years of the model fit.

Future penguin mortality is assumed to depend on the projected sardine biomass according to the relationship fitted (Figure 4). When calculating projected values of adult mortality, strictly uncertainty about the value of $\hat{\sigma}$ (which relates to the variability about the assumed biomass–mortality relationship) should be taken into account. However, results obtained using the maximum likelihood estimate of $\hat{\sigma} = 0.088$ are nonetheless informative.

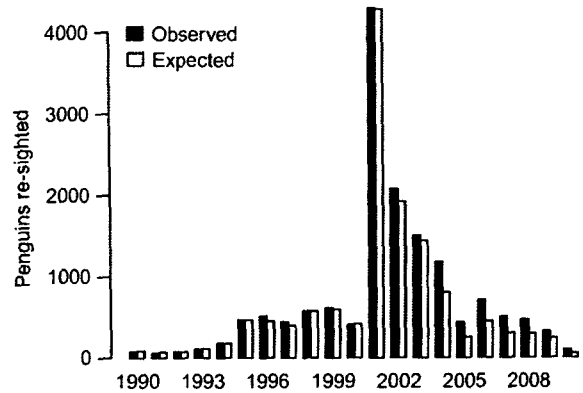


Figure 5. Comparison of observed and expected (posterior mode) numbers of banded penguins re-sighted each year.

Results and discussion

Population model

When viewed overall the model fits the data very well, with the one exception of the systematic trend of more observed than expected re-sightings of tagged penguins from 2002 to 2010 (Figure 5). It is possible to force the expected numbers of re-sightings to match the observed data exactly, which results in higher re-sighting probabilities over this period. Although the fit to the moult data remains acceptable when this is done, the tag–recapture likelihood suffers considerably (Supplementary Table S10). This suggests that it is the re-sighting histories of the birds that are not compatible with some assumptions of the recapture model being used; consideration of either or both of age-dependent mortality and of heterogeneous re-sighting probability factors might improve the fit of the model to the re-sighting numbers. Importantly though, the key result relating the penguin projections is insensitive to forcing the model fit in this way (see Supplementary Table S12 and Figure S12).

The posterior distribution percentiles (see Supplementary Table S8) for the parameter β of the relationship between sardine biomass and penguin mortality show that this increase in mortality at low biomass is substantial and well determined. The shape of this relationship (Figure 4) suggests that penguins gain very little additional benefit as the sardine biomass index increases above $B_5 = 0.25$, which corresponds to some 336 000 t (west of Cape Agulhas). However, penguin mortality increases rapidly as sardine biomass drops lower, from about $M = 0.13$ up to roughly $M = 0.6$. The model applied prefers the relationship to flatten as the biomass index approaches zero.

The Bayesian 95% probability intervals for adult survival (Figure 6) and adult moulters (Figure 7) are fairly narrow, reflecting relatively precise estimation. In contrast, the probability intervals for the estimated number of penguins immigrating to Robben Island are rather wide.

The estimates for transient-related (first year after banding) apparent mortality rates are comparatively large in the years 1990–1992 and 2001–2003 (Supplementary Figure S5; note that these transient rates for the first year of tagging differ from the natural mortality rates in subsequent years which are shown in Figure 6). This may suggest that penguins were emigrating from Robben Island in those years, or that a large proportion of the birds tagged were visitors rather than residents. Alternatively, poor quality of either the tagging or the tags in those years might be the cause.

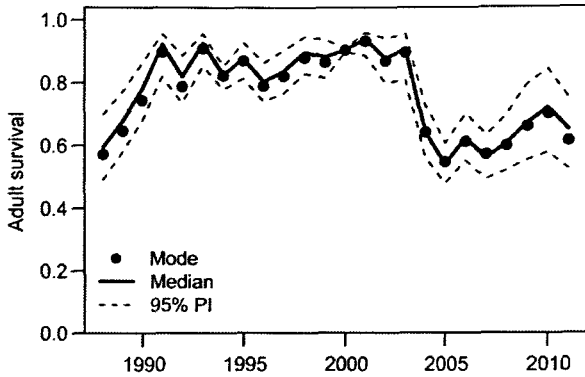


Figure 6. Time-series of estimated adult penguin annual survival rates for Robben Island at the joint posterior mode (black circles). The medians and 95% probability intervals of the Bayesian posterior distributions are joined by lines.

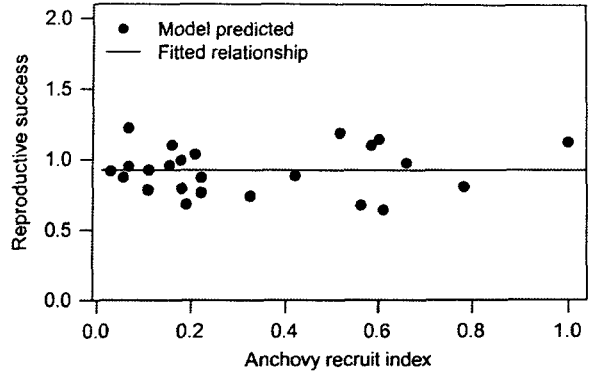


Figure 8. Estimated (posterior mode) and predicted values of penguin reproductive success plotted against an index of anchovy recruitment (prey abundance).

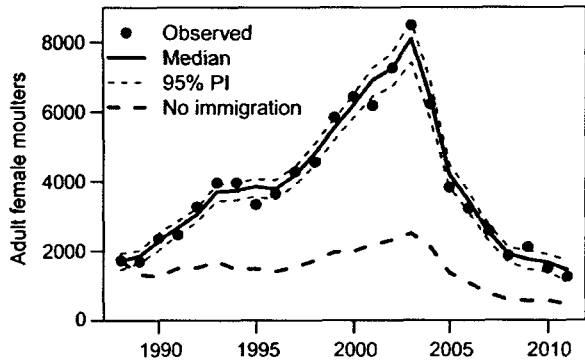


Figure 7. Time-series of female moulting penguins at Robben Island from observations (black circles). The medians and 95% probability intervals of the Bayesian posterior distributions for the model-predicted moult counts are joined by solid thick and light dashed lines, respectively. The thick dashed line indicates the median trajectory for the same demographic parameter estimates had the immigration estimated by the model not occurred.

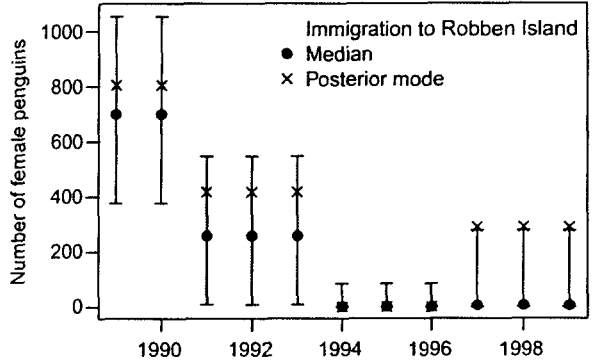


Figure 9. Median (black circle) and posterior mode (cross) numbers of 3-year-old female penguins estimated to have immigrated to Robben Island each year, with associated 90% probability intervals.

Figure 8 shows annual predictions by the model of penguin reproductive success plotted against the anchovy recruit index, illustrating the somewhat surprising lack of any dependence as mentioned in the Reproductive success section.

A notable result is the large number of penguins estimated to immigrate to Robben Island from 1989 to 1993 (Figure 9). This warrants further investigation to determine compatibility with data for the most likely source of these immigrants (the Dyer Island colony). The model predicts that the Robben Island population would scarcely have been self-sustaining without immigration (Figure 7), showing only a moderate increase in abundance during the years of high sardine biomass (1997–2003). This suggests that most increases in the size of the Robben Island colony during the 1990s are attributable to immigrants.

This observation has implications for future expectations of penguin abundance at Robben Island. Because penguins have apparently stopped immigrating to the colony in large numbers, it may be overly optimistic to assume that numbers at the colony will increase rapidly in the future, even if sardine biomass in the region increases substantially.

Projections

Twenty-year projections for penguin abundance have been calculated for two different assumptions concerning the spatial distribution of future sardine biomass (Figure 10), reflecting proportions west of Cape Agulhas similar to those observed in, alternatively, 1984–1998 or 1999–2012. A key statistic of interest is the median 20-year projection of the number of observable adult penguins, which is comparable with the historical adult moult count time-series to which the model is fitted. The ratio of this statistic to the most recent adult penguin moult count as predicted by the model gives the proportional change in penguin numbers over the projection period (Table 3). This ratio can be compared for different fishery management options and also for alternative sardine spatial distribution assumptions. These results are robust across a range of sensitivities tested (Supplementary material, Sensitivity tests).

Overview

The model of the dependence between a predator and its key prey developed here is more rigorous than most approaches used to assess the ecosystem effects of fishing because it integrates data from different sources in a statistically defensible manner.

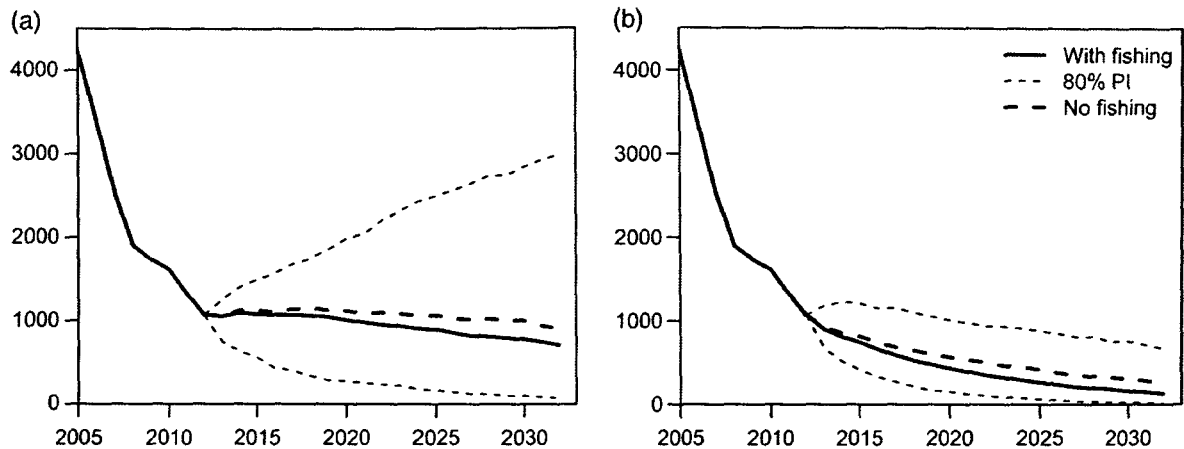


Figure 10. Comparison of median projected penguin numbers with fishing under Interim OMP-13, and without fishing, for future sardine distributions similar to those observed in (a) 1984–1998 and (b) 1999–2012. The 80% probability intervals are indicated for the projections under Interim OMP-13. Projections commence at the posterior mode in 2012.

Table 3. Projected median numbers of adult female penguins at the Robben Island colony in 2032 with and without fishing (N_{2032}), the associated proportional changes P from numbers in 2012 ($N_{2012} = 1067$), and the percentage proportional change per year, for alternative assumptions regarding the future spatial distributions of the sardine resource.

| | 1984–1998 sardine distribution | | | 1999–2012 sardine distribution | | |
|-----------------|--------------------------------|------|----------------------|--------------------------------|------|----------------------|
| | N_{2032} | P | % year ⁻¹ | N_{2032} | P | % year ⁻¹ |
| With fishing | 712 | 0.67 | -2.0 | 129 | 0.12 | -10.0 |
| Without fishing | 909 | 0.85 | -0.8 | 256 | 0.24 | -6.9 |

Specifically, the model includes abundance estimates from moult counts as well as survival estimates inferred from tag–recapture data.

The sardine biomass–penguin mortality relationship (Figure 4) predicts that average adult penguin mortality increases only when sardine biomass drops below a certain threshold. This threshold is estimated to be at an index of about $B_S = 0.25$ (one-quarter of the maximum observed biomass). When assuming a future spatial distribution of sardine similar to 1999–2012, 52% of the projected distribution that is generated assuming Interim OMP-13 is below the index $B_S = 0.25$, resulting in a drop in the adult penguin survival rate. Hence, the natural death rate frequently exceeds the reproduction rate, and consequently, the penguin population declines (Figure 10b).

In contrast, when assuming that the future spatial distribution of sardine is similar to that of the 1984–1998 period, only 13% of the projected sardine distribution lies below the critical value. In this case, the sardine biomass is at a level where the average penguin adult survival rate is as high as possible most of the time, and population abundance is stable in median terms (Figure 10a). Furthermore, sardine abundance higher than this would provide negligible additional benefit to penguins, as average survival is not predicted to increase with increasing biomass above approximately $B_S = 0.25$.

The relationship indicates that sardine is probably a more important prey species for penguins than anchovy, at least at certain

times of the year. Although diet studies indicate that anchovy accounts for the majority of consumption during the breeding season when adult penguins catch it for provisioning chicks (Crawford *et al.*, 2011), sardine may be the preferred prey of adults during spring and summer when they must gain condition in preparation for moulting and breeding. Indeed, Sherley *et al.* (2013) found that the length of time taken for chicks to fledge at Robben Island was related to the sardine biomass in the preceding November. A possible reason for the preference for sardine over anchovy is that each sardine caught is likely to be larger and more nutritious than each anchovy, thus providing a better energy return for the foraging effort exerted. Several studies have estimated the calorific content of sardines as higher than that of anchovies with the mean values of 6.59 and 6.03 kJ g⁻¹ wet mass, respectively (Balmelli and Wickens, 1994).

The impact of fishing on penguin numbers through the reduction in total sardine biomass by the fishery is rather small, especially when compared with other factors influencing the dynamics. The median projection for penguins assuming future spatial distributions of sardine similar to 1984–1998 is virtually flat (Table 3 and Figure 10a). Even in the absence of fishing, only a small increase in penguin abundance is predicted. One reason for this relatively small projected effect is that the design of OMP-13 is relatively conservative (by global standards) with regard to the sardine resource. Under simulation testing, the average sardine biomass at the end of the 20-year projection period is 75% of the pristine average abundance, and 45% higher than the rather low 2011 biomass from which the projections of this paper commence (de Moor and Butterworth, 2012b).

These projections may seem surprising, as the penguin population grew rapidly in the early- to mid-1990s (before the sardine boom) at sardine biomass levels that were similar to those now projected. However, the analyses suggest that the main reason for the growth in the Robben Island penguin population over that period in the 1990s was immigration, not any substantial excess of the reproduction rate over the death rate (Figure 7). Without immigration, the population would have grown very little even in the years of high sardine abundance. This is seemingly because there is minimal additional benefit to penguin adult survival when sardine

biomass increases above about one-quarter of the maximum level that has been observed. This last result suggests that Robben Island offers a marginal breeding location for penguins, even under optimal feeding conditions. As it appears that the colony was barely self-sustaining even during periods when sardine biomass was high, it may be unreasonable to expect any substantial growth in penguin numbers at the island if the conditions of the last two decades persist, unless additional birds again immigrate from elsewhere.

There are several reasons that could explain why the Robben Island penguin population increased little apart from as a result of immigration. Most immigrants were likely to be pre-breeders, and first-time breeders are expected to have a relatively low success rate, improving in subsequent years as partners gain experience (Wolfaardt *et al.*, 2008). The two major oil spills off the west coast caused great disruption to the population, and the subsequent reproductive performance of penguins that had been oiled was negatively affected (Wolfaardt *et al.*, 2008). Finally, removal from many islands of guano, in which penguins prefer to construct nest burrows, has resulted in reduced breeding success for the penguin population overall (Frost *et al.*, 1976). Most penguins at the colony now nest under vegetation, as much of the soil is too sandy for constructing stable burrows. Evidence that breeding success at surface nests is lower than that for artificial nest boxes or nests in buildings suggests that vegetation does not provide optimal nesting habitat for penguins (Sherley, 2010). Surface nests may be more susceptible to predators such as feral cats and kelp gulls (Underhill *et al.*, 2006), especially if guarding adults vacate their nests for some reason (e.g. to alleviate heat stress).

Conventionally, poor feeding conditions for seabirds are thought to primarily affect reproduction (e.g. Einoder, 2009; Cury *et al.*, 2011). The breeding season is usually the period when food requirements are greatest as additional foraging is necessary for provisioning chicks (Pichegru *et al.*, 2009). If food within the penguin foraging range of the breeding colony is scarce, adults can abstain from breeding or abort a breeding attempt, preserving themselves in anticipation of better conditions in a subsequent season.

However, no relationship was found between estimated penguin reproductive success at Robben Island and forage fish abundance. Adult survival changes appear to have had a much larger impact on the population trend than variations in breeding success. In fact, the available data indicate that breeding success may have increased on average during the past decade when the Robben Island population was in decline (Sherley *et al.*, 2013). Furthermore, anchovy abundance has remained high during this period (Butterworth *et al.*, 2012), which should have provided an adequate food source for provisioning chicks.

In a meta-analysis of seabird populations from various world-wide locations, Cury *et al.* (2011) found that breeding success was reduced when prey abundance dropped below approximately one-third of the maximum observed level. In this study, however, it was instead penguin adult survival that was found to be correlated with prey abundance. Nevertheless, a consistent pattern is that in both studies, seabirds exhibit a negative response only once prey abundance drops below a relatively low level. Additional prey availability above this threshold provides little, if any, additional benefit to the birds.

While the result that prey availability has a larger effect on adult survival than on breeding success is surprising, it is not unprecedented. Sandvik *et al.* (2005) found through a tag–recapture analysis that prey abundance affected adult survival in some seabird species in the western Barents Sea. They note that a decrease in

adult survival is likely to have a dramatic effect on the population of a longer-lived species, as seems to have been the case here for the African penguin.

Fishing stress and consequent reduced fish biomass may result in environmental anomalies having a more severe effect than would be the case in a pristine ecosystem (Watermeyer *et al.*, 2008). The recent low sardine recruitment in several consecutive years has resulted in a marked decline in the resource. It may be that the disproportionately higher fishing pressure on the west coast contributed to the current relatively low sardine biomass proportion west of Cape Agulhas (Coetzee *et al.*, 2008), exacerbating the situation for Western Cape penguins.

EAF advancement

This work provides a framework for making an objective assessment of the impact of fishing from an EAF perspective by evaluating its effect on the population trend of a dependent predator. Under this framework, the impact of fishing on a predator caused by any management procedure suggested for a fishery can be evaluated. The goal is to prevent not only overfishing in the conventional single-stock assessment context, but also “ecosystem overfishing” (Powers and Monk, 2010), using penguin performance in this case as an ecological indicator of the state of the ecosystem (Boersma, 2008). Avoiding such ecosystem overfishing should help to preserve both the functioning of the ecosystem and the productivity of the target stock.

The recent downward trend in penguin abundance, in particular at Robben Island, is certainly worrying, and reasons for this decline should continue to be investigated. However, the results of this study suggest that the reason most commonly suggested for the decrease in penguin abundance—heavy fishing pressure—is unlikely to be the primary cause, unless the mechanisms for this negative interaction have not been reflected appropriately in the analyses conducted here. Thus, levels of pelagic fishing permitted by the OMP tested are unlikely to have a substantial effect on penguin abundance at Robben Island. In particular, this effect is small when compared with the effect of changes in the spatial distribution of sardine.

The coupling of the penguin population model to the sardine operating model provides an objective assessment of the impact of fishing on Robben Island penguins. This reflects the application of rigorous quantitative methods in which data from a variety of sources are integrated in a statistically defensible manner. Similar techniques are typically used in a rigorous single-species fisheries assessment. Here, however, they have been applied to a non-target predator species which is dependent for food on fish stocks under harvest. This is important in the context of advancing the EAF concept. It is unusual for approaches as quantitative as this to be implemented to address an EAF issue. Nevertheless, some modelling work has been conducted relating to the dependence of predators on Antarctic krill *Euphausia superba* (Thomson *et al.*, 2000; Plagányi and Butterworth, 2012; Watters *et al.*, 2013), in response to requests for scientific advice by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Although krill catches are currently fairly low, it has been recognized that they could nonetheless make an appreciable ecosystem impact if they are concentrated in small localized areas that simultaneously serve as important foraging grounds for dependent predators. A number of models were therefore developed to assess and evaluate current and future potential impacts of fishing on land-based predators such as penguins and seals. The models were used to explore alternative scenarios involving subdivision of the precautionary catch limit for krill among 15 small-scale management units (SSMUs)

in the Scotia Sea. Similar predator–prey interaction models have also been developed to explore factors affecting Steller sea lions *Eumetopias jubatus* in the Bering Sea (Fay and Punt, 2006; Kinzey and Punt, 2009). Although still very rare, there is at least one example of a whole ecosystem model being fit to similar data to those used in stock assessments (e.g. Gaichas *et al.*, 2011). However, this requires very large datasets and computation resources.

Ecosystem models of varying quality (and rarely conditioned on data) are commonly being applied, typically in a strategic rather than tactical context, to provide guidance as to recommended caps on harvest levels to protect ecosystem biodiversity. In South Africa, the widespread initial response to the decline in penguin numbers was to suggest that this was a consequence of reduction in the abundance of their prey caused by the pelagic fishery. Perhaps, the main guidance emanating from this work is to caution that marine ecosystem interactions are not necessarily straightforward, so that the temptation to jump to such conclusions before conducting careful and desirably quantitative analyses should be avoided.

Supplementary data

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

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