TRACE document

This is a TRACE document ("TRAnsparent and Comprehensive model Evaludation") which provides supporting evidence that our model presented in:

Florian Weller, Richard B. Sherley, Lauren J. Waller, Katrin Ludynia, Deon Geldenhuys, Lynne J. Shannon, Astrid Jarre. System dynamics modelling of the *Endangered* African penguin populations on Dyer and Robben islands, South Africa. Ecological Modelling

was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

The rationale of this document follows:

Schmolke A, Thorbek P, DeAngelis DL, Grimm V. Ecological modelling supporting environmental decision making: a strategy for the future. Trends in Ecology and Evolution 2010; 25:479-486.

and uses the updated standard terminology and document structure in:

Grimm V, Augusiak J, Focks A, Frank B, Gabsi F, Johnston ASA, Liu C, Martin BT, Meli M, Radchuk V, Thorbek P, Railsback SF. 2014. Towards better modelling and decision support: documenting model development, testing, and analysis using TRACE. Ecological Modelling 2014; 280:129-139.

and

Augusiak J, Van den Brink PJ, Grimm V. Merging validation and evaluation of ecological models to 'evaludation': a review of terminology and a practical approach. Ecological Modelling 2014; 280:117–128.

African Penguin Pressure Model – TRACE documentation
(version 2016_02)

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Table of contents

Each section contains an executive section summary in the form of an annotated table of contents. Blue text contains local hyperlinks.

1   Problem formulation

1.1   Section summary
This TRACE element provides supporting information on: The decision-making context in which the model will be used; the types of model clients or stakeholders addressed; a precise specification of the question(s) that should be answered with the model, including a specification of necessary model outputs; and a statement of the domain of applicability of the model, including the extent of acceptable extrapolations.

This element contains the following sub-sections:

- 1.2 – Context – modelling African penguin populations [3]
  The rapid decline in African penguin populations necessitates the development of management tools. A system dynamics environment enables the use of sparsely parameterized processes and qualitative data in the construction of a model that attempts to capture all known influences on penguin colonies in South Africa.
- 1.3 – Requirements and outputs [4]
  The model is intended to aid management decisions of conservation stakeholders by comparing and prioritizing pressure influences and by examining the likely effects of management actions. Current implementations focus on two specific colonies (on Robben and Dyer islands).

1.2   Context – modelling African penguin populations
The African penguin (*Spheniscus demersus*) is endemic to Southern Africa and breeds at 28 sites in South Africa and Namibia (Crawford et al., 1995; 2011). It is currently classified as "Endangered" on the IUCN Red List of Threatened Species (IUCN, 2010) in recognition of a rapid population decline that has reduced the South African population from ~ 570 000 breeding pairs at the beginning of the 20th century to ~17 000 pairs in 2013 (Crawford et al., 2008, 2011, 2014), a loss of ~97%. Factors thought to contribute to that rapid decline include competition for food with commercial fisheries, predation by seals, sharks and terrestrial predators, oiling, loss of habitat from historic guano harvesting, interspecific competition for nesting sites, disease, and human disturbance (Crawford et al., 1995; Whittington et al., 2000; DEA, 2013). There is an urgent need for modelling tools to provide guidance for management strategies that can assist in recovering the negative trend in penguin populations.

Under the Ecosystem Approach to Fisheries (see Garcia et al., 2003), to which South Africa is committed (Cochrane et al., 2004), it has become increasingly important to explore means of assessing ecosystem effects of fishing and of providing management advice in the light of multiple factors affecting marine ecosystems. The modelling of a vulnerable marine predator in mathematical frameworks linked to traditional fish stock assessment models is restricted by the necessity for the factors and relationships involved to be well parameterized. Difficulties associated with parameter estimation due to scarcity of data suggest that explicit consideration of multiple pressures driving penguin population dynamics necessitates a move to a different paradigm. In a system dynamics framework expert opinion can be incorporated to qualitatively define relationships that would not be included under traditional stock assessment modelling. Such a model can attempt to include all known influences on a penguin population, even if they would normally be omitted from modelling due to data scarcity. A mediated, participatory modelling approach (van den Belt, 2004; Starfield and Jarre, 2011) allows the effective participation of key stakeholders, including those outside academia.

Inputs were sought throughout the entire process from conceptualization of the model and throughout model development and interpretation of model results. Selection of pressures and structure of pressure processes were developed with a group of researchers from the University of Cape Town and the South African National Biodiversity Institute, researchers and managers from government organisations (the Department of Environmental Affairs, Branch Oceans and Coasts, and Cape Nature), and members of conservation organisations (BirdLife South Africa), who met regularly to guide model parameterization and development.

1.3   Requirements and outputs

Both the required flexibility and accessibility can be provided by a system dynamics approach, which is a computer-aided modelling approach that can be used to understand dynamic systems characterized by interdependence, mutual interaction, information feedback, and circular causality (System Dynamics Society, 2013). This is particularly useful when, as in this case, there are significant feedback loops and the system may involve non-linearity and relationships best defined by a graph. In addition, model components and interactions can be graphically depicted on-screen, which aids stakeholders in understanding the model structure and the relationships between variables.

The Penguin Pressure Model is a system dynamics model intended for the examination of the effects of various external pressures, food availability and food competition by commercial fishing on a penguin population while accounting for stage-structured demography and stochasticity. It is intended less as a predictive tool than as a method of exploring the effect of a variety of different inputs on long-term trends. The model's main objective is to aid in the prioritization of management efforts by carrying out comparative analyses of different pressure impacts and by exploring scenarios that simulate the effect of management strategies. Required outputs are thus mostly relative and comparative (e.g., identification of limiting factors or trade-offs between pressure-alleviation actions) and need to indicate ranges and trends in likely outcomes, given the known sources of uncertainty and stochasticity in the system. Results are intended for the use of governmental agencies, conservation organizations, and other stakeholders involved in planning, facilitating and implementing conservation strategies for African penguins.

Separate models are being constructed for individual penguin colonies, based on availability of data and urgency of localized management interventions. While a multi-colony, meta-population model is planned for future development, at the current stage, models are intended to provide inference only for their specific target colony. At this point, models for the colonies at **Robben Island** (Table Bay, near Cape Town) and **Dyer Island** (near Gansbaai) have been finalized. These two models are discussed in this document.

2   Model description

2.1   Section summary

This TRACE element provides supporting information on: The model. Provide a detailed written model description. For individual/agent-based and other simulation models, the ODD protocol is recommended as standard format. For complex submodels it should include concise explanations of the underlying rationale. Model users should learn what the model is, how it works, and what guided its design.

This element contains the following subsections:

- 2.2 - Model structure [6]
  The model is implemented in a system dynamics environment (Vensim) and is based on a structure of stocks (age classes) and flows (transition to the next age class); no individuals are tracked. Eight age classes are distinguished. All major model processes have stochastic components driven either by random sampling from records or variation around a configurable mean.
  The full model, executable using the free Vensim Model Reader (http://vensim.com/vensim-model-reader/), is available as an online supplementary file to Weller et al. (2016).
- 2.3 - Demographic model equations [7]
  The equations used to drive the demographic processes of the modelled population are described.
  - 2.3.1 - Initial setup [7]
    The population at the start of the simulation is set to a stable equilibrium state that will result in population stasis in the absence of all other influences (including food availability). This base state is then modified by pressure processes.
  - 2.3.2 - Population dynamics [7]
    Details of processes governing age class survival, breeding, and density effects.
- 2.4 – Pressures [12]
  Pressures affect the penguin population by modifying survival rates or directly removing penguins from age classes. Individual pressure processes are described in detail.
  - 2.4.1 - Food availability [13]
    Changes in small pelagic fish biomass are modelled separately for two food zones (close to the colony and used during breeding; further afield and used during the rest of the year), based on resampled biomass and fisheries catch records.
    - 2.4.1.1 – Zone One [14]
    - 2.4.1.2 – Zone Two [14]
    - 2.4.1.3 – Equilibrium food level [16]
  - 2.4.2 – Oiling [16]
    Catastrophic (oil spills) and chronic (frequent small-scale pollution) oiling.
  - 2.4.3 – Predation [17]
    Predation by terrestrial predators, sharks, fur seals, and kelp gulls. The impact of seal and gull predation can be modified through culling.
    - 2.4.3.1 – Shark and terrestrial predation [17]
    - 2.4.3.2 – Seal predation [17]
    - 2.4.3.3 – Gull predation [18]
  - 2.4.4 - Human disturbance [19]
    Human disturbance is implemented as an increase in gull predation when parents are driven from the nest.
  - 2.4.5 – Flooding [19]
    Rain and wave flooding.
  - 2.4.6 - Heat waves [19]
    Short periods of extreme heat.
- 2.5 - Summary of changes between model versions [19]

Where the model has changed from the previous version published in Weller et al. (2014), details are provided throughout this document in red font. This subsection provides a short summary of the changes to model processes noted in this section.

2.2   Model structure

The model was implemented in Vensim Professional V6.0.0.1 (Ventana Systems), an environment for system dynamics modelling. The full model, executable using the free Vensim Model Reader (http://vensim.com/vensim-model-reader/), is available as an online supplement to Weller et al. (2016). Figure 2 gives a diagrammatic overview of the structure of the demographic model.
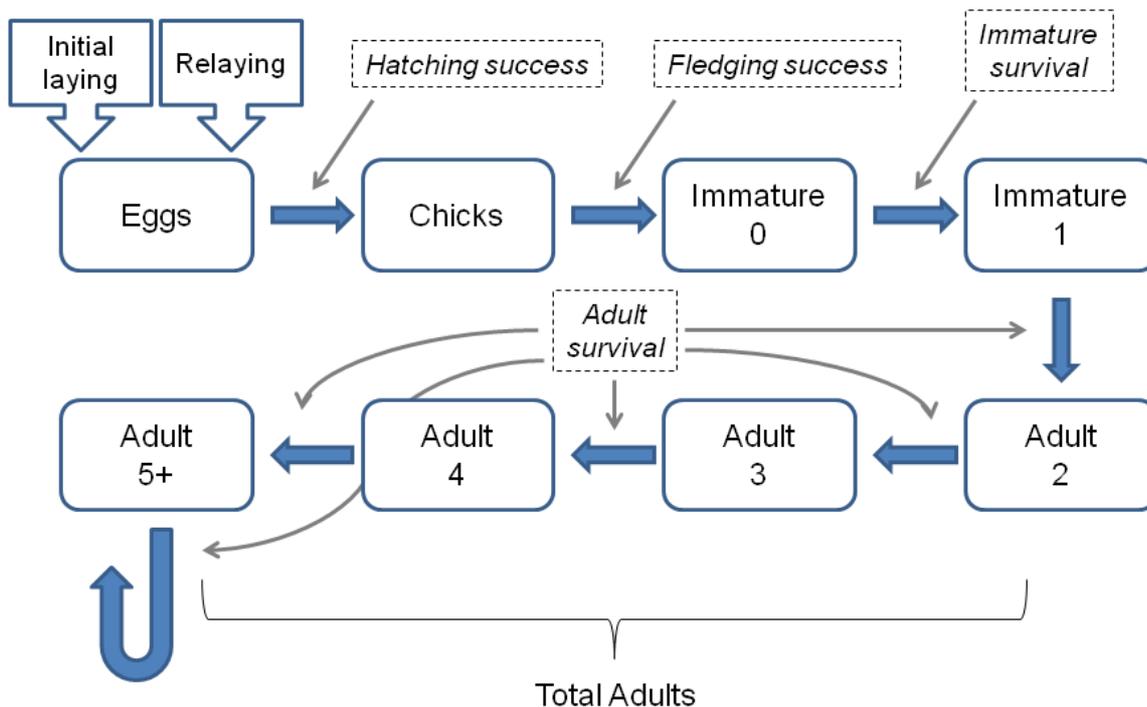

Figure 2.   Penguin population structure as implemented in the model.

Eight age classes are distinguished: Eggs, Chicks, two Immature age classes (immature penguins born in year y and immature penguins born in year $y-1$) and four Adult age classes (adults aged 2, 3, 4 and 5 or older). The model uses a monthly time step. The main dynamics of the model are monthly mortality and annual survival.

The adult penguins form breeding pairs that lay eggs. Eggs hatch after one month and the chicks fledge after another three months. The immature penguins leave the island to forage, returning during their second year of life to moult into adult plumage. Adult penguins and those in the second immature class share a single mortality rate throughout the year (subject to modification by pressure influences). Mortality for the first immature class can vary among months as this stage can be of variable length (eggs can be laid February–August on Robben and Dyer Islands, while molting is mostly restricted to November and December (Crawford et al., 2006a)). Populations at end of month in each age class are determined by number of individuals at beginning of month and class-specific survival rate. At the end of each year, surviving penguins in these age classes move to a higher age until they have reached age class Adult 5+ where they remain.

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Eggs are laid in initial and relaid clutches. They experience monthly mortality and progress to the Chicks age class after one month with a class-specific survival rate. Chicks are modelled similarly to eggs but progress to the first immature age class after three months with a chick-specific survival rate.

All major process groups in the model have stochastic components, either in the form of random sampling from a database or parameter-controlled variation around a configurable mean.

2.3 Demographic Model Equations

This subsection provides the equations used to describe the demographic processes of the modelled penguin population.

A model year runs from January (index 0 at initiation, 12 in following years) to December (11). Some quantities in the model update annually in January or December, which is indicated by 'Jan' or 'Dec' instead of 'month t' in the equations.

2.3.1 Initial set up

Survival rates for each age class, breeding proportions and breeding success are shown in Table 3 and are based on initial estimates by Crawford et al. (1999). These estimates were adjusted to take into account the structure of the current model (3.3.1, 6.3).

At model initialization, each individual in the starting population is assigned to an immature or adult age class based on its age next 'birthday' as at 1 January. The number of adult penguins from age 2 upwards is set at an initial chosen amount. This is assumed to be the total number of adult penguins at the beginning of the first year of simulation (January or time 0). The model then calculates how many penguins are in each adult age group by assuming the population is initially in equilibrium (see Equ. 1–5). The survival probability used in this calculation is the mean adult survival rate given by Crawford et al. (1999). The equilibrium population is used as a stable base state to which other influences are then applied. In this hypothetical state, the population exactly maintains its size if all pressures are absent, including food availability (prey abundance). See 2.4.1.3, 3.3.8.2.5 and 7.2.3.1 for details on the interaction between equilibrium population and long-term mean food conditions.

The number of immature penguins aged 1 at the beginning of the year is calculated by dividing the number of penguins aged 2 by the annual survival probability. The number of eggs, chicks and immature penguins aged 0 that year are each set to zero, as the first eggs are laid in February.

2.3.2 Population Dynamics

This section gives an overview of the equations used in the individual parts of the model. Table 3 provides the values and sources of parameters. Table 1 defines symbols used in equations.

Symbol	Definition
$A_{i,t}$	Number of adult penguins aged i in month t
$A_{i,t}^d$	Number of adults aged i that die in month t
A_i^s	Number of adults aged i that survive to the end of the year
$I_{i,t}$	Number of immature penguins aged i in month t
$I_{i,t}^d$	Number of immatures aged i that die in month t
I_i^s	Number of immatures aged i that survive to the end of the year
C_t	Number of chicks in month t
C_t^d	Number of chicks that die in month t
C_t^s	Number of chicks that successfully fledge in month t

E_t	Number of eggs in month t
E_t^d	Number of eggs that die in month t
E_t^s	Number of eggs that successfully hatch in month t
s_t^a	Annual survival rate in month t of adults and immatures aged 1
s_t^i	Proportion of penguins born that year that survive to the end of the year
s_t^c	Fledging success of chicks in month t
s_t^e	Hatching success of eggs in month t

Table 1. Symbols used in model equations

2.3.2.1 Adult penguins

Adult penguins experience mortality in month t according to the equation:

$$A_{i,t}^d = A_{i,t}\left(1 - (s_t^a)^{\frac{1}{12}}\right) for\ i = 2, \dots, 5 \qquad (1)$$

At the end of each year, surviving adult penguins advance to the next age class according to the equations:

$$A_i^s = A_{i,Dec} - A_{i,Dec}^d\ for\ i = 2, \dots, 5 \qquad (2)$$

$$A_{i,Jan} = A_{i-1,Dec}^s - A_{i,Dec}^s\ for\ i = 3,4 \qquad (3)$$

$$A_{2,Jan} = I_{1,Dec}^s - A_{2,Dec}^s \qquad (4)$$

$$A_{5,Jan} = A_{5,Dec}^s - A_{4,Dec}^s \qquad (5)$$

2.3.2.2 Immature penguins

Immature penguins aged 1 experience mortality in month t according to the equation:

$$I_{1,t}^d = I_{1,t}\left(1 - (s_t^a)^{\frac{1}{12}}\right) \qquad (6)$$

At the end of each year, surviving immature penguins move up to the first adult age class according to the equation:

$$I_1^s = I_{1,Dec} - I_{1,Dec}^d \qquad (7)$$

$$I_{1,Jan} = I_{0,Dec} - I_{1,Dec}^s \qquad (8)$$

The total proportion of immature penguins aged 0 (I_0) that survive from fledging to the end of the year is determined by the same immature survival rate. However, this age class is modelled as seven subclasses to represent the different periods (from one month to seven months) that the penguins will spend in this age class. They experience a monthly fractional mortality depending on the time between fledging and the end of the year. This method ensures that the effects of various pressures act appropriately on this age class. The equation to determine monthly mortality in subclass j is:

$$I_{0,j,t}^d = I_{0,j,t}\left(1 - (s_t^i)^{\frac{1}{j}}\right) for\ j = 1, \dots, 7 \qquad (9)$$

2.3.2.3 Eggs

The hatching period for eggs is assumed to be one month as it is usually an average of 40 days (Williams and Cooper, 1984). Eggs experience monthly mortality according to the equation:

$$E_t^d = E_t(1 - s_t^e) \qquad (10)$$

The eggs that do not die hatch after a month and become chicks as per equation 13. Eggs are increased by first clutches and by clutches that are relaid following clutch loss, brood loss or successful fledging of a brood by a breeding pair (see 2.3.2.5).

2.3.2.4 Chicks

Chicks fledge after three months. This value was chosen as hatching-fledging intervals vary between 60 and 130 days, with an average of 90 days at St. Croix Island (Randall, 1995) and annual means of 68–78 days from 2001 to 2009 at Robben Island (Sherley et al., 2013a). Each month chicks experience mortality in month t according to the equation:

$$C_t^d = C_t \left(1 - (s_t^c)^{\frac{1}{3}}\right) \qquad (11)$$

After three months, remaining chicks are assumed to have fledged successfully and move into age class I_0 according to the following equations:

$$C_t^s = E_{t-3}^s s^c \qquad (12)$$

$$C_t = C_{t-1} + E_t^s - C_t^d - C_t^s \qquad (13)$$

s^c is the product of the monthly survival rates over the fledging period.

2.3.2.5 Breeding parameters

The following details how the model calculates the number of eggs laid each month. The number of eggs laid in month t is the sum of the number of first clutches laid in month t and clutches laid following clutch or brood loss, or the successful fledging of a brood.

2.3.2.5.1 Calculation of breeding pairs

The number of potential breeding pairs (PBP) is calculated as:

$$PBP_t = \frac{\sum_i A_{i,t} b_i}{2} \qquad (14)$$

b_i is the proportion of penguins aged i that are able to breed that year. The proportion of penguins able to breed in each age group is calculated from age at first breeding estimates. Each b_i is sampled from a truncated normal distribution with means and standard deviations taken from Crawford et al. (1999). It is assumed that all penguins able to breed can find a mate; once mated, pair fidelity is high (ca. 90%; Crawford et al., 1994) and first time breeders can emigrate to other colonies to find a mate (Whittington et al., 2005).

The actual number of breeding pairs (ABP) is:

$$ABP_t = PBP_t * B \qquad (15)$$

B is the proportion of potential pairs that do breed that year and varies with food availability in the previous two years (shift in mean; see 2.4.1.2).

2.3.2.5.2 Initial egg laying

The laying rate (L) is the percentage of breeding pairs that lay their first clutch in month t. The majority of pairs (23% each month) lay their first clutch between February and April each year. 27% lay between May and July (9% each month) with 4% laying their first clutch in August (Shannon and Crawford, 1999; Crawford et al., 1999). Clutch size (C) is determined as the weighted average of nests with 1 or 2 eggs per pair. The number of eggs laid per month (initial clutches) is:

$$Number\ of\ eggs\ laid\ in\ month\ t = \ ABP_t * L_t * C_t \qquad (16)$$

2.3.2.5.3 Relaying

Clutch loss, brood loss and successfully fledging at least one chick can result in a proportion of breeding pairs laying a second clutch two months after one of those events. Second clutches can only be laid until August (last month for initial clutches) to prevent clutches being laid at unrealistic times of the year.

The decision to relay is likely to be strongly influenced by the current food situation, as adults will not attempt to raise a clutch if there is insufficient food to sustain their offspring and offset their own energy investment. Additionally, relaying is more likely early in the breeding season (Jan–Feb) when no great investments have yet been made in a previous clutch. Relaying probability is thus

$$Relaying\ probability\ in\ month\ t = m_{Rc/b/s} + V_t^F + V_t^R + V_t^S \qquad (17)$$

where $m_{Rc/b/s}$ is the empirical mean for the three cases (R_c, R_b, R_s; see 3.3.2), V_{Ft} is food-driven variation, V_{Rt} is random variation, and V_{St} is seasonal variation.

As the main determinant of relaying decision, V_{Ft} is assumed to constitute 90% of empirically observed variation and is driven by the Zone 1 food index (range -1 to +1; see 2.4.1.1). Thus, V_{Ft} = trunc ($3 \times$ r $R_{c/b/s}$) $\times$ Zone 1 food index $\times$ 0.9, where trunc ($3 \times$ r $R_{c/b/s}$) is the range of variation as determined by the standard deviation (r R_c, r R_b, r R_s; see 3.3.2), if necessary truncated at 0 and 1 and scaled to the interval.

V_{Rt} represents non-food-driven influences, e.g., demographic composition and climate, and drives the remaining 10% of empirical variation by varying normally with mean $m_{Rc/b/s}$ and standard deviation r $R_{c/b/s} \times 0.1$. The ranges of V_{Ft} and V_{Rt} sum to $3 \times$ r $R_{c/b/s}$ and have a mean of 0. V_{St} is the mean multiplied by a monthly adjustment (Jan: 0.25, Feb: 0.15, Mar/Apr: 0, Jun: -0.15, Jul: -0.25; based on Crawford et al., 1999). The net effect of V_{St} across the year is neutral, but it serves to weight relaying probability towards the early months of the breeding season. V_{St} is not applied to relaying after successful fledging, as this will always be relatively late in the season.

Earlier version [Weller et al. (2014)]: Probability of relaying was determined entirely by normal variation around *m* for each of the three relaying cases. The update introduces the expected link to an already modelled environmental driver (food availability).

2.3.2.5.4   Nest calculations

Nest calculations take into account the chance of nests containing one or two eggs and the resulting survival probabilities for individual chicks and entire broods.

Let C be the clutch size (as set in the model) and let n_1 and n_2 be the number of one egg and two egg nests respectively.

By definition:

$$C = \frac{E_t}{n_1 + n_2} \qquad (18)$$

But

$$E_t = n_1 + 2n_2 \qquad (19)$$

Therefore

$$C = \frac{E_t}{E_t - n_2} \qquad (20)$$

It follows that the number of nests containing two eggs is calculated as

$$n_2 = \frac{E_t(C-1)}{C} \qquad (21)$$

The number of nests containing one egg is then:

$$n_1 = \frac{E_t}{C} - n_2 \qquad (22)$$

The number of 1 chick nests and 2 chick nests is calculated from the number of 1 egg and 2 egg nests. As a 2 chick nest can only occur if both eggs of a 2 egg nest hatch:

$$number\ of\ 2\ chick\ nests = n_2(s_t^e)^2 \qquad (23)$$

1 chick nests occur when an egg from a 1 egg nest hatches or when only one egg from a 2 egg nest hatches. This is calculated as:

$$number\ of\ 1\ chick\ nests = n_1 s_t^e + 2n_2 (s_t^e)^2 (1 - s_t^e) \qquad (24)$$

The factor of 2 is due to the fact that either of the two eggs in the nest can survive. The number of whole clutches lost each month is:

$$clutch\ loss\ at\ time\ t = n_1(1 - s_t^e) + n_2(1 - s_t^e)^2 \qquad (25)$$

The number of broods lost and the number of broods successfully fledged for 1 chick nests is easily found as the chick either survives for three months or dies before the end of the period.

Brood loss and success for 2 chick nests are slightly more complicated as the survival of the two chicks is not necessarily independent. The scenarios that can occur over the course of three months are shown in Table 2.

Chicks alive at end of a period				Result
Start of month 1	End of month 1	End of month 2	End of month 3	
2	2	2	2	Success
2	2	2	1	Success
2	2	2	0	Loss in month 3
2	2	1	1	Success
2	2	1	0	Loss in month 3
2	2	0	0	Loss in month 2
2	1	1	1	Success
2	1	1	0	Loss in month 3
2	1	0	0	Loss in month 2
2	0	0	0	Loss in month 1

Table 2. Brood success scenarios for 2 chick nests.

Assuming independence, number of broods lost and number of broods successfully fledged is derived by multiplying the number of 2 chick nests by the appropriate survival probabilities for each scenario. When this approach was applied to actual data from Robben Island, it resulted in an underestimation of brood loss and an overestimation of brood success. This suggests that the fates of the two chicks are not independent. Adjustment factors for brood loss and for brood success were therefore computed as the mean values required to closely reproduce the observed data:

$$brood\ success = bs_1 + bs_2 * 0.77 \qquad (26)$$

$$brood\ loss = bl_1 + bl_2 * 1.38 \qquad (27)$$

where bs_1 and bs_2 are respectively the number of one chick and two chick broods fledged successfully and bl_1 and bl_2 are the number of one and two chick broods that are lost. Thus, these factors serve to down-weight the effective number of successful broods and up-weight the effective number of lost broods originating from two-chick nests, before the probability of relaying is calculated. The same adjustment was used for Dyer Island.

2.3.2.6 Density effects

Three levels of penguin population size with an effect on the breeding proportion of potential pairs were specified. The highest of these thresholds is the carrying capacity. If this value is reached, the number of penguins able to breed is severely restricted in the model (the mean breeding proportion is reduced by 60%). Note that while an asymptotic falling-off of breeding proportion on approaching the threshold would be more realistic, no data are available to model this, and the practical consequences of the current implementation are minimal, as realistic forecast scenarios will rarely if ever involve population sizes near carrying capacity.

A lower threshold is set at a small population size where low competition for resources is assumed to cause a small increase from base mean breeding proportion (+20%). The lowest model threshold simulates an Allee effect (negative density dependence) at very small population sizes that results in a decrease from base mean breeding proportion of 10%.

2.4 Pressures

The model incorporates pressures that act on the penguin population, including predation, food availability, climate, disease and disasters such as oiling. Pressures can effect all age classes (with direct effects on immatures and adults, and secondary effects on the survival of eggs and chicks of affected parents), or eggs and chicks in the nest only. Figure 3 presents an overview of pressures.
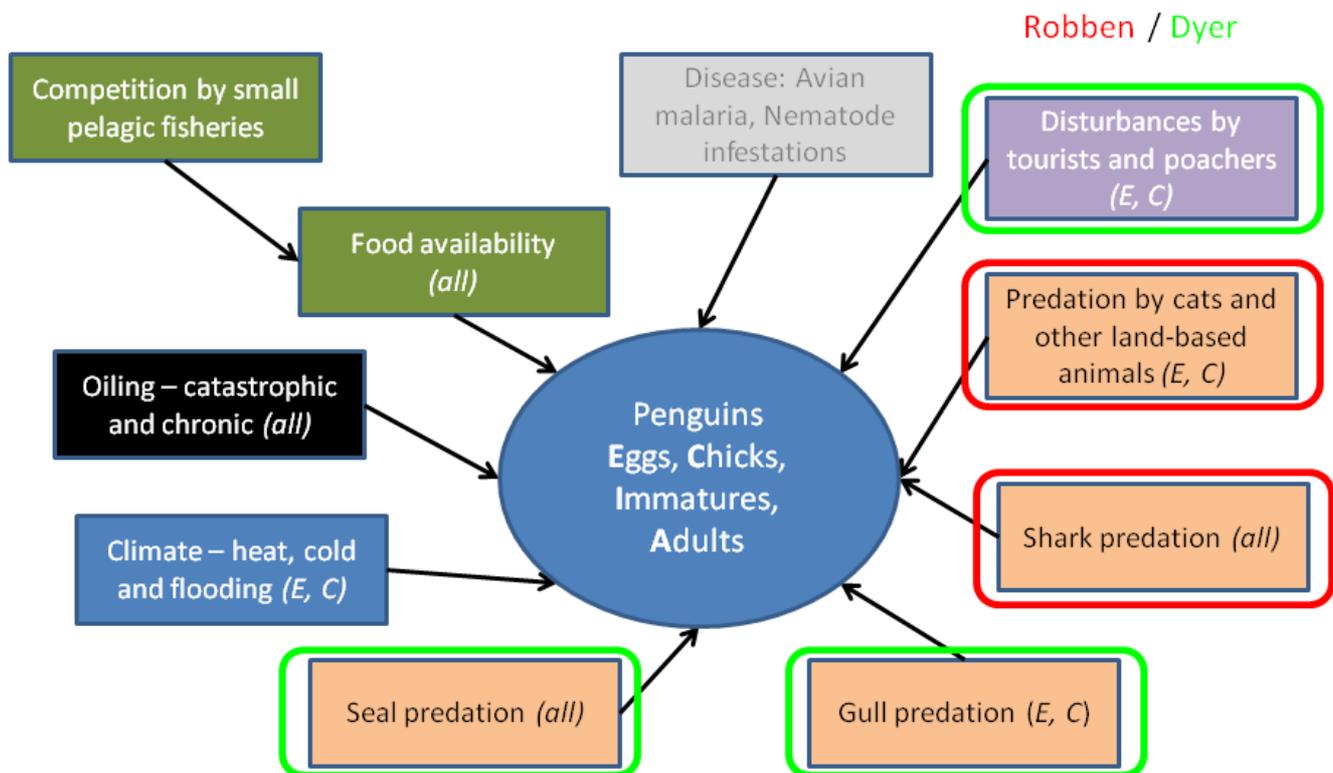

Figure 3. Pressures affecting the modelled penguin population. Pressures in red outlines are active only in the Robben Island model, those in green outlines only in the Dyer Island model. Disease effects are currently not implemented.

Food availability (available biomass of small pelagic prey fish) and its reduction by small pelagic fisheries are applicable to all modelled colonies, as are the effects of catastrophic (oil spills) and chronic (recurrent small-scale) oiling and several climate/weather pressures. Presence of predation pressures varies by colony, with land-based and shark predation only reported from Robben Island, and seal and gull predation only a factor on Dyer Island. Disease pressures do not appear to play a noticeable role in these colonies (pers. comm. Nola Parsons), and are currently unimplemented. Other more subtle pressures, such as competition with other predators for food, were regarded as outside the model's scope for the time being.

The effect of each individual pressure is implemented either as the removal of a portion of an age class, in the case of disasters/once-off disturbances, or is factored into the monthly survival rate through a logit function.

This ensures that the resulting survival probability (implemented as an inverse logit function) will remain between 0 and 1.

2.4.1 Food availability

For modelling food availability, the model distinguishes two zones surrounding the colonies. Nesting penguins are restricted to foraging in Zone 1, which extends 15 nautical miles (28 km) from the colonies for Robben and Dyer islands (e.g. Petersen et al., 2006), while Zone 2 is a larger general region that provides small pelagic prey to penguins when they are not rearing chicks.

The data used for food availability modelling are based on biomass surveys of sardines and anchovies carried out by the Department of Agriculture, Forestry and Fisheries, Branch Fisheries (DAFF) in May and November from 1983–2013. Based on results in Waller (2011) and additional analyses, research surveys for specific areas were used. Figure 1 shows approximate strata boundaries – note that May and November strata occupy the same areas (DAFF, unpublished data courtesy Dr Carl van der Lingen). May surveys record fish recruits, while November surveys record spawners. Zone 1 biomass was based on records for May Stratum D (Cape Columbine to Cape Point) for Robben Island, and on May Stratum C (Cape Point to Cape Agulhas) for Dyer Island; these strata contain the respective colony islands. Zone 2 was based on different combinations of November Strata A, B and C for both colonies (see below for details).

See 3.3.8.2 for a discussion of choice of survey region and specific drivers.
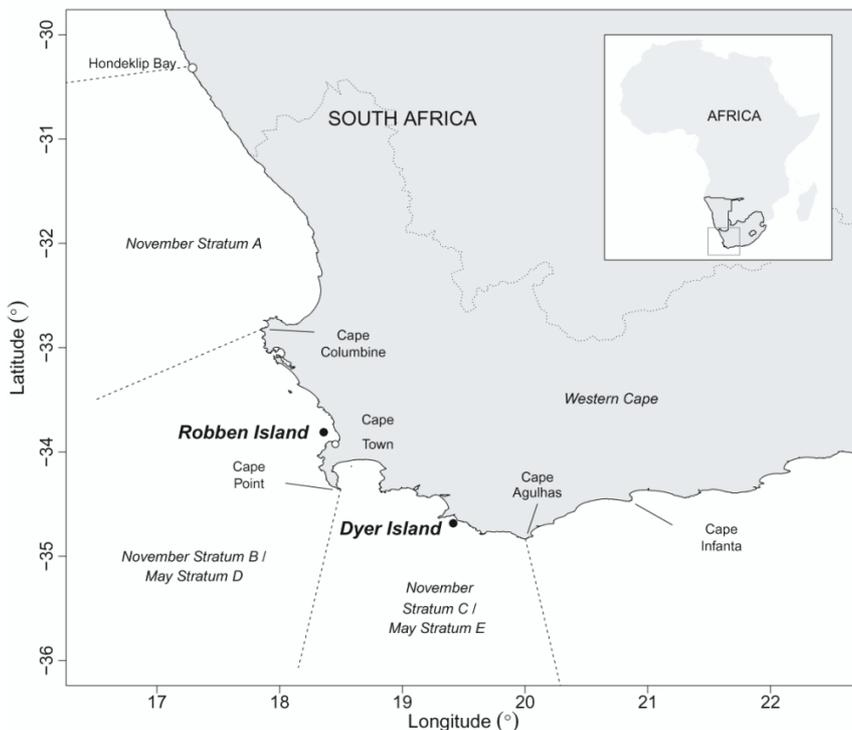

Figure 4.   Location of Robben Island and Dyer Island African penguin colonies on the coast of South Africa. The approximate stratum boundaries used in the DAFF biomass surveys (sardines and anchovy) are shown by dotted lines

As the biomass data show no significant autocorrelation, they are sampled with replacement (together with the appropriate catch data) to produce a time series for use in the model. Samples are drawn from a continuous distribution interpolated from annual records for the years 1983–2013. Resampling is driven by a probability density function (PDF) based on the recorded biomass estimates for the two main prey species (anchovy and sardines) in the respective food zones.

Earlier version [Weller et al. (2014)]: Individual annual records were randomly sampled with replacement. The update provides automatic weighting of sampling by probability density and prevents the recurrence of a limited number of identical input states.

Data about the biomass amounts removed by the sardine and anchovy fisheries are based on recorded catches in the (partially fractional) fishing blocks around the colonies that cover the Zone 1 areas (DAFF unpublished data, as used by Sherley et al., 2013a). If a fishing catch record is required together with a biomass resample, the date of the original biomass record closest to the resample is found, then the series of monthly catch records associated with that year is returned, thus preserving catch-biomass associations that would realistically occur for a given biomass level.

2.4.1.1 Zone One

The recruit biomass of anchovy and sardine in Stratum D (Robben) / E (Dyer) is used to indicate prey availability in Zone 1. The abundance of food in this zone will have an impact on chicks and eggs as low food abundance can lead to adult penguins abandoning nests to find food and high food abundance increases breeding success (Crawford et al., 2006b; Sherley et al., 2013a). Combined tonnage of sardine and anchovy recruits is used as driver.

One sample is drawn each year from the biomass distribution for the respective stratum, which is then used as that year's mean monthly available biomass. A variable portion of this is assumed to be close enough to the island to be available for the penguins each month. Monthly variation around the annual base value is determined by a normal distribution with a mean equal to the sampled value of the May recruit biomass. A logit-like restriction is added: the distribution is truncated symmetrically to x, where x is the smaller of {mean biomass – minimum biomass, maximum biomass – mean biomass}, and standard deviation is set to $x / 3$. Thus possible variation is largest when the annual base is close to the median of recorded values, and converges to 0 as the base approaches recorded minimum/maximum biomass values. This prevents unrealistic drops or spikes in biomass close to the extremes, and gives more weight to the annual base rather than monthly variability in driving overall food availability.

Earlier version [Weller et al. (2014)]: The logit-like restriction was not present.

In the model, the biomass available around the island is decreased by fishing before becoming available to the penguins. The monthly fishing catch corresponding to the biomass record most closely matching the generated biomass sample is selected from the records and subtracted from the sample. Available catch data only cover a small subsection of the survey strata (~ 850 km^2 of ~ 4 800 km^2 in the case of Robben Island). In the absence of more detailed information about the availability of fish in the area, the model assumes biomass to be uniformly available across each stratum.

The resulting prey tonnage for sardine and anchovy is summed and then converted to a food index with range {-1; 1} relative to the minimum and maximum range of total recruit biomasses on record. The index value is derived by taking the integral of the biomass record PDF for the range {sample tonnage; median recorded tonnage} and dividing by the integral for the range {x; median recorded tonnage}, where x is minimum recorded tonnage for samples below median, and maximum recorded tonnage for samples above median.

Earlier version [Weller et al. (2014)]: Robben Island Zone 1 survival response was based on fixed index values of -1/-0.67/-0.33/0/0.33/0.67/1. These were derived from a custom function with vertices at biomass values of median biomass × 0 / ⅓ / ⅔ / 1 / 1 + σ / 1 + 2σ / 1 + 3σ, where σ is the standard deviation of median biomass.

The index is then multiplied by a food effect parameter (currently 0.5 for either colony) and factored into chick and egg survival rates (which are then modified by further pressures). Thus, at minimum food (index = -1) survival is decreased by 50%, at maximum food (index = 1) increased by 50%.

2.4.1.2 Zone Two

Food availability has an important impact on breeding by affecting the decision to breed in any one year, as well as breeders' condition and breeding success (Crawford et al., 1999; Sherley et al., 2013a). Breeding condition is largely determined by the ability of an adult penguin to provision sufficiently, such that it survives the moult fast and afterwards is adequately able to replace condition in order to breed. Adult penguins make use of the available anchovy and sardine spawners during these periods. In the model, food availability in Zone 2 affects

the survival rates of adult and immature penguins, as well as the proportion of breeders among sexually mature penguins.

Current analyses indicate that for both the Robben and Dyer Island colonies, relationships exist

- between adult survival and the current year's log-transformed sardine tonnage in November Stratum C
- between immature survival and the current year's log-transformed sardine tonnage west of Cape Agulhas (November Strata A, B and C)
- between breeding proportion and the energy content (kJ) of summed anchovy and sardine tonnage in November Stratum C, lagged for two years

The survival response to resampled food availability for adults and immatures is based on the predicted values from log-linear models fitted to these drivers (Fig. 5). Monthly survival rates thus derived are used as base values that are further modified by other pressures.

Note that the curves in Fig. 5 are further shifted before evaluation to accommodate assumptions about the model base (equilibrium) state – see 3.3.8.2.1 for details.
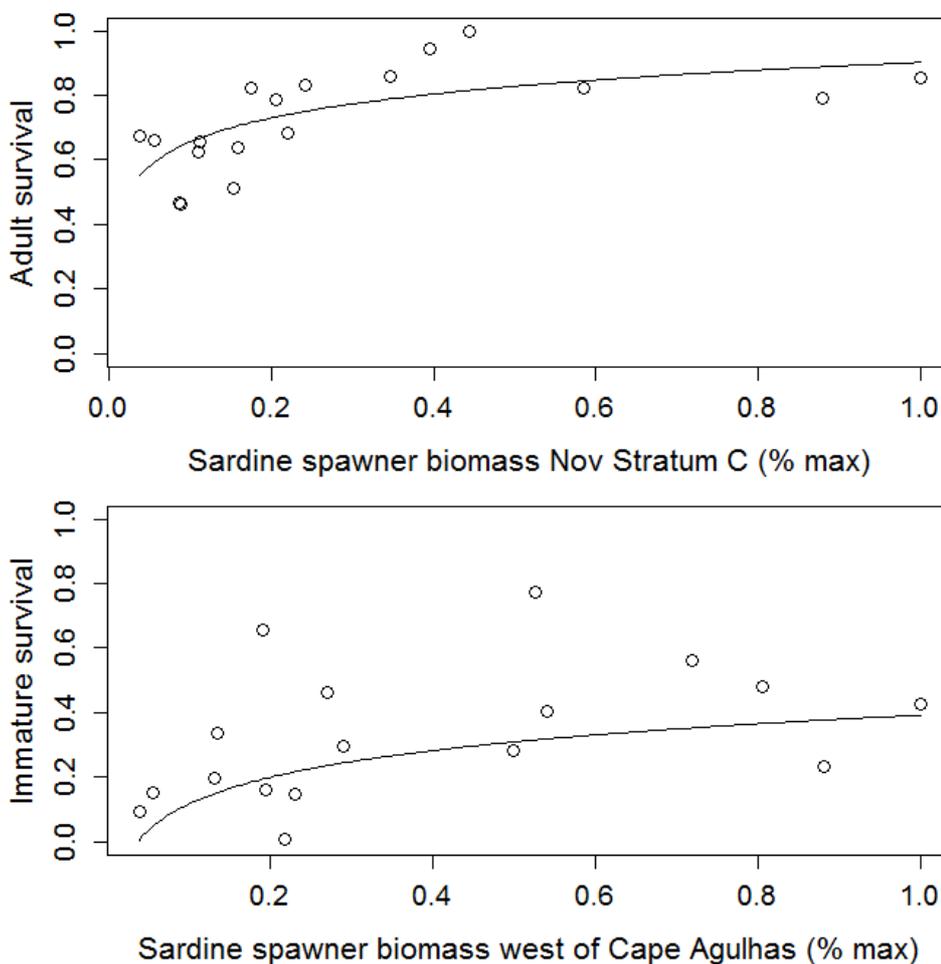

Figure 5.   Predicted values from log-linear models used as basis for functional response of survival to food biomass. (above) Adult survival as a function of sardine spawner biomass in November stratum C ($R^2 = 0.47$). (below) Immature survival as a function of sardine spawner biomass west of Cape Agulhas ($R^2 = 0.29$). Y axis shows biomass as % of maximum recorded biomass for the period 1983–2013.

The monthly proportion of breeders among sexually mature penguins varies normally around an empirical mean and with empirical truncation (see 2.3.2.5.1, and Table 3), and is linked to food availability through a shift in the mean. The shift is driven by the combined energy content (kJ) of sardine and anchovy spawners in November Stratum C, lagged by two years (Waller 2011), which is converted into a food index with range {-1;1}

analoguously to the Zone 1 food index (see above). Under the assumption that food availability explains roughly 50% of variation in breeding proportion (Crawford et al. 1999), shift range is set ~ equal to normal variation range (roughly ±0.15), i.e. the index is mulitplied by 0.15. This value is added to the mean before the monthly breeding proportion is drawn.

Earlier version [Weller et al. (2014)]: Zone 2 biomass driver for adult/immature survival at Robben Island was identical to earlier and current breeding proportion driver (energy content of combined November Stratum C sardine and anchovy). Survival response to the driver was modelled analoguous to earlier Zone 1 survival response function (semi-linear response, fixed index values derived from a custom function) (see 2.4.1.1)

See 3.3.8 for details on choice of survey region and biomass drivers.

Note that for egg and chick processes, the adjusted mean survival rates given in Table 3 are used as base values and a modification driven by a single food effect parameter is applied to them. In contrast, for immature and adult processes, response curves were constructed from survival rate time series, the adjusted mean rates were used to shift the curves relative to the model equilibrium state (see 3.3.8.2.1), and food-influenced survival rates are read from the curves. There is thus no single food effect parameter that governs immature/adult survival response. This difference is due to the lack of sufficient data on egg and chick survival to allow the fitting of response curves, forcing the postulation of an approximately linear relationship.

2.4.1.3   Equilibrium food level
Resampled food availability is evaluated for its effect on penguin survival in relation to the food availability level at which the penguin population is assumed to be in equilibrium (no population size change – model base state in absence of pressures). However, the most common food availability level (long-term mean) would be expected to result in moderate growth (while below the upper carrying capacity threshold) rather than in population stasis. It was found that a value of 75% of the food biomass long-term median has support as threshold below which the investigated penguin populations would experience decline from poor food availability alone. This level was therefore chosen as the equilibrium (zero growth) food level for the model base state. This means that under randomly resampled biomass and in absence of all pressures, the population will experience some growth (see 7.2.3). See 3.3.8.2.5 for details of the associated analysis.

Earlier version [Weller et al. (2014)]: The equilibrium food level was assumed to be equal to the long-term mean, i.e. the population on average maintained its size under random food resampling absent all pressures. The update brings model behaviour better in line with observed seabird population dynamics (see 3.3.8.2.5).

2.4.2 Oiling
Following Shannon and Crawford's (1999) model, oiling is split into catastrophic oiling and chronic oiling. Catastrophic oiling occurs on average every 15 (Robben)/ 22 (Dyer) years, implemented as a Poisson process whose mean value is the monthly rate at which oil spills occur. Catastrophic oiling directly affects 24% (Robben)/ 33% (Dyer) of the adult and immature penguins (Whittington et al., 2000; Ludynia et al., 2014) and indirectly affects a smaller proportion of chicks and eggs through the loss of parents. This proportion is taken as 0.24/0.33 times the percentage of penguins currently parents of chicks and eggs, respectively. Based on SANCOBB records of responses to past oil spills, it is assumed that the spill is cleaned up within the month. Chronic oiling at Robben and Dyer Islands is mostly caused by vessels flushing their bilge tanks close to shore and by leakage from unrecovered wrecks. Events occur on average every three months and are assumed to affect ~ 0.01% of adults and immatures and a still smaller portion of chicks and eggs (as per catastrophic oiling).

Adult penguins that are oiled are assumed to be admitted for cleaning and rehabilitation. Of these, 90% (Robben)/ 84% (Dyer) are rehabilitated to the model colony one month after the oiling event. They are now marked as having been oiled and, as a result, have a lower chance to breed (Wolfaardt et al., 2008a) although their model survival rates remain the same as penguins that have never been oiled. Chicks born to oiled parents are assumed to have a reduced fledging success. The reduction is set at 50% and assumed to represent both the lower proportion of breeders among oiled adults and the lowered survival of their chicks (Barham et al., 2007; Wolfaardt et al., 2008b; Sherley, 2010).

2.4.3 Predation

There are four different sources of predation pressure in the model: sharks, terrestrial predators, seals, and gulls. The former two are implemented as survival rate modifications varying around a base level of predation, the latter two as more complex processes that directly subtract a percentage of penguins from an age class.

2.4.3.1 Shark and terrestrial predation

Sharks and terrestrial predators are thought to be an active influence on Robben Island but not on Dyer Island. Sharks are a direct danger to adult and immature penguins, and an indirect danger to chicks and eggs through the removal of parent penguins. Land predators target chicks and eggs directly. These include predators such as mole snakes (*Pseudaspis cana*), feral cats (*Felis catus*) and pied crows (*Corvus albus*), all of which are known to take chicks and eggs on Robben Island (Crawford et al., 1995; Underhill et al., 2009).

These types of predation are largely unobservable in action on Robben Island, and data are sparse. The model therefore works on the assumption that a base level of predation takes place under normal circumstances, and that estimates of mean survival rates already include its impact. The abundance of predators is represented on a scale of -1 to 1, with a value of 0 representing an average abundance of predators that year. Average abundance has no influence on penguin survival rates, a negative value represents increased predation and thus lowered survival, and a positive value represents relief from predation and a boost to survival. Abundance is multiplied by an age class-specific effect strength (see Table 3) before being factored into survival rates, remaining constant throughout the year.

For terrestrial predation, abundance varies annually around a mean of 0 according to a truncated normal distribution with a standard deviation of 0.3. For shark predation, shark abundance is assumed to be connected to the availability of small pelagic fish in the general area, while penguin captures are incidental and scale with abundance. However, no specific data exist to describe this relationship to fish biomass. A qualitative connection is therefore used that allows shark abundance to vary between -1 and 1 when food availability in Zone 1 is at median values, but shifts the mean and increasingly restricts possible variation when food values become more extreme. Abundance varies normally around a mean of x, truncated at $x - bound$ and $x + bound$, and a standard deviation of $bound / 3$; where x is an index between -1 and 1 describing Zone 1 food biomass (similar to the penguin Zone 1 index – see 2.4.1.1 – but without added monthly variation), and *bound* is abs(1 - x). This creates a logit-like restriction on variance, forcing shark abundance to follow food availability near the bounds.

2.4.3.2 Seal predation

Cape fur seals (*Arctocephalus pusillus pusillus*) predate on adult penguins at Dyer Island. Seal predation is implemented as an annual reduction in adult numbers by 7.5%. Predation is assumed to take place from April to October only (7 months), and the loss is applied fractionally over these months, with weightings based on relative predation strength across this period.

A secondary effect on eggs and chicks from loss of parental care is applied to a proportion of eggs and chicks equal to "monthly predation loss rate × proportion among breeders that have eggs or chicks". The effect is taken as a loss of 2/3 of chicks (assuming that a remaining single parent may be able to fledge chicks, depending on their age) and of all eggs (as a single parent cannot successfully incubate eggs).

2.4.3.2.1 Seal control

The culling of individual seals observed to engage in seabird predation has at times been implemented at several seabird colonies, including Dyer Island (Ludynia et al., 2014). While some data exist on the effectiveness of seal culling to lessen predation on other seabirds (du Toit et al., 2004; Makhado et al., 2009), very little is known about its application in penguin conservation. However, various assumptions can be made based on field observations at Dyer Island.

Seal predation on Dyer Island seabirds focuses on Cape cormorants (*Phalacrocorax capensis*) during the summer months and, at lower magnitude, on penguins during their winter breeding season (Makhado et al., 2013a). It was found that the shooting of seals seen predating on Cape gannet (*Morus capensis*) at Malgas Island was able to prevent further attacks for a short time, but that attacks continued after a few days, when

other seals resumed the practice (Makhado et al., 2009). Observations indicate that penguin predation is more difficult and attempted more rarely by fewer seals. These seals are suspected to be individuals that have become skilled at attacking seabirds by preying on gannets or cormorants (D. Geldenhuys, L. Waller, unpublished data; M. Meyer, H. Oosthuizen, pers. comm.). Predation on penguins is therefore likely to be more susceptible to control by removal of the individual seals observed to engage in it (*sensu* Votier et al., 2004), with longer holdover periods for the deterrent effect. In addition, the number of individuals capable of, or interested in, penguin predation is likely influenced by the number who successfully practiced the behaviour in the preceding summer.

In seal control scenarios in the model, these relationships are implemented as separate effects of culling effort during the winter/spring penguin breeding season (April–October) and during the preceding summer months. During winter, weather and sea conditions limit monthly culling (carried out from a small boat) to an average of 2 days/month, however that amount of effort may be sufficient to prevent penguin predation for up to 6 weeks (D. Geldenhuys, unpublished data). Thus, a monthly cull at full effort/effectiveness would reduce penguin adult loss by seal predation by 100% of the base amount for that month and by 50% for the following month. Lower effort would reduce predation by a lower percentage for one month only. Culling efforts during the 5 summer months, while penguins are not directly affected, are implemented as a lowering of the base amount of predation experienced by penguins during the winter. Allowing a holdover deterrent period of 2 days for each day of summer culling, 10 active days/month for each of 5 summer months would keep the summer predation-free and thus lower base predation during the winter by 100%; therefore, each day/month of culling throughout the summer is assumed to lower winter base predation by 10%.

Monthly penguin loss rates (% of unmodified base) for April–October may thus be described, in the case of no culling at all, as {100} for all months; in the case of 2 days/month of summer culling and no winter culling, as {80} for all months; and in the case of 2 days/month of summer culling and full winter culling in August only, as {80/80/80/80/0/40/80}.

Very little is known about interannual (as opposed to short-term) changes in fur seal predation on seabirds in response to control measures. As a default, the model uses the same fixed rate of predation as the base rate for each year, i.e., predation neither increases in absence of culling nor decreases in response to culling across years. Investigation of interannual effects currently requires specific modification of the code base.

2.4.3.3   Gull predation

In the Dyer Island model, gull predation takes place from February to October and is implemented as a reduction in egg and chick numbers. Maximum number of predated nests per month is calculated as $nests_{max}$ = total nests × maximum predation rate × percentage of surface nests. Maximum monthly losses are thus $nests_{max}$% of eggs and $nests_{max}$% of chicks 15 days old or younger. In the absence of local data on the distribution of predation rates, actual monthly predation rate is determined by using a PDF based on observation of gull predation on penguin nests at Bird Island, Algoa Bay, in Pichegru (2013). A frequency-weighted egg loss rate is drawn from the frequency distribution of daily losses recorded in that study, converted to a fraction of maximum recorded egg losses, then applied as fraction of maximum nest predation rate on Dyer Island. Bird Island egg loss rates are thus taken to represent shifts in predation pressure as exerted on available nests as a whole, rather than either eggs or chicks specifically, and to exemplify pressure under "normal" circumstances (in absence of intensifying factors).

Egg and chick losses are further modified by several such factors. In the event of a hot spell, losses increase by 10%. If food availability is below the long-term median, -50% of the Zone 1 food index (see 2.4.1.1) is applied to losses as a multiplier, to a maximum of × 1.5 in the case of lowest recorded food biomass. Short-term human disturbance (see 2.4.4) is assumed to increase predation rates by a factor of 10 (Ludynia et al., 2014), by driving all adults away from nests for a time; however, each human disturbance event is assumed to affect only a single day in that month (each individual event is applied at 1/30 strength).

Gull control for penguin conservation management can be simulated in the model by employing the same mechanisms that are used for fur seal control, but as gull predation was found to be of little impact at Dyer Island (Weller et al., 2016), no specifics have been developed at this time.

2.4.4   Human disturbance

Moderate human disturbance represents short-term displacement of penguins from their nests, allowing gulls unhindered access to eggs and chicks for a short period. Heavy human disturbance happens more rarely and refers to events that may displace penguins for a longer term, putting nestlings at risk of death from exposure. Moderate disturbance is implemented as an increase in kelp gull predation pressure (see above) and happens with a mean frequency of 1 month (multiple events per month are possible). Heavy disturbance occurs with a mean frequency of 120 months and affects egg and chick mortalities directly, increasing each by 50%.

2.4.5   Flooding

In the model, flooding by rainwater in storm events occurs in a similar way to oil spills. Floods occur randomly by sampling from a Poisson distribution with a mean of 1/60 (Robben) / 1/36 months (Dyer). Only chicks and eggs are affected. A modelled flood event will kill 10% (Robben) / 25% (Dyer) of chicks and 30% (Robben) / 25% (Dyer) of eggs that month.

In addition to rain flooding, a percentage of low-lying surface nests on Dyer Island may be affected by wave swells of sufficient height, with the loss of all eggs and chicks in flooded nests (Ludynia et al., 2014). In the model, 3% of all nests are assumed to be at risk from wave flooding, at a mean frequency of 36 months.

2.4.6   Heat waves

Penguin chicks and eggs are vulnerable to extremes of heat, which can affect the chicks and eggs throughout the year although the magnitude of the effect is dependent on the time of year. A hot spell has a much higher impact during the summer months, when the temperature is likely to be higher, than during winter, with interpolated values for spring and autumn. Hot spells occur with a frequency of 1/36 months, and during summer reduce the survival rates of eggs by 40% and those of chicks by 12%; in winter, 1/4 of these values is applied.

2.5   Summary of changes between model versions

The model engine used in the original Robben Island model (Weller et al., 2014) was subjected to major upgrades before being employed for the Dyer Island colony. While the previous version is no longer in use, and Robben Island results have been updated using the new model version, details of the previous version are provided in several sections in colored font to document continued model evolution. Changes to model structure between these versions are summarized below and detailed in the respective subsections.

Randomized food biomass resampling (2.4.1) for use in scenarios was changed to sample from a continuous, interpolated distribution, driven by a probability density function (PDF) based on the frequency distribution of recorded biomass estimates. This helps avoid recurrent model states and ensures correct weighting of resamples based on their record frequency.

Fitted survival response curves (2.4.1.2) were constructed for adult and immature penguins based on newly selected drivers, replacing the previous linear approximation that mapped a food index value (-1 to +1) to the recorded range of biomass estimates. The curves directly relate biomass values to observed survival rates and provide a more realistic response mechanism.

The accuracy of the linear response (2.4.1.2) was enhanced in the case of egg and chick survival (to Zone 1 food availability) and breeding proportion (to Zone 2 food availability), were the data did not permit the fitting of specific response curves. Food index values are now derived using the biomass driver's PDF, ensuring exact mapping of biomass resamples to biomass frequency distributions.

The equilibrium food level (2.4.1.3) (food availability level of zero population growth) was re-estimated and changed from its previous value of long-term biomass median to 75% of the median, following the reasoning that a penguin population (free from other pressures) should experience moderate growth rather than stasis

under the most commonly encountered food conditions. This implies that using randomly resampled food, the population will now increase in the absence of other pressures.

Changes of lesser consequence were made to <u>monthly variation in Zone 1 food availability</u> (<u>2.4.1.1</u>) and the determination of <u>relaying probability</u> (<u>2.3.2.5.3</u>).

<u>Choice of biomass drivers</u> (<u>2.4.1.2</u>) for the survival of adult and immature age classes was changed based on the analysis of newly published data (Sherley et al. 2014a).

See section <u>3</u> (Data evaluation) for details on these changes.

3   Data evaluation

3.1   Section summary

This TRACE element provides supporting information on: The quality and sources of numerical and qualitative data used to parameterize the model, both directly and inversely via calibration, and of the observed patterns that were used to design the overall model structure. This critical evaluation will allow model users to assess the scope and the uncertainty of the data and knowledge on which the model is based.

This element contains the following subsections:

- 3.2 – Use of expert opinion parameters [22]
  The models were parameterized using published data where available and expert opinion where these were lacking. Further information about the source of expert opinion parameterization is given here.
- 3.3 – Parameters used in the model [22]
  A table of all parameters used in the models is presented giving their value and provenance and additional notes. Subsections expand on individual groups of parameters.
  - 3.3.1 – Basic demographic parameters [25]
    Mean survival rates, age class transfer times, and starting population. Survival rates are based on literature but calibrated for population stability in absence of pressures.
  - 3.3.2 – Breeding and relaying [27]
    Mean breeding and sexually mature age class proportions, relaying probabilities under different scenarios, and adjustment parameters. Largely based on published values, with some expert opinion additions; adjustment parameters were calibrated to model.
  - 3.3.3 – Shark and terrestrial predation [28]
    Effects of shark and terrestrial predation on age classes. In absence of specific data, these are based on expert opinion.
  - 3.3.4 – Seal predation [29]
    Age class loss rates with seasonal adjustment. Largely based on published values, with some expert opinion additions.
  - 3.3.5 – Gull predation and human disturbance [30]
    Egg/chick loss rates by gull predation, distribution of loss rates, and impacts of aggravating effects (low food availability, hot spells, and moderate human disturbance); and impacts of heavy human disturbance. Largely based on expert opinion and application of data from other localities.
  - 3.3.6 – Oiling [31]
    Age class impacts and frequency of catastrophic and chronic oiling, rehabilitation rates, and long-term impacts. Based on published data.
  - 3.3.7 – Climate and flooding [32]
    Age class impacts and frequency of rain and wave flooding and hot spells. Based on currently unpublished data and expert opinion.
  - 3.3.8 – Food availability [32]
    Sources of small pelagic fish biomass and fisheries catch data, and food availability impacts on age classes and breeding. Based on published and unpublished data, correlation analyses (shown), and expert opinion.
    - 3.3.8.1 – Biomass resampling [33]
      Details of the sources and process used for food biomass resampling.
    - 3.3.8.2 – Food zone determination, biomass drivers, and survival response [34]
      Details of analyses used to determine age class drivers (prey type and food zones) and survival response curves.
      - 3.3.8.2.1 – Adult and immature survival response – Robben Island [34]
      - 3.3.8.2.2 – Adult and immature survival response – Dyer Island [35]

3.2   Use of expert opinion parameters

A strength of the system modelling approach adopted in this study is that it involves stakeholders and harnesses their inputs from conceptualization of the model and throughout model development and interpretation of model results, employing a participatory/mediated modelling approach (van den Belt, 2004; Starfield and Jarre, 2011). Selection of pressures and structure of pressure processes were developed with a group of researchers from the University of Cape Town and the South African National Biodiversity Institute, researchers and managers from government organisations (the Department of Environmental Affairs, Branch Oceans and Coasts, and Cape Nature), and members of conservation organisations (BirdLife SA), who met regularly to guide model parameterization and development. Several ecological processes were considered both crucial for a realistic model but lacking in published data for parameterization. Where these were nonetheless considered reasonably well understood by the participating researchers, parameters were based on expert opinion. In these cases, we attempted to keep relationships qualitative rather than quantitative as far as possible, and to emphasize connection to well-parameterized higher-level drivers and known boundaries (e.g., recorded food biomass).

Sensitivity tests to help evaluate these processes and parameters are presented in section 7.

3.3   Parameters used in the model

Table 3 presents a complete list of parameters used in the model, their values in the Robben and Dyer Island implementations, and basic notes on their use and source. Individual groups of parameters are discussed in detail in the subsections below.

Penguin population parameters	Robben Is. value	Dyer Is. value	Reference/Notes
Mean survival rates are modified by population pressures and result in population equilibrium in absence of pressures. Other population parameters are constants.			
Mean egg survival	0.657*	0.59	Robben Is.: Shannon & Crawford, 1999
Mean chick survival	0.597*	0.7	Dyer Is.: Ludynia et. al., 2014 (calibrated to produce equilibrium population in absence of pressures)
Mean immature survival	0.51	0.51*	
Mean adult survival	0.88*		
Immature emigration rate	N/A	0.5*	Reduction in immatures entering first adult age class; calibrated vs equilibrium value and field estimate of immature survival
Laying rate	Lookup table		Shannon & Crawford, 1999
Hatching time	1		Averaged from Shannon & Crawford, 1999
Fledging time	3		Averaged from Shannon & Crawford, 1999
Starting population (adults)	3500	4950	Robben Is.: moult counts, from Crawford et al., 2011. Dyer Is.: extrapolated from nest counts, from Makhado et al., 2013b Rounded to nearest 50.
Breeding parameters	Robben Is.	Dyer Is.	Reference/Notes

	value	value	
Base mean proportion of breeding adults in population (*mean bp*)	0.834		Shannon & Crawford, 1999
Proportion of breeding adults in population	stochastic		Follows a truncated normal distribution with mean of *mean bp* × (*febp* + density effects adjustment factor), and standard deviation of 0.05; truncation at 0.69 and 1 (Shannon & Crawford, 1999)

Breeding parameters for age class *x* follow a truncated normal distribution with mean $b\{x\}$ and standard deviation $r\,b\{x\}$ where $x = 2,\dots,5$.

	value	value	
Sexually mature proportion of age class 2 (*b2*)	0.05		
Variation in b2 (*r b2*)	0.05		
b3	0.33		
r b3	0.3		Shannon & Crawford, 1999
b4	0.74		
r b4	0.07		
b5	1		

Relaying parameters describe the probability for relaying after completing or losing the first clutch. They vary monthly around a mean $R\{x\}$ with variation driven by food availability, seasonal adjustments, and a down-scaled truncated normal distribution with standard deviation $r\,R\{x\}$ where x = c (clutch loss), b (brood loss) or s (brood survival).

	value	value	Sources: Robben Is.: Shannon & Crawford, 1999 Dyer Is.: Ludynia et al., 2014 Beta distribution parameters:
Probability for relaying after clutch loss (*Rc*)	0.31	0.24	Robben: α = 6.033, β = 13.745; Dyer: α = 49.766, β = 154.193
Variation (SD) in *Rc* (*r Rc*)	0.101	0.03	
Rb	0.22	0.07	
r Rb	0.153	0.058	Robben: α = 1.370, β = 4.912; Dyer: α = 1.249, β = 16.847
Rs	0.22	0.04	
r Rs	0.114	0.043	Robben: α = 2.642, β = 9.476; Dyer: α = 0.957, β = 20.792
Monthly seasonal adjustment to relaying probability (*VS*)	Lookup table		Expert opinion. Jan: 0.25, Feb: 0.15, Mar/Apr: 0, Jun: -0.15, Jul: -0.25.
Adjustment to number of broods lost	1.38[*]		
Adjustment to number of successful broods	0.77[*]		Calculated with reference to Crawford et al., 2011

Predation and disturbance	**Robben Is. value**	**Dyer Is. value**	**Reference/Notes**
Shark and terrestrial predator abundance varies annually between -1 and 1 following a truncated normal distribution with a standard deviation of truncation distance / 3. Simplified, penguin survival rates are unmodified at average predator abundance (**0**), multiplied by *predation effect* at abundance = **1** and by (2-*predation effect*) at abundance = **-1**. These processes are only active in the Robben Island model.			
Shark predation effect on adults	0.9	N/A	
Shark predation effect on immatures	0.9	N/A	
Shark predation effect on chicks	0.95	N/A	Expert opinion. Full positive/negative effect size is multiplied into age class survival at maximum/minimum predation strength. Effect range is thus ±5% / ±10% survival.
Shark predation effect on eggs	0.95	N/A	
Terrestrial predation effect on chicks	0.9	N/A	
Terrestrial predation effect on eggs	0.9	N/A	
Fur seal and gull predation directly subtract from monthly population size during the months that they are active. Gull predation is increased by low food situations, hot spells, and moderate human disturbance. Heavy and moderate human disturbance occur based on a Poisson distribution with means of 1/frequency. These processes are only active in the Dyer Island model.			
Annual adult loss to seal predation	N/A	0.075	Ludynia et al., 2014

Proportion of chicks lost to parents predated by seals	N/A	0.66	
Proportion of eggs lost to parents predated by seals	N/A	1	Expert opinion
Monthly weighting of seal predation strength	N/A	Internal lookup	Based on Johnson et al., 2006
Proportion of surface nests predated by gulls	N/A	0.15	Expert opinion
Egg/chick loss per day	N/A	Internal lookup	Based on Pichegru et al., 2013
Low food effect on gull predation	N/A	0.5	Expert opinion. If Zone 1 food index is below median, losses are multiplied with 0.5× index
Hot spell effect on gull predation	N/A	0.1	Expert opinion. Losses increased by 10%.
Moderate human disturbance effect on gull predation	N/A	10	Expert opinion. Losses multiplied by 10
Mean moderate human disturbance frequency (months)	N/A	1	Expert opinion
Heavy human disturbance effect on egg and chick survival	N/A	0.5	Expert opinion. Survival rates multiplied by 0.5
Mean heavy human disturbance frequency (months)	N/A	120	Expert opinion

Catastrophic and chronic oiling	Robben Is. value	Dyer Is. value	Reference/Notes
Catastrophic and chronic oiling occurences follow a Poisson distribution with mean of 1/frequency.			
Rehabilitation rate after oiling	0.9	0.84	Calculated from SANCCOB data
Reduction in fledging success for chicks of oiled parents	0.5		Based on Wolfaardt et al. (2008) and Sherley (2010). Includes lowered proportion of breeders among oiled adults.
Mean catastrophic oiling frequency (months)	180	264	Based on Wolfaardt et al., 2008
Proportion of adults affected	0.24	0.33	Robben Is.: Whittington et al., 2000
Proportion of immatures affected	0.1	0.14	Dyer Is.: Ludynia et al., 2014
Mean chronic oiling frequency (months)	3		
Proportion of adults affected	0.008	0.009	Calculated from SANCCOB data
Proportion of immatures affected	0.0006	0.0007	

Climate and floods	Robben Is. value	Dyer Is. value	Reference/Notes
Hot spells and floods occur according to a poisson distribution with a mean of 1/frequency. Wave flooding occurs only in the Dyer Island model.			
Mean rain flooding frequency (months)	60	36	
Proportion of chicks lost	0.1	0.25	
Proportion of eggs lost	0.3	0.25	
			Expert opinion
Mean wave flooding frequency (months)	N/A	36	
Proportion of chicks lost	N/A	0.03	
Proportion of eggs lost	N/A	0.03	

The effect of extreme hot spells is weighted by month using a lookup table, with full effect applied in summer months and 1/4 effect in winter months. Chick and egg survival rates are multiplied by the weighted effect.

Mean months between extreme hot spells	36	Expert opinion

Effect on chicks	0.12	
Effect on eggs	0.4	

Food availability	Robben Is. value	Dyer Is. value	Reference/Notes
Annual biomass and catch data in the model are sampled with from distributions based on recorded data. Egg and chick survival and breeding proportion are driven by linear indices (-1 to 1) relative to the minimum, median and maximum of recorded data, with median biomass corresponding to an absence of effect; adult and immature survival are mapped to response curves fitted to biomass records. Biomass in the region around the island (Zone 1) is treated as a variable portion of a larger volume, and is normally distributed with a mean of that volume's May (recruit) biomass and a standard deviation equal to that of the recorded data (with logit-like constraints). Biomass in the region farther out (Zone 2) is based on several metrics of that volume's November (spawner) biomass and expressed in terms of tonnage and/or caloric value of prey species.			
Biomass data	Internal lookup		Data from Department of Agriculture, Forestry and Fisheries (unpublished)
Fisheries catch data	Internal lookup		
Food effect on immature survival	Internal lookup		Survival rates are based on functional response curves fitted to survival estimates in Sherley et al. (2014a)
Food effect on adult survival	Internal lookup		
Food effect on egg survival	0.5		Expert opinion. Full positive/negative effect size is multiplied into age class survival at maximum/minimum food availability (Zone 1 index), with approximately linear interpolation
Food effect on chick survival	0.5		
Food effect on breeding proportion (*febp*)	0.15		Based on Crawford et al., 1999. Food effect is 0.15 × Zone 2 index
Food effect on relaying probability (V_F)	0.9		Expert opinion. Food effect is 0.9 × Zone 1 index
Caloric value in kj value [sardine]	8.59		Bouwhuis et al., 2007
Caloric value in kj value [anchovy]	6.74		

Density effects	Robben Is. value	Dyer Is. value	Reference/Notes
Density parameters are constants.			
Number of adults below which breeding proportion is reduced due to Allee effects	200		Expert opinion. Reduction in breeding proportion by 10%
Number of adults below which breeding proportion is increased due to low resource competition	1500		Expert opinion. Increase in breeding proportion by 20%
Carrying capacity	25000		Current reduced Benguela upwelling ecosystem carrying capacity (Crawford et al., 2007)

Table 3. Parameters used in the Robben and Dyer Island models. * = parameter was calibrated to model fit

3.3.1. Basic demographic parameters

Penguin population parameters	Robben Is. value	Dyer Is. value	Reference/Notes
Mean survival rates are modified by population pressures and result in population equilibrium in absence of pressures. Other population parameters are constants.			
Mean egg survival	0.657[*]	0.59	Robben Is.: Shannon & Crawford, 1999
Mean chick survival	0.597[*]	0.7	Dyer Is.: Ludynia et. al., 2014 (*: calibrated to produce equilibrium population in absence of pressures)
Mean immature survival	0.51	0.51[*]	
Mean adult survival	0.88[*]		
Immature emigration rate	N/A	0.5*	Reduction in immatures entering first adult age class; calibrated vs equilibrium value and field estimate of immature survival
Laying rate	Lookup table		Shannon & Crawford, 1999

Hatching time	1		Averaged from Shannon & Crawford, 1999
Fledging time	3		Averaged from Shannon & Crawford, 1999
Starting population (adults) for scenarios starting from the present	3500	4950	Robben Is.: moult counts, from Crawford et al., 2011. Dyer Is.: extrapolated from nest counts, from Makhado et al., 2013b Rounded to nearest 50.

Table 3.1.   Demographic parameters. * = parameter was calibrated to model fit

Mean survival rates for the four age classes (egg, chicks, immatures, and adults) are of fundamental importance in determining model behaviour. The demographic model is based to a large part on the structure and parameters used in the Dassen Island model by Shannon and Crawford (1999), and survival estimates reported there were used as basis for the Robben Island model. Use of these parameters leads to a declining population unless immigration is introduced, as reported by Crawford et al. (2008). The number of chicks fledged per breeding attempt (0.225–0.594, mean of 0.389) was within the observed range of values on Robben Island from 1989 to 1995 (Crawford et al., 1999), although higher values were estimated in later studies (see below). This level of breeding success is insufficient to replace adult penguins lost each year.

Both animal movement between colonies and an unknown number of unidentified pressures are likely to have influenced the original estimates. The use of a constant immigration value to stabilise the population is not a realistic option. In the current absence of reliable estimates of immigration processes, several base survival parameters were therefore adjusted in the Robben Island model to simulate a population unaffected by either of these influences. Test runs showed that a long-term stable population (over 100 years) could be achieved with an adult survival rate of 0.880 (originally 0.860) and that the number of chicks fledged per breeding attempt (clutch size × egg survival × chick survival) should be just over 0.7. This agrees with long-term averages recorded for the colony (e.g. 0.62 chicks per pair in Crawford et al., 2006b; 0.70 chicks per pair in Sherley et al., 2012). This adjustment was implemented as an egg survival rate of 0.657 (originally 0.548) and chick survival of 0.597 (originally 0.370), thus producing 0.704 chicks fledged per breeding attempt.

Note that several survival rates are presented with three-digit precision. The increased precision was introduced for the calibration of the equilibrium base population intended to remain stable over 100 years. A lower (two-digit) precision is more realistic for field estimates, and has been used for all parameter values in the model that were not subject to calibration (for details on calibrated parameters, see 6.3).

Earlier version [Weller et al. (2014)]: Mean egg survival in the Robben Island model was 0.649 instead of 0.657. The parameter was further calibrated to increase long-term stability of population development under equilibrium conditions, but remains well within the reported range (Sherley et al., 2013a).

Parameters for the Dyer Island model were handled similarly, using estimates from Ludynia et al. (2014). Estimated survival rates were 0.590 for eggs, 0.700 for chicks, 0.247 for immatures, and 0.545 for adults. While egg and chick survival were in the range found for artificial nests at Robben Island, both adult and immature survival were considerably lower. It is likely that adult survival is impacted by fur seal predation, which strongly adds to adult mortality and was found to have a very strong influence on population development in the model (7.2.9). Immature survival estimates may be negatively affected by additional factors in addition to pressures present in the model. There was a relatively high loss rate of the silicone rubber bands used in mark-recapture estimation of penguin numbers at Dyer Island (4–20% per year; Ludynia et al., 2014), leading to underestimates in resighting and survival rates. An even stronger effect may derive from the high emigration rates from Dyer Island to other colonies estimated for immature penguins (> 90%), allowing negligible recruitment of young penguins to the colony (Ludynia et al., 2014).

Using these estimates as provided did not produce a viable equilibrium model population. The low adult and immature survival rates led to extinction within 5–10 years. It was found that raising both values to the equilibrium levels used in the Robben Island model (adult survival: 0.88, immature survival: 0.51) resulted in a stable configuration in combination with the unaltered egg and chick survival estimates. This setup is a reasonable assumption, as the different sets of added-on pressures can be regarded as one of the crucial

differences between the colonies. However, generating robust estimates of movement rates between African penguin colonies is presently difficult, hampered by a paucity of marked individuals (Sherley et al., 2014a). This is currently being addressed through a nationwide programme to mark individuals with subcutaneous transponders

A reasonable working assumption of the magnitude of emigration of juveniles from Dyer Island can be made from the observation that combining the increased equilibrium immature survival rate (0.51) with removing 50% of immatures before they enter the first adult stage approximates the effects of the original low field estimate (0.247). This emigration rate of 50% agrees with the findings of a study on hand-reared chicks from Dyer Island, in which six of 12 individuals that went on to breed did so at this colony (Sherley et al., 2014b). Thus, a conservative immature emigration rate of 50% was used by default for all management scenarios at that colony.

For Robben Island, the model currently does not by default use a representation of immigration, as estimates were considered too uncertain. However, several management scenarios have been presented with an additional alternative setup that investigates the effects of possible ongoing immigration (Weller et al., 2016).

Survival rates for both colony implementations were thus modified within reasonable bounds to produce a base population configuration that is in equilibrium in the absence of all pressures considered in the model. The underlying assumption was that factoring in the pressures at their implemented impact strength will then produce a realistic population response. For tests of this assumption see 6.2.

For predictive runs starting from the present, current best estimates of population size should be used as starting population. For the Robben Island results presented in Weller et al. (2014), these were based on moult counts of ~3500 individuals (Crawford et al., 2011), which still appears applicable. For Dyer Island, moult counts are not representative, as penguins moulting there often choose a different colony for breeding. Therefore, a starting population size of 4950 adults was extrapolated from nest counts of ~1500 breeding pairs in 2013 (Makhado et al., 2013b) using an empirical conversion factor of breeding pairs to total adult individuals of 3.2 (Crawford and Boonstra, 1994).

3.3.2 Breeding and relaying

Breeding parameters	Robben Is. value	Dyer Is. value	Reference/Notes
Base mean proportion of breeding adults in population (*mean bp*)	0.834		Shannon & Crawford, 1999
Proportion of breeding adults in population	stochastic		Follows a truncated normal distribution with mean of *mean bp* × (*febp* + density effects adjustment factor), and standard deviation of 0.05; truncation at 0.69 and 1 (Shannon & Crawford, 1999)

Breeding parameters for age class *x* follow a truncated normal distribution with mean $b\{x\}$ and standard deviation $r\,b\{x\}$ where $x = 2,\ldots,5$.

Sexually mature proportion of age class 2 (*b2*)	0.05		
Variation in b2 (*r b2*)	0.05		
b3	0.33		
r b3	0.3		Shannon & Crawford, 1999
b4	0.74		
r b4	0.07		
b5	1		

Table 3.2.   Breeding parameters

The mean proportion of breeders among sexually mature adults, and the proportion of sexually mature individuals within each age class, follow the model of Shannon & Crawford (1999). While the age class-specific proportions are likely subject to food influences, currently available data appear insufficient for

modelling a relationship (Crawford et al., 1999; Whittington et al., 2005). The effect of assuming overall lowered breeding age under good food conditions was however explored in some scenarios (6.2.1; Weller et al., 2016).

In the calculation of variation around breeding proportion, *febp* refers to the influence of food availability (see 2.4.1.2 and 3.3.8.2.4), and adjustment factor to density effects (see 2.3.2.6 and 3.3.9).

Breeding parameters	Robben Is. value	Dyer Is. value	Reference/Notes
Relaying parameters describe the probability for relaying after completing or losing the first clutch. They vary monthly around a mean $R\{x\}$ with variation driven by food availability, seasonal adjustments, and a down-scaled truncated normal distribution with standard deviation $r R\{x\}$ where x = c (clutch loss), b (brood loss) or s (brood survival).			
			Sources: Robben Is.: Shannon & Crawford, 1999 Dyer Is.: Ludynia et al., 2014 Beta distribution parameters:
Probability for relaying after clutch loss (Rc)	0.31	0.24	Robben: α = 6.033, β = 13.745; Dyer: α = 49.766, β = 154.193
Variation (SD) in Rc ($r Rc$)	0.101	0.03	
Rb	0.22	0.07	Robben: α = 1.370, β = 4.912; Dyer: α = 1.249, β = 16.847
$r Rb$	0.153	0.06	
Rs	0.22	0.04	Robben: α = 2.642, β = 9.476; Dyer: α = 0.957, β = 20.792
$r Rs$	0.114	0.043	
Monthly seasonal adjustment to relaying probability (V_S)	Lookup table		Expert opinion. Jan: 0.25, Feb: 0.15, Mar/Apr: 0, Jun: -0.15, Jul: -0.25.
Adjustment to number of broods lost	1.38[*]		
Adjustment to number of successful broods	0.77[*]		Calculated with reference to Crawford et al., 2011

Table 3.3.   Relaying parameters. * = parameter was calibrated to model fit

Mean probabilities for additional attempts at nesting after a previous nesting attempt either failed or succeeded were taken from Shannon and Crawford (1999) (Robben) and Ludynia et al. (2104) (Dyer), based on nest tracking studies. Monthly seasonal adjustment to relaying probability (V_S) is based on expert opinion of the relative likelihood of a relaying attempt being undertaken, based on how much time remains in the preferred annual breeding season window and the likely amount of resources expended so far. See 2.3.2.5.3 for details on relaying probability calculations. Note that as only 10% of variation are random and thus driven by a down-scaled (× 0.1) distribution, the normal distribution parameters used for that purpose (mean and sd) are given; to visualize the complete distribution, a beta distribution using the given parameters should be used.

The adjustments to numbers of lost/successful broods are calibration multipliers applied to **two chick** broods only. They serve to down-weight the effective number of successful broods and up-weight the effective number of lost broods originating from two-chick nests, before the probability of relaying is calculated. These are empirical parameters that were introduced to match model output to observed data, in the apparent presence of an unaccounted-for correlation among chick survivals in two chick nests (see 2.3.2.5.4).

3.3.3   Shark and terrestrial predation

Predation	Robben Is. value	Dyer Is. value	Reference/Notes
Shark and terrestrial predator abundance varies annually between -1 and 1 following a truncated normal distribution with a standard deviation of truncation distance / 3. Simplified, penguin survival rates are unmodified at average predator abundance (**0**), multiplied by *predation effect* at abundance = **1** and by (2-*predation effect*) at abundance = **-1**. These processes are only active in the Robben Island model.			
Shark predation effect on adults	0.9	N/A	Expert opinion. Full positive/negative effect size is multiplied into age class survival at maximum/minimum predation
Shark predation effect on immatures	0.9	N/A	

Shark predation effect on chicks	0.95	N/A	strength. Effect range is thus ±5% / ±10% survival.
Shark predation effect on eggs	0.95	N/A	
Terrestrial predation effect on chicks	0.9	N/A	
Terrestrial predation effect on eggs	0.9	N/A	

Table 3.4.　　　Shark and terrestrial predation parameters

While observed cow shark aggregations around main Robben Island penguin landing sites indicate that shark predation takes place (C. Da Silva (DAFF), pers. comm.), equivalent observations and/or discovery of shark attack victims are lacking for Dyer Island (Ludynia et al., 2014). Given that such observations have also been reported from the penguin colonies at both St Croix and Bird islands, this is unexpected. The chumming of sharks in the course of the thriving cage diving industry in the vicinity of Dyer Island may be a possible explanation.

Predation by cats is thought to have been a strong effect on Robben Island before the cat culls in 2005 and 2006 (de Villiers et al., 2010). Currently, there are low predator populations (feral cats *Felis catus*, pied crows *Corvus albus*, kelp gulls *Larus dominicanus*), and cat stomach content analyses after 2009 (C. Wilke (DAFF), pers. comm.) indicate low penguin consumption. Dyer Island appears to be free of terrestrial predators that could prey on penguin eggs or chicks (Ludynia et al., 2014).

Lacking more concrete data, predation effects on Robben Island penguins were chosen to be low impact (maximum of ±10% survival from direct predation, and ±5% from indirect effects by removal of parents). In the absence of a parameterized model to drive monthly predation pressure changes, terrestrial predation process essentially acts as a centered source of small random changes in survival rate until better data can be included. Shark predation is assumed to be connected to fish biomass in Zone 1, and extremely low or high biomass values will force shark abundance to grow or decline in parallel (2.4.3.1), however this relationship is speculative.

Earlier version [Weller et al. (2014)]: Shark predation effect on adult and immature survival was 0.8, that on egg and chick survival was 0.9, and terrestrial predation effect on egg and chick survival was 0.85. The impact of all these predation types was lowered based on assessment of model outcomes and information from conservation professionals. Shark predation also followed an unmodified normal distribution as in terrestrial predation, without a link to food biomass.

3.3.4　Seal predation

Predation	Robben Is. value	Dyer Is. value	Reference/Notes
Fur seal predation directly subtract from monthly population size during the months that it is active. This process is only active in the Dyer Island model.			
Annual adult loss to seal predation	N/A	0.075	Ludynia et al., 2014
Proportion of chicks lost to parents predated by seals	N/A	0.66	Expert opinion
Proportion of eggs lost to parents predated by seals	N/A	1	
Monthly weighting of seal predation strength	N/A	Internal lookup	Based on Johnson et al., 2006

Table 3.5.　　　Seal predation parameters

Cape fur seals (*Arctocephalus pusillus pusillus*) are known to predate on seabirds at Namibian and South African colonies, although this is considered to be play rather than a feeding behaviour (du Toit et al., 2004; Makhado et al., 2006, 2013a). Predation rates do not appear to be related to the number and birth rates of seals at nearby colonies nor to fish availability, but are rather linked to whichever seabird species is most abundant at the time (Ludynia et al., 2014). On Dyer Island, the annual loss rate of adult penguins to seal predation is

estimated at 7–8% of total adults (Makhado et al., 2013a), while it appears to be negligible on Robben Island and is unimplemented in that model.

The proportion of chicks of predated adults that are lost is assumed to be 0.66, as a single remaining parent may be able to fledge some chicks, depending on their age. That of eggs is assumed to be 1, as a single remaining parent cannot successfully incubate eggs.

African penguins are subject to seal predation principally during their winter breeding season (Makhado et al., 2006). A clear seasonal variability in attacks and penguin casualties was found at Dyer Island (Johnson et al., 2006), with highest predation rates in August followed by September and October. To represent this, monthly loss rates are weighted using fractions of 0.1 for April–June, 0.25 for August, and 0.175 for September and October (summing to 1).

The process for simulating seal control measures uses several rough estimates of culling effectiveness and persistence. To keep these integrated with the description of the process, they are covered in 2.4.3.2.1.

3.3.5 Gull predation and human disturbance

Predation and disturbance	Robben Is. value	Dyer Is. value	Reference/Notes
Gull predation directly subtracts from monthly population size during the months that it is active. Gull predation is increased by low food situations, hot spells, and moderate human disturbance. Heavy and moderate human disturbance occur based on a Poisson distribution with means of 1/frequency. This process is only active in the Dyer Island model.			
Proportion of surface nests predated by gulls	N/A	0.15	Expert opinion
Egg/chick loss per day	N/A	Internal lookup	Based on Pichegru et al., 2013
Low food effect on gull predation	N/A	0.5	Expert opinion. If Zone 1 food index is below median, losses are multiplied with 0.5× index
Hot spell effect on gull predation	N/A	0.1	Expert opinion. Losses increased by 10%.
Moderate human disturbance effect on gull predation	N/A	10	Expert opinion. Losses multiplied by 10
Mean moderate human disturbance frequency (months)	N/A	1	Expert opinion
Heavy human disturbance effect on egg and chick survival	N/A	0.5	Expert opinion. Survival rates multiplied by 0.5
Mean heavy human disturbance frequency (months)	N/A	120	Expert opinion

Table 3.6.   Gull predation and human disturbance parameters

Kelp gulls (*Larus dominicanus*) prey on eggs and young chicks of African penguins throughout the breeding season (Seddon and van Heezik, 1991; Pichegru, 2013). Predation rates may be exacerbated if adult penguins are forced to leave the nest unguarded due to prolonged partner absences when prey is scarce (Seddon and van Heezik, 1991), during heat waves when they have to seek out the water to cool off (Randall 1995), or due to human disturbance (Voorbergen et al., 2012). Surface nests are at substantially higher risk of being predated than burrows and nest boxes (du Toit et al., 2003). Chicks are generally only taken while they are still relatively small; a threshold age of 15 days was used in the model.

A recent increase in kelp gull breeding pairs on Dyer Island after 2000, reaching ~600 pairs in 2012, suggests that gull predation may now play an enhanced role in limiting penguin breeding success in that colony (Ludynia et al., 2014). While there are no published estimates of predation rates, a rough maximum predation level of 15% of surface nests was estimated from observational data (D. Geldenhuys (Cape Nature), pers. comm.).

Under the assumption that patterns of egg and chick losses to gull predation are principally driven by gull foraging behaviour applicable to different colonies, observational data from Bird Island, Algoa Bay (Pichegru,

2013) were used to determine the frequency distribution of losses. These data cover 116 days and record the number of eggs lost per day (chick losses were not recorded). The distribution is strongly right-skewed, with a maximum of 25 and a median of 2 attacks. This was standardized to 1 and then treated as percentage of susceptible nests attacked, equally affecting eggs and chicks. A frequency-weighted draw from this distribution is used as monthly predation rate.

Nesting penguins on Dyer Island are subject to disturbance by moult counts, which are carried out on an approximately monthly basis. A mean frequency of 1/month was therefore used. While this practice is in abeyance as of 2015 to aid penguin recruitment (D. Geldenhuys, pers. comm.), it is likely that it may be resumed at some point in the future. Disturbance of a catastrophic nature happens much more rarely and may be caused by oil spills, helicopter landings, or illegal boat landings by poachers (Ludynia et al., 2014). These events were assumed to happen once every 10 years on average. The gull predation-connected effects of disturbance and of low food (see 2.4.1.1) and hot spells (see 2.4.6) are based on expert opinion.

3.3.6 Oiling

Catastrophic and chronic oiling	Robben Is. value	Dyer Is. value	Reference/Notes
Catastrophic and chronic oiling occurences follow a Poisson distribution with mean of 1/frequency.			
Rehabilitation rate after oiling	0.9	0.84	Calculated from SANCCOB data
Reduction in fledging success for chicks of oiled parents	0.5		Based on Wolfaardt et al. (2008) and Sherley (2010). Includes lowered proportion of breeders among oiled adults.
Mean catastrophic oiling frequency (months)	180	264	Based on Wolfaardt et al., 2008
Proportion of adults affected	0.24	0.33	Robben Is.: Whittington et al., 2000
Proportion of immatures affected	0.1	0.14	Dyer Is.: Ludynia et al., 2014
Mean chronic oiling frequency (months)	3		
Proportion of adults affected	0.008	0.009	Calculated from SANCCOB data
Proportion of immatures affected	0.0006	0.0007	

Table 3.7.   Oiling parameters

Data from SANCCOB (Southern African Foundation for the Conservation of Coastal Birds) on penguins admitted from Robben and Dyer Island was used to determine the frequency of chronic oiling, and the effect both types of oiling have on adult and immature penguins (e.g. Parsons and Underhill, 2005). The data consist of the date of admission, date of release or death and age of penguin (adult or immature), and were collated to give an indication of the number of penguins oiled in each oil spill (an oil spill was defined as covering all admission dates less than a week apart) as well as the average number of months between oil spills. Proportions of adults affected by catastrophic oil spills are taken studies treating individual spill events (Whittington et al., 2000; Ludynia et al., 2014).

27% of de-oiled birds never breed again (Wolfaardt et al., 2008a) and those that do breed again have ~10% lower chick survival than non-oiled birds (Sherley 2010), confirming previous results for the *Apollo Sea* spill (Wolfaardt et al., 2008a) and the *Treasure* spill (Barham et al., 2007). These effects were combined into an overall reduction in fledging success of 50%. Ongoing observations suggest that this effect persists for the life of the breeding adult (unpublished data), which is how it is treated in the model.

Mean catastrophic spill frequency depends on spills of which magnitude are taken into account, as well as on the evaluated period. The time frame for inference was restricted to that given by the oldest reliable penguin loss records (1953 for Robben Island, 1948 for Dyer Island). Robben Island has since then been subject to four spills that were deemed to have had substantial impacts on penguins (*Esso Essen* 1968, *Unknown* 1972, *Apollo Sea* 1994, *Treasure* 2000), and Dyer Island to three (*Esso Wheeling* 1948, *Wafra* 1971, *Unknown* 1995)

(Wolfaardt et al., 2009; Ludynia et al., 2014), resulting in mean occurrence frequencies of 180 (Robben) / 264 (Dyer) months.

Earlier version [Weller et al. (2014)]: A lower frequency of 600 months was used for Robben Island, based on the two extreme events (*Apollo Sea* and *Treasure*) that had occurred over the last century. A more restricted time frame and accounting for smaller but still substantial events was subsequently considered more appropriate. For a discussion of penguin losses attributed to individual oil spills, see Wolfaardt et al. (2009).

3.3.7 Climate and flooding

Climate and floods	Robben Is. value	Dyer Is. value	Reference/Notes
Hot spells and floods occur according to a poisson distribution with a mean of 1/frequency. Wave flooding occurs only in the Dyer Island model.			
Mean rain flooding frequency (months)	60	36	Expert opinion
Proportion of chicks lost	0.1	0.25	Unpublished data (R. Sherley) (Robben); expert opinion (Dyer)
Proportion of eggs lost	0.3	0.25	
Mean wave flooding frequency (months)	N/A	36	
Proportion of chicks lost	N/A	0.03	Expert opinion
Proportion of eggs lost	N/A	0.03	
The effect of extreme hot spells is weighted by month using a lookup table, with full effect applied in summer months and 1/4 effect in winter months. Chick and egg survival rates are multiplied by the weighted effect.			
Mean hot spells frequency (months)	36		Expert opinion
Effect on chicks	0.12		Unpublished data (R. Sherley)
Effect on eggs	0.4		

Table 3.8. Climate and flooding parameters

Few data are available on the specifics of climate events that effect the colonies at Robben and Dyer islands. The mean frequency of hot spells and flooding, as well as the proportion of eggs and chicks lost to wave flooding, are rough estimates based on field observations. The effect strengths of rain flooding on Robben Island, and of hot spells in both colonies, are based on analyses of nestling survival that are currently still unpublished.

Earlier version [Weller et al. (2014)]: The model had a hot spell effect on eggs and chicks of 0.5, and a proportion of eggs and chicks lost to rain flooding of 0.4. Recent data indicate that both these loss ratios were too high (R. Sherley, unpublished data). The model also contained a cold spell process, implemented analogous to hot spells, with a survival effect of 0.7 on eggs and chicks and a mean frequency of 40 months. As cold spells frequently overlap with rain flooding events and the effects could not be sufficiently distinguished from each other (R. Sherley, unpublished data), this process was removed from the model.

3.3.8 Food availability

Food availability	Robben Is. value	Dyer Is. value	Reference/Notes

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Annual biomass and catch data in the model are sampled with from distributions based on recorded data. Egg and chick survival and breeding proportion are driven by linear indices (-1 to 1) relative to the minimum, median and maximum of recorded data, with median biomass corresponding to an absence of effect; adult and immature survival are mapped to response curves fitted to biomass records. Biomass in the region around the island (Zone 1) is treated as a variable portion of a larger volume, and is normally distributed with a mean of that volume's May (recruit) biomass and a standard deviation equal to that of the recorded data (with logit-like constraints). Biomass in the region farther out (Zone 2) is based on several metrics of that volume's November (spawner) biomass and expressed in terms of tonnage and/or caloric value of prey species.

Biomass data	Internal lookup	Data from Department of Agriculture, Forestry and Fisheries (unpublished)
Fisheries catch data	Internal lookup	
Food effect on immature survival	Internal lookup	Survival rates are based on functional response curves fitted to survival estimates in Sherley et al. (2014a)
Food effect on adult survival	Internal lookup	
Food effect on egg survival	0.5	Expert opinion. Full positive/negative effect size is multiplied into age class survival at maximum/minimum food availability (Zone 1 index), with approximately linear interpolation
Food effect on chick survival	0.5	
Food effect on breeding proportion (*febp*)	0.15	Based on Crawford et al., 1999. Food effect is 0.15 × Zone 2 index
Food effect on relaying probability (V_F)	0.9	Expert opinion. Food effect is 0.9 × Zone 1 index
Caloric value in kj value [sardine]	8.59	Bouwhuis et al., 2007
Caloric value in kj value [anchovy]	6.74	

Table 3.9.   Climate and flooding parameters

The impact of food availability on variation around mean breeding proportion (shift in mean of ±0.15) is based on the finding that food-based variation makes up ~50% of total variation, which spans a change in breeding proportion of ~0.3 (Crawford et al. 1999) (see 2.4.1.2). The proportion of variation in relaying probability that is food-driven (0.9) is an estimate based on the assumption that food availability is the main determinant of relaying (see 2.3.2.5.3 for calculation). Energy values of prey species are based on caloric measurements in Bouwhuis et al. (2007).

3.3.8.1   Biomass resampling
Biomass data for the years 1983–2013 were sourced from the Department of Agriculture, Forestry and Fisheries (DAFF). Biomass records are sorted into 12–20 range intervals and their frequency distribution is used as a PDF in resampling (Fig. 6); i.e., values are drawn from the sampling domain defined by the records, but no individual records are resampled. This provides a smooth continuum of resampled values while preventing the recurrence of a small number of parameter states, and ensures correct weighting by giving less weight to rare extremes and more to values close to the biomass median.

Note that this approach is only used when the entire time series of records is resampled, but not for resampling from a restricted time range, as standardized PDFs cannot be constructed by the model on the fly. Simulations using restricted time ranges (e.g. to investigate the effects of a specific historical prey distribution regime) thus resample individual annual records without weighting (uniform distribution), and should consequently be considered as using slightly less sound data streams.
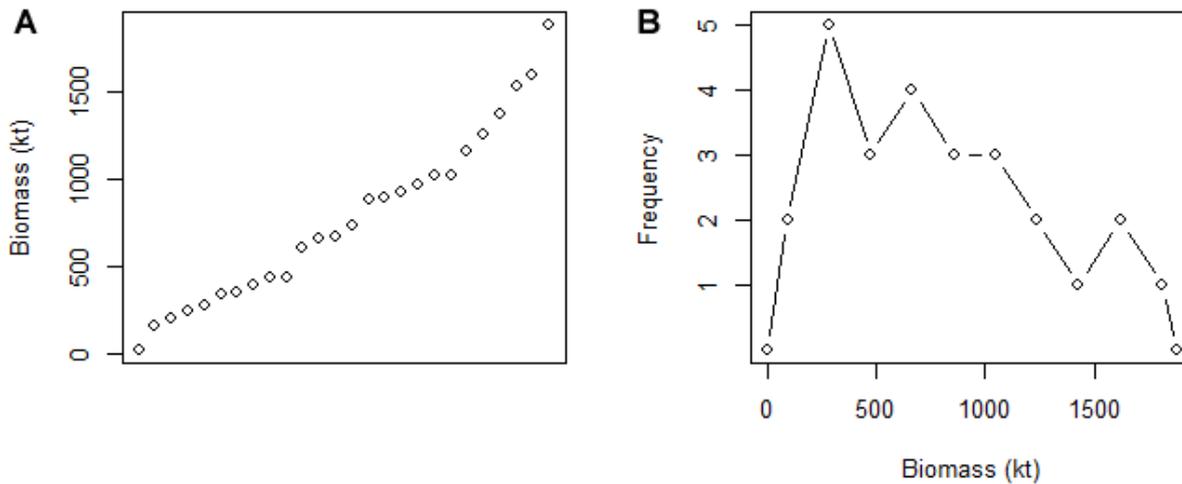
Figure 6.   Construction of the probability density function (PDF) for resampling from biomass records. Anchovy biomass records 1987–2012 are used as an example. A) Records ordered by size. B) Frequency count of records, using 12 size intervals. After standardizing the area under the curve over the frequency distribution to 1, the curve is used as a PDF for resampling interpolated biomass records.

There are two time series of annual records, one based on surveys carried out in May of each year and recording sardine and anchovy recruits (used for Zone 1 processes), and one in November recording spawners (used for Zone 2 processes). The surveyed area varies annually, which is of no consequence for Zone 2 processes, but important for Zone 1 calculation, as here only a fraction of the total May survey area (sea area proportion of a circle 15 nautical miles (28 km) in diameter around the colony) is considered. Zone 1 areas were divided by averages of May survey areas (D for Robben, E for Dyer) over the time of interest to derive a generalised factor of 0.175, used for both colonies. Thus annual mean Zone 1 biomass is taken as 17.5% of resampled annual recruit biomass.

Monthly fisheries catch data for sardine and anchovy were also sourced from DAFF records, at the resolution of 10 km^2 fishing blocks. The fractional blocks making up the Zone 1 area around each colony were summed to provide monthly total catches, which are then retrieved as annual series based on the value of the drawn annual mean recruit biomass (see 2.4.1.1).

3.3.8.2   Food zone determination, biomass drivers, and survival response

3.3.8.2.1   Adult and immature survival response – Robben Island
Adult survival in both models is driven by the natural log of the tonnage (t) of Stratum C sardine spawners, and immature survival by the natural log of the tonnage of sardine spawners combined for all November strata west of Cape Agulhas – A,B and C (see Figure 4).

Relationships between adult and immature survival and food availability on Robben Island were modelled using survival rates estimated in multi-state capture-mark recapture (CMR) analyses for the Robben Island population from 1994/95 to 2011/12 (Sherley et al., 2014a). Since we used the annual survival rates as response variables, and these were estimated rather than observed without error, the survival rates were weighted by their standard errors in all analyses. For adult survival, the 1999/2000 estimate was omitted because it was indistinguishable from a survival rate of 1 (i.e. not robustly estimated) and for immature survival, the 2008/2009 estimate was omitted because it was not estimable in the CMR model.

We first used generalized additive models (GAM) using the 'gam' function in the 'mgcv' package (Wood, 2011) for R v. 3.0.2 (R Core Team, 2013) with the LOESS smoother term selected by cross-validation (Zuur et al., 2009) to assess evidence for non-linear relationships between adult/immature African penguin survival and anchovy/sardine biomass and energy content. For adult survival, the best supported GAM model was for sardine spawner biomass in November survey stratum C (AICc weight = 0.79, ΔAICc to the next best model = 2.7) and the smoother term was significant (F = 6.66, d.f. = 3.30, p = 0.004). The model (red line in Figure 7)

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was almost asymptotic and a subsequent comparison to a log-linear model (blue line in Figure 7) indicated little difference in relative model fits (ΔAICc = 0.5). Given the greater simplicity and robustness for predictions of linear models, we thus favoured the log-linear fit for adult survival. For immatures the best supported GAM model was for sardine spawner biomass summed west of Cape Agulhas (consisting of November survey strata A, B and C; AICc weight = 0.86, ΔAICc to the next best model = 4.1) and the smoother term was significant (F = 6.34, d.f. = 1.21, p = 0.019). Again, there was little to choose between the GAM model and a log-linear fit (ΔAICc = 0.6), so we used the latter model.

Earlier version [Weller et al. (2014)]: Adult and immature survival were previously linked to the sum of the energy content (kJ) of the sum of sardine and anchovy spawners in November Stratum C and used an approximately linear response mapping function, analogously to current breeding proportion among adults.
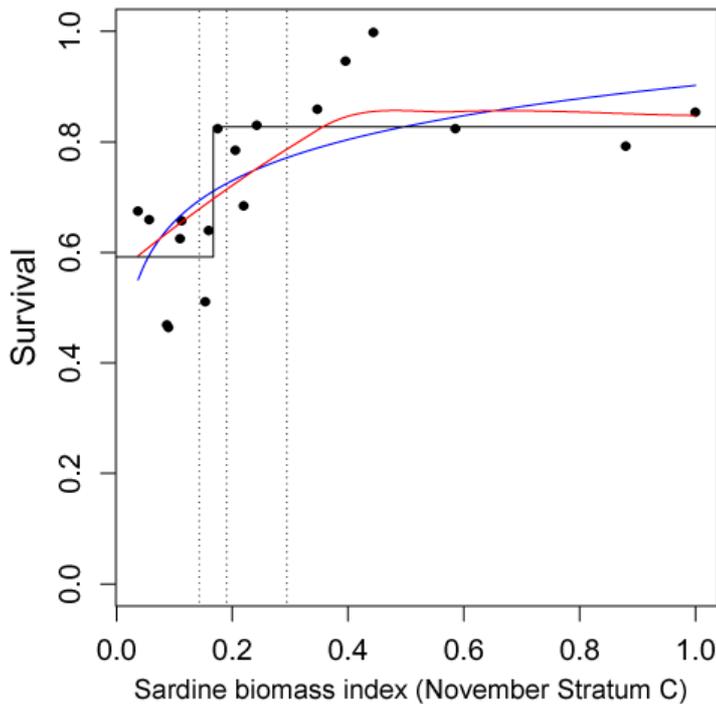
Figure 7.   Adult penguin survival estimates, relative to November Stratum C sardine spawner biomass divided by maximum recorded biomass. Blue curve: log-linear model; red curve: GAM model; black curve: step function. Dotted lines from left to right: 75% of median biomass, median biomass, mean biomass.

Response curves were further adapted for use in the pressure model, which uses higher base penguin survival rates than estimated in the field (due to its pressure-free equilibrium population base state; see 3.3.1). For each age class, response curves were mapped to the entire recorded range of survival estimates, then shifted upwards on the y axis (survival) such that mean survival (adults: 0.88, immatures: 0.51; for both colonies) mapped to the equilibrium biomass level (see 2.4.1.3), with survival rates capped at 0.99.

3.3.8.2.2   Adult and immature survival response – Dyer Island
Waller (2011) found no significant relationship between number of breeding or moulting penguins on Dyer Island and fish biomass in any stratum of the November spawner surveys, possibly because population development is currently being dominated by the effects of seal predation (Ludynia et al., 2014; Weller et al., 2016). However, a comparison to the situation on Robben Island suggests that biomass found in November Stratum C (identical to May Stratum E) may be a useful driver. Although those analyses (above) cannot be repeated for Dyer Island because no time series of annual survival rates are available here, it is reasonable to assume that this applies to the Dyer Island colony (which is situated in this stratum) as well. The survival-food relationship for Robben Island immatures was equivalently retained. Consequently, Zone 2 biomass for the purpose of driving adult survival was defined as sardine spawner biomass only in November stratum C, and for

immature survival, as sardine spawner biomass only west of Agulhas (November strata A, B and C). The functional response curves fitted to the Robben Island parameters were used in both models.

3.3.8.2.3 Egg and chick survival response

Because current data do not admit fitting a regression model of adequate quality, the functional response of egg and chick survival (Zone 1) and breeding proportion (Zone 2) to food biomass at either colony could not be connected to response curves the same manner as for adult and immature survival. A transformation into an index multiplier relative to minimum/maximum recorded tonnage (t) (see 2.4.1.1) is used until better data become available. It should be noted that the long-term relationship between penguin breeding success (which integrates egg and chick survival) and anchovy recruitment biomass is linear (Sherley et al., 2014c), which adds plausibility to this temporary response function solution.

For both colonies, the biomass stratum used as driver for egg/chick survival is the May (recruit) stratum the colony is located in (D for Robben Island, E for Dyer Island).

3.3.8.2.4 Breeding proportion

There are indications that there is a relationship between the energy content (kJ) of anchovies and sardine in Stratum C over the previous two years and the variation in breeder numbers on Robben Island (adjusted R^2 of 61%; Waller 2011). As the Dyer Island model uses the same stratum as a driver for adult survival, and in the absence of Dyer-specific data, this relationship was used for both models and the same approximately linear mapping as for egg/chick survival response was employed (above).

3.3.8.2.5 Equilibrium food level

Resampled food availability is evaluated for its effect on penguin survival in relation to the food availability level at which the penguin population is assumed to be in equilibrium (no population size change – model base state in absence of pressures). However, this level should be *lower* than the most common food availability level (long-term mean), as the latter would be expected to result in moderate growth rather than in population stasis. For example, in a global comparison of the response of seabird breeding success to food availability, Cury et al. (2011) found that the long-term mean of prey abundance constituted an approximate threshold below which breeding success started to decline. With the limited time since the re-establishment of the Robben Island penguin colony, we suggest that the median constitutes a more robust measure for our purposes than the mean, but assume that in the long term both would be reasonably similar.

This interpretation is supported by current penguin survival data. The GAM fits indicated good evidence for non-linear relationships. Figure 7 (above) shows adult penguin survival fitted to Stratum C spawner biomass as a log-linear model (blue, AICc = −21.5), a GAM model (red, AICc = −22.0) and a step function (black, AICc = −32.5). Dotted lines from left to right indicate 75% of median, median, and mean biomass. The step function indicates a critical threshold between 75% and 100% of median, below which the population is unlikely to be in equilibrium under natural conditions. The relationship between the penguin population growth rate [(Nt-Nt-1)/Nt-1] at Robben Island and biomass suggests a similar conclusion (Figure 8, below) (note: biomass estimates are from west of Cape Agulhas, following better model fit). Here the level of zero population growth (equilibrium) based on the step function (AICc = −2.99) is equal to biomass median (left dotted line), and that based on the log-linear model (left dotted line; AICc = −2.37) is slightly above the median.

Together these analyses indicate that a biomass level slightly below median is likely to result in zero population growth. Therefore, 75% of biomass median is assumed to be the equilibrium food level for the model base state. This means that under randomly resampled biomass and absent all pressures, the population will experience some growth, and will approximately double over 20 years. See 7.2.3 for sensitivity test results for this parameter choice.

Earlier version [Weller et al. (2014)]: The equilibrium food level was assumed to be equal to the long-term mean, i.e. the population on average maintained its size under random food resampling absent all pressures.
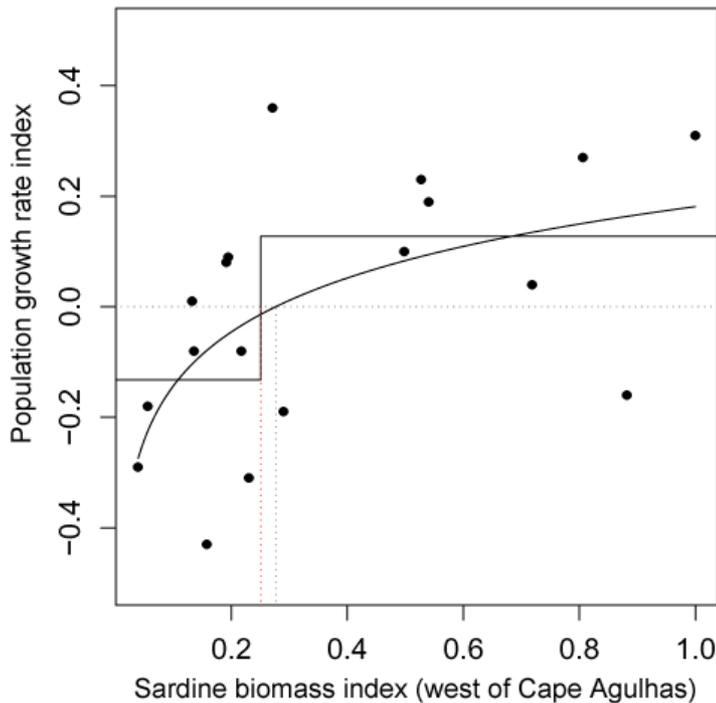
Figure 8.　　　African penguin population growth rate estimates, relative to November sardine spawner biomass west of Cape Agulhas divided by maximum recorded biomass. Log-linear model and step function are shown. Left dotted line: intersection of step function and zero growth level, and median biomass; right dotted line: intersection of log-linear model and zero growth level.

3.3.9　Density effects

Density effects	Robben Is. value	Dyer Is. value	Reference/Notes
Density parameters are constants.			
Number of adults below which breeding proportion is reduced due to Allee effects	200		Expert opinion. Reduction in breeding proportion by 10%
Number of adults below which breeding proportion is increased due to low resource competition	1500		Expert opinion. Increase in breeding proportion by 20%
Carrying capacity	25000		Current reduced Benguela upwelling ecosystem carrying capacity (Crawford et al., 2007)

Table 3.9　　　Climate and flooding parameters

The very low population level represents a threshold at which Allee effects come into comes into play (Courchamp et al., 1999), for reasons such as gender imbalance or decreased foraging efficiency. The existence of such a threshold for African penguins is likely (Ryan et al., 2012; Sherley et al. 2014a). In the absence of concrete data, a population size of 200 adults was assumed.

The low threshold represents a population level at which resource competition is decreased sufficiently that the proportion of breeders benefits (Sherley et al., 2014a). A population size of 1500 adults is a conservatively low value (R. Sherley, pers. comm.).

The carrying capacity of the modelled colony is typically close to the theoretical maximum number of penguins the island could sustain. This was set at 2.5×10^4 for each single-colony model, based on estimates of the current reduced carrying capacity of the entire Benguela upwelling ecosystem (Crawford et al., 2007). Colony-scale overpopulation effects on adult survival were not taken into account, as immature penguins would likely settle in other colonies if the island was overpopulated (Crawford et al., 2007).

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3.4   Summary of changes between model versions (Robben Island data)

Some parameters used in the original Robben Island model (Weller et al., 2014) were updated in the course of model development. While the previous version is no longer in use, and Robben Island results have been updated using the new model version, details of the previous version are provided in several sections in colored font to document continued model evolution. Changes to model data between these versions are summarized below and detailed in the respective subsections.

Mean egg survival (3.3.1) was calibrated upwards from 0.649 to 0.657, to increase long-term population stability under equilibrium conditions.

Predation effect strengths (3.3.3) were reduced for shark (adults and immatures 0.8 to 0.9, eggs and chicks 0.9 to 0.95) and terrestrial predation (eggs and chicks 0.85 to 0.9) to better conform to field information and expected model behaviour. Shark predation was linked to small pelagic food biomass to drive the mean and restrict the bounds of shark abundance variation.

Catastrophic oil spill frequency (3.3.6) was increased from 600 months to 180 months, based on re-interpretation of available data on spill occurrence and severity.

Climate effects (3.3.7) were reduced based on new analyses. Hot spell effects on eggs and chicks were lowered from 0.5 to 0.4 for eggs and 0.12 for chicks, and the proportion of nestlings lost to rain flooding was lowered from 0.4 to 0.3 for eggs and 0.1 for chicks. Cold spell effects were removed from both models because these events could not be sufficiently distinguished from occurrences of rain flooding.

Food drivers of adult and immature survival (3.3.8.2.1) were changed from the energy content (kJ) of the sum of sardine and anchovy spawners in November Stratum C, to sardine spawner biomass in Stratum C for adults, and sardine spawner biomass west of Agulhas (November Strata A, B and C) for immatures.

The equilibrium food level (3.3.8.2.5) was changed from the long term median of Zone 2 food biomass, to 75% of the median, causing the population to experience some growth at the most common food availability level rather than remain stable.

Carrying capacity (3.3.9) was reduced from a 'pristine ecosystem' value of 3×10^6 to a more current estimate of 2.5×10^4.

4 Conceptual model evaluation

4.1 Section summary

This TRACE element provides supporting information on: The simplifying assumptions underlying a model's design, both with regard to empirical knowledge and general, basic principles. This critical evaluation allows model users to understand that model design was not ad hoc but based on carefully scrutinized considerations.

This element contains the following subsections:

- 4.2 – Earlier models [39]
  The core of the model is based on the earlier demographic model by Shannon and Crawford (1999), from which it was adapted to a system dynamics platform and extended.
- 4.3 – Spatial and temporal scale [39]
  Implementations of the model are developed to cover individual colonies and the foraging zones found to be associated with them. A time step of one month is used to conform with the quality of most available data. Simulations are generally designed to be evaluated for a time span of 20 years.
- 4.4 – Stochasticity [40]
  This subsection provides details about the several different types of stochastic processes used by the model.
- 4.5 – Basic model assumptions [41]
  This section lists a number of basic assumptions made in the design of the model.

4.2 Earlier models

The demographic processes of the pressure model are based to a large extent on those used in the model of Shannon and Crawford (1999). It employs a 3 month time step and annual survival and mortality. Their model was intended to specifically explore the effects of egg harvesting and oiling on the Dassen island colony, using population parameters estimated for the Robben Island colony, but was not set up to model other pressures or integrate food availability as a driver. Its population model core (2.3) was translated into a systems dynamic framework and extended with relaying calculations (2.3.2.5) and pressure processes (2.4).

Motivations for the shift in modelling environment to system dynamics were the enhanced ability to explore heterogeneity and variability in environmental drivers, greater ease in integrating qualitative and resampled data and setting up feedback relationships, a framework that allows the creation of a library of modular pressure processes, and a graphical user interface that enables participatory model development and provides advanced output options.

The pressure model is being developed in versions incorporating cumulative improvements. A proof-of-concept prototype was developed into a functional simulation prototype (Cecchini, 2012) which was further expanded into a model suitable as a management decision tool for the Robben Island (Weller et al., 2014) and Dyer Island colonies (Weller et al., 2016).

4.3 Spatial and temporal scale

4.3.1 Spatial scale

Separate models are being developed for individual penguin colonies rather than for the meta-population as a whole. This is based on the finding that each colony is subject to a different combination of drivers and pressures, and thus would have to be treated at least as a separate sub-model (Crawford et al, 1999; Ludynia et al., 2014). Available data are generally also colony-specific, and quality and availability of demographic data influence the choice of target colonies, as some colonies have received much more thorough and consistent research coverage than others. While adult penguins tend to remain faithful to a colony after their first breeding season (Crawford et al., 2001, 2010), there is migration of juveniles and young adults between colonies, which makes development of a meta-population model crucial; however, migration remains difficult to estimate due to paucity of marked individuals (Sherley et al. 2013b, 2014a). Further developments in this area would greatly

improve the predictive power of the pressure model. Transponder studies currently underway include chicks from the majority of colonies and are expected to yield additional data in the near future.

Spatial inference of each colony model is for a breeding period foraging zone extending 15 nautical miles (28 km) from the colony (Zone 1) and a larger general region providing prey to penguins when they are not rearing chicks (Zone 2). For specifics, see 2.4.1 and 3.3.8.2.

4.3.2 Temporal scale

The model uses a time step of one month. Some processes in the model would be more realistically represented by using shorter time scales; e.g., development of nestlings and changes in nestling mortality are more accurately tracked in weekly increments. However, a weekly time step would constitute empty resolution for several other data sources, particularly for the main driver (food availability) and for several other pressures (fisheries catch, seal predation, moderate human disturbance), all of which use monthly data. A larger time step (e.g. quarterly, as in Shannon and Crawford, 1999) would reduce model uncertainty, but discard finer-grained data for the above processes, several of which are well parameterized with monthly data records. It was therefore decided that current data availability favoured a monthly time step.

Analyses, including those used for further calibration of model parameters, were generally restricted to a simulation time frame of 20 years. This was regarded as suitable because shorter periods would conflict with the relatively long generation time of African penguins (~4 years; Crawford et al., 1999), the susceptibility of model outputs to stochasticity in the short term, and the intended use of the model as a strategic planning tool for mid- to long-term conservation actions; and because longer simulation periods would become increasingly dependent on absence of changes in current input estimates (e.g., anchovy and sardine distribution in the Agulhas region, magnitude of fisheries takes, and seal predation levels).

4.4 Stochasticity

The model uses several levels of stochastic representation for processes where a range of inputs and/or responses is indicated by the data. In descending order of specificity, these are:

- PDF-driven resampling
  Where a sufficiently long time series of input values for a process is available, input for simulation is determined by resampling with replacement from a database. Under the assumption that the long-term distribution of values constitutes the best guide to relative frequency of values, weighting for the sampling process is determined by a PDF constructed by interpolation from the data's frequency distribution (see 3.3.8.1). Sampling is carried out using Vensim function RANDOM LOOKUP. Note that this method will not resample individual records, but values from a contiguous sampling domain defined by those records, thus reducing the likelihood of the occurrence of repetitive model states. This approach is used for determining food availability (3.3.8) and gull predation rate (3.3.5).
- Normal variation
  Where normal distributions are used and either standard deviation or truncation distance is unknown or undefined, following common practice, truncation distance is set as 3 × stdev ([a]), or inversely, stdev is set as truncation distance / 3 ([b]).
  - Normal variation with adjustments
    Where variation following a normal distribution can be assumed and some further impact on the distribution is known, a normal distribution with additional adjustments is employed. This approach is used for biomass availability in Zone 1 (logit-like restriction to truncation[b]; 2.4.1.1), shark abundance (logit-like restriction to truncation[b]; 2.4.3.1), and breeding proportion among sexually mature adults (food-driven shift in mean; 2.3.2.5.1, 2.4.1.2).
  - Normal variation without adjustments
    Unadjusted normal distributions are used for terrestrial predation intensity ([b]; 2.4.3.1), the proportion of each adult age class that is sexually mature (3.3.2), and the random component of relaying probability ([a]; 2.3.2.5.3).
- Poisson processes

Poisson processes with an expected mean of "1 / mean number of months between events" are used to determine the occurrence of rare events. The event happens if the drawn value is > 0, and happens multiple times if the value is > 1.

This approach is used for chronic and catastrophic oiling (2.4.2), moderate and catastrophic human disturbance (2.4.4), rain flooding and wave flooding (2.4.5), hot spells (2.4.6), and the frequency randomization options for seal and gull control regimes (currently undocumented). For cumulative occurrence probabilities for these processes, see 7.3.

Earlier version [Weller et al. (2014)]: Maximum value of Poisson draws was capped at 1, i.e. no event could happen more than once per month. The update removes this arbitrary restriction.

- Uniform variation
  Uniform random variation is employed for a few processes that have no direct connection to ecological processes. This approach is used for random year determination if specific year ranges of food records are resampled (3.3.8.1) and for the intensity randomization options for seal and gull control regimes (currently undocumented).

4.5   Basic model assumptions

The simplifying assumptions made in the implementation of each pressure process are described in the relevant subsections of section 2 (Model description) and 3 (Data evaluation). However, some general assumptions were made about the behaviour of the population as a whole, which are listed below.

- *Unless specifically manipulated, estimates for environmental parameters remain at current levels or within current bounds of variation for the duration of the simulation (usually 20 years).*
  This particularly concerns predation pressure by fur seals and kelp gulls, which fundamentally depends on predator population levels. While the seal population at Dyer Island has remained approximately stable over the last 20 years (A. Makhado, pers. comm.), gull numbers have increased markedly in the recent past (Ludynia et al., 2014). However, due to lack of data there is no basis for estimating likely future changes in population size for either species, nor the effects in terms of predation pressure such a change might have. The default assumption is thus a continuance of the current estimates.
  The occurrence of climate and catastrophic oiling events can be considered buffered against short-term changes by their low frequency, and food biomass availability by the long time series that is resampled.

- *The penguin population is in demographic equilibrium at time zero.*
  This is almost certainly untrue for any start date but a necessary and generally recommended modelling practice to establish a model base state (Renshaw, 1993).

- *All adult age classes are assumed to share a common survival rate.*
  This assumption is generally made due to the difficulty of estimating the age of individual adults in the field (as age classes do not differ in size) and resulting lack of data on age-specific survival rates (e.g., Crawford et al., 2011). Behavioural differences at sea are believed to be minor.

- *The survival rate of immature penguins between 1 and 2 years of age is equal to the adult survival rate.*
  See previous assumption; model-based age-specific survival rates are under investigation but cannot yet be estimated with confidence (Sherley et al., 2014a).

- *The survival rate for immature penguins aged less than 1 year is lower due to e.g. inexperience in foraging and predator avoidance.*
  This is generally true in seabirds (e.g., Sæther and Bakke 2000) and has been demonstrated for African penguins in particular (Whittington 2002).

- *The penguin population is not subject to immigration*
  This is untrue (Sherley et al., 2013b, 2014a; Ludynia et al., 2014) but a necessary simplification until suitable data on migration are available. Note that this assumption was relaxed in modifying base

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survival parameters for an equilibrium population ([3.3.1](#)) and in assuming no unpaired penguins of breeding age ([2.3.2.5.1](#)). Note also that a model-derived amount of **emigration** is used in all management scenarios of the Dyer Island model ([3.3.1](#)).

5   Implementation verification

5.1   Section summary

This TRACE element provides supporting information on: (1) whether the computer code for implementing the model has been thoroughly tested for programming errors and (2) whether the implemented model performs as indicated by the model description.

This element contains the following sub-sections:

- 5.2 – Code testing and verification [43]
  The model code is compiled and error-checked on execution. Processes were tested extensively during and after model construction.
- 5.3 – User interface [43]
  The model is displayed in flow graph form and can be edited on-screen. Data is loaded from an external spreadsheet source for easy manipulation of parameters. A free model reader for read-only exploration and execution of model files is available.
- 5.4 – Output and output options [44]
  Time series of all variables are stored at arbitrary replication and can be exported or displayed in-program as tables or various types of graphs.
- 5.5 – Extensibility [44]
  The model is modular by design and easily extendable with further processes or to new colonies. Construction of a meta-population model is likely to require the use of additional data exchange programs.

5.2   Code testing and verification

Vensim models are compiled at run-time, which includes the usual suite of code and consistency checks. The engine at this time also checks for circular definitions and other similar issues that may occur in a feedback-heavy model environment. Emergent errors such as exceeded data ranges are logged and reported during model execution.

During model construction, internal consistency and desired output of individual processes or process groups were tested by tracking the behaviour of involved variables in simplified (isolated process) or manipulated (extreme input values) model runs. Sensitivity tests were used to verify process behaviour over a range of inputs in the completed model (see 7.2).

5.3   User interface

Vensim provides a graphical user interface that displays the model as a flow graph, with nodes and links representing individual equations (or systems of equations) and data sources, which can be edited on the same interface (Fig. 9). Multiple other options for code display and management also exist, such as searchable parameter lists, text-only mode, causal trees etc. For users that do not have access to a commercial version of Vensim, a free Model Reader is available (http://vensim.com/vensim-model-reader/) that allows exploration and execution but not alteration of provided model files.

The large majority of parameters is read on execution from a Microsoft Excel spreadsheet that acts as external database. This allows easy manipulation of runs, including changing environmental parameter ranges, switching pressures on or off, and manipulating demographic parameters, without requiring alteration of the model code. Aside from simplifying tests during model construction and evaluation, this setup also enables easier access by stakeholders during mediated model-building.

The engine also supports the inclusion of a layer of 'gaming variables' that allow on-the-fly graphical manipulation of model parameters, however this has not been implemented in the current version of the model.
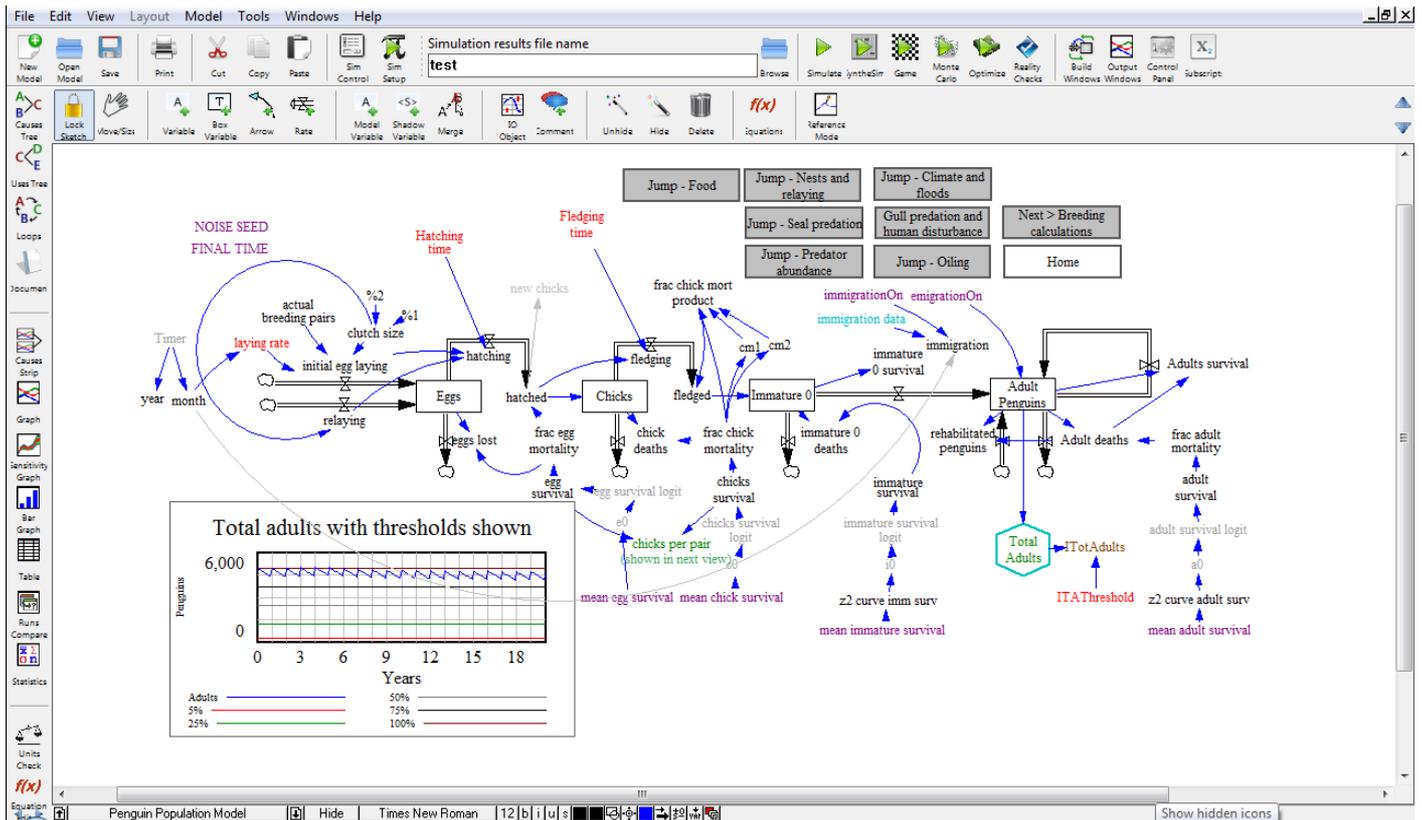
Figure 9   Vensim graphical user interface, showing the demographic core model. Submodels are accessed by a series of custom links (top of model). Various types of graphical output for individual parameters can be integrated into the model view (bottom left: total adult population trace).

5.4   Output and output options

Model runs can be saved as files and loaded for display singly or in combination for on-screen comparison. Time series of all variables over an arbitrary number of replicate runs are stored and can either be exported as text files for further processing, or displayed in-program as bar graphs, line graphs, or tables. For the purposes of the pressure model, useful options are the display of variable time series for individual runs (e.g., Fig. 9, bottom left), the percentile display of output distribution across replicates (e.g., Fig. 12, top), and the export of replicate time series for further visualization with tools like R (e.g., Fig. 12, bottom). Execution is very fast for models of this size and allows standard use of high replicate numbers (5000 replicates used throughout this document).

5.5   Extensibility

The configuration of the model was kept expressly modular by design, as it is intended to be adapted to individual colonies with separate pressure configurations. While extension to a new colony is not trivial, it is largely a matter of external data preparation rather than changes in model structure. Further pressures or other processes may be added at any time and can be switched on or off from the external spreadsheet source.

An eventual goal is the construction of a meta-model that combines several colony models and enables accurate real-time simulation of migration between them. As Vensim currently does not support parallel processing of multiple models, this will likely require a) the construction of a combination model, b) a workaround solution featuring sequential simulations of colonies in assumed migration sequence, or c) the adoption of an external data exchange agent (e.g., MetaModel Manager; Pollak and Lacy, 2013) to mediate between models run in separate simultaneous instances of Vensim. Option c) may be challenging to implement but is probably the most potent solution, while a) should be avoided as it may destabilize the code, introduce hard-to-detect errors and would require rebuilding for each new colony. Option b) may present a useful interim approach, if the migration 'source' or 'sink' status of individual colonies can be determined with acceptable accuracy.

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6 Model output verification

6.1 Section summary

This TRACE element provides supporting information on: (1) how well model output matches observations and (2) how much calibration and effects of environmental drivers were involved in obtaining good fits of model output and data.

This element contains the following subsections:

6.2 Fit to observed population development

Estimates of adult penguin population sizes made at colonies contain a measure of uncertainty. Specifically, they may be derived from counts of individuals undergoing moult, or from counts of nests or nest sites that are then converted into total adult numbers using a suitable conversion factor (Crawford and Boonstra, 1994). Nest counts may tend to overestimate breeding adult numbers because penguins can use multiple nests in a season. While moult counts may be regarded as more reliable (Kemper, 2007), both methods are frequently subject to bias. Therefore, the model's population predictions were put into the context of estimate series derived from both moult counts (taken from Robinson, 2013) and nest counts (taken from Makhado et al., 2013b). Scenarios were run in 5000 replicates with random noise streams driving stochastic processes.

6.2.1 Robben Island

This scenario attempts to replicate recorded population developments at the Robben Island colony from 1988–2012, using various assumptions to produce a range of possible trajectories approximating observed population dynamics. Using default pressure parameters and realistic timing of the two oil spills recorded during that period (Wolfaardt et al., 2008), the behaviour of the modelled population did not match the dynamics indicated by the two record series (Figure 10, lower shaded series), showing that the output space of the model using standard parameterization (which is largely based on the means of field estimates) did not encompass the trajectory taken by the population in that period.

Several ecologically sound assumptions about specific circumstances active between 1988 and 2012 were therefore made.

- Although immigration was an important factor for the period 1992–2003 (Crawford et al., 1999, 2008), there is currently no immigration process in the standard model setup. Here, we attempted to provide rough estimates of available immigrants from other colonies in the Western Cape and Namibia, under the assumptions that these numbers would provide an approximate upper bound for penguins choosing to breed at Robben Island during this period. Immigrants were assumed to be of age class I1 (two-year old immatures) and were added into the population in January of each year. Rough maximal estimates of available immigrants for the period 1990–2012 were produced using the following formulas:

  Western Cape: annual penguin population estimate × breeding success × immature survival × immigration rate

where the sum of the annual penguin population estimate for all Western Cape colonies (1990–2012) is taken from Makhado et al. (2013b); breeding success (clutch size × egg survival × chick survival) uses the mean Robben Island estimate of 0.39; immature survival is the mean for Robben and Dassen island from 1994/95 to 2011/12 of 0.42 (Sherley et al., 2014a); and immigration rate of 0.2 is a conservative estimate based on Sherley et al. (2014a).

Namibia: annual penguin population estimate × overall survival rate × immigration rate

where the sum of the annual penguin population estimate for the main Namibian colonies (1992–2009) is based on unpublished data from the Ministry of Fisheries and Marine Resources (J. Kemper, unpublished data); the overall survival rate for adults at Namibian colonies is 0.74 (Crawford et al., 2011); and the immigration rate of 0.025 is based on an approximate calculation carried out using the state-base model results described in Sherley et al. (2014a). Numbers of estimated immigrants per year are given in Table 4, together with a forecast of numbers for 2015–2035 (based on prediction from linear regression of recorded time series).

- Mean age at first breeding among African penguins can be assumed to respond to food availability and demographic factors (Crawford et al., 1999), but data on the nature of this response are still scarce (Whittington et al., 2005). As there is insufficient parameterization for a process simulating its relationship to food availability, the mean proportion of each adult age class that is sexually mature is fixed in the model, with a small amount of normal variation (3.3.2). However, the rapid increase in population size at Robben Island between 1990 and 2004/5 suggests that age at first breeding was lower than average during this period. To simulate this, default sexual maturity proportions for adults aged 2–5 (5%, 33%, 74%, 100%) were increased (50% for age 2, 100% for older) for the period 1988–2004, and reset to default values thereafter.

- Following a sustained upsurge in small pelagic fish abundance in the early 2000s (Coetzee et al., 2008), it is possible that marine predator populations increased more strongly over several years than is implied by the food biomass link currently implemented for shark predation in the model (2.4.3.1). A more pronounced shift in predation pressure from relatively low (mean of -0.5 in a range of -1 to 1) until 2003 to relatively high (mean of +0.5) afterwards was therefore included in the scenario.

Using these assumptions, model output replicates recorded population dynamics with acceptable accuracy (Figure 10, upper shaded series). Recruitment between 1990 and 2004/5 still appears to have been larger than can be accounted for by recognized factors, as was population decline from 2008 onwards. The latter can be largely addressed by assuming a cessation of immigration at this point (not shown). This scenario demonstrates the difficulty of forecasting the likelihood of individual timelines within the range of variation when incorporating a large number of incompletely understood influences.
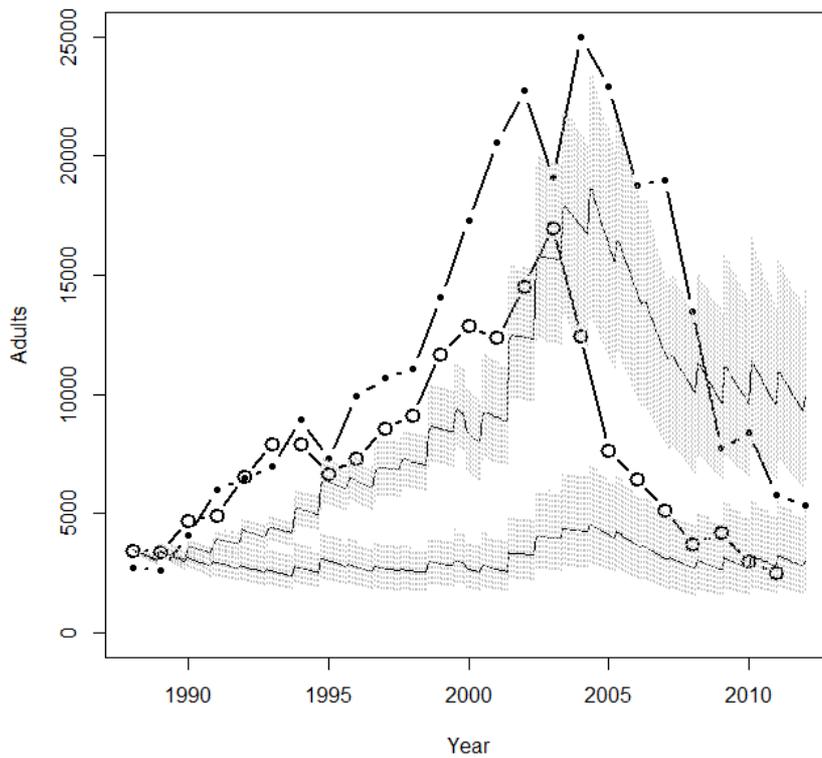
Figure 10.   Recorded population development (number of adult African penguins) at the Robben Island colony 1988–2012, compared to model output using recorded food biomass for that period (5000 replicates). Empty circles: population based on moult count records; black dots: population exrapolated from nest counts. Lower shaded series: modelled series using default pressure parameters. Upper shaded series: modelled series using default pressure parameters and adding immigration, changes in shark predation, and changes in age at first breeding. Shaded ranges indicate 95% confidence intervals.

Year	West Coast immigrants	Namibian immigrants	Combined immigrants	Year	Forecast combined immigrants
1990	303	N/A	303	2015	130
1991	284	N/A	284	2016	121
1992	320	136	456	2017	112
1993	126	144	270	2018	103
1994	241	112	353	2019	95
1995	214	124	338	2020	86
1996	178	109	287	2021	77
1997	173	102	275	2022	68
1998	140	99	239	2023	59
1999	167	106	273	2024	50
2000	170	91	261	2025	41
2001	190	107	297	2026	32
2002	173	121	295	2027	24
2003	160	108	268	2028	15
2004	182	74	256	2029	6
2005	176	85	261	2030	0

2006	152	59	211	2031	0
2007	120	66	186	2032	0
2008	143	89	233	2033	0
2009	115	80	196	2034	0
2010	118	N/A	118	2035	0
2011	119	N/A	119		
2012	159	N/A	159		

Table 4. Left: estimates of immigrants used in the Robben Island realistic scenario. No estimates of Namibian population sizes to base immigrant numbers on were available for 1990/91 and 2010/11/12. Right: forecast number of combined immigrants for 2015–2035, based on prediction from linear regression of 1990–2012 numbers.

6.2.2 Dyer Island

This scenario uses the time series of recorded small pelagic biomass from 1990–2012 to attempt a replication of recorded population developments at Dyer Island. While moult counts are generally regarded as a more reliable indication of the size of the resident population (Kemper, 2007), in the case of the Dyer Island penguin colony they can be expected to be misleading because a substantial percentage of penguins breeding on the island do not moult there (Waller 2011). Modelled population numbers were therefore compared only to adult numbers extrapolated from nest counts using an empirical conversion factor of 3.2 (Crawford and Boonstra, 1994). Model output is based on annual means of the period May–July (peak breeding season at this colony), with all pressures enabled and a single known oil spill of unidentified origin occurring in 1995 (Wolfaardt et al., 2008). A 1990 starting population of 27 500 adults is assumed (Underhill et al., 2006).

Figure 11 shows recorded (large dots) and modelled (shaded) time series, with model output range (95% CI) indicated by the shaded range. The lower series represents model output using default model parameters, which provides values that are slightly lower than in the nest count series. As recruitment into the adult population at Dyer is probably strongly reduced by unmodelled high emigration of immatures to other colonies, an immature emigration rate of 50% (annual reduction in numbers entering the first adult age class) has been included in all model runs; this roughly corresponds to lowering immature survival from the equilibrium state value (0.51) to the original estimate of 0.247 (3.3.1; Ludynia et al., 2014). When this reduction is omitted, the modelled population remains slightly above recorded numbers (upper shaded series). Taking uncertainty in nest counts and conversion into account and considering that the nest count series likely has an upwards bias, this suggests that the default parameterization captures population dynamics well at this colony.
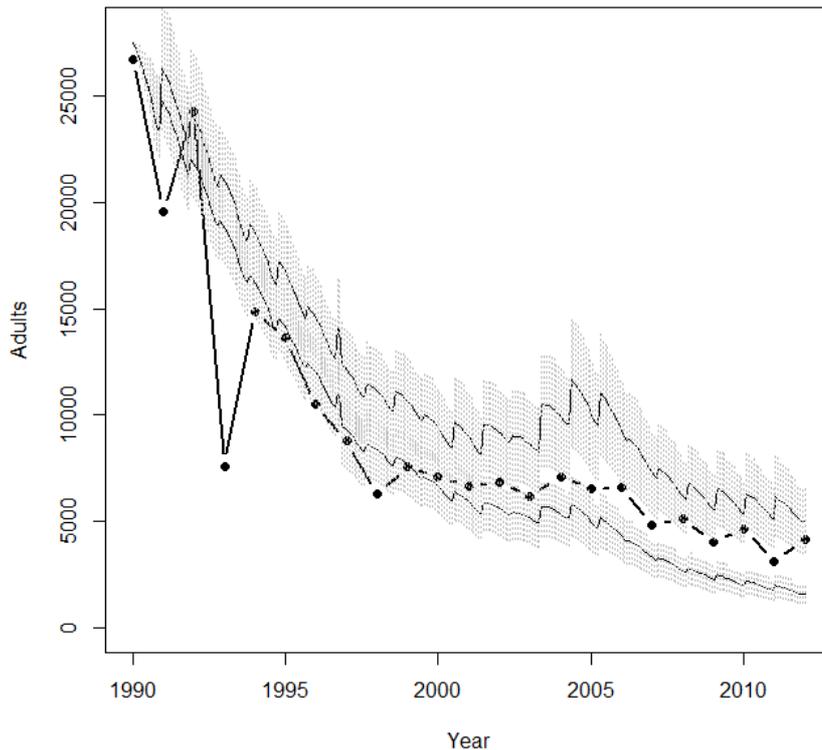
Figure 11.   Recorded population development (number of adult African penguins) at the Dyer Island colony 1990–2012 (black circles), compared to model output using recorded food biomass for that period (5000 replicates). Upper shaded series: modelled series using default pressure parameters without immature emigration. Lower shaded series: modelled series using default pressure parameters with immature emigration (50%). Shaded ranges indicate 95% confidence intervals.

While the model thus allows a closer fit of simulated population development to historic records in the case of one colony than in the other, we conclude that given the uncertainty of the available data, the model performs sufficiently well to be useful in evaluating strategic scenarios.

6.3   Calibrated parameters

Several parameters that were originally based on field estimates or literature were calibrated further once the model was set up. Details about calibration are given in the indicated subsections in section 2 (Model description) and 3 (Data evaluation).

Mean age class survival values were adjusted upwards from field estimates to derive parameterization for a hypothetical equilibrium population in absence of all pressures. This population state is then modified by pressure influences to produce a realistic population response to environmental influences. In effect, field estimates are recorded with pressures active, which are then i) subtracted to generate a stable base state and ii) added on again to generate realistic population behaviour. The latter process is governed by pressure parameter estimates, the former by in-model calibration. Calibration was performed by adjusting survival rates to produce a population that remained as close as possible to its starting size over a period of 100 years, while keeping each rate within the recorded range of values for its age class. Affected parameters are egg and chick survival (Robben), immature survival (Dyer), and adult survival (both) (3.3.1).

Immature emigration rates from Dyer Island (50%) were calibrated such that the number of immatures entering the first adult age class approximately matched that resulting from using the original, lower immature survival estimate (3.3.1), while simultaneously producing a good fit to recorded population developments (6.2.2).

The number of chicks successfully fledged or lost in two chick nests as compared to one chick nests was adjusted when a comparison to recorded breeding success rates (Crawford et al., 2006b; Sherley et al., 2012) showed that an apparent lack of independence between chick survivals in two chick nests was not being addressed. Empirical adjustment factors wered added to match the expected outcome (2.3.2.5.4).

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7 Model analysis

7.1 Section summary

This TRACE element provides supporting information on: (1) how sensitive model output is to changes in model parameters (sensitivity analysis), and (2) how well the emergence of model output has been understood.

This element contains the following subsections:

7.2 Pressures in isolation

7.2.1 Overview

The impact of processes representing individual pressures was evaluated in isolation from the effects of other parameters. Table 5 lists the influence of all implemented pressures in the Robben and Dyer Island models at base strength, in terms of median change in adult population size over 20 years (5000 replicates), with pressures

acting in isolation on the equilibrium population (note that this implies an absence of any immigration/emigration influences).

Process impacts were also tested for their sensitivity to changes in input parameters. Generally, sensitivity was tested separately for changes in effect strength (e.g., proportion of adult penguins affected by an oil spill) and effect frequency (e.g., mean occurrence interval of oil spills), where applicable. Modifications were evaluated at five levels: current implementation ('base'); two levels of small changes – 'low' and 'high' (90% and 110% of base value); and two extremes – 'very low' and 'very high' (50% and 150% of base value). Value permutations are listed in Table 6. Tests of modified values were run for a period of 20 years, with 5000 replicates, in an equilibrium population with a starting size of 3500 (Robben; Crawford et al., 2011) / 4950 adults (Dyer; Makhado et al, 2013b). Results are presented in the form of a) a population trace of 100 years duration that shows adult population development in the long term under base conditions, and b) a level comparison graph that shows distribution of population sizes after 20 years for each level of modification. These are presented and discussed in the subsections below. Note that in the former, the point in time listed in Table 5 occurs early in the trace (after 20 years); and that in the latter, the darkest shaded interval represents the mode, which may differ from the median in strongly skewed distributions.

	Median change in adult population size over 20 years	
Pressure	**Robben Island**	**Dyer Island**
Food availability (resampling 1988–2012)	+ 110%	+ 95%
Immature emigration	N/A	- 66%
Catastrophic oiling	- 13%	- 14%
Chronic oiling	- 30%	- 38%
Rain flooding	- 3%	- 7%
Hot spells	- 5%	- 6%
Wave flooding	N/A	- 3%
Shark predation	± 0%	N/A
Terrestrial predation	± 0%	N/A
Seal predation	N/A	- 76%
Gull predation	N/A	- 10%
Gull predation incl. moderate human disturbance	N/A	- 12%
Heavy human disturbance	N/A	- 5%

Table 5. Effect of pressures at base strength and in isolation, on equilibrium adult penguin population size after 20 years (5000 replicates). All pressures (except food availability) were tested with food disabled as a driver.

	Parameter (frequencies) / Strength of parameter influence (others)					
Parameter	**Very low**	**Low**	**Base**	**High**	**Very high**	**Model**

Food availability

Egg and chick survival	0.75	0.55	0.5	0.45	0.25	Robben
						Dyer
Food link to breeding proportion	0.075	0.135	0.15	0.165	0.225	Robben
						Dyer

Equilibrium food level

Percent of median food availability	100	82.5	75	62.5	50	Robben
						Dyer

Immature emigration

Immatures removed before entering A2 class	0.25	0.45	0.5	0.55	0.75	Dyer

Catastrophic oiling

Adults affected	0.120	0.216	0.240	0.264	0.360	Robben
	0.165	0.300	0.330	0.363	0.495	Dyer
Immatures affected	0.050	0.090	0.100	0.110	0.150	Robben
	0.070	0.126	0.140	0.154	0.210	Dyer
Frequency	270	198	180	162	90	Robben
	396	290	264	238	182	Dyer

Chronic oiling

Adults affected	0.004	0.0072	0.008	0.0088	0.012	Robben
	0.0045	0.0081	0.009	0.0099	0.0135	Dyer
Immatures affected	0.0003	0.00054	0.0006	0.00066	0.0009	Robben
	0.0004	0.0006	0.0007	0.0008	0.0015	Dyer
Frequency	5	4	3	2	1	Robben
						Dyer

Shark predation

Adult and immature survival	0.99	0.99	0.9	0.81	0.45	Robben
Egg and chick survival	0.99	0.99	0.95	0.855	0.48	Robben

Terrestrial predation

Egg and chick survival	0.99	0.99	0.9	0.81	0.45	Robben

Seal predation

Adult loss	0.038	0.068	0.075	0.083	0.113	Dyer
Chick loss	0.33	0.594	0.66	0.726	0.99	Dyer

Gull predation

Maximum proportion of predated nests	0.075	0.135	0.15	0.165	0.225	Dyer
Low food effect	0.25	0.45	0.5	0.55	0.75	Dyer

Moderate human disturbance effect	5	9	10	11	15	Dyer
Moderate human disturbance frequency	1.5	1.1	1	0.9	0.5	Dyer

Rain flooding

Egg loss	0.15	0.27	0.3	0.33	0.45	Robben
	0.125	0.225	0.25	0.275	0.375	Dyer
Chick loss	0.05	0.09	0.1	0.11	0.15	Robben
	0.125	0.225	0.25	0.275	0.375	Dyer
Frequency	90	66	60	54	30	Robben
	54	39	36	32	18	Dyer

Wave flooding

Egg and chick loss	0.025	0.027	0.03	0.033	0.045	Dyer
Frequency	54	39	36	32	18	Dyer

Hot spells

Egg loss	0.2	0.36	0.4	0.44	0.6	Robben
						Dyer
Chick loss	0.06	0.118	0.12	0.132	0.18	Robben
						Dyer
Frequency	54	39	36	32	18	Robben
						Dyer

Heavy human disturbance

Egg and chick survival	0.25	0.45	0.5	0.55	0.75	Dyer
Frequency	180	132	120	108	60	Dyer

Table 6. Parameter modifications used in sensitivity tests. Very low = 50%, low = 90%, base = 100%, high = 110%, very high = 150%; capped at 0.99. Base level of modified parameters is that shown in Table 3.

7.2.2 Mean Survival Values

As the mean survival values are central to the population model, it was expected that changes to these values would significantly affect population development for both colonies. Using base values, equilibrium populations remained within a few percent ($\pm$) of starting numbers over 50 years. However, an increase of 10% in adult survival parameters led to populations reaching carrying capacity (25000) within 25 years, followed by a continued increase despite a reduction in breeding proportion by 60%. A decrease of 10% invariably led to extinction within 50 years. Equivalent changes to the three other survival rates respectively led to a decrease by 50% of starting size over 30 years and by 75% over 100 years, and numbers reaching carrying capacity within 90 years.

As expected, changing these fundamental estimates produces significant changes in the model results. This part of the model is particularly dependent on comprehensive field data and their ecologically sensible adjustment to model requirements, as estimates of real survival parameters must be modified to compensate for unmodelled influences. Recent estimates of survival rates for the Robben Island colony suggest preliminary values of ~ 0.87 for adults and ~ 0.43 for immatures (Abadi et al., unpublished data), yet immature survival in the model needs to be higher to simulate an unpressured population. As more data become available, it will be possible to

replace such adjustments with explicitly modelled dynamics, e.g. the influence of migration between colonies on mark-recapture estimates of immature and adult survival at specific locations (Abadi et al., unpublished data).

7.2.3 Food availability

Food availability is the main stochastic driver of the model, due to the high responsiveness of the population to the underlying resource flow. There is a wide range of outcomes based on the high variance of the resampled biomass data. As the equilibrium food level is assumed to be lower than the median of resampled food values (75% of median; 3.3.8.2.5), the population will grow in the absence of other pressures, doubling within 20 years and reaching carrying capacity within 30–50 years (Fig. 12, top). Note that there is relatively little variability among effect strength levels, as the parameters varied in the sensitivity tests are restricted to egg and chick survival and breeding proportion, while adult and immature survival are driven by fitted response curves that cannot reasonably be varied widely (see 3.3.8.2).
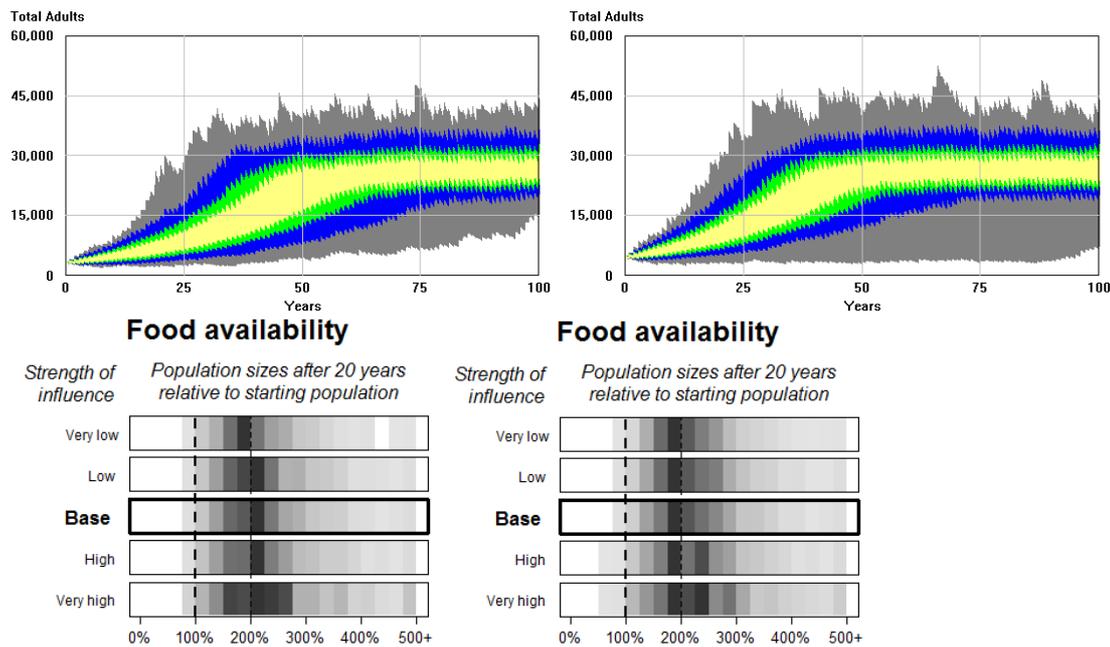
Figure 12.   African penguin population development (number of adults) under the influence of food availability in isolation, across 5000 replicates with random noise streams, at Robben (left) and Dyer islands (right). Top: Population development at base level over 100 years. Color ranges indicate the probability that any individual model run would fall within the respective band (50%, 75%, 95%, 100%). Bottom: Population development after 20 years, using five levels of pressure parameter modification (Table 6). Distributions are shaded by relative frequency of intervals within each level (10% intervals, darkest shade indicates mode interval).

7.2.3.1   Equilibrium food level

The food biomass level at which the population holds stable at its current size (barring other influences) was set to 75% of the long-term biomass median, based on several data analyses (3.3.8.2.5). If randomly resampled biomass (i.e., median biomass over sufficiently many replicates) is used as input, an equilibrium level equal to biomass median will on average result in no population growth; at the implemented level of 75%, the population will approximately double over 20 years, with even lower levels rapidly increasing growth over time (Fig. 13).

As the baseline for population growth or decline, this is a sensitive parameter, and alterations will significantly change model response to provided biomass data. While our analyses of correlations between biomass and penguin survival and reproduction (3.3.8.2.5) allow for some confidence here, further corroboration from other colonies is certainly desirable.
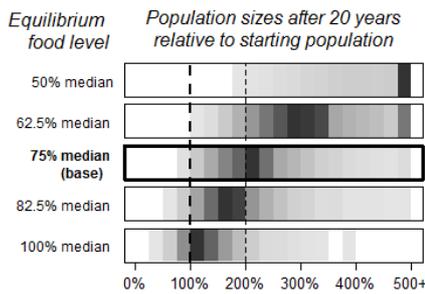
Figure 13. African penguin population development (number of adults) under the influence of food availability in isolation, a different equilibrium food levels (expressed as % of long-term food biomass median). Population development after 20 years across 5000 replicates with random noise streams is shown, using five levels of parameter modification (Table 6). Distributions are shaded by relative frequency of intervals within each level (10% intervals, darkest shade indicates mode interval).

7.2.4 Immature emigration

An immature emigration level of 50% was used in all Dyer Island management scenarios (see 3.3.1 for details). Together with predation by fur seals on adult penguins, this is the dominant pressure in the Dyer Island model. As expected, the removal at this point of half of the annual recruitment into the pool of breeding adults severely limits the ability of the population to compensate for losses due to other pressures, and on its own already leads to a median loss in adult population years of 66% over 20 years (Fig. 14, left; Table 6).

As emigration is implemented as a fixed direct loss of individuals, there is no variability in trajectories from the pressure process itself (Fig. 14, right). The pressure is moderately sensitive to changes in implemented strength, however, the 'very low' strength level (25% emigration rate) will still nearly halve the population over 20 years.

Since the impact of emigration is both pronounced and possibly somewhat intransigent to management actions (due to current lack of understanding of the exact causes), it presents a problem when modelling management scenarios, as population decline from emigration losses will tend to overpower the effects of most pressure mitigations. To cover possible developments, such scenarios will thus need to include variants where the lowering of emigration rates as a result of other management actions is assumed (Weller et al., 2016). Further investigations into the causes of emigration and the source or sink status of individual colonies, presumably through tagging and tracking studies, are urgently needed in this respect.
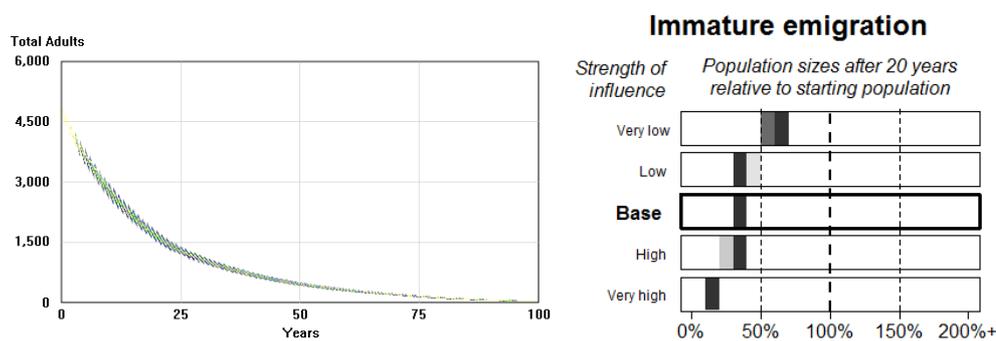

Figure 14. African penguin population development (number of adults) under the influence of immature emigration in isolation, across 5000 replicates with random noise streams, at Dyer Island. Left: Population development at base level over 100 years. Color ranges indicate the probability that any individual model run would fall within the respective band (50%, 75%, 95%, 100%). Right: Population development after 20 years, using five levels of pressure parameter modification (Table 6). Distributions are shaded by relative frequency of intervals within each level (10% intervals, darkest shade indicates mode interval).

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7.2.5   Catastrophic oiling

Catastrophic oiling occurs very rarely (mean frequency of 180 months (Robben) / 264 months (Dyer)) but with high impact, leading to a wide spread of possible outcomes (Fig. 15, top) with a median population loss of ~14% over 20 years. Sensitivity to changes in both strength (Fig. 15, middle) and frequency (Fig. 15, bottom) is low.
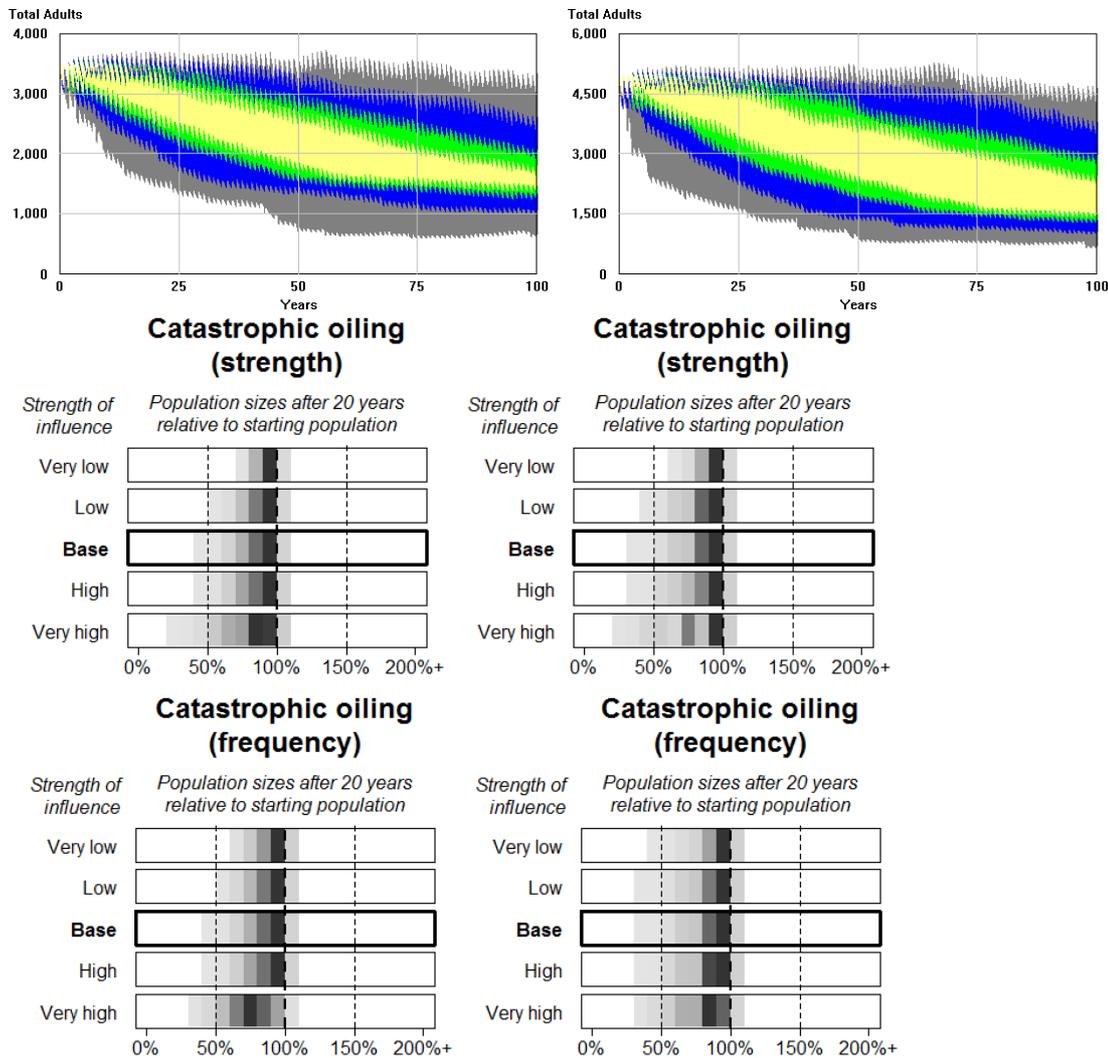

Figure 15.   African penguin population development (number of adults) under the influence of catastrophic oiling in isolation, across 5000 replicates with random noise streams, at Robben (left) and Dyer islands (right). Top: Population development at base level over 100 years. Color ranges indicate the probability that any individual model run would fall within the respective band (50%, 75%, 95%, 100%). Below: Population development after 20 years, using five levels of pressure strength modification (middle) or pressure frequency modification (bottom) (Table 6). Distributions are shaded by relative frequency of intervals within each level (10% intervals, darkest shade indicates mode interval).

7.2.6   Chronic oiling

Chronic oiling events have a smaller individual impact, but occur much more frequently (mean frequency 3 months), resulting in a consistent and strongly negative impact (Fig. 16, top) that is somewhat responsive to modifications in strength (Fig. 16, middle) and more so to further increases in frequency (Fig. 16, bottom). Mean population loss over 20 years at Robben Island is approximately twice that of catastrophic oiling (30%), and larger at Dyer Island (38%). This difference between colony models appears to be due to the small differences in estimated rehabilitation percentage (90% (Robben) / 84% (Dyer)) and even smaller increases in estimated number of affected penguins at Dyer Island (+ 0.1% of adults, + 0.01% of immatures).
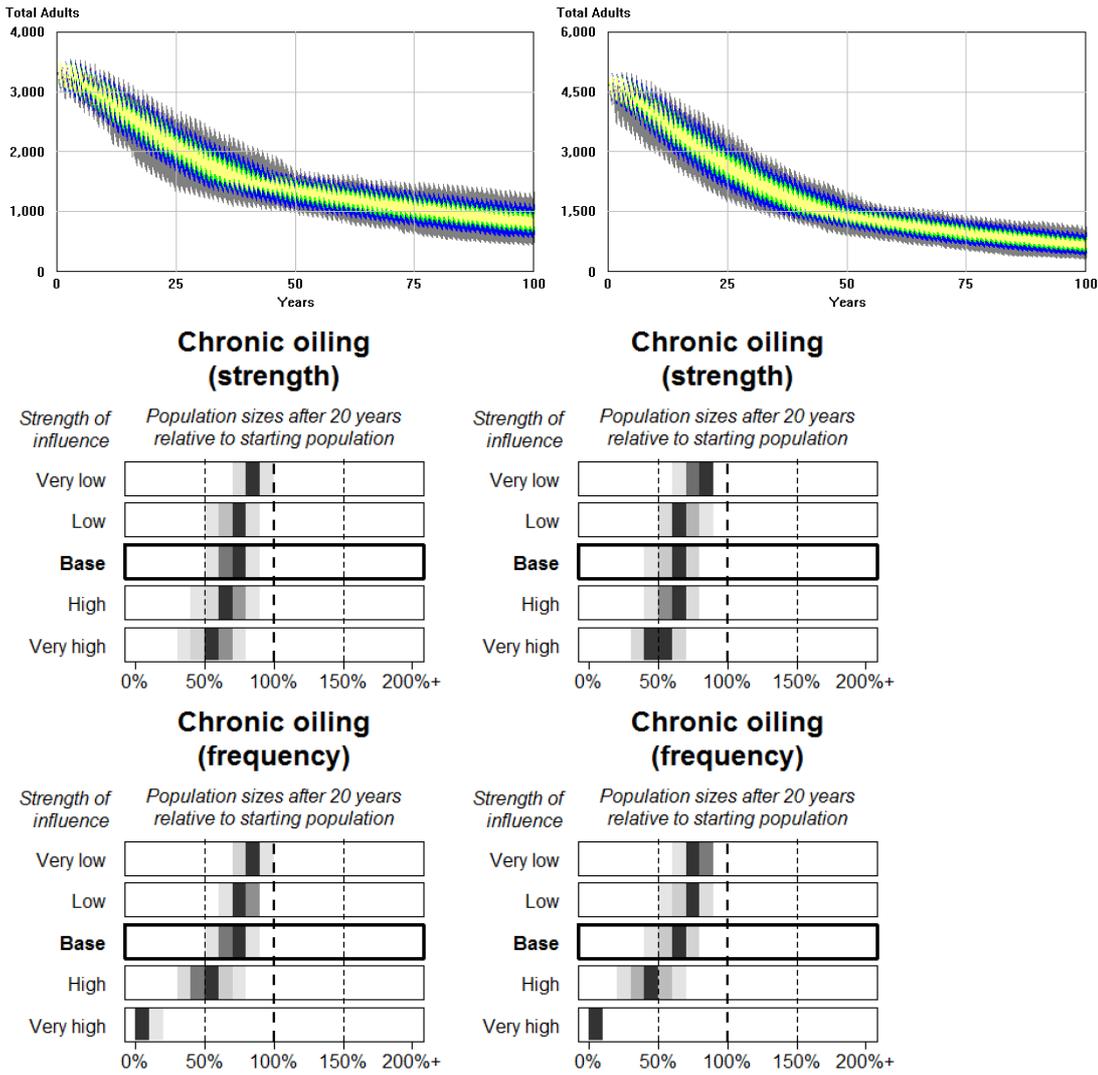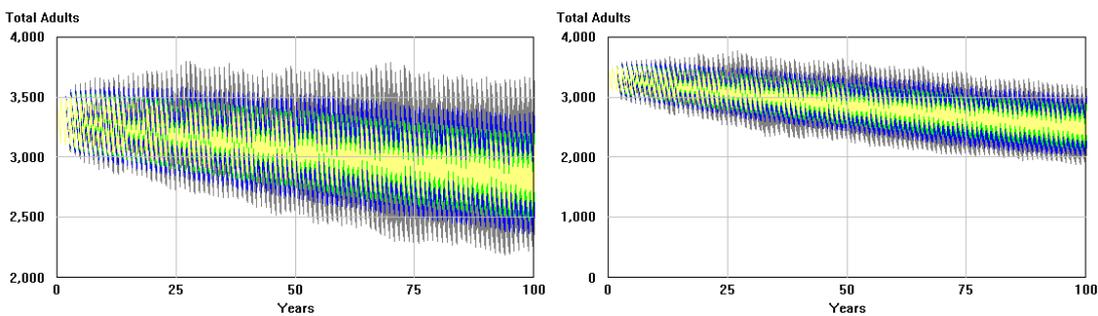
Figure 16. African penguin population development (number of adults) under the influence of chronic oiling in isolation, across 5000 replicates with random noise streams, at Robben (left) and Dyer islands (right). Top: Population development at base level over 100 years. Color ranges indicate the probability that any individual model run would fall within the respective band (50%, 75%, 95%, 100%). Below: Population development after 20 years, using five levels of pressure strength modification (middle) or pressure frequency modification (bottom) (Table 6). Distributions are shaded by relative frequency of intervals within each level (10% intervals, darkest shade indicates mode interval).

7.2.7 Rain flooding, wave flooding and hot spells

Hot spells, rain flooding and wave flooding are relatively weak pressures that occur at moderate to low frequencies and have small impacts on the population (Table 6). The negative impact on population development is low to medium, with very little responsiveness to changes in implemented strength. The largest relative variability is in the impact of rain flooding. Fig. 17 shows traces and sensitivity test results for Robben Island, Fig. 18 for Dyer Island.
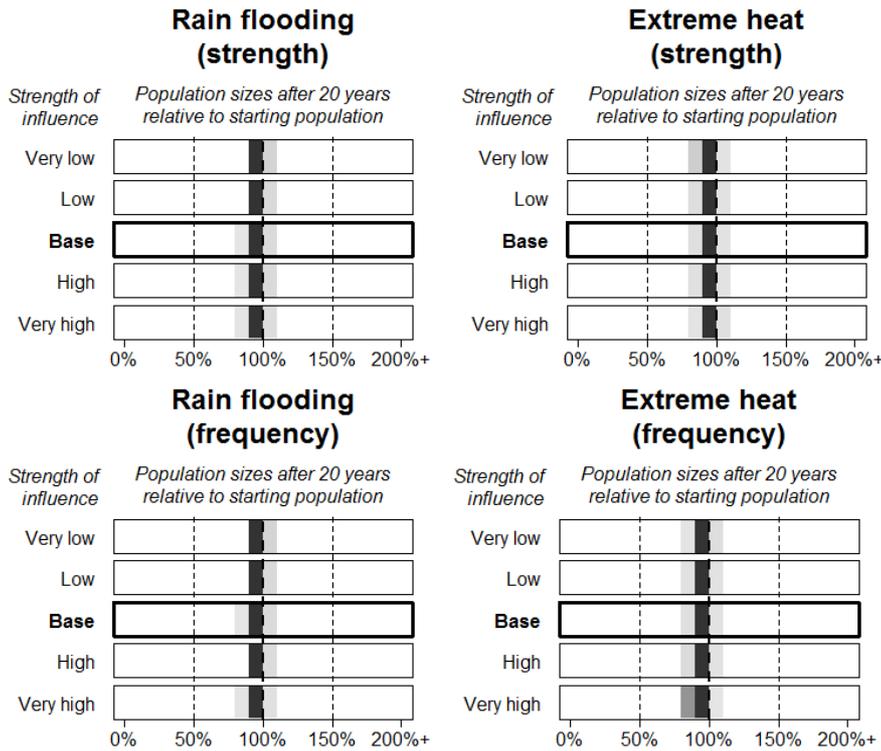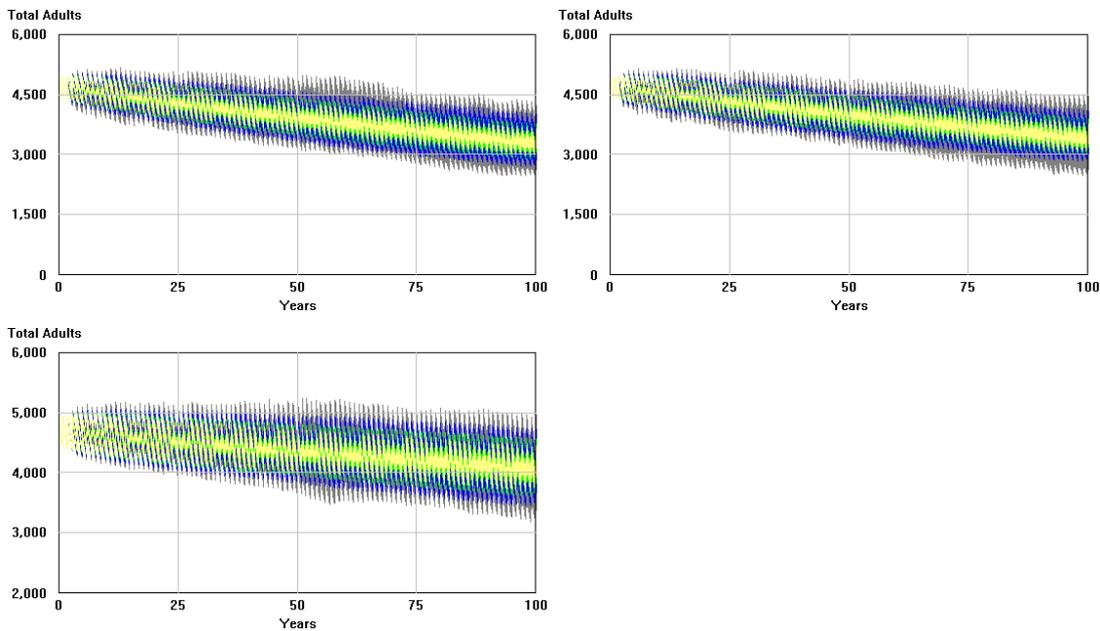
Figure 17. African penguin population development (number of adults) under the influence of rain flooding (<u>left</u>) and hot spells (<u>right</u>) in isolation, across 5000 replicates with random noise streams, at <u>Robben Island</u> (*wave flooding is not implemented in this model*). <u>Top</u>: Population development at base level over 100 years. Color ranges indicate the probability that any individual model run would fall within the respective band (50%, 75%, 95%, 100%). Below: Population development after 20 years, using five levels of pressure strength modification (<u>middle</u>) or pressure frequency modification (<u>bottom</u>) (Table 6). Distributions are shaded by relative frequency of intervals within each level (10% intervals, darkest shade indicates mode interval).
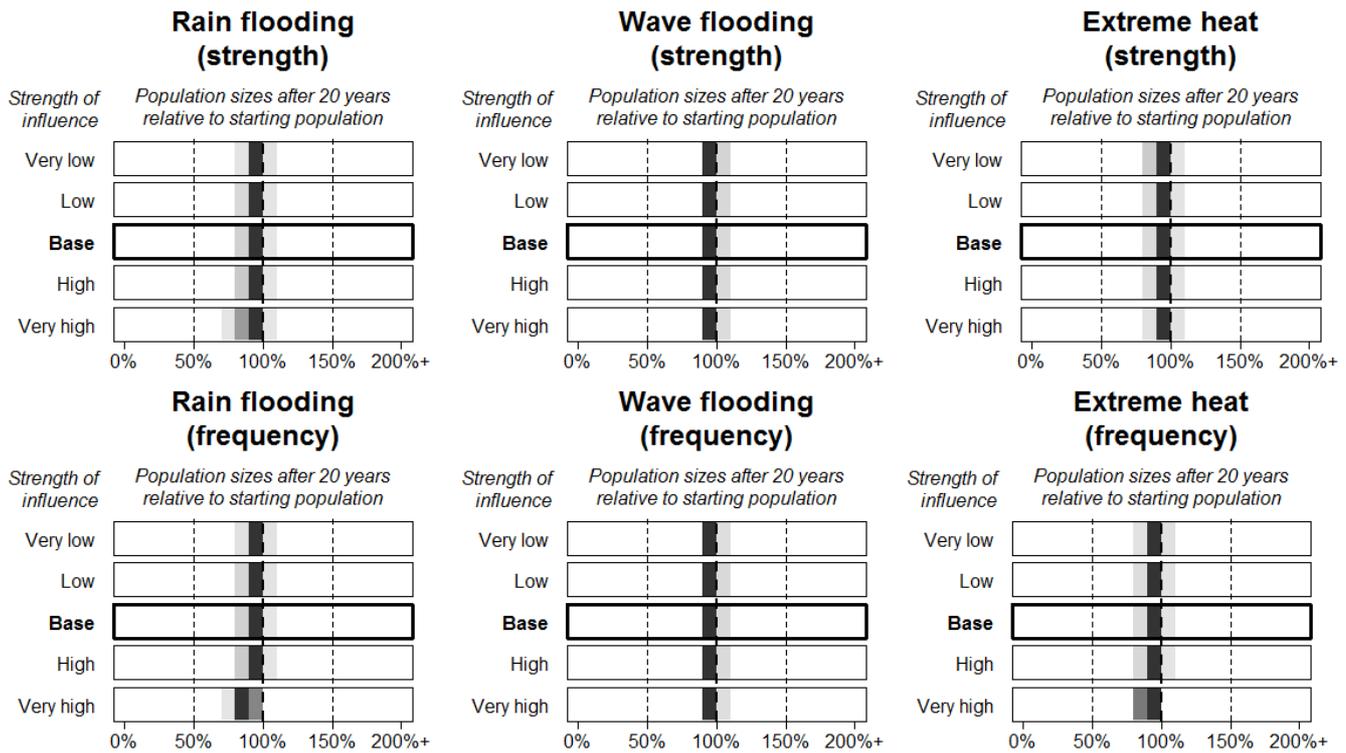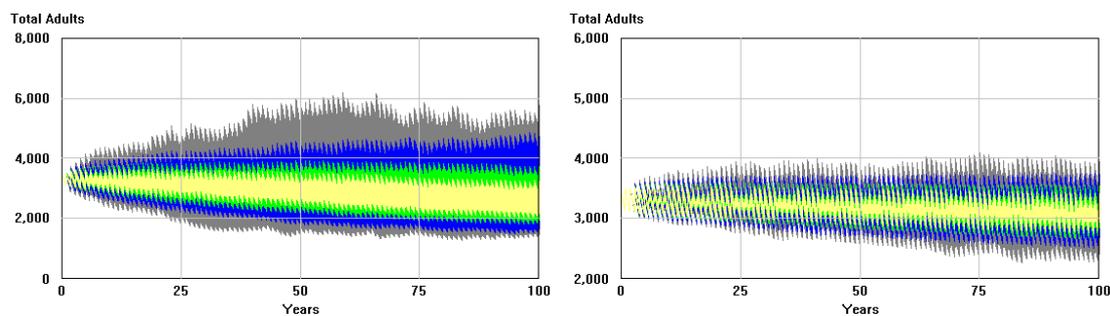
Figure 18.　African penguin population development (number of adults) under the influence of rain flooding (<u>left</u>), wave flooding (<u>middle</u>) and hot spells (<u>right</u>) in isolation, across 5000 replicates with random noise streams, at <u>Dyer Island</u>. <u>Top</u>: Population development at base level over 100 years. Color ranges indicate the probability that any individual model run would fall within the respective band (50%, 75%, 95%, 100%). Below: Population development after 20 years, using five levels of pressure strength modification (<u>middle</u>) or pressure frequency modification (<u>bottom</u>) (Table 6). Distributions are shaded by relative frequency of intervals within each level (10% intervals, darkest shade indicates mode interval).

7.2.8　Sharks and terrestrial predation

The effects of shark predation in the Robben Island model are centered at zero, with a slight negative bias in the long term (Fig. 19, top left). The process is largely insensitive to further decreases in influence strength, but acquires a wider spread and a strong negative outcome bias at increased values (Fig. 19, bottom left). Terrestrial predation is less impactful (Fig. 19, top right), and final population sizes are generally within 10% of starting numbers at base level (Fig. 19, bottom right). It is generally insensitive to changes in implemented influence strength. These differences between predation types are reasonable in that land-based predators primarily prey on eggs and chicks, while seals, sharks etc. take adult and immature penguins, which in a long-lived species with low and late-onset reproduction will have a larger cumulative effect on population dynamics (Sæther and Bakke, 2000).

Shark predation pressure in the model is connected to Zone 1 food biomass (2.4.3.1), which will impart negative or positive bias to variation in individual runs; however, in massively replicated scenarios the randomized nature of biomass resampling itself ensures an overall absence of bias.
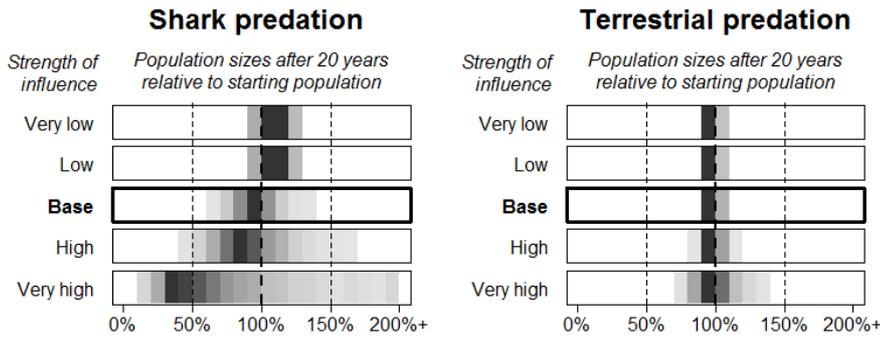

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Figure 19. African penguin population development (number of adults) under the influence of shark (left) and terrestrial predation (right) in isolation, across 5000 replicates with random noise streams, at Robben Island. Top: Population development at base level over 100 years. Color ranges indicate the probability that any individual model run would fall within the respective band (50%, 75%, 95%, 100%). Bottom: Population development after 20 years, using five levels of pressure parameter modification (Table 6). Distributions are shaded by relative frequency of intervals within each level (10% intervals, darkest shade indicates mode interval).

7.2.9   Seal predation

Predation by fur seals on adult penguins is the dominant negative pressure in the Dyer Island model (closely followed by immature emigration). In contrast to any other modelled pressure, this pressure in isolation will drive the equilibrium population to extinction in the long term, using the currently implemented impact estimates (Fig. 20, left). This behaviour must be considered in the absence of any enhanced density dependence functionality, for the implementation of which no data are as yet available. Median loss of the adult population over 20 years is 76% (Table 6).

As seal predation is implemented as a fixed direct loss of individuals, there is no variability in trajectories from the pressure process itself (Fig. 20, right), although the interaction with other influences, particularly food availability, still imparts considerable variation to scenario outcomes. The pressure is moderately sensitive to changes in implemented strength (loss ratio of adults and secondary losses of eggs and chicks); however, the 'very low' strength level, corresponding to a loss of 3.75% of adults per year, will still halve the population over 20 years.
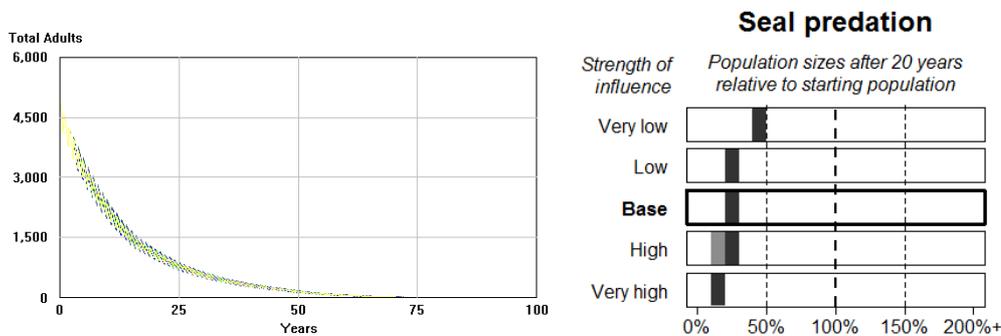

Figure 20. African penguin population development (number of adults) under the influence of fur seal predation in isolation, across 5000 replicates with random noise streams, at Dyer Island. Left: Population development at base level over 100 years. Color ranges indicate the probability that any individual model run would fall within the respective band (50%, 75%, 95%, 100%). Right: Population development after 20 years, using five levels of pressure parameter modification (Table 6). Distributions are shaded by relative frequency of intervals within each level (10% intervals, darkest shade indicates mode interval).

7.2.10 Gull predation and moderate human disturbance

Kelp gull predation as currently parameterized has a considerably lower impact than seal predation (median loss of 10% over 20 years; Table 6). The pressure shows dynamics similar to the climate pressures, with relatively consistent outcomes and low sensitivity to parameter variation (Fig. 21). It is notable that increasing the estimated number of predated surface nests from 15% to 22.5% (a 50% increase) does not result in a strong increase in effect (Fig. 21, middle left; level 'very high').

The pressure of moderate human disturbance is implemented as an increase in gull predation during a disturbance event and, when enabled in addition to base gull predation, will raise median losses from gulls to 12% over 20 years, with negligible sensitivity to variations in effect strength or frequency (Fig. 21, bottom).

The effect of gull predation in the model is lower than what might be expected when the recent rapid increase of the gull population on Dyer Island is taken into consideration (Ludynia et al., 2014). Current parameterization of predated nest ratio is based on incidental observations (D. Geldenhuys, unpublished data). A dedicated study of gull predation behaviour on the island is warranted and might lead to substantial changes in model results.
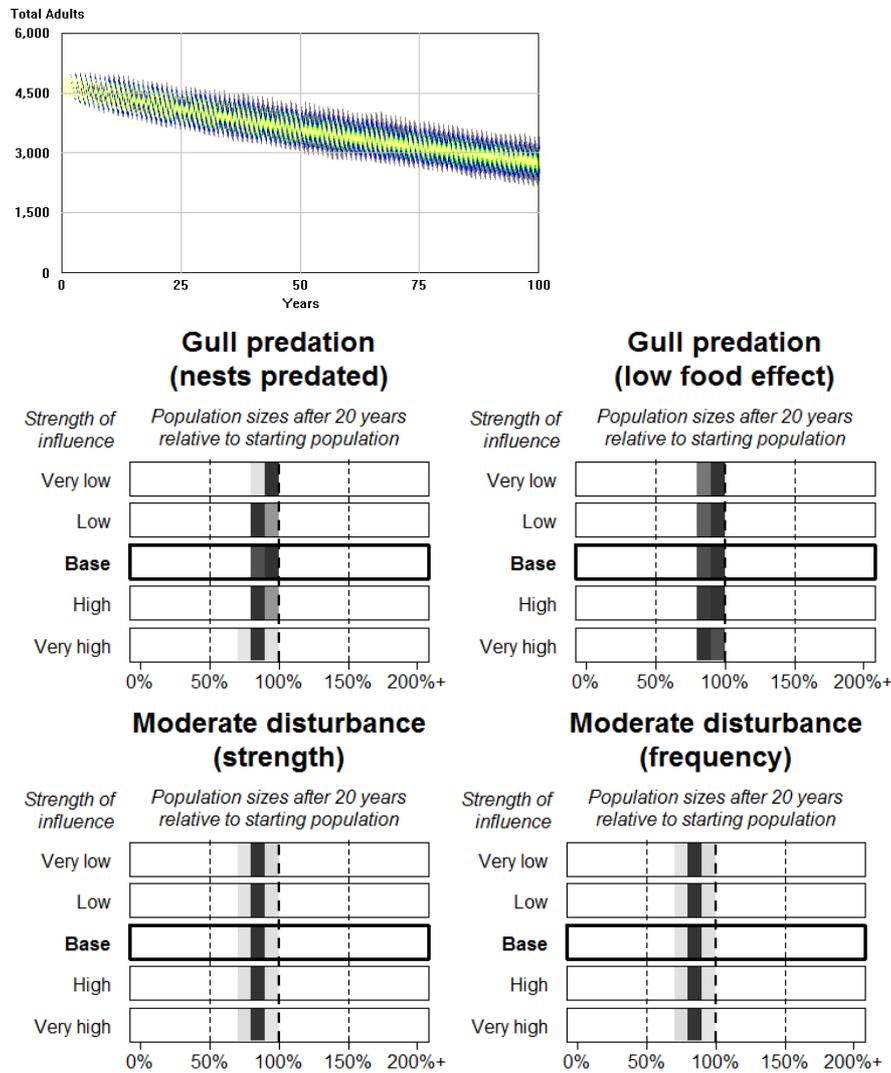

Figure 21.   African penguin population development (number of adults) under the influence of gull predation in isolation, across 5000 replicates with random noise streams, at Dyer Island. Top: Population development at base level over 100 years. Color ranges indicate the probability that any individual model run would fall within the respective band (50%, 75%, 95%, 100%). Below: Population development after 20 years, using five levels of parameter modification (Table 6), for number of nests predated (middle left), low food effect (middle right), and moderate disturbance strength (bottom left) and frequency (bottom right). Distributions are shaded by relative frequency of intervals within each level (10% intervals, darkest shade indicates mode interval).

7.2.11 Heavy human disturbance

Heavy human disturbance occurs very rarely (mean frequency 120 months) and at a high severity that however only affects eggs and chicks and has no long-term effects; impact on population development over 20 years is therefore relatively low (-5%; Table 6), and dynamics and sensitivity are more comparable to the climate pressures than to catastrophic oiling (Fig. 22).
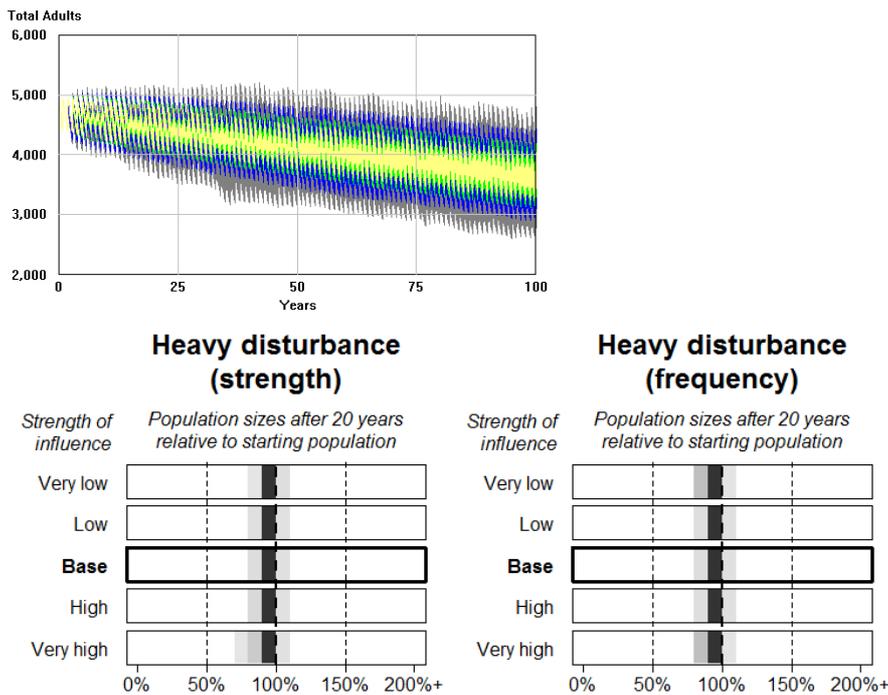
Figure 22. African penguin population development (number of adults) under the influence of heavy human disturbance in isolation, across 5000 replicates with random noise streams, at Dyer Island. Top: Population development at base level over 100 years. Color ranges indicate the probability that any individual model run would fall within the respective band (50%, 75%, 95%, 100%). Bottom: Population development after 20 years, using five levels of pressure parameter modification (Table 6) for strength (left) and frequency (right). Distributions are shaded by relative frequency of intervals within each level (10% intervals, darkest shade indicates mode interval).

7.3   Process test summary

The output of all individual processes remains within bounds that appear ecologically sensible and agree with the implementation intent. Sensitivity analysis shows that overall population trajectories are most heavily affected by changes to adult survival (as expected), while variation in population development in the model is primarily driven by food availability and to a lesser degree by catastrophic oil spill events. Chronic oiling has a high and consistent impact, while terrestrial predation, climate events and flooding have low and consistent impacts. The Dyer Island population is dominated by the invariable and strongly negative effects of immature emigration and seal predation on adults. The model is moderately robust to changes in implemented influence strength and event frequency of all environmental pressures.

It is notable that processes of higher sensitivity to parameter choice coincide with those for which relatively good data are already available (i.e., food availability, catastrophic oiling). The two dominant pressures in the Dyer Island model remain comparatively poorly parameterized, but display a strong negative impact regardless of reasonable changes in parameterization.

7.4   Rare event determination

To determine whether an event with an associated mean frequency (such as oiling and climate events) occurs in the model in a given month, a value is drawn from a Poisson function with an expected mean of 1/frequency. The event happens if the drawn value is > 0, and happens multiple times if the value is > 1. The likelihood of multiple events in any one month is generally small except for moderate human disturbance. Mean event frequency (ef) and resulting cumulative probability of more than one event occurring in any one month (cp) are given below for each affected pressure.

- catastrophic oiling: $ef = 1/180$ (Robben), $1/264$ (Dyer); $cp < 0.001$

- climate events: $ef = 1/60$ (rain flooding Robben), $1/36$ (others); $cp < 0.001$

- chronic oiling: $ef = 1/3$, $cp = 0.045$

- moderate human disturbance: $ef = 1$, $cp = 0.26$
- heavy human disturbance: $ef = 1/120$, $cp < 0.001$

8   Model output corroboration

This TRACE element provides supporting information on: How model predictions compare to independent data and patterns that were not used, and preferably not even known, while the model was developed, parameterized, and verified. By documenting model output corroboration, model users learn about evidence which, in addition to model output verification, indicates that the model is structurally realistic so that its predictions can be trusted to some degree.

The output of the pressure model is difficult to corroborate against independent observations. As far as records of South African penguin population dynamics go, these were either used in the parameterization of the present models and are tested against the respective records in section 6, or otherwise seem inapplicable because of the complex and voluminous colony-specific parameterization employed – it is unlikely that environmental circumstances at other colonies are comparable to those used in the model, or even known well enough to pronounce on similarity. This is even more of an issue if other seabird species are taken into consideration.

While the corroboration of the output of individual sub-models is being suggested as an alternative in such circumstances (Grimm et al., 2014), this too appears infeasible because records to compare against will typically contain a multitude of influences, and linking a population dynamic to the specific process covered by the submodel will be largely speculative. This may seem most defensible in the case of South African fur seal predation, the pressure identified as having the strongest single effect on penguins in the Dyer Island model. However, no penguin-specific assessment of fur seal predation impacts beyond those used for parameterization are available, and while impacts on other seabirds have been studied, those results by and large are not comparable. Fur seal predation on other species tends to be targeted, focused on fledglings rather than adults, and at much higher volume; thus Makhado et al. (2006) found Cape gannet fledgling losses of 30-83% at Malgas Island (an impact that appears to have been instrumental in a colony size reduction by 25% between 2001 and 2005), well beyond the estimated 7.5% of adult penguins lost at Dyer Island.

It appears that the best opportunities for model corroboration, outside the replication of the dynamics of the colony specifically targeted, will arise when further penguin colonies with similar pressure configurations are prepared for modelling, and once the respective data have been prepared and differences in parameterization can be assessed.

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