Limitation of population recovery: a stochastic approach to the case of the emperor penguin

Stéphanie Jenouvrier, Christophe Barbraud, Henri Weimerskirch and Hal Caswell

S. Jenouvrier (sjenouvrier@whoi.edu) and H. Caswell, Biology Dept, MS-34, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA. – SJ, C. Barbraud and H. Weimerskirch, Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, FR–79360 Villiers en Bois, France.

Major population crashes due to natural or human-induced environmental changes may be followed by recoveries. There is a growing interest in the factors governing recovery, in hopes that they might guide population conservation and management, as well as population recovery following a re-introduction program. The emperor penguin *Aptenodytes forsteri* population in Terre Adélie, Antarctica, declined by 50% during a regime shift in the mid-1970s, when abrupt changes in climate and ocean environment regimes affected the entire Southern Ocean ecosystem. Since then the population has remained stable and has not recovered. To determine the factors limiting recovery, we examined the consequences of changes in survival and breeding success after the regime shift. Adult survival recovered to its pre-regime shift level, but the mean breeding success declined and the variance in breeding success increased after the regime shift. Using stochastic matrix population models, we found that if the distribution of breeding success observed prior to the regime shift had been retained, the emperor penguin population would have recovered, with a median time to recovery of 36 years. The observed distribution of breeding success after the regime shift makes recovery very unlikely. This indicates that the pattern of breeding success is sufficient to have prevented emperor penguin population recovery. The population trajectory predicted on the basis of breeding success agrees with the observed trajectory. This suggests that the net effect of any factors other than breeding success must be small. We found that the probability of recovery and the time to recovery depend on both the mean and variance of breeding success. Increased variance in breeding success increases the probability of recovery when mean success is low, but has the opposite effect when the mean is high. This study shows the important role of breeding success in determining population recovery for a long-lived species and demonstrates that demographic mechanisms causing population crash can be different from those preventing population recovery.

Animal and plant populations are commonly reduced by natural or human-induced environmental changes. Often these crashes are followed by recoveries, whereas sometimes the recovery of a population may fail. Gardmark et al. (2003) pointed out the critical need to understand the factors affecting population recoveries given the current high rate of population declines, mainly caused by human activities. They defined recovery as a re-growth of a population after a crash to a size of one order of magnitude to the pre-decline population size. However, for long-lived vertebrate species for which a population decrease of 20–30% corresponds to a marked decrease, this definition of a threshold of one order of magnitude may be to be too large. The definition of recovery depends thus on the life history traits of a species.

The study of recovery can be considered in the context of studies of population regulation and population limitation. Sinclair (1989) clarified the distinction between these phenomena. Population regulation refers to the tendency of a population to return to equilibrium when perturbed. Limiting factors determine the abundance at equilibrium.

The concept of 'recovery' implies return to something, and the appearance of the word 'equilibrium' reminds us that these concepts pre-date the modern appreciation of non-equilibrium and transient phenomena in ecology. Population regulation could now legitimately include the processes that cause a population to return to a cycle, invariant loops, or strange attractor. Population limitation could refer to the determination of the level at which populations oscillate, as well as the abundance at equilibrium.

Here, our focus is on the pattern of recovery from perturbation. When a population is perturbed by some factor, and the perturbing factor is removed, we have an intuitive expectation that the population will recover. This recovery depends on population growth, and so the primary focus is on the factors determining population growth rates (Gardmark et al. 2003). To the extent that the population is recovering from a decline, density-dependent factors may be unimportant (unless, perhaps, the decline has been severe enough to trigger an Allee effect), which allows linear demographic analysis to be applied in a powerful fashion.

Long-lived species have low population growth rates resulting from their life histories (late recruitment, low fertility and high adult survival, Stearns 1992). Therefore, for such species, recovery can be slow, resulting in a greater risk of extinction. If the traits most likely to influence recovery are identified, then conservation and population management programs are able to target these traits as areas of focus. Understanding the processes affecting the recovery of a population following a re-introduction program might guide conservation actions.

Population crashes followed by a lack of recovery may arise when there is an abrupt change in the environment. Marine ecosystems are especially subjected to abrupt changes in climate and ocean environment, which affect the whole ecosystem, from phytoplankton to top predators (e.g. Humboldt current, Alheit 2004). Such abrupt environmental change from one stationary environmental state to another is defined as a regime shift.

Long-lived marine predators are useful indicators of regime shifts because they integrate the effect of climatic forcing on lower trophic levels (Furness and Greenwood 1993). A major regime shift in the Southern Ocean ecosystem began in the early 1970s, and continued for about 10 years. It affected many marine predator populations (Reid and Croxall 2001, Weimerskirch et al. 2003, Ainley et al. 2005, Jenouvrier et al. 2005b). During this regime shift, some populations increased rapidly (e.g. Adelie penguin Pygoscelis adeliae; Ainley et al. 2005), whereas other decreased dramatically (e.g. emperor penguin Aptenodytes forsteri; Jenouvrier et al. 2005b, Weddell seals Leptonychotes weddellii; Ainley et al. 2005). These different population responses were caused by differences in environmental effects on life history traits among the different species (Croxall et al. 2002, Jenouvrier et al. 2005a). Among populations that declined during the regime shift, few recovered rapidly; most of them exhibited little or no change in abundance up to decades after the decline (Ainley et al. 2005, Jenouvrier et al. 2005b).

Emperor penguin populations in Terre Adélie, Antarctica, declined by 50% during the Southern Ocean ecosystem regime shift in the late 1970s (Ainley et al. 2005, Jenouvrier et al. 2005b). Since then, the population has remained stable and has not recovered. In order to understand the factors preventing population recovery, we determined how changes in the vital rates influenced the growth of the emperor penguin population before, during and after the late 70s regime shift.

The time necessary for a population to recover depends on its growth rate (Gardmark et al. 2003). Fluctuations in the emperor penguin population growth rate are mostly caused by the variations in two key vital rates: (1) adult survival and, (2) breeding success (Jenouvrier et al. 2005a). Adult survival declined during the regime shift, but eventually recovered to the levels prevailing before the regime shift (Barbraud and Weimerskirch 2001). Hence, adult survival variations cannot explain the lack of emperor penguin population recovery. Breeding success, however, has followed a different pattern. Mean breeding success declined during the regime shift. In contrast to adult survival, mean breeding success continued to decline after the regime shift. In addition, variance in breeding success increased due to a higher frequency of extensive breeding failure (Barbraud and Weimerskirch 2001, Ainley et al. 2005).

In this study we first explore the effect of breeding success on population recovery after the regime shift occurred. If the observed change in breeding success is responsible for the lack of population recovery, breeding success observed prior the regime shift should lead to population recovery with high probability. On the other hand, the breeding success during and after the regime shift should lead to a much lower probability of recovery. Secondly, we explore the effects of changes in both the mean and variance of breeding success on population recovery. To address these two questions, we developed stochastic population models structured by stages (Caswell 2001), and calculated the probability of population recovery and the time until the population recovered fully, similar to calculations of quasi-extinction probability and time to quasi-extinction in population viability analysis (Lande and Orzack 1988).

Material and methods

Data description

Emperor penguins breed in winter on Pointe Géologie Archipelago (66°40′S, 140°01′E), Terre Adélie, Antarctica, and forage within the pack ice on fish, cephalopods and krill (Offredo 1986, Cherel 2008). Censuses of breeding emperor penguins and fledged chicks have been conducted every year since 1962 (Fig. 1a). Capture–recapture surveys have occurred since 1968, although marking was halted in 1988 due to concerns that flipper banding was impacting penguin welfare (see Jenouvrier et al. 2005a for more details).

A regime shift is defined as a rapid change from one relatively stable state to another. There are a number of methods designed for a detection of regime shifts in time series (Rodionov 2005). We applied a method based on a sequential t-test and F-tests that reliably detect the timing of a regime shift (Rodionov 2004). Here we used both the times series of the number of breeding pairs and chicks, and we found that the regime shift occurred from 1972 to 1981 (Jenouvrier et al. 2009), as shown by Fig. 1a.

Breeding success is calculated as the proportion of pairs that successfully breed, i.e. laying an egg and fledging a chick, every year from 1962 to 2005. Breeding success per decade is shown in the boxplot in Fig. 1b.

To to test whether breeding success differed among the pre-regime shift, regime shift, and post-regime shift periods, after accounting for yearly variation, we used generalized linear models with a logit link. We used two models that included the effect of year and period, with the year effect nested within period for the second model (LOGISTIC procedure of SAS). We also used a logistic mixed model with period as a fixed effect and year as a random effect (GLIMMIX procedure of SAS).

Model description

Two stochastic population models were constructed for the study: the effect on population recovery of (1) breeding
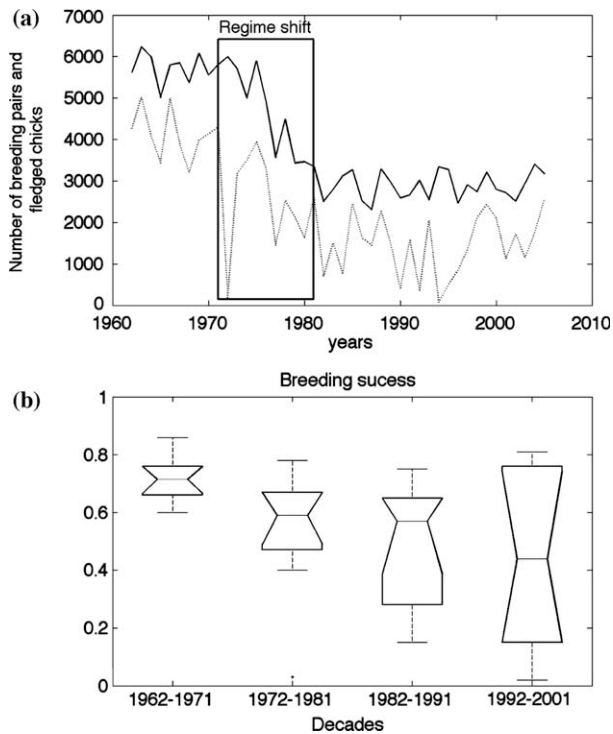
Figure 1. (a) number of breeding pairs (black line) and fledged chicks (dotted line) of emperor penguins in Terre Adélie, Antarctica between 1962 and 2005. (b) box plot of breeding success per decade since 1962. The box shows the minimum and maximum values (ends of the whiskers), interquartile range (length of the box), and median (line through the box).

To disentangle the effect of the mean and variance of a breeding success on population growth rate, we used a model based on a set of matrices A_t in which breeding success is drawn independently at each time t from a beta distribution. The beta distribution is a continuous probability density defined on the interval [0, 1] and parameterized by two positive shape parameters, typically denoted by a and b. The shape parameters are calculated as:

$$a = m^2/v - m^3/v - m$$

and

$$b = a/m \times (1 - m)$$

where m is the mean and v the variance of breeding success. In this model, all the other vital rates are constant and set to their observed mean after the regime shift (i.e from 1982–2005).

Probability of recovery and time to recovery

To estimate the potential for population recovery under a particular set of vital rates, we generated stochastic simulations using Eq. 1 for a period of 1000 years. To project the population from t to t+1, we used, as an initial condition, a population vector proportional to the stable age distribution of the mean of the matrices A_t from 1982–2005, with the size of the breeder class set equal to the mean observed number of breeding pairs during this period. Figure 2 shows some population projections from 1982 to 2100. We define a population projection to have recovered if its size

success after the regime shift and, (2) the respective effects of changes in the mean and variance of breeding success. We call those two models (1) the matrix-selection model and, (2) the beta distribution model.

Both models are based on the emperor penguin life cycle as described in Jenouvrier et al. (2005a). This model has seven stages, including breeding adults, non-breeding adults, and five age classes of pre-breeding birds. We describe population dynamics with a time-varying matrix population model:

$$\mathbf{n}(t + 1) = \mathbf{A_t}\mathbf{n}(t) \tag{1}$$

where $\mathbf{n}(t)$ is a vector of abundances of the stages and the matrix $\mathbf{A_t}$ projects the population from t to t+1. The matrix $\mathbf{A_t}$ contains the following vital rates from t to t+1: proportion of birds attempting to breed, adult survival and fecundity. Fecundity is calculated as the product of breeding success and survival during the first year at sea (see Jenouvrier et al. 2005a for parameter estimation).

The matrix-selection model uses the set of 44 year-specific matrices $\mathbf{A_t}$ obtained from the vital rates estimated annually from t=1962 to t=2005 (Jenouvrier et al. 2005a). This set of matrices includes the observed variation and covariation in the vital rates. To project population from t to t+1, a matrix $\mathbf{A_t}$ is randomly selected from the subset of year-specific matrices corresponding to a specified period before (1962–1971), during (1972–1981), or after (1982–2005) the regime shift.
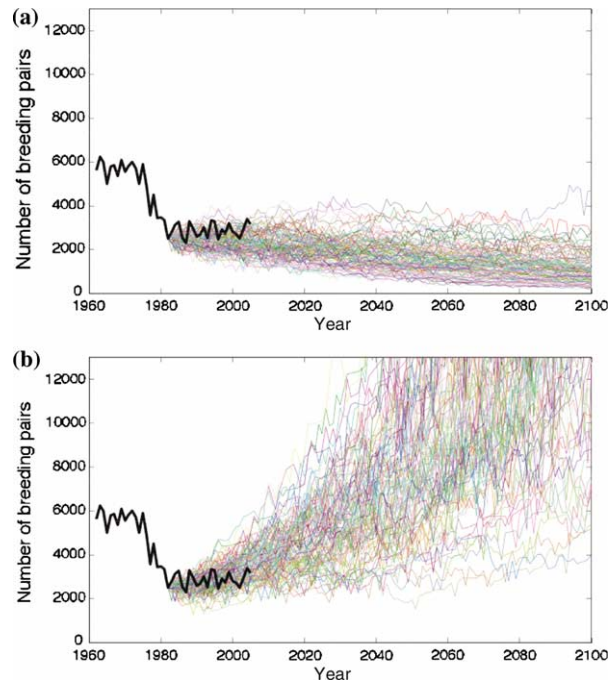

Figure 2. Number of breeding pairs of emperor penguins in Terre Adélie, observed between 1962 and 2005 (thick black line) and projected to 2100 (thin color lines). Population projections are calculated with the matrix-selection stochastic model using a subset of population matrices $\mathbf{A_t}$ from (a) before the RS (i.e. 1962–1971), and (b) after the RS (i.e. 1982–2001).

exceeds the mean observed population size prior to the regime shift (i.e from 1962–1971). The first time at which a population projection recovers is denoted t_r. The probability of recovery (P) is the proportion of the population projections that recover within 1000 years. Among the population projections that recover, the time to recovery (T) is calculated as the median of the distribution of t_r.

Results

The median and minimum of breeding success decreased strongly and the variability of breeding success increased over the last decade (Fig. 1b). The mean and standard deviation per decade since 1962 were: 0.72 ± 0.08, 0.55 ± 0.21, 0.50 ± 0.21 and 0.46 ± 0.30. The breeding success differed across the three periods (i.e. pre-regime shift, regime shift and post-regime shift) (LOGISTIC and GLIMMIX procedures: $p < 0.0001$ and $p = 0.0496$ respectively).

If the observed changes in breeding success are responsible for the failure of the population to recover after the regime shift, we would expect two patterns to appear in the results. First, the breeding success values (mean and variance) observed prior the regime shift should lead to recovery with high probability. Second, the breeding success values during and after the regime shift should lead to a much lower probability of recovery. As expected, we found that all population projections from the matrix-selection model using the pre-regime shift vital rates recovered (P = 100%), with a mean time to recovery of T = 36 years (Fig. 2a, 3a). In contrast, almost none of the projections from the matrix-selection model using vital rates from after the regime shift recovered (P < 1%, Fig. 2b, 3b). Our results demonstrate that the post-regime shift distributions of breeding success have been sufficient to prevent emperor penguin population recovery.

The observed decrease in breeding success is related to an increase in the frequency of years with very low breeding success (Table 1). When we excluded years where breeding success was lower than 0.4 during the post-regime shift era (1982–2005), the mean breeding success increased from 0.52 to 0.62 and the variance was reduced from 0.25 to 0.02. Under these hypothetical conditions recovery would be certain (P = 100%), although slower than with pre-regime shift values (T = 119 years).

This suggests that the probability of recovery P and the time to recovery T depend on both the mean and the variance of breeding success. We used the beta distribution model to explore this dependence. Not surprisingly, we found that P increases with increases in mean breeding success (Fig. 4a). Increased variance in breeding success increases P if mean success is lower than $\beta^* = 0.68$, but has the opposite effect if mean success is higher than β^*. Interestingly, β^* corresponds to the breeding success for which the deterministic growth rate is equal to one. A breeding success above β^* at time t results in a population increase from t to t + 1, while breeding success below β^* results in a population decrease. Below β^*, increasing variance increases the possibility of breeding success being above β^* at year t, causing the population to grow and eventually increase P. On the other hand, above β^*,
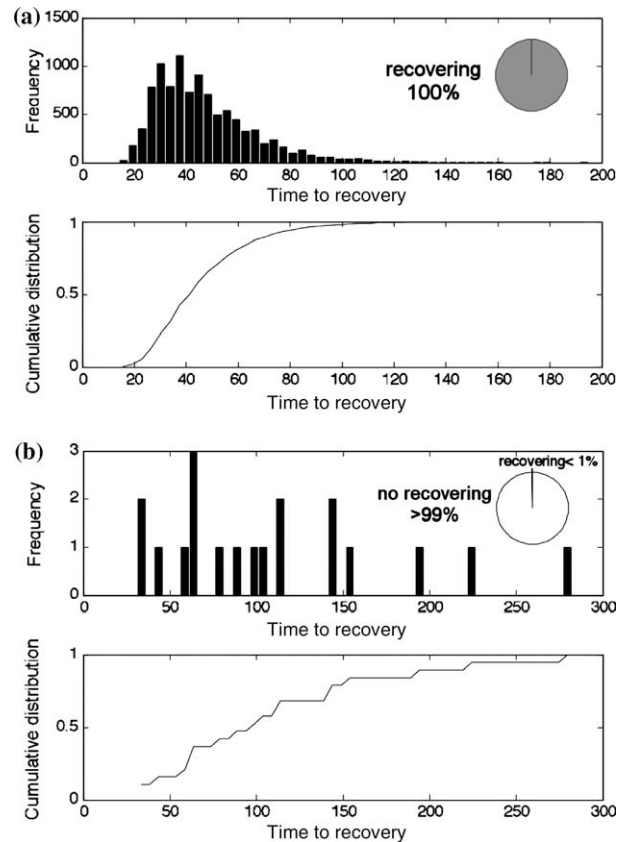

Figure 3. Probability of recovery and distribution of the time to recovery for population projections with breeding success from (a) before the RS (A_t from 1962 to 1971) and (b) after the RS (A_t from 1982 to 2001). Each figure has two panels; higher panel: distribution of the time to recovery given that the population recovered, with the proportion of population trajectories that recovered illustrated by the inside pie chart, and lower panel: the cumulative probability of the time to recovery. These results were obtained by computing 10 000 population trajectories over a period of time of 1000 years.

an increasing the variance increases the possibility of breeding success being below β^* at year t, which ultimately decreases P.

The median time to recovery T, increases until reaching a maximum and then decreases as mean breeding success increases, especially for low variance. For low values of breeding success mean and variance, the probability of recovery P is very small, and the few cases where recovery takes place occur early. As mean breeding success increases, P increases, and T increases initially, then decreases. Higher variance reduces T, especially for mean breeding success below β^* (Fig. 4b). Likewise, the probability of recovery below β^*, an increase in breeding success variance has more chance of producing a breeding success above β^* at year t, that ultimately reduces T.

Discussion

Breeding success has been sufficient to prevent the emperor penguin population recovery

Our results demonstrate that the distribution of breeding success after the population crash has been sufficient to

Table 1. Number of years where breeding success is lower than a specified threshold before and after the regime shift (RS). Mean and variance of the breeding success after the RS (1982–2005) when those lower breeding success years are excluded. Probability of recovery (P) and time to recovery (T) calculated with the matrix-selection model for a reduced sub-set of population matrix after the RS for which those years with breeding successes lower than the threshold are excluded.

Threshold	Number of events with BS <threshold		mean	variance	P (%)	T (yr)
	Before the RS (1962–1971)	After the RS (1982–2005)				
0.1	0	1	0.50	0.049	<1	111
0.2	0	4	0.56	0.032	32	249
0.3	0	6	0.59	0.024	81	230
0.4	0	8	0.62	0.017	100	119
0.5	0	11	0.69	0.008	100	69

prevent emperor penguin population recovery in Terre Adelie. This shows that breeding success can limit population recovery even for a long-lived species, and demonstrates that the demographic mechanisms causing population decline can be different from those preventing recovery. The model based on breeding success alone agrees with the observed population trajectory. This implies that the net effect of any other factors limiting recovery must be small. Our results cannot rule out the possibility of two or more factors with large effects of opposite sign that exactly or nearly cancel each other out.

Population growth rates of long-lived species are usually more elastic to adult survival than to breeding success (Sæther and Bakke 2000). Changes in adult survival can thus have a large impact on population growth rate, such as the penguin population crash during the regime shift (Barbraud and Weimerskirch 2001, Jenouvrier et al. 2005a). However, changes in breeding success may still contribute to population fluctuations, especially if adult survival varies less than breeding success (Jenouvrier et al. 2005a). Indeed, variability is selectively disadvantageous for long-lived species, and the variations of vital rates who has greatest impact on the population growth rate are expected to be buffered against temporal variability (Gaillard and Yoccoz 2003).

Our results show that both the reduced mean and the increased variance in post-regime shift breeding affected population recovery of emperor penguins. The decrease in mean and increase in variance of breeding success is caused by more frequent years with severe breeding failure after the regime shift. Severe breeding failure (breeding success <0.4) was not observed before the regime shift, but occurred in 33% of the years after the regime shift. If breeding success had retained the mean and variance observed prior the regime shift, the population would almost certainly have recovered, with a median time to recovery of 36 years.

Limitation of population recovery or population size can be explained at any of a series of hierarchical levels. At the level of demographic rates, we have shown that recovery is limited by breeding success. A second level of explanation would involve the ecological factors that directly affect breeding success (e.g. chick predation, food limitation). A third level would involve the processes determining those factors (e.g. predators facing reduced competition from other species, or parental foraging limited by sea ice conditions). This chain of causation could be pursued indefinitely.

In the present case, it is not known which of the many factors that affect breeding success are responsible for the higher frequency of severe breeding failure. Possibilities include chick mortality due to predation by the southern giant petrel *Macronectes giganteus* and prolonged blizzards (Jouventin 1975). However, observations from the colony indicate that predation from giant petrels is an unlikely cause of the decrease in breeding success because (1) the giant petrel population strongly declined during the last 40 years (Micol and Jouventin 2001), and (2) the frequency of
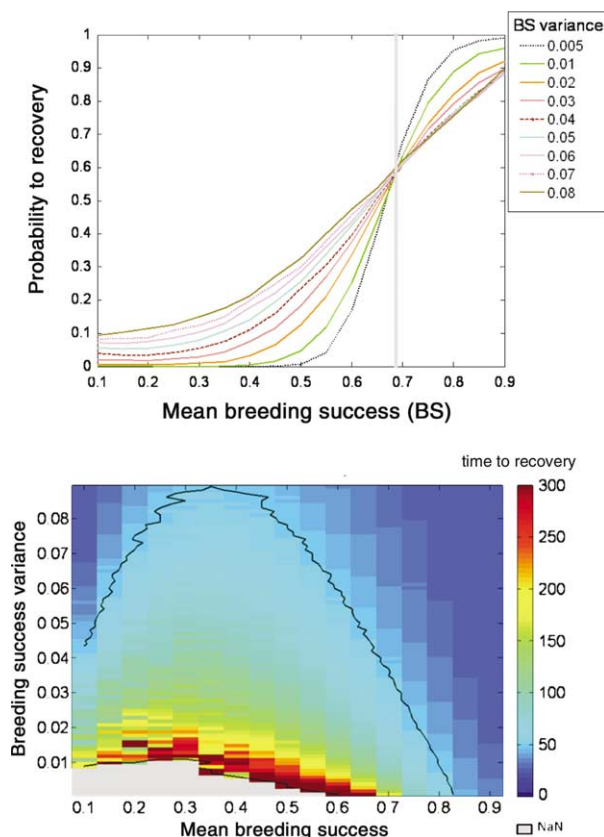

Figure 4. (a) Probability of recovery (P) and (b) time to recovery (T), as a function of the mean and variance of breeding success in the beta distribution model. In (a), the grey vertical line indicates the value of breeding success for which the deterministic growth rate is equal to one. In (b) the color scale gives values of T. The grey area represents the mean-variance space in which none of the population trajectories recover. The black contour is T = 50 years. These results were computed with 10 000 stochastic simulations.

predation at the colony is low and relatively stable (Barbraud and Weimerskirch unpubl.).

Other possible causes for the observed decrease in breeding success relate to higher energetic costs of parental care due to changes in penguin nesting and/or foraging habitat. Sea ice characteristics may cause longer foraging trips between the colony and the nearest open water leading to higher energetic costs and reduced breeding success (Wienecke and Robertson 1997). A recent study of ice dynamics from 1992 to 1999 in Terre Adélie (Massom et al. unpubl.), suggests that poor breeding seasons coincided with large extent of ice that resulted in longer distances to foraging sites. Another potential factor affecting foraging and nesting success is the presence of icebergs. Giant icebergs in the southwest Ross Sea modified the foraging routes of resident incubating adult penguins, which resulted in adult abandonment of chicks and high chick mortality (Kooyman et al. 2007). However, giant icebergs have not affected the Pointe Géologie colony since its discovery. Finally, premature ice break-up may have contributed to fledging failure (Budd 1962). To estimate the relative importance of each of these potential factors and to disentangle the ecological factors influencing emperor penguins breeding success in Terre Adélie, process-oriented studies during the breeding season (foraging studies, impact of storms or ice break out on breeding success, etc.) are needed.

Our model is stage-classified, because age-specific data are not available and because the ecological differences among stages are greater than those among ages. Because it does not include age classes, our model cannot include effects of senescence. If senescence affects breeding success (Bennett and Owens 2002), it might contribute to the low recruitment after the shift in ecological conditions.

The important role of variance and covariance in vital rates

Most studies of the time to recovery project the intrinsic deterministic growth rate (Raimondoa and Donalds 2003). Deterministic models assume a fixed environment and constant vital rates over time. However, natural population experience variations in their environment (e.g. climatic variations) that affect vital rates. To include stochasticity in vital rates several stochastic models have been developed (reviewed by Caswell 2001). These different models may produce divergent estimates of probability of and time to recovery since they produce different population growth rate estimates (Ramula and Lehtila 2005).

Adult survival and breeding success of emperor penguins are nearly independent of each other (correlation $r = -0.004$). Thus covariance effects (reviewed by Ramula and Lehtila 2005) are unlikely to be important. To estimate the probability of recovery and time to recovery, covariation among vital rates should usually be included in stochastic models (Coulson et al. 2005), as we do with the matrix-selection model.

We showed that the variance in breeding success affects population recovery, and the relationship changes according to whether or not the mean breeding success is lower or higher than β^* (breeding success where the deterministic growth rate is equal to one). Indeed, below β^*, an increase in variance is more likely to produce a breeding success above β^* at year t, causing the population to grow between t and $t+1$ and eventually recover. On the other hand, above β^*, increasing the variance is more likely to produce a breeding success below β^* at year t, which ultimately decreases the chance of population recovery.

Changes in the variance of vital rates can be as important as changes in mean (Boyce et al. 2006, Morris et al. 2008), and our results emphasize their importance in limiting population recovery. Ecologist should pay more attention to the effects of the variance and covariance of the vital rates on population dynamics using stochastic demographic models.

Conclusion

Population recovery arises in numerous situations (reviewed by Gardmark et al. 2003), such as resurgence of an invasive species following a control program (e.g. black-tailed prairie dogs, Knowles 1986, Wisdom and Mills 1997) or recovery of species after habitat disturbance, such as seabird populations recovering from oilspills (e.g. harlequin duck *Histrionicus histrionicus*, Esler 2002, herring gull *Larus argentatus* and common tern *Sterna hirundo* Samuels and Ladino 1984). Many studies of recovering populations relate to harvesting by fisheries, which has led to rapid declines of many marine fishes. Indeed, few fish populations recovered rapidly after harvesting; most of them exhibited little or no change in abundance up to 15 years after a decline (Hutchings and Reynolds 2004). Hutchings (2001) suggested that recovery was independent of exploitation rate, and that factors other than fishing may be considerably more important to recovery. Our results show that the demographic rates limiting recovery may differ from those causing population decline. Therefore, understanding the factors influencing population recovery is fundamental for species conservation and management, and we provide here a general modeling approach in which to do so.

References

Alheit, J. 2004. Regime shifts in the Humboldt Current ecosystem. – Progr. Oceanogr. 60: 201–222.

Ainley, D. et al. 2005. Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean, 1950s to the 1990s. – Antarct. Sci. 17: 171–182.

Barbraud, C. and Weimerskirch, H. 2001. Emperor penguins and climate change. – Nature 411: 183–186.

Bennett, P. M. and Owens, I. P. F. 2002. Evolutionary ecology of birds: life history, mating system and extinction. – Oxford Univ. Press.

Boyce, M. S. et al. 2006. Demography in an increasingly variable world. – Trends Ecol. Evol. 21: 141–148.

Budd, G. M. 1962. Population studies in rookeries of the emperor penguin *Aptenodytes forsteri*. – Proc. Zool. Soc. Lond. 139: 365–388.

Caswell, H. 2001. Matrix population models. – Sinauer.

Cherel, Y. 2008. Isotopic niches of emperor and Adélie penguins in Adélie Land, Antarctica. – Mar. Biol. 54: 813–821.

Coulson, T. et al. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. – J. Anim. Ecol. 74: 789–801.

Croxall, J. P. et al. 2002. Environmental change and Antarctic seabirds populations. – Science 297: 1510–1514.

Esler, D. et al. 2002. Harlequin duck population recovery following the 'Exxon Valdez' oil spill: progress, process and constraints. – Mar. Ecol. Progr. Ser. 241: 271–286.

Furness, R. W. and Greenwood, J. J. D. 1993. Birds as monitor of environmental change. – Chapman and Hall.

Gaillard, J. M. and Yoccoz, N. G. 2003. Temporal variation in survival of mammals: a case of environmental canalization? – Ecology 84: 3294–3306.

Gardmark, A. et al. 2003. The ecology of recovery. – Ann. Zool. Fenn. 40: 131–144.

Hutchings, J. A. 2001. Influence of population decline, fishing, and spawner variability on the recovery of marine fishes. – J. Fish Biol. 59: 306–322.

Hutchings, J. A. and Reynolds, J. D. 2004. Marine fish population collapses: consequences for recovery and extinction risk. – BioScience 54: 297–309.

Jenouvrier, S. et al. 2005a. Long-term contrasted responses to climate of two Antarctic seabirds species. – Ecology 86: 2889–2903.

Jenouvrier, S. et al. 2005b. Evidence of a shift in cyclicity of Antarctic seabirds dynamics link to climate. – Proc. R. Soc. Lond. B 272: 887–895.

Jenouvrier, S. et al. 2009. Demographic models and IPCC climate projections predict the decline of an emperor penguin population. – Proc. Natl Acad. Sci. USA 106: 1844–1847.

Jouventin, P. 1975. Mortality parameters in emperor penguins *Aptenodytes forsteri*. – In: Stonehouse, B. (ed.), The biology of penguins. Macmillan Press, pp. 435–446.

Knowles, C. J. 1986. Population recovery of black-tailed prairie dogs following control with zinc phosphide. – J. Range Manage. 39: 249–250.

Kooyman, G. et al. 2007. Effects of giant icebergs on two emperor penguin colonies in the Ross Sea, Antarctica. – Antarct. Sci. 19: 31–38.

Lande, R. and Orzack, S. 1988. Extinction dynamics of age-structured populations in a fluctuating environment. – Proc. Natl Acad. Sci. USA 85: 7418–7421.

Micol, T. and Jouventin, P. 2001. Long-term population trends in seven Antarctic seabirds at Pointe Geologie (Terre Adelie). Human impact compared with environmental change. – Polar Biol. 24: 175–185.

Morris, W. et al. 2008. Longevity can buffer plant and animal populations against changing climate variability. – Ecology 89: 19–25.

Offredo, C. 1986. The diet of emperor penguins *Aptenodytes forsteri* In Adélie Land, Antarctica. – Ibis 128: 409.

Raimondoa, D. C. and Donalds, J. S. 2003. Responses of cycads with different life histories to the impact of plant collecting: simulation models to determine important life history stages and population recovery times. – Biol. Conserv. 111: 345–358.

Ramula, S. and Lehtila, K. 2005. Importance of correlations among matrix entries in stochastic models in relation to number of transition matrices. – Oikos 111: 9–18.

Reid, K. and Croxall, J. P. 2001. Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. – Proc. R. Soc. Lond. B 268: 377–384.

Rodionov, S. 2004. A sequential algorithm for testing climate regime shifts. – Geophys. Res. Lett. 31: L09204.

Rodionov, S. 2005. A brief overview of the regime shift detection methods. – In: Velikova, V. and Chipev, N. (eds), Large-scale disturbances (regime shifts) and recovery in aquatic ecosystems: challenges for management toward sustainability. UNESCO-ROSTE/BAS Workshop on Regime Shifts, pp. 17–24.

Sæther, B. E. and Bakke, O. 2000. Avian life history variation and contribution of demographic trait to the population growth rate. – Ecology 81: 642–653.

Samuels, W. B. and Ladino, A. 1984. Calculations of seabird population recovery from potential oilspills in the mid-Atlantic region of the United States. – Ecol. Modell. 21: 63–84.

Sinclair, A. R. E. 1989. Population regulation in animals. – In: Cherrett, J. M. (ed.), Ecological concepts: the contribution of ecology to an understanding of the natural world. Blackwell, pp. 197–241.

Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press.

Weimerskirch, H. et al. 2003. Trends in bird and seal populations as indicators of a system shift in the southern ocean. – Antarct. Sci. 15: 249–256.

Wisdom, M. J. and Mills, L. S. 1997. Sensitivity analysis to guide population recovery: prairie-chickens as an example. – J. Wildlife Manage. 61: 302–312.

Wienecke, B. C. and Robertson, G. 1997. Foraging space of emperor penguins *Aptenodytes forsteri* in Antarctic shelf water in winter. – Mar. Ecol. Progr. Ser. 159: 249–253.