1   **Bottom-up effects of a no-take zone on endangered penguin**

2   **demographics**

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Abstract

Marine no-take zones can have positive impacts for target species and are increasingly important management tools. However, whether they indirectly benefit higher-order predators remains unclear. The endangered African penguin (*Spheniscus demersus*) depends on commercially exploited forage fish. We examined how chick survival responded to an experimental three-year fishery closure around Robben Island, South Africa, controlling for variation in prey biomass and fishery catches. Chick survival increased by 18% when the closure was initiated, which alone led to a predicted 27% higher population compared with continued fishing. However, the modelled population continued to decline, likely because of high adult mortality linked to poor prey availability over larger spatial scales. Our results illustrate that small no-take zones can have bottom-up benefits for highly mobile marine predators, but are only one component of holistic, ecosystem-based management regimes.

1. Introduction

Anthropogenic actions, including industrial fishing, have profoundly altered marine ecosystems and rapid action is required to rehabilitate the oceans [1]. Marine Protected Areas (MPAs) are increasingly designated to protect benthic habitats and species, but their efficacy for highly mobile species is unclear [2,3]. This problem is exacerbated when fisheries closures are designed to benefit mobile, upper-trophic level predators by protecting their prey [4]. In particular, behaviourally mediated change or unrelated natural fluctuations in prey may mask population-level responses to closures [4–6].

The endangered African penguin *Spheniscus demersus* could benefit from MPAs [7]. This southern African endemic, a short-range (20–40 km) forager when breeding [6], feeds on commercially exploited forage fish (sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*) [8]. Decreased availability of these fish off western South Africa has been linked to a 69% reduction in penguin numbers between 2001 and 2013 [9]. Purse-seine fisheries may deplete stocks [10,11] and without spatial management, the South African fishery can remove adult sardine and anchovy recruits from waters adjacent to penguin colonies [6]. The species' worsening conservation status led to the implementation of experimental fishing closures around four colonies between 2008 and 2014. An initial ban at St. Croix Island (33° 48' S, 25° 46' E) reduced penguin foraging effort, but did not influence breeding success, adult body mass or chick growth [6,7]. Therefore the efficacy of these closures at the population-level and whether they should continue, have been the subject of much debate [12].

From 2011 to 2013, a 20 km radius around Robben Island (33° 48' S, 18° 22' E), South Africa, was closed to purse-seine fishing. Chick survival is heavily influenced by the rate and amount of food delivered to the nest, so should respond if closure increases prey availability above baseline levels [6]. We examined whether penguin chick survival varied between years with (2011–2013) and without (2001–2010) fisheries closure and used a demographic

model to examine the impact on population growth. Crucially, we used biomass estimates to account for variation in prey availability, penguin population estimates to control for density-dependent effects and catch data from outside the closure to control for changes in fishing activity over larger spatial scales.

2. Materials and Methods

(a) Penguin data

Data were from 1054 African penguin nests monitored at Robben Island between 2001 and 2010 and 447 nests between 2011 and 2013 (electronic supplementary material, table S1). We calculated the number of days each chick was exposed to potential mortality (nestling days) then estimated failure rates and standard errors (SE) for each year independently using parametric survival models in R v.3.0.2. We used nest identity as a shared frailty term, an exponential error distribution [13] and an exponential distribution to transform the failure rates to annual estimates of chick survival [8]. An island-wide census in May each year estimated the annual breeding population [14].

(b) Fish biomass and catch data

To account for changing prey availability we used hydro-acoustic survey estimates of the adult biomass (excluding age 0 juveniles) of sardine west of Cape Agulhas during November prior to penguin breeding and the recruit (age 0) biomass of anchovy in May of the breeding season from 2001 to 2013. Although no catches were taken within the closed area, fishing continued outside (figure 1). To account for possible effects of this on closure efficacy [6], we used annual sardine and anchovy catch data from the 30 nautical mile (55.6 km) fishing blocks around Robben Island (see electronic supplementary material).

(c) Analysis of closure effect

We considered candidate models similar in form to linear models, with additive fixed effects and normally distributed residuals (table 1 and electronic supplementary material, table S2).

87 The annual chick survival estimates $(\phi_{c,y})$, transformed to the logit scale, formed the

88 response variable. As these were estimated rather than observed directly, we modelled them

89 as originating from a latent normal distribution so that $\mathrm{logit}(\phi_{c,y}) \sim N(\varphi, \hat{\tau}_y)$, where φ is the

90 unknown true mean survival and $\hat{\tau}_y$ is the standard error for year y. The 'Closure' variable

91 (Open = 0, Closed = 1) was included in each candidate model (except the null model), with

92 the catch, biomass and census data added to account for changing conditions experienced

93 by the breeding population over time. Models were fitted using Monte-Carlo Markov Chain

94 estimation using the 'rjags' and 'coda' libraries for R v.3.0.2, non-informative priors and

95 three chains of length 1 000 000 (first 10 000 samples discarded as burn-in, no thinning).

96 Models were compared using penalized expected deviance (PED) and considered well

97 supported if their ΔPED was smaller than the associated SE under repeated sampling [15].

98

99 (d) Demographic model structure

100 We constructed a matrix model with one juvenile, three immature and one adult stage

101 classes. We assumed a post-breeding census and that all individuals mature at 4 years [16].

102 The model was:

103
$$N_{t+1} = \mathbf{A}N_t$$

104 (1)

105 where N_t is a vector holding the numbers in each stage at time t, and $\mathbf{A}$ is the population

106 projection matrix:

107
$$\mathbf{A} = \begin{bmatrix} 0 & 0 & 0 & 0 & F \\ \phi_j & 0 & 0 & 0 & 0 \\ 0 & \phi_a & 0 & 0 & 0 \\ 0 & 0 & \phi_a & 0 & 0 \\ 0 & 0 & 0 & \phi_a & \phi_a \end{bmatrix}$$

108 (2)

109   For $\mathbf{A}$, ϕ_j = first year survival (0.343) and ϕ_a = immature and adult survival (0.743), as

110   studies suggest they are equivalent [17]. Fecundity (F) = $P \times f \times R \times \phi_a$, where P =

111   breeding probability (assumed to be 1); f = proportion of females in the population

112   (assumed to be 0.5); and $R = E \times B \times \phi_e \times \phi_c$, where E = clutch size (1.86 eggs) [18], B =

113   breeding frequency (1.27 clutches per annum) [18], ϕ_e = egg survival (0.548) [18] and ϕ_c =

114   chick survival. Using a starting population of 8512 pairs in 2004 [14] we first modelled the

115   observed population trajectory for 2005–2013. We then simulated the population trajectory

116   over 10 years (2014–2023) in the presence and absence of closure by modifying the ϕ_c

117   component of F with the mean closure effect from the best supported model above.

118

119   **3. Results**

120   Three models were well supported (ΔPED/SE < 1), all containing positive closure effects

121   (table 1; electronic supplementary material, figure S1). The model with the lowest PED

122   (model 1, table 1) and the third best model (model 5) were nested in the simpler model 7

123   (Table 1), which accounted for changes in sardine biomass and closure status. Based on

124   this (most parsimonious) model, chick survival in 'Closed' years was 0.658 (95% credible

125   intervals: 0.523–0.773) versus 0.470 (0.395–0.546) in 'Open' years at mean sardine biomass

126   (figure 1).

127

128   The demographic model reproduced the decline at Robben Island (figure 2), predicting 1349

129   pairs in 2013 (1.06% below the census figure). Without closure (ϕ_c = 0.470), the population

130   growth rate (λ) = 0.815 and the 2023 population = 175 pairs. With closure (ϕ_c = 0.658), λ =

131   0.835 and the 2023 population = 222 pairs, a 26.9% increase. However, the projected

132   population continued to decline in both cases and the difference (47 pairs) represented 3.5%

133   of the 2013 population.

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4. Discussion

After controlling for long-term variation in prey availability, our results demonstrate that small-scale fishing closures can provide demographic benefits for penguins. Although the closure was relatively small, and catches continued at its boundary, chick survival was 18% higher on average when fishing was excluded, likely because of decreased prey depletion within the foraging range of breeding birds [5–7,10]. The population difference predicted to accrue over time supports the continuation of this closures programme [6].

Although our analysis suggests that if current conditions on the west coast prevail these closures will be insufficient to allow population recovery (figure 2), we only modelled an impact on chick survival. Population dynamics in long-lived vertebrates are often least sensitive to variation in fecundity. Thus a key question remains whether small-scale closures can improve adult or juvenile survival. For African penguins elsewhere, closures decreased energy expenditure during provisioning [7], which may improve survival over time. Detecting such effects would require analysis of capture-mark-recapture data and a longer period of closures. In turn, this would allow for robust assessment of the magnitude of the population-level impacts of small-scale no-take zones.

Assessments of this kind are important to fully elucidate the role for targeted, small-scale fisheries closures in marine conservation. MPAs can contribute towards the conservation of marine predators, but rarely protect highly-mobile species throughout their life-cycle [2,3,19]. African penguins feed far from colonies when not breeding and have suffered poor adult survival over the last decade as the regional abundance of sardine fell below a critical threshold [17,20]. It is becoming increasingly clear that fishing can exacerbate forage fish population collapses [11], with consequences for predators [21]. The recent adult mortality observed in African penguins easily offsets the improved chick survival noted here. As a consequence, the conservation of African penguins (and many other marine predators) is likely to require strategies to maintain forage fish populations above critical thresholds

163 [11,20,21] and spatial protection at various scales (i.e. MPA networks) [2]. In summary, our

164 results support the use of small-scale fishing closures to conserve marine predators [4–6]

165 but highlight the importance of integrating them into holistic, ecosystem-based management

166 regimes.

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Author contributions

177 R.B.S., R.J.M.C., and C.D.v.d.L. contributed data. R.B.S. wrote the first draft and analysed

178 the data with help from H.W., R.A., and S.C.V. All authors contributed to interpretation,

179 revisions and approved the final version.

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184 **Competing interests.** We have no competing interests.

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249 **Tables**

250 **Table 1.** Model selection results for analyses relating African penguin chick survival to

251 closure status.

| Model No.	Model	$\overline{D}$	P_{opt}	PED	ΔPED	SE	ΔPED/SE	Closure effect
1	AB+SB+C	−8.16	112.1	103.9	0.0	0.00	0.00	+
7	SB+C	−8.79	122.2	113.4	9.5	11.91	0.80	+
5	SB+AC+C	−8.74	122.1	113.4	9.5	10.74	0.88	+
6	SB+SC+C	−8.93	129.7	120.8	16.9	14.45	1.17	+
3	AB+SC+C	−8.73	134.5	125.8	21.9	17.74	1.23	+
17	Null model	−8.90	215.3	206.4	102.5	33.48	3.06	NA

252 $\overline{D}$ = expected deviance; P_{opt} = optimism penalty applied to model; PED = penalised

253 expected deviance ($\overline{D}$ + P_{opt}); ΔPED = difference in *PED*; SE = standard error associated

254 with Δ*PED*; ratio of Δ PED/SE, indicating model support; AB = anchovy biomass; SB =

255 sardine biomass; SC = sardine catch; AC = anchovy catch; C = closure status. The top

256 five and the null model are shown.

257
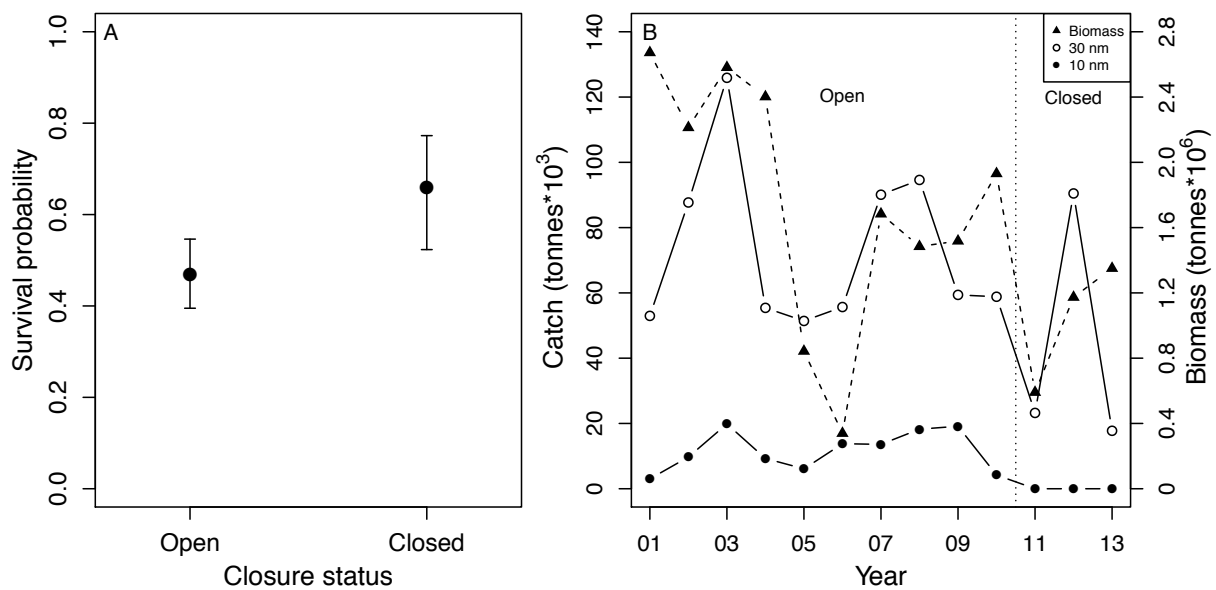
Figures

Figure 1. A: Mean (±95% credible intervals) chick survival during 2001–2010 (Open) and 2011–2013 (Closed) from model 7 (Table 1). B: Combined sardine (November surveys) and anchovy (May surveys) biomass off western South Africa (▲) and combined catches within 10 nm (entirely encompassed by the closure; ●) and 30 nm of Robben Island (○). The vertical line indicates the onset of closure.

266
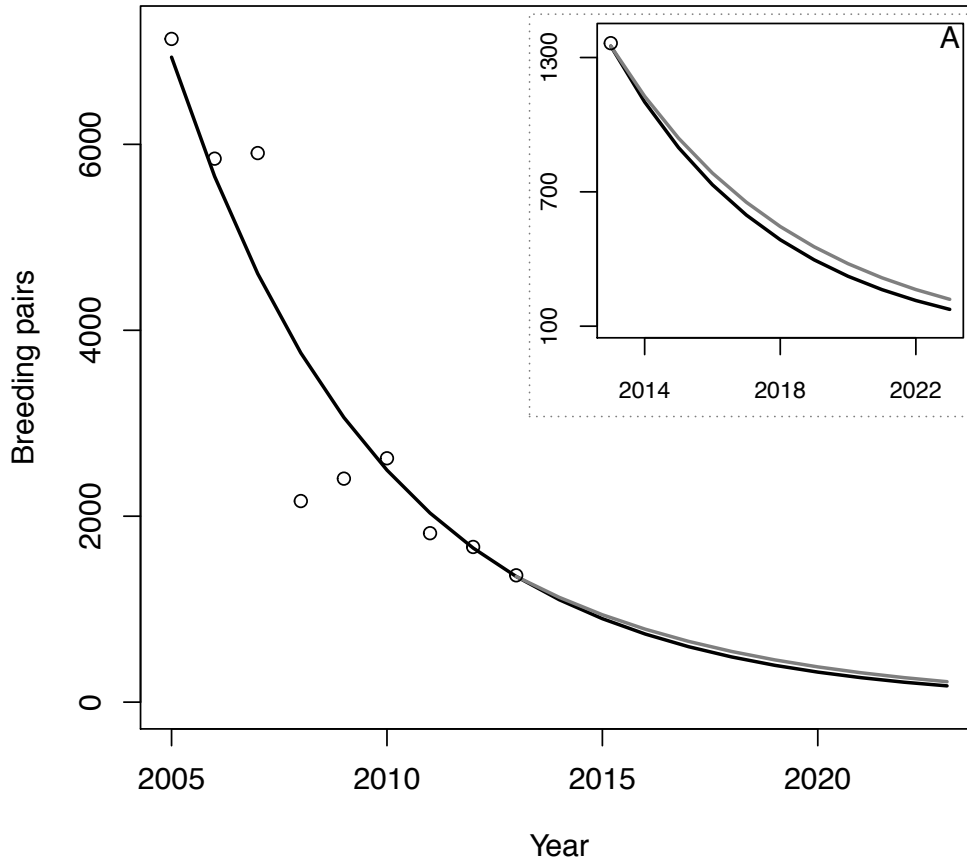
Figure 2. Observed (○) and modelled African penguin breeding population (pairs) if fishing
continued for 2005–2023 (black line) and if fishing was excluded within 20 km of the island
from 2014–2023 (grey line). A: 2014–2023 projections on a scale from 100 to 1400 pairs.