

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

2 **demographics**

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17

18 **Abstract**

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

30

31 **1. Introduction**

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

39

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

53

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

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

63

## 64 **2. Materials and Methods**

### 65 (a) Penguin data

66 Data were from 1054 African penguin nests monitored at Robben Island between 2001 and  
67 2010 and 447 nests between 2011 and 2013 (electronic supplementary material, table S1).  
68 We calculated the number of days each chick was exposed to potential mortality (nestling  
69 days) then estimated failure rates and standard errors (SE) for each year independently  
70 using parametric survival models in R v.3.0.2. We used nest identity as a shared frailty term,  
71 an exponential error distribution [13] and an exponential distribution to transform the failure  
72 rates to annual estimates of chick survival [8]. An island-wide census in May each year  
73 estimated the annual breeding population [14].

74

### 75 (b) Fish biomass and catch data

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

83

### 84 (c) Analysis of closure effect

85 We considered candidate models similar in form to linear models, with additive fixed effects  
86 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  $\text{logit}(\phi_{c,y}) \sim N(\varphi, \hat{\tau}_y)$ , where  $\varphi$  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  $\Delta\text{PED}$  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:

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

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

$$107 \quad \mathbf{A} = \begin{bmatrix} 0 & 0 & 0 & 0 & F \\ \phi_j & 0 & 0 & 0 & 0 \\ 0 & \phi_a & 0 & 0 & 0 \\ 0 & 0 & \phi_a & 0 & 0 \\ 0 & 0 & 0 & \phi_a & \phi_a \end{bmatrix} \quad (2)$$

108

109 For  $\mathbf{A}$ ,  $\phi_j$  = first year survival (0.343) and  $\phi_a$  = 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],  $\phi_e$  = egg survival (0.548) [18] and  $\phi_c$  =  
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  $\phi_c$   
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 ( $\Delta\text{PED}/\text{SE} < 1$ ), 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 ( $\phi_c = 0.470$ ), the population  
130 growth rate ( $\lambda$ ) = 0.815 and the 2023 population = 175 pairs. With closure ( $\phi_c = 0.658$ ),  $\lambda$  =  
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.

134

135 **4. Discussion**

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

142

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

152

153 Assessments of this kind are important to fully elucidate the role for targeted, small-scale  
154 fisheries closures in marine conservation. MPAs can contribute towards the conservation of  
155 marine predators, but rarely protect highly-mobile species throughout their life-cycle [2,3,19].  
156 African penguins feed far from colonies when not breeding and have suffered poor adult  
157 survival over the last decade as the regional abundance of sardine fell below a critical  
158 threshold [17,20]. It is becoming increasingly clear that fishing can exacerbate forage fish  
159 population collapses [11], with consequences for predators [21]. The recent adult mortality  
160 observed in African penguins easily offsets the improved chick survival noted here. As a  
161 consequence, the conservation of African penguins (and many other marine predators) is  
162 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.

167

168 **Data accessibility.** The data are in the electronic supplementary material or Dryad digital  
169 repository: <http://dx.doi.org/10.5061/dryad.t446r>.

170

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175

#### 176 **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.

180

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183

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

185



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248

249 **Tables**

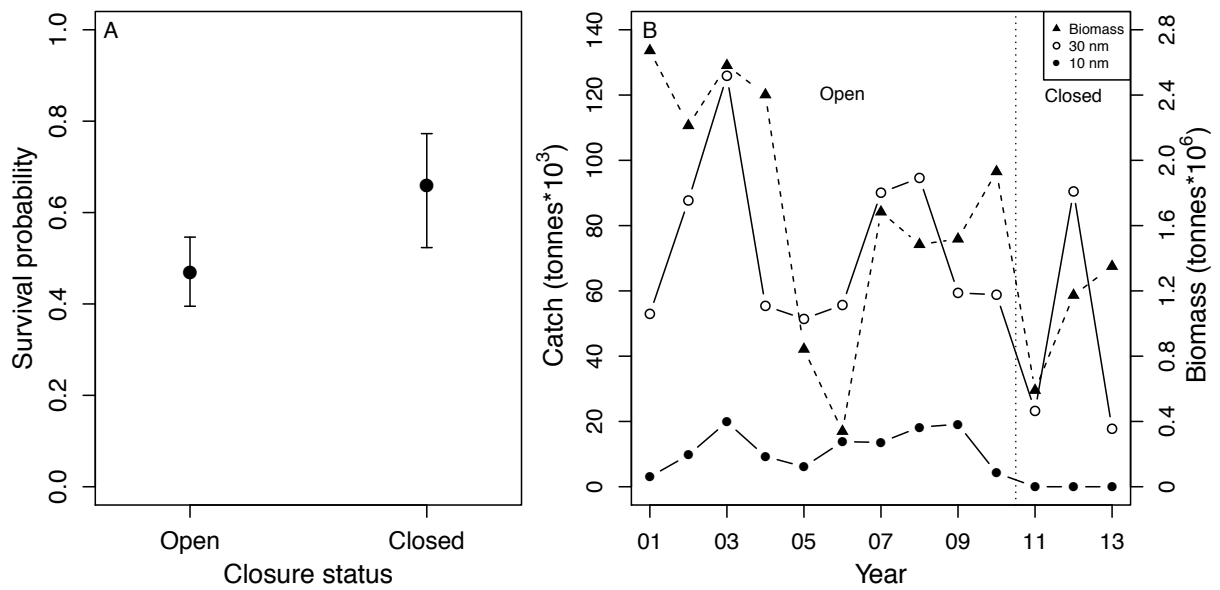
250 **Table 1.** Model selection results for analyses relating African penguin chick survival to  
 251 closure status.

Model No.	Model	$\bar{D}$	$P_{opt}$	$PED$	$\Delta PED$	SE	$\Delta PED/SE$	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  $\bar{D}$  = expected deviance;  $P_{opt}$  = optimism penalty applied to model; PED = penalised  
 253 expected deviance ( $\bar{D} + P_{opt}$ );  $\Delta PED$  = difference in  $PED$ ; SE = standard error associated  
 254 with  $\Delta PED$ ; ratio of  $\Delta PED/SE$ , 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

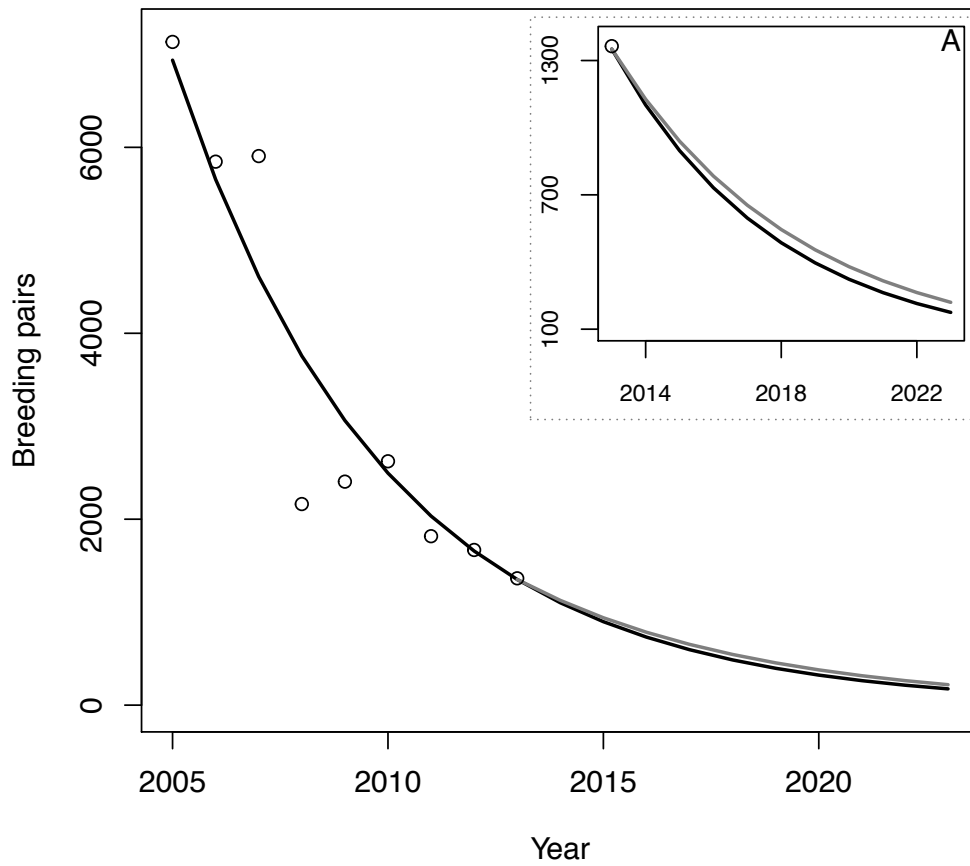
258 **Figures**



259

260 **Figure 1.** A: Mean ( $\pm 95\%$  credible intervals) chick survival during 2001–2010 (Open) and  
 261 2011–2013 (Closed) from model 7 (Table 1). B: Combined sardine (November surveys) and  
 262 anchovy (May surveys) biomass off western South Africa ( $\blacktriangle$ ) and combined catches within  
 263 10 nm (entirely encompassed by the closure;  $\bullet$ ) and 30 nm of Robben Island ( $\circ$ ). The  
 264 vertical line indicates the onset of closure.

265



266

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