

1 **Defining ecologically-relevant scales for spatial protection using long-term data**

2 **on an endangered seabird and local prey availability**

3

4 **Abstract:** Human activities are important drivers of marine ecosystem functioning. However,
5 separating the synergistic effects of fishing and environmental variability on the prey base of non-
6 target predators is difficult, often because prey availability estimates on appropriate scales are
7 lacking. Understanding how prey abundance at different spatial scales links to population change
8 can help integrate the needs of non-target predators into fisheries management by defining
9 ecologically-relevant areas for spatial protection. We investigated the local population response
10 (number of breeders) of the bank cormorant *Phalacrocorax neglectus*, a range-restricted endangered
11 seabird, to the availability of its prey, the heavily-fished west coast rock lobster *Jasus lalandii*.
12 Using Bayesian state-space modeled cormorant counts at three colonies, 22 years of fisheries-
13 independent data on local lobster abundance and generalized additive modeling, we determined the
14 spatial-scale pertinent to these relationships in areas of differing lobster availability. Cormorant
15 numbers responded positively to lobster availability in the intermediate and high abundance
16 regions, but not where regime shifts and fishing pressure have depleted lobster stocks. The
17 relationships were strongest at 20-30 km, greater than the cormorants' foraging range when
18 breeding, and may have been influenced by prey availability for non-breeding birds, prey switching
19 or prey ecology. Our results highlight the importance of considering the scale of ecological
20 relationships in marine spatial planning and suggest that designing spatial protection around focal
21 species can benefit marine predators across their full life cycle. We propose the precautionary
22 implementation of small-scale marine protected areas, followed by robust assessment and adaptive-
23 management, to confirm population-level benefits for the cormorants, their prey and the wider
24 ecosystem, without negative impacts on local fisheries.

25 **Introduction**

26 Environmental change and direct anthropogenic influences are profoundly impacting marine
27 ecosystem functioning, with negative consequences for upper-trophic-level predators (e.g. Hobday
28 et al. 2015). One possible solution is implementing Marine Protected Areas (MPAs) where human
29 activities – particularly fishing – are restricted (McCay & Jones 2011). However, given the potential
30 socio-economic impacts, governments may be reluctant to restrict fishing without clear evidence for
31 ecological benefits, making even adaptive-management (where management is adjusted as
32 understanding improves) of MPAs difficult (Mangel 2010). Thus, MPAs have strong support in
33 conservation policy, but integrating them into ecosystem-based fisheries management remains a
34 major challenge (McCay & Jones 2011). Indeed, their efficacy in protecting dependent predators by
35 increasing access to prey resources remains unclear; separating the influence of fishing and
36 environmental variability is problematic because it requires long time-series straddling a closure
37 and fisheries-independent prey availability data on appropriate scales are usually lacking (e.g.
38 Daunt et al. 2008; Sherley et al. 2015). Moreover, even the largest of MPAs may have limited
39 benefits for upper-trophic-level predators if the mobility of such species is not considered (Agardy
40 et al. 2011; Hays et al. 2014).

41

42 In light of these caveats, analyzing long-term datasets on the relationship between focal predator
43 populations and the changing abundance of their prey at different spatial scales could help identify
44 situations where small-scale protected areas meet the ecological requirements of threatened taxa
45 throughout their life-cycle. The resulting ecologically-relevant MPAs could play an important role
46 in broader marine spatial planning agendas by helping governments create effective MPAs
47 networks – arguably more effective than few large-scale MPAs (De Santo 2013; McCauley 2014) –
48 by raising public support for protected areas via flagship species (Lee et al. 2015), and by
49 encouraging stakeholders to treat MPA implementation as policy experiments (Mangel 2010; Fox et
50 al. 2012).

51 In South Africa, the interactions between the endangered bank cormorant *Phalacrocorax neglectus*
52 and its main prey, the west coast rock lobster *Jasus lalandii* (hereafter rock lobster), offer an
53 opportunity to develop ecologically-relevant MPAs. Lobsters are generally heavily fished, but
54 readily benefit from protected areas (Lester et al. 2009; Moland et al. 2013), while dependent
55 fisheries can ultimately benefit from MPAs through spill-over effects (Goñi et al. 2010). Rock
56 lobster is South Africa's third most valuable marine resource. Catches peaked at 16 000 t in the
57 1950s, then declined following overfishing to < 5 000 t after 1960 (Pollock et al. 2000). A formal
58 stock assessment procedure was introduced in 1997, with a spatial component added in 2006, but
59 the stock remains well below target levels (de Moor et al. 2015). Today, the fishery is
60 acknowledged to be in a poor state (de Moor et al. 2015; Sink 2016) with the available biomass
61 estimated at < 3% of 'pristine' (see Blamey et al. 2015). Individual lobster growth rates also
62 declined during the 1970s and 1980s, while in the 1990s a 'regime shift', characterized by increased
63 upwelling and wind variability, coincided with an eastward expansion in the lobster's distribution
64 (Blamey et al. 2012). Consequently, the percentage of landings taken north and west of Cape Town
65 (Areas 1–7, Fig. 1) declined from ~ 60% to < 10% between the late-1980s and 2000, while the
66 reverse occurred south of Cape Town (Area 8, Fig. 1; Cockcroft et al. 2008).

67

68 These changes in lobster abundance and distribution mediated top-down and bottom-up ecosystem
69 effects (Blamey et al. 2015; Crawford et al. 2015). The bank cormorant, which feeds extensively on
70 rock lobster in South Africa (Crawford et al. 2015), decreased from ~ 9 000 breeding pairs in the
71 late-1970s to fewer than 2 600 breeding pairs in 2015, of which < 800 were in South Africa (Cook
72 2015). Several threats contributed to this decline including oiling, disturbance and bycatch in
73 lobster pots (Cooper 1985; Cook 2015). However, food shortage is considered the key factor
74 (Crawford et al. 2008, 2015) given the bank cormorants' restricted foraging range (~10 km when
75 breeding; Ludynia et al. 2010) and the importance of rock lobster in their diet (Cooper 1985;
76 Crawford & Cooper 2005).

77 Landings of rock lobster in the offshore fishery and bank cormorant numbers have been correlated
78 in the past (Crawford et al. 2008), while cormorant extirpation at Lambert's Bay and colonization at
79 Stony Point followed a significant decline and increase in lobster abundance respectively (Fig. 1;
80 Cockcroft et al. 2008). Moreover, the marine environment within 1.8 km of Robben Island (Fig. 1)
81 has been closed to rock lobster fishing since 1960 (Pollock 1987) and that island supported the
82 largest bank cormorant colony in South Africa until 2015 (~100 pairs; Sherley et al. 2012). With
83 commercial fishing prohibited, breeding habitat may have been limiting colony growth rather than
84 prey availability (Sherley et al. 2012).

85

86 In light of this, bank cormorant conservation could benefit from excluding lobster fishing around
87 other colonies. Crucially, although South Africa is implementing a network of 22 new MPAs (the
88 Phakisa Network), the designation process has been criticized for ignoring the poor status of the
89 west coast rock lobster (Sink 2016), precisely because ecological and fisheries benefits of no-take
90 lobster areas have been demonstrated previously (Lester et al. 2009; Goñi et al. 2010; Moland et al.
91 2013). In this context, we examined the link between the number of bank cormorant breeders
92 (hereafter the 'local population response') and rock lobster availability at increasing distances
93 around three key breeding colonies, two north of Cape Town, where rock lobster abundance has
94 declined and one to the east of Cape Point (Fig. 1), where rock lobsters have increased. We aimed
95 to evaluate the spatial scale over which availability is most influential to these birds and, ultimately,
96 recommend management strategies that could provide for robust tests of whether MPAs can
97 produce sustained benefits for neritic seabirds without impacting local fishing communities.

98

99 **Methods**

100 *Bank cormorant counts*

101 We used counts of bank cormorant breeding pairs from three colonies: Jutten Island (33°05'S;
102 17°57' E); Dassen Island (33°25'S; 18°05'E); and Stony Point (34°22'S; 18°53'E) (Fig. 1). These

103 colonies were chosen because (1) 1–3 counts were conducted during austral winter, around peak
104 breeding in most years between 1987 and 2015 (Crawford et al. 2008, 2015); (2) they are
105 distributed towards the north, center and east of the area of operation of the South African rock
106 lobster fishery (Crawford et al. 2008); and (3) fisheries-independent estimates of rock lobster
107 abundance were available for adjacent waters for 1993–2015 (excluding 2000, see below). At all
108 sites, the cormorant nests are clustered on adjacent boulders within c. 100 m of each other.

109

110 Of a possible 69 counts between 1993 and 2015, five were not made (all at Stony Point, Fig. 2) and
111 one count was considered unreliable because it was made outside the main breeding period (2011 at
112 Dassen Island, Fig. 2). To estimate these missing counts, and account for the unknown observation
113 error in the remaining data, we used all available counts from 1987 and a state-space model (SSM)
114 to generate annual time-series of the local population response for each colony between 1993 and
115 2015 (Fig. 2). We specified an exponential growth model on the log scale, where the state process
116 was $\log(N_{t+1,i}) = \log(N_{t,i} + r_{t,i})$, with $r_{t,i} \sim \text{Normal}(\bar{r}_i, \sigma_{r,i}^2)$ and observation process $y_{t,i} =$
117 $N_{t,i} + \varepsilon_{t,i}$, with $\varepsilon_{t,i} \sim \text{Normal}(0, \zeta_{y,i}^2)$, where $y_{t,i}$ are observed data, $N_{t,i}$ the estimated population
118 size, $\varepsilon_{t,i}$ the observation error with variance $\zeta_{y,i}^2$, and $r_{t,i}$ the population growth rate, varying around
119 a long-term mean \bar{r}_i with process error $\sigma_{r,i}^2$ for year t at colony i (Kéry and Schaub 2012). We ran
120 three chains of 200,000 iterations in JAGS (v. 4.1.0; Plummer 2003), using the *jagsUI* library (v.
121 1.3.7) in R (v. 3.2.3; R Core Team 2015), with vague priors, burn-in of 20,000 samples and no
122 thinning (see Supporting Information for model code).

123

124 *Rock lobster data*

125 The west coast of South Africa is divided into 14 commercial harvesting areas for rock lobster (Fig.
126 1). Fisheries Independent Monitoring Surveys (FIMS), designed to obtain information on, *inter*
127 *alia*, relative rock lobster abundance, began in Areas 5–8 in 1993 (Cockcroft et al. 2008; Fig. 1).

128 For 1993–1999 and 2001–2015, annual FIMS sampling occurred over two-weeks between January
129 and May; no sampling occurred in 2000 due to logistic constraints. Within each area, five lobster
130 traps were deployed at each of 110–160 sampling stations annually (Fig. 3); ~75% of stations were
131 visited twice, with the remainder sampled once. At each visit, traps were set, left for 15–20 hours,
132 recovered and the number of lobsters caught was recorded. We used FIMS data from three
133 locations: (1) Areas 5 and 6 for Jutten Island, (2) Areas 6 and 7 for Dassen Island and (3) Area 8 for
134 Stony Point (Fig. 1; Supporting Information). In this last case, it was necessary to use data sampled
135 only in Area 8 as FIMS data were not collected east of this (Area 12).

136

137 *Data Analysis*

138 We used the GPS positions of each FIMS station (Fig. 3) to measure their distance from their
139 adjacent bank cormorant colony in ARCGIS v. 10.2 (Environmental Systems Research Institute,
140 Redlands, USA) and categorize them into four distance intervals: 0–5 km; 0–10 km; 0–20 km; and
141 0–30 km radius around each colony. For Stony Point, we used a location on the coast (Hangklip
142 Lighthouse, 34°23.2'S, 18°49.7' E), 5 km west of Stony Point and on the border of FIMS survey
143 Area 8 as a proxy for the colony location (Fig. 1). By the start of our study, Area 8 and those east of
144 Hangklip Lighthouse (Areas 12–14) combined both contributed around 40% to the total recreational
145 catch of rock lobster (Cockcroft & Mackenzie 1997) suggesting similar abundance in these regions.

146

147 We calculated catch per unit effort (CPUE) as total number of lobsters caught divided by number of
148 traps set for each distance interval at each colony. CPUE may be influenced by social interactions
149 within and around traps, such as large lobsters, once caught, excluding other, smaller lobsters from
150 entering traps (e.g. Ihde et al. 2006). We therefore also used the proportion of total traps set that
151 contained lobsters (TCL) for each distance interval to index the available abundance around each
152 colony.

153 We compared the bank cormorant response (from the SSM) and rock lobster indices between
154 colonies using ANOVA and Tukey’s Honest Significant Difference (HSD). Because seabirds often
155 show non-linear responses to their prey (e.g. Cury et al. 2011), we examined the relationship
156 between the local population response and rock lobster availability using Generalized Additive
157 Models (GAMs, *mgcv* library for R; Wood & Augustin 2002). To account for the uncertainty
158 associated with the estimated cormorant counts, we weighted each observation by its relative
159 standard deviation (SSM posterior SD/SSM posterior mean).

160

161 The explanatory variables were CPUE and TCL within 5, 10, 20 and 30 km of the breeding locality
162 for Dassen Island and Jutten Island. For Stony Point, the FIMS stations within 5 km of our colony
163 proxy were not sampled in all years, so we used the 10, 20 and 30 km intervals only (Fig. S1). In
164 addition, because a regime shift occurred in the inshore waters of South Africa’s west coast between
165 2003 and 2007 (Blamey et al. 2012, 2015), we included a binary covariate denoted ‘Regime’ to
166 account for this change, with years 1993–2004 = 0 and 2005–2015 = 1. The models tested allowed
167 for additive effects between Regime, and the smoother (see below) for the two measures of rock
168 lobster availability and each distance interval. Thus the maximal models took the form: $Y_i = \alpha +$
169 $S(X_i) + \text{Regime}_i + \varepsilon_i$, where Y_i is the SSM estimated local population response in year i ; α the
170 intercept; $S(X_i)$ is the nonparametric smoothing function, specifying the effect of the lobster
171 covariate X_i on each cormorant count with $\text{Regime}_i = 0$ if a count was from 1993–2004 and = 1
172 otherwise; and $\varepsilon_i \sim N(0, \sigma^2)$ is the residual error. The degrees of freedom of the smoothing
173 functions were selected automatically by generalized cross validation (GCV), with the option for
174 the function to be linear (e.g. $S(X_i) = \beta \times X_i$, where β is the slope).

175

176 Models were run separately for each distance category and island. We also specified models
177 containing only the Regime term and null (intercept only) models (see Supporting Information for

178 the full model set). Inference was based on model selection using Akaike's Information Criterion
179 for small samples sizes (AICc), with models with $\Delta\text{AICc} \leq 2$ considered well supported (Burnham
180 & Anderson 2002). Finally, we checked residual plots for normality, heterogeneity of variance and
181 an absence of auto-correlation ('acf' function in R v. 3.0.2; Supporting Information).

182

183 **Results**

184 *Bank cormorant population trends*

185 Bank cormorants at Jutten Island decreased from a mean (SD) of 47.1 (6.9) pairs for 1993–2004 to
186 21.4 (15.5) pairs for 2005–2015 (Fig. 2). The mean (95% credible intervals, CI) population growth
187 rate (λ) = 0.89 (0.80–0.99), confirming significant decline. At Dassen Island, λ = 0.98 (0.87–1.09),
188 suggesting moderate decline to stability (Fig. 2); the difference between the means (SD) of 41.3
189 (10.9) pairs for 1993–2004 and 52.2 (6.0) for 2005–2015 was marginally not significant (Tukey's
190 HSD: p = 0.06). The population at Stony Point increased from ~6 pairs in 1993 (1993–2004 mean =
191 12.3, SD = 4.6 pairs) to ~60 pairs in 2009 (2005–2015 mean = 36.3, SD = 11.8 pairs; Fig. 2) and
192 λ = 1.12 (1.003–1.25). With the exception of Jutten and Dassen islands for 1993–2004 (p = 0.62),
193 the mean differences in breeding pairs between the colonies were all significant for the two regime
194 periods (all p -values < 0.01).

195

196 *Rock lobster availability*

197 Rock lobster availability was generally greatest around Stony Point, intermediate around Dassen
198 Island and least around Jutten Island at all distances (Fig. S1). For example, mean (SD) CPUE for
199 the 0–30 km interval was 2.3 (2.7) around Jutten Island, 15.4 (13.6) for Dassen Island, and 177.0
200 (54.9) at Stony Point. The differences between locations were significant at all four distances for
201 both CPUE and TCL (Tukey's HSD: all p -values < 0.002).

202

203 *Relationships between the local population response and rock lobster availability*

204 Given the significant differences outlined above, we modelled the relationships for each colony
205 separately. For Jutten Island, no models showed significant effects of rock lobster availability (all p -
206 values > 0.05). At Dassen Island, two models had good AICc support (Supporting Information); the
207 cormorant local population responded positively to the proportion of TCL within 20 km (GAM:
208 effective degrees of freedom (edf) = 1, $F = 6.7$, $p = 0.018$, deviance explained [dev.] = 47.0%) and
209 30 km (edf = 1, $F = 6.7$, $p = 0.018$, dev. = 47.1%) of the colony (Fig. 4a). Regime was significant in
210 both models ($p = 0.005$ and $p = 0.006$ respectively). The next best model ($\Delta\text{AICc} = 2.01$) also
211 contained a marginally significant linear effect of TCL within 10 km (edf = 1, $F = 4.5$, $p = 0.048$).
212 The deviance explained by TCL + Regime at Dassen Island increased from ~38% at 5 km to ~47%
213 at 20 and 30 km (Fig. 4b). At Stony Point, only the model containing a positive, non-linear response
214 between the cormorants' local population and TCL within 30 km (edf = 2.99, $F = 4.6$, $p = 0.017$,
215 dev. = 80.5%; Fig. 4c) and a significant Regime effect ($t = 7.7$, $p < 0.001$) was well supported
216 (Supporting Information).

217

218 **Discussion**

219 Not accounting for the scale of ecological processes in spatial planning can result in protected areas
220 that fail to meet their conservation objectives, even when they cover vast areas (e.g. De Santo 2013;
221 Hays et al. 2014). In the oceans, $< 5\%$ of species may have $> 10\%$ of their home range covered by
222 MPAs (Klein et al. 2015) and effectively conserving mobile species likely requires both small- and
223 broad-scale actions (Boyd et al. 2008; Sherley et al. 2017). Here, we show how modelling the
224 functional link between a predator and their prey can be used to identify both good candidate
225 species and relevant scales for spatial protection. Our results suggest that MPAs with no-take of
226 lobster at ≥ 20 km around bank cormorant colonies (see Supporting Information for an example)
227 would benefit the conservation of this endangered seabird (Crawford et al. 2015). Coupling these
228 closures with adaptive management would provide robust tests of whether such MPAs can produce

229 sustained benefits for seabirds without impacting fisheries, helping elucidate the role for small-
230 scale, localized no-take zones that protect the prey of threatened predators within marine spatial
231 planning (Agardy et al. 2011).

232

233 *Regional differences in the response of bank cormorants to lobster availability*

234 The positive response of bank cormorants to lobster availability at Dassen Island and Stony Point,
235 but not at Jutten Island (despite Saldanha Bay being an area of zero lobster catch) is consistent with
236 the general deterioration of the coastal marine environment off north-west South Africa (Blamey et
237 al. 2012; Crawford et al. 2015). Together the patterns at the three colonies are also consistent with
238 theoretical expectations: an asymptotic-type response where rock lobster was abundant (Stony
239 Point, Fig. 4c), a linear response in the area of intermediate lobster abundance (Dassen Island, Fig.
240 4a) and no apparent response at Jutten Island, where regime shifts and fishing pressure had already
241 made rock lobster scarce by 1993 (Cockcroft & Mackenzie 1997; Cockcroft et al. 2008).

242

243 Marine predators often show asymptotic responses to changing prey availability (Moustahfid et al.
244 2010; Cury et al. 2011) and many seabirds buffer impacts on their survival or fecundity of severe
245 decreases in their preferred prey by targeting other organisms (e.g. Smout et al. 2013). Together,
246 these mechanisms can produce sigmoidal functional responses (i.e. type III; Fig. 5), particularly in
247 demersal or benthic predators (Moustahfid et al. 2010). Indeed, bank cormorants will feed on other
248 organisms when rock lobsters are scarce; at Jutten Island and in Namibia they now eat mainly lower
249 energy fish and crustaceans (Crawford & Cooper 2005; Ludynia et al. 2010; BMD, unpubl, data).
250 Thus, prey switching may sustain small colonies (see Crawford et al. 2008) and could have diluted
251 any response to changing lobster abundance at Jutten Island (cf. Smout et al. 2013; Fig. 5).

252 *Scaling the link between rock lobsters and bank cormorants in space and time*

253 The strong response to rock lobster availability at 20-30 km may result from the life-history traits of
254 palinurid lobsters. Bank cormorants mostly eat lobster < 60 mm carapace length (CL; Avery 1983),
255 though lobsters up to 82 mm CL have been recorded in diet samples (n = 281, BMD and J. Cooper,
256 unpubl. data). At ~ 60 mm CL, rock lobsters begin to move from inshore habitats to deeper waters
257 (Pollock & Beyers 1981) and ~ 95% of lobsters in FIMS traps were between 60–90 mm CL (DAFF,
258 unpubl. data). Hence the local population response to lobster availability beyond the cormorants'
259 foraging range (~ 10 km) may result from the size class of lobsters most commonly caught in FIMS
260 traps tending to be in deeper water, farther offshore.

261

262 Alternatively, or in addition, this pattern may relate to food availability during the non-breeding
263 period, which can influence seabird survival, fecundity and population dynamics (e.g. Salton et al.
264 2015). Non-breeding bank cormorants appear to remain within 20 km of shore and close to breeding
265 colonies (Cooper 1981, 1985). Thus the strong relationship at Dassen Island may be explained by
266 shallow water reefs ~ 20–30 km north and south of the island, reefs that are close to sites of high
267 lobster pueruli settlement (Groeneveld et al. 2010) and where FIMS consistently catch lobster of the
268 size consumed by cormorants (DAFF, unpubl. data). Coupling fine-scale lobster abundance data
269 from baited remote underwater video systems (BRUVS, Roberson et al. 2017) with data on
270 cormorant habitat use (from animal-borne loggers, Ludynia et al. 2010) may clarify this in future.

271

272 *Implications for marine spatial planning*

273 No-catch MPAs can be powerful tools for managing reef-dwelling organisms like lobster (Lester et
274 al. 2009), with increased size, weight, egg production and biomass benefiting fishing yields through
275 spillover effects (e.g. Goñi et al. 2010; Kerwath et al. 2013). However, they are usually most
276 effective in raising yields – and protecting dependent predators – when implemented alongside
277 fisheries management at regional scales (Hopf et al. 2016). The changes in the marine environment,

278 including marked reductions in lobster densities off north-west South Africa, are likely to limit
279 lobster recovery in that area, even in the complete absence of fishing (de Moor et al. 2015). In turn,
280 the null response at Jutten Island suggests lobster no-take zones north of Dassen Island are unlikely
281 to benefit bank cormorants. Prioritizing networks of MPAs where links between predators and the
282 availability of their prey at relevant spatial scales are strongest would help managers avoid the
283 socio-economic costs of placing fishery closures where conservation benefits are unlikely to accrue.

284

285 In contrast, Dassen Island's cormorants responded strongly to rock lobster availability, despite the
286 observed regime shifts (Fig. 4). Lobster landings in Area 7 and bank cormorants at Dassen Island
287 (Fig. 1) both decreased between 1987 and 1994, after which lobster catches increased while
288 cormorant numbers remained low (Crawford et al. 2008). Additionally, the lobster catch legal size
289 limit was reduced from 89 to 75 mm CL in 1993 (Pollock et al. 1997), increasing competition with
290 the industry for the largest lobsters taken by the birds (up to 82 mm CL, see above). It is likely,
291 therefore, that fishing decreased rock lobster availability for bank cormorants at Dassen Island
292 during our study period (Crawford et al. 2008).

293

294 Dassen Island and Robben Island to the south (Fig. 1) hold ~20% of South Africa's remaining bank
295 cormorant population, making them priorities for no-take lobster areas. Moreover, both sites are
296 already under consideration for forms of spatial planning (Sherley et al. 2015, Sink 2016) and
297 precautionary implementation of MPAs to protect bank cormorants would contribute to the Phakisa
298 Network's aim of holistic environmental sustainability (Sink 2016). However, MPAs are
299 increasingly designated to protect non-targeted marine predators (e.g. Notarbartolo di Sciara et al.
300 2008; Ludynia et al. 2012; Boersma et al. 2015) without robust assessments of how they impact of
301 prey availability for predators (but see Sherley et al. 2015). Indeed, studies examining how MPAs
302 influence predator-prey dynamics appear rare (see Barnett & Semmens 2012), and data necessary to
303 undertake multispecies assessments in this regard are generally lacking. In such circumstances,

304 long-term data on focal species can be used to improve conservation outcomes at the ecosystem
305 level (Argady et al. 2011; Lee et al. 2015). In South Africa, experimental 20 km purse-seine fishing
306 closures around Dassen and Robben islands are being assessed for benefits to endangered African
307 penguins *Spheniscus demersus* (Sherley et al. 2015). These same closures offer potential to protect
308 endangered Cape cormorants *P. capensis*, which have a similar foraging range and diet to African
309 penguins (Cook et al. 2012). However, both species target highly mobile pelagic prey and non-
310 breeders move widely (e.g. Sherley et al. 2017), so any effects of fishing restrictions may only
311 become apparent over long-time scales (Mangel 2010; Sherley et al. 2015).

312

313 Adult bank cormorants, in contrast, target relatively sedentary, benthic prey and adult birds should
314 remain within a 20 km MPA year round (Cooper 1981). Hence they may show strong population-
315 level responses to spatial protection. Crucially, non-invasive methods (using video and time-lapse
316 cameras) exist to measure changes in breeding success and foraging effort (Sherley et al. 2012;
317 Botha 2014), allowing closures to be assessed against baseline data or control sites relatively
318 quickly (e.g. 3–4 years; Sherley et al. 2015). As such, bank cormorants offer a potential bridge
319 between single and multispecies conservation planning in this ecosystem; the precautionary and
320 experimental implementation of MPAs of 20 km radius around Robben and Dassen Island would
321 offer potential protection for three endangered seabird species and could stand to benefit local
322 lobster and line-fish fisheries through the kind of spill-over effects already demonstrated in South
323 Africa and elsewhere (Goñi et al. 2010; Kerwath et al. 2013).

324

325 Continuing to collect lobster abundance data inside and outside these MPA, plus data on fisheries
326 catches, would quickly provide insights into the benefits or impacts for local fisheries (e.g. Kerwath
327 et al. 2013). In tandem, a period of robust assessment of their impacts on non-harvested predators'
328 (penguins and cormorants) population dynamics would provide valuable information for MPA
329 management worldwide (Fox et al. 2012). Moreover, as data on the habitat use of these predators

330 improve, and new methods to study ocean ecosystems – like BRUVS (Roberson et al. 2017) –
331 provide more accurate, near-real time prey abundance data, applying dynamic ocean management to
332 these MPAs may become possible (Maxwell et al. 2015). The ability to rapidly adjust no-take zones
333 would help reduce impacts on local fisheries while maintaining ecologically-relevant protection
334 (Maxwell et al. 2015), and expanding to monitoring lobster abundance east of Cape Point could
335 provide a leading indicator of change in the inshore environment to guide future protected areas.

336

337 In conclusion, small-scale, targeted MPAs can individually solve localized, species-specific,
338 conservation problems and, in so doing, contribute to ecosystems approaches to fisheries
339 management (Argady et al. 2011). Moreover, explicitly treating these MPAs as policy experiments
340 – combining precautionary designation, adaptive management and impact evaluation – could help
341 guide the creation of effective MPA networks worldwide (Fox et al. 2012), providing resilience
342 against the impacts of future environmental change on coastal marine ecosystems.

343

344 **Supporting Information**

345 JAGS code (Appendix S1), additional figures (Appendix S2), full candidate model set and model
346 selection results (Appendix S3), are available online. The authors are solely responsible for the
347 content and functionality of these materials. Queries (other than absence of the material) should be
348 directed to the corresponding author.

349

350 **Literature Cited**

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500

501 **Figure Legends**

502 *Figure 1. The west coast of South Africa (A) with the three bank cormorant colonies at Jutten*
503 *Island, Saldanha Bay (insert B), Dassen Island (in A) and Stony Point (insert C), used in this study*
504 *to test the relationship with west coast rock lobster availability from 1993 to 2015. South Africa's*
505 *commercial fishing areas for rock lobster are shown (Areas 1 to 14), as are other localities*
506 *mentioned in the text.*

507
508 *Figure 2. The number of breeding pairs of bank cormorants counted annually (points) and the*
509 *state-space model (SSM) estimated local population response (lines) at Jutten Island (○, dotted*
510 *line), Dassen Island (●, solid line) and Stony Point (▼, dashed line), 1993–2015. The grey shaded*
511 *areas show the Bayesian 95% credible intervals around each SSM estimate.*

512
513 *Figure 3. Positions of Fisheries Independent Monitoring Survey (FIMS) stations for west coast rock*
514 *lobster around Jutten Island, Dassen Island and Stony Point (small grey circles). Large black*
515 *concentric circles represent the radii of 5, 10, 20 and 30 km around each study colony that served*
516 *to identify the FIMS stations used in the analyses. Due to the absence of FIMS stations to the east of*
517 *Stony Point, Hangklip Lighthouse (5 km west of Stony Point) was used as a proxy for Stony Point's*
518 *location.*

519
520 *Figure 4. Results of GAM modelling of the effects of West Cost rock lobster availability on the*
521 *estimated bank cormorant local population response (number breeding), 1993–2015. (A) The linear*
522 *fit between bank cormorant pairs and the proportion of traps containing lobsters (TCL) within the*
523 *30 km (TCL 30) distance interval from the best fitting model for Dassen Island (dev. = 47.1%); (B)*
524 *the percentage deviance in bank cormorant pairs explained by models containing the Regime*
525 *covariate and TCL at the 5, 10, 20 and 30 km distance intervals around Dassen Island; (C) the*
526 *relationship bank cormorant pairs and TCL 30 from the best fitting mode for Stony Point (dev. =*

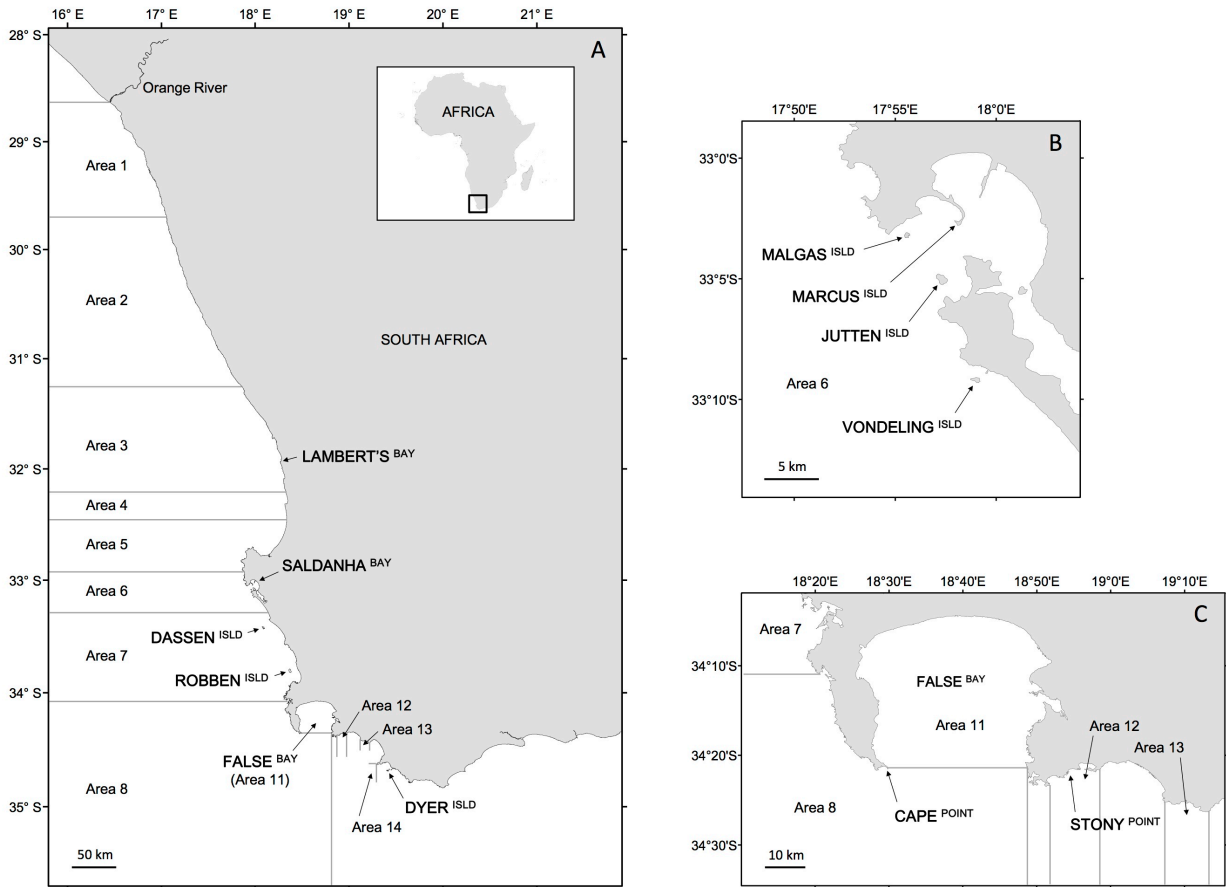
527 80.5%). In A and C , $s(x,y)$ is the smoothing term, with x the explanatory variable and y the
528 estimated degrees of freedom of the smoothing term. The pointwise 95% confidence intervals (grey
529 area) and the partial residuals around the significant covariate effects (◆) are shown.

530

531 *Figure 5. Hypothetical type III functional response curves for the change in the proportion of west*
532 *coast rock lobster in the diet of bank cormorants (dark grey curve) and the change in bank*
533 *cormorant breeding success (light grey curve) in relation to the abundance/availability of west*
534 *coast rock lobster. Across a wide range of prey availability, sigmoidal predator-prey functional*
535 *response curves can result from a combination of mechanisms like predator satiation and prey*
536 *switching (e.g. Moustahfid et al. 2010). The vertical lines approximate the relative range of prey*
537 *availability experienced by the bank cormorants at Jutten Island (dotted lines), Dassen Island (solid*
538 *lines) and Stony Point (dashed lines) during the study period, as indexed by the proportion of traps*
539 *containing lobsters (TCL).*

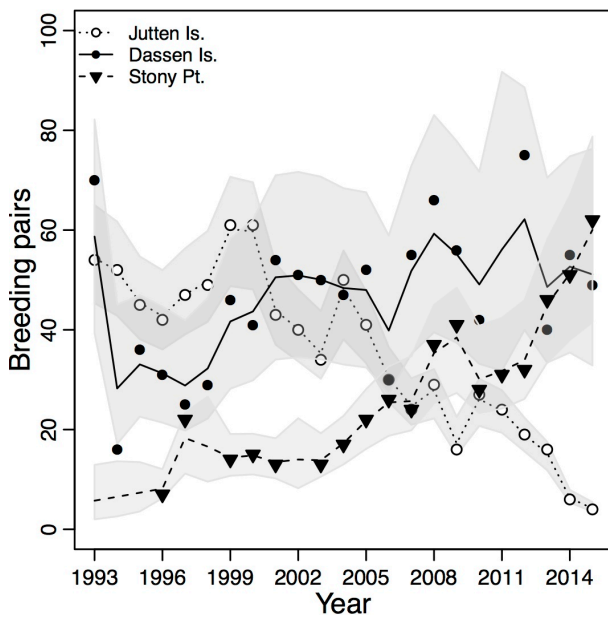
540 **Figures**

541 **Figure 1**



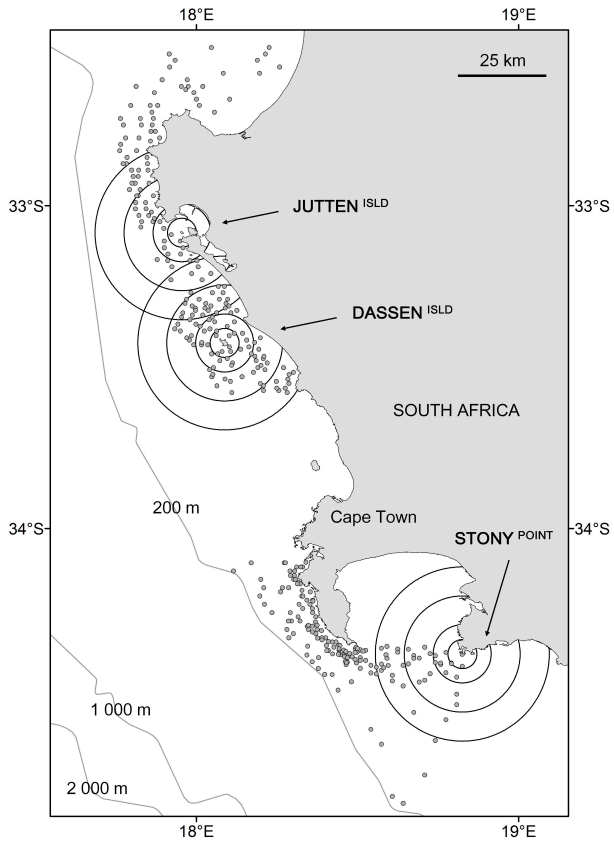
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543 **Figure 2**



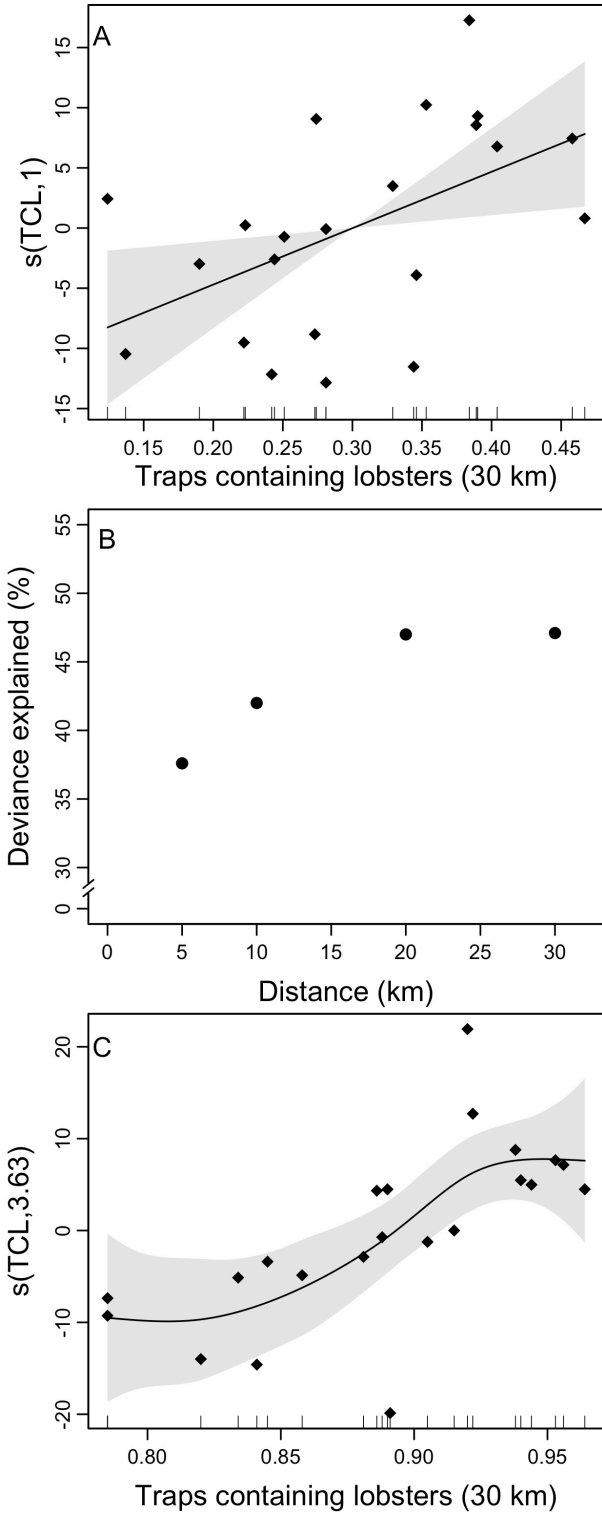
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545 Figure 3



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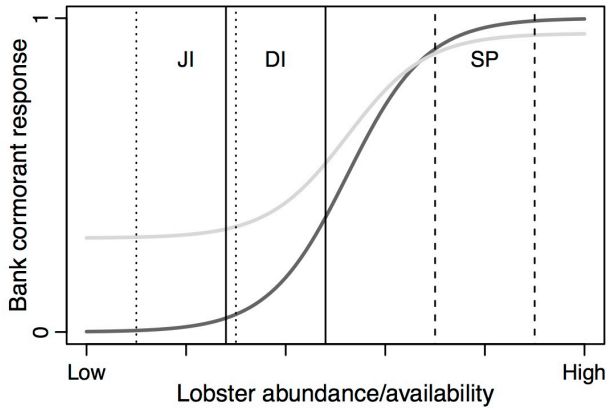
547 Figure 4



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550 Figure 5



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552