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

2   # on an endangered seabird and local prey availability

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25 **Abstract**: Human activities are important drivers of marine ecosystem functioning. However,

26 teasing apart the synergistic effects of fishing and environmental variability on the prey base of

27 non-target predators is difficult, often because estimates of prey availability on appropriate scales

28 are lacking. Hence, understanding the links between direct measures of prey abundance and

29 population change can help integrate the needs of non-target predators into fisheries management.

30 Here we investigated the local population response (number of breeders) of bank cormorants

31 *Phalacrocorax neglectus*, an Endangered seabird, to the availability of its prey, the heavily-fished

32 West Coast rock lobster *Jasus lalandii*. Using Bayesian state-space modelled counts of cormorants

33 at three colonies, 22 years of fisheries-independent data on local lobster abundance and generalized

34 additive modelling, we determined the spatial-scale pertinent to these relationships in areas of

35 differing lobster abundance. Cormorant numbers responded positively to rock lobster availability in

36 the regions of intermediate and high abundance, but not where regime shifts and fishing pressure

37 have made rock lobster scarce. However, the spatial scale (30 km) at which the relationships were

38 strongest was greater than the cormorants' foraging range when breeding. Prey availability in the

39 non-breeding season, prey switching and prey ecology can all influence neritic seabirds and should

40 be considered in marine spatial planning. Crucially, though, our results highlight the potential for

41 small-scale marine protected areas (MPAs) to benefit top predators over their full-life cycle by

42 protecting their prey. Precautionary implementation of MPAs, with robust assessment and adaptive-

43 management, could protect predators and their prey without negatively impacting dependent

44 fisheries.

45

Introduction

47 Environmental change and direct anthropogenic influences are profoundly altering marine

48 ecosystem functioning, with negative consequences for upper-trophic-level predators (e.g.

49 McCauley et al. 2015; Trathan et al. 2015). Climate-change induced fluctuations are altering

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50 nutrient availability, changing species distributions, seasonality and production (Brander 2010).

51 Where species are also subject to fishing pressure, these impacts can be exacerbated (Essington et

52 al. 2015; Hobday et al. 2015; Young et al. 2015).

53

54 One possible solution to maintain ecosystem resilience is Marine Protected Areas (MPAs);

55 however, their efficacy in protecting dependent predators by increasing access to forage resources

56 remains unclear. In particular, separating the influence of fishing and environmental variability can

57 be difficult (Daunt et al. 2008), often because fisheries-independent estimates of prey availability on

58 the appropriate scale are lacking (Sherley et al. 2013). Although there is growing evidence that

59 spatial fishing restrictions can benefit upper-trophic-level predators (e.g. Daunt et al. 2008, Sherley

60 et al. 2015), robust tests of their ability to meet management goals generally requires long-term

61 datasets straddling the closure (Kerwath et al. 2013, Moland et al. 2013). Governments, however,

62 may be reluctant to curb fishing effort without clear evidence for an ecological benefit (see Sherley

63 et al. 2015). In such circumstances, analysis of long-term datasets on the relationship between

64 predator populations and the changing abundance of their prey can help identify ecologically

65 relevant species and spatial scales for potential management action (e.g. Furness 2007).

66

67 In South Africa, the interactions between the *Endangered* bank cormorant *Phalacrocorax neglectus*

68 and its main prey, the west coast rock lobster *Jasus lalandii* (hereafter rock lobster), may offer an

69 opportunity to develop ecologically-relevant MPAs. Rock lobsters are generally heavily fished and

70 have high potential population growth rates, so readily benefit from fisheries closures (Lester et al.

71 2009). Rock lobster is South Africa's third most valuable marine resource, but catches peaked at 16

72 000 t in the 1950s, then declined following overfishing to < 5 000 t after 1960 (Pollock et al. 2000;

73 van der Lingen et al. 2006). Catch restrictions were enforced (Cockcroft & Payne 1999), but growth

74 rates also declined during the 1970s and 1980s following 'regime shifts' in the Benguela ecosystem

75 and the population has not recovered (van der Lingen et al. 2006; Blamey et al. 2012). Another

3

76   regime shift in the early-to-mid 1990s, characterized by increased upwelling and wind variability,

77   also coincided with an eastward expansion in the lobster's distribution (Blamey et al. 2012).

78   Consequently, the percentage of rock lobster landings taken north and west of Cape Town (Areas

79   1–7, Fig. 1) declined from ~60% to < 10% between the late-1980s and 2000, while the reverse

80   occurred south of Cape Town (Area 8, Fig. 1; Cockcroft et al. 2008).
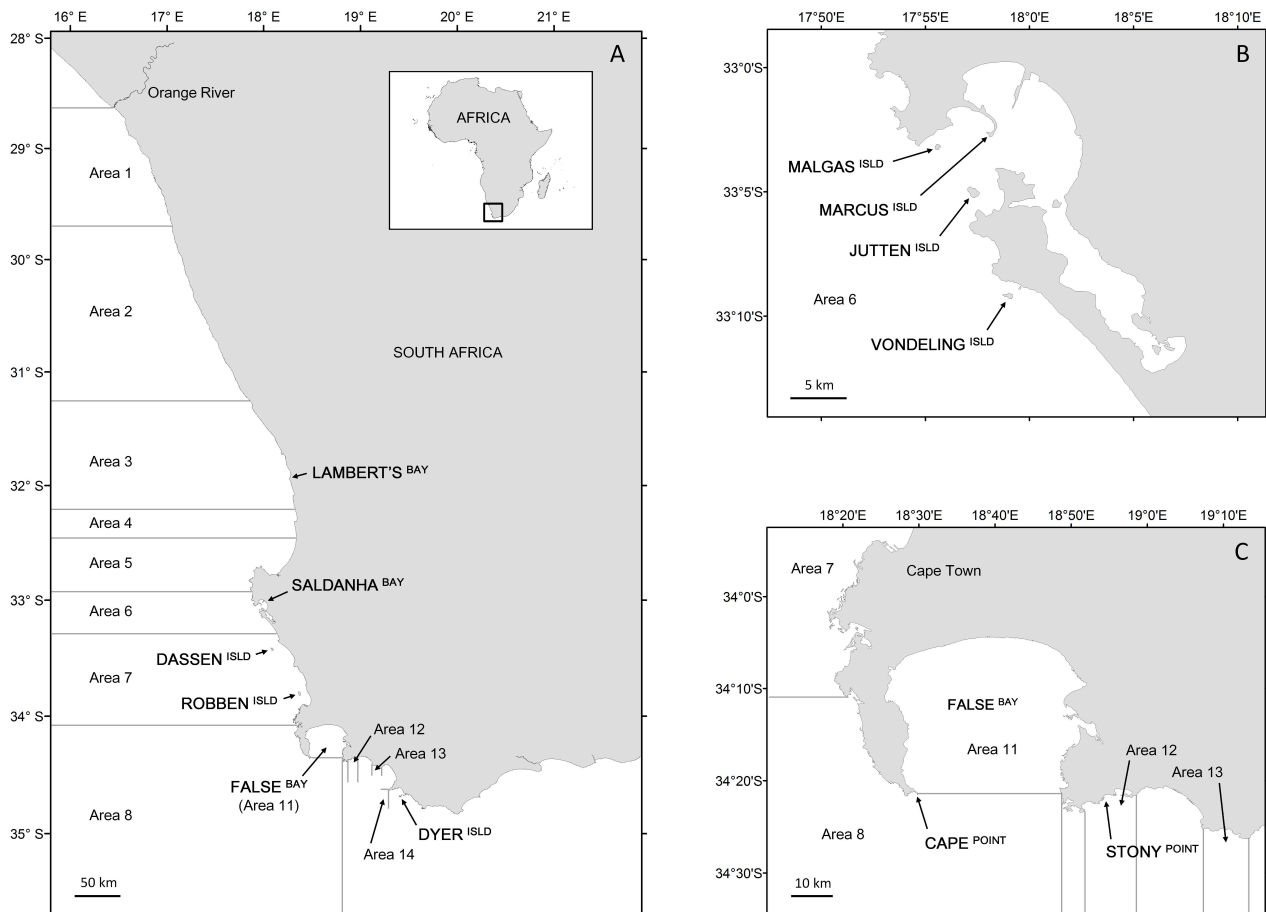
81

82   Figure 1. The west coast of South Africa (A) with the three bank cormorant colonies at Jutten Island,

83   Saldanha Bay (insert B), Dassen Island (in A) and Stony Point (insert C), used in this study to test the

84   relationship with West Coast rock lobster availability from 1993 to 2015. South Africa's commercial

85   fishing areas for rock lobster are shown (Areas 1 to 14), as are other localities mentioned in the text.

86

87   These changes in lobster abundance and distribution mediated top-down and bottom-up changes in

88   the ecosystem (e.g. Blamey et al. 2014; Crawford et al. 2015). The bank cormorant, the system's

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89 only endemic seabird that feeds on rock lobster (Crawford et al. 2015), decreased from ~9 000

90 breeding pairs in the late-1970s to fewer than 2 600 breeding pairs in 2015 (Cook 2015). Several

91 factors are thought to have contributed to the decline (see Cook 2015), but food shortage is

92 considered the key factor (Crawford et al. 1999, 2008). Bank cormorants typically forage within 10

93 km of their colonies when breeding, diving to depths of ≤ 50 m to catch a wide variety of benthic

94 prey, such as crustaceans, cephalopods, other mollusks and fish (mostly Clinidae) (Cooper 1985;

95 Ludynia et al. 2010). However, rock lobster forms an important component of their diet in South

96 Africa (Cooper 1985; Crawford & Cooper 2005; Crawford et al. 2008).

97

98 Landings of rock lobster in the offshore fishery and bank cormorant numbers have been correlated

99 in the past (Crawford et al. 2008), while the localized extirpation and colonization at Lambert's Bay

100 and Stony Point respectively followed a significant decline in rock lobster north of Cape Town and

101 an increase in lobster abundance east of Cape Point (Fig. 1; Cockcroft et al. 2008; Crawford et al.

102 2008; Blamey et al. 2012). Moreover, the marine environment within 1.8 km of Robben Island,

103 Table Bay, has been closed to rock lobster fishing since 1960 (Pollock 1987). Until the most recent

104 census in 2015, that island supported the largest bank cormorant colony in South Africa (~100

105 pairs; Crawford et al. 2008; Sherley et al. 2012). With commercial fishing prohibited, the past

106 growth of the colony may have been limited by breeding space rather than prey availability (Sherley

107 et al. 2012). Given all of the above, the conservation of bank cormorants could stand to benefit from

108 excluding lobster fishing close to other nesting colonies.

109

110 To test this idea, we examined the relationship between the number of bank cormorant breeders

111 (hereafter the 'local population response') and the availability of rock lobster at increasing distances

112 around three key breeding colonies, two north of Cape Town, where rock lobster abundance has

113 declined and one to the east of Cape Point (Fig. 1), where rock lobsters have increased. We set out

114 to evaluate the importance of rock lobster as a prey species driving bank cormorant population

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115 change and determine the spatial scale of rock lobster availability most influential to these birds.

116 Ultimately, we aimed to recommend a strategy that could be implemented, with adaptive-

117 management, to provide a robust test of whether MPAs can produce sustained benefits for neritic

118 seabirds without impacting fisheries.

119

Materials & Methods

120

121 *Bank cormorant data*

122 We used counts of bank cormorant breeding pairs from three colonies: Jutten Island, Saldanha Bay

123 (33°05'S; 17°57' E); Dassen Island (33°25'S; 18°05'E) and Stony Point (34°22'S; 18°53'E) (Fig. 1).

124 These colonies were chosen because (1) counts were conducted 1–3 times during the austral winter,

125 around the peak of the breeding season in most years between 1987 and 2015 (Crawford et al. 1999;

126 Meyer 2014); (2) because of their distribution towards the north, center and east of the area of

127 operation of the rock lobster fishery off South Africa (Crawford et al. 1999); and (3) fisheries-

128 independent rock lobster data were available for the waters adjacent to each colony for 1993–2015

129 (excluding the year 2000, see below). Field data were collected by staff of the Department of

130 Environmental Affairs (cormorant counts) and Department of Agriculture, Forestry and Fisheries

131 (lobster data).

132

133 Of a possible 69 counts that could have been made between 1993 and 2015, five were not made (all

134 at Stony Point, Fig. 2) and one count was considered unreliable because it was made outside the

135 main breeding period (2011 at Dassen Island, Fig. 2). To estimate these missing counts, and account

136 for the unknown observation error in the remaining data, we used all the available counts from 1987

137 and a state-space model (SSM) to generate annual time-series of the local population response for

138 each colony between 1993 and 2015 (Fig. 2). Following Kéry and Schaub (2012), we specified an

139 exponential growth model on the log scale, where the state process was $\log(N_{t+1,i}) = \log(N_{t,i} +$

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140   $r_{t,i}$),   with $r_{t,i} \sim Normal(\bar{r}_i, \sigma_{r,i}^2)$ and   the   observation   process $y_{t,i} = N_{t,i} + \varepsilon_{t,i}$,   with

141   $\varepsilon_{t,i} \sim Normal(0, \varsigma_{y,i}^2)$, where $y_{t,i}$ are the observed count data, $N_{t,i}$ the estimated population size, $\varepsilon_{t,i}$

142   the observation error with variance $\varsigma_{y,i}^2$, and $r_{t,i}$ is the population growth rate, which varies around a

143   long-term mean $\bar{r}_i$ with process error $\sigma_{r,i}^2$ for year t at colony i. We ran three chains of 200,000

144   iterations in the JAGS software (v. 4.1.0), called from the *jagsUI* R library (v. 1.3.7), using vague

145   priors, a burn-in of 20,000 samples and no thinning (see Supporting Information for model code).
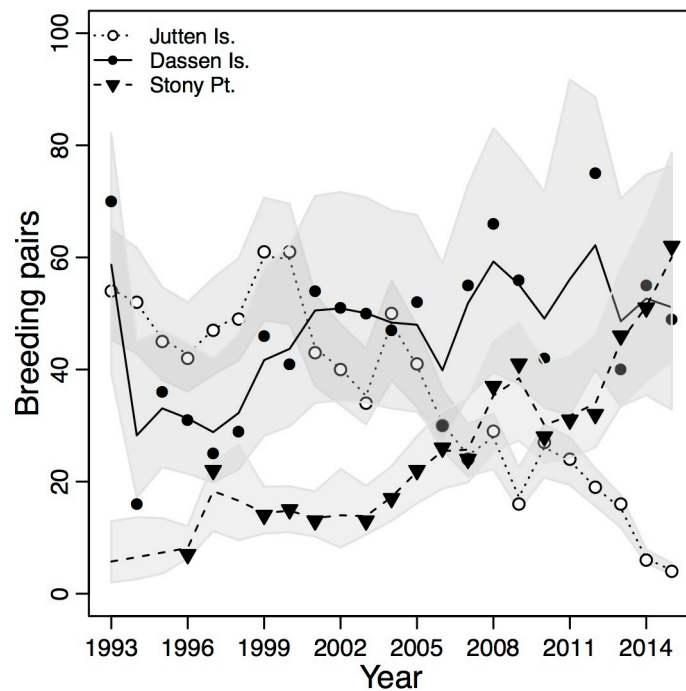

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147   Figure 2. The number of breeding pairs of bank cormorants counted annually (points) and the state-space

148   model (SSM) estimated local population response (lines) at Jutten Island (○, dotted line), Dassen Island

149   (●, solid line) and Stony Point (▼, dashed line), 1993–2015. The grey shaded areas show the Bayesian

150   95% credible intervals around each SSM estimate.

151

152   *Rock lobster data*

153   The west coast of South Africa is divided into 14 commercial harvesting areas for rock lobster (Fig.

154   1). Fisheries Independent Monitoring Surveys (FIMS), designed to obtain information on *inter alia*

155   the relative abundance of the rock lobster, began in Areas 5–8 in 1993 (Cockcroft et al. 2008; Fig.

156   1). For the years 1993–1999 and 2001–2015, annual FIMS sampling occurred over two-weeks

7

157   between January and May; data were not collected in 2000 due to logistic constraints. Within each

158   area, five lobster traps were deployed at each of 110–160 sampling stations each year (Fig. 3).

159   Around 75% of stations were visited twice during the two-weeks, with the remainder sampled once.

160   At each visit, the traps were set, left for 15–20 hours, then recovered. The number of lobsters in

161   each trap was recorded. We used FIMS data sampled in three locations: (1) in Areas 5 and 6 for

162   Jutten Island, (2) in Areas 6 and 7 for Dassen Island and (3) in Area 8 for Stony Point (Fig. 1;

163   Supporting Information). In this last case, it was necessary to use data sampled only in Area 8 as

164   FIMS data were not collected east of this (Area 12).
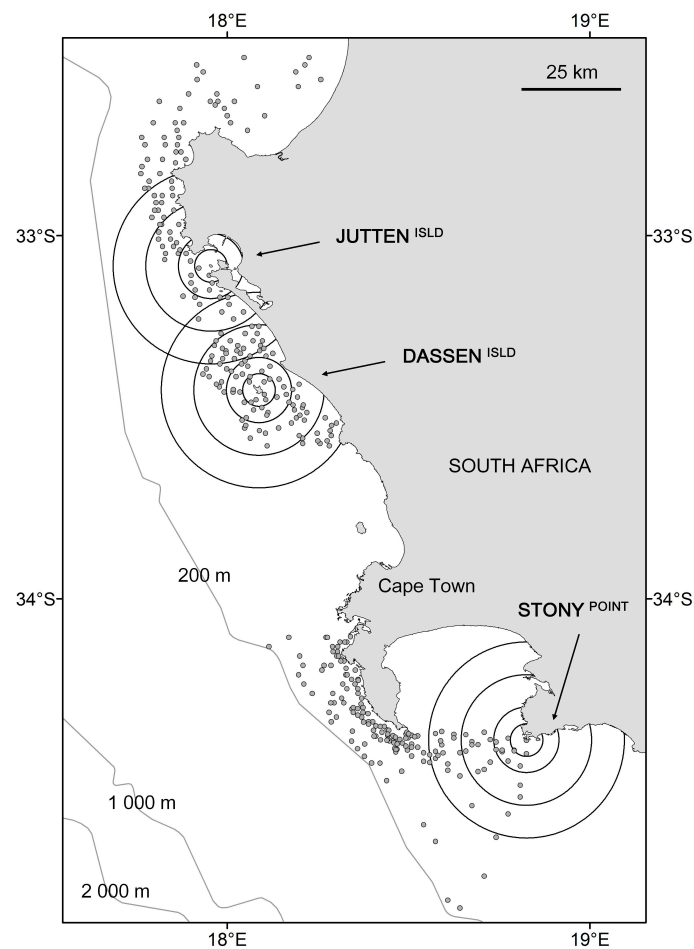
165

166   Figure 3. Positions of Fisheries Independent Monitoring Survey (FIMS) stations for West Coast rock

167   lobster around Jutten Island, Dassen Island and Stony Point (small grey circles). Large black concentric

168   circles represent the radii of 5, 10, 20 and 30 km around each study colony that served to identify the

169   FIMS stations used in the analyses. Due to the absence of FIMS stations to the east of Stony Point,

170   Hangklip Lighthouse (5 km west of Stony Point) was used as a proxy for Stony Point's location.

8

172   We used the GPS positions of each FIMS station (Fig. 3) to measure the distance to their adjacent

173   bank cormorant colony in ARCGIS v. 10.2 (Environmental Systems Research Institute) and

174   categorize them into one of four distance intervals: 0–5 km; 0–10 km; 0–20 km; and 0–30 km

175   radius around each colony. For Stony Point, we used a location on the coast (Hangklip Lighthouse,

176   34°23'12"S, 18°49'39" E), 5 km west of Stony Point and on the border of FIMS survey Area 8 as a

177   proxy for the colony location (Fig. 1). By the start of our study, Area 8 and those east of Hangklip

178   Lighthouse (Areas 12–14) combined both contributed around 40% to the total recreational catch of

179   rock lobster (Cockcroft & Mackenzie 1997) suggesting similar abundance in these regions.

180

181   We calculated the Catch Per Unit Effort (CPUE) as the total number of lobsters caught divided by

182   the number of traps set at all stations for each distance interval at each colony. CPUE may be

183   influenced by social interactions within and around traps, such as large lobsters, once caught,

184   excluding other, smaller lobsters from entering the traps (Richards et al. 1983; Ihde et al. 2006). We

185   therefore also used the proportion of the total traps set that contained lobsters (TCL) for each

186   distance interval to index the available abundance around each colony.

187

188   We compared the bank cormorant local population response (from the SSM) and rock lobster

189   indices between the three colonies using ANOVA and Tukey's Honest Significant Difference

190   (HSD). Because seabirds often show non-linear responses to their prey (e.g. Cury et al. 2011), we

191   examined the relationship between the bank cormorant population size and rock lobster availability

192   using Generalized Additive Models (GAMs, *mgcv* library for R; Wood & Augustin 2002). To

193   account for the uncertainty associated with the estimated bank cormorant counts, we weighted each

194   observation by its relative standard deviation (SSM posterior SD/SSM posterior mean).

195

196   The explanatory variables were CPUE and TCL within 5, 10, 20 and 30 km of the breeding locality

197   for Dassen Island and Jutten Island. For Stony Point, the FIMS stations within 5 km of our colony

198   proxy were not sampled in all years, so we used the 10, 20 and 30 km intervals only (Fig. S1). In

199   addition, because a regime shift occurred in the inshore waters of South Africa's west coast between

200   2003 and 2007 (Blamey et al. 2012, 2015), we included a binary covariate denoted 'Regime' to

201   account for this change, with years 1993–2004 = 0 and 2005–2015 = 1. The models tested allowed

202   for additive effects between Regime, and the smoother (see below) for each of the two measures of

203   rock lobster availability, and for each distance interval. Thus the maximal models took the form: Y_i

204    $= \alpha + S(X_i) + \text{Regime}_i + \varepsilon_i$, where Y_i is the SSM estimate of the local population response in year

205   i; α the intercept; $S(X_i)$ is the nonparametric smoothing function, specifying the effect of the

206   lobster covariate X_i on each bank cormorant count with $\text{Regime}_i = 0$ if a count was from 1993–2004

207   and $= 1$ otherwise; and $\varepsilon_i \sim N(0, \sigma^2)$ is the residual error. The degrees of freedom of the

208   smoothing functions were selected automatically by generalized cross validation (GCV), with the

209   option for the function to be linear (e.g. $S(X_i) = \beta \times X_i$, where β is the slope).

210

211   The models were run separately for each distance category and island. In addition, we specified a

212   model containing only the Regime term and null (intercept only) model (see Supporting

213   Information for the full model set). Inference was based on model selection using Akaike's

214   Information Criterion adjusted for small samples sizes (AICc), with models with ΔAICc ≤ 2

215   considered to have good support (Burnham & Anderson 2002). Finally, we checked residual plots

216   for normality, heterogeneity of variance and an absence of auto-correlation (using the 'acf' function

217   in R v. 3.0.2; Supporting Information).

218

219

220 **Results**

221 *Bank cormorant population trends*

222 Bank cormorants at Jutten Island decreased from a mean (SD) of 47.1 (6.9) pairs for 1993–2004 to

223 21.4 (15.5) pairs for 2005–2015 (Fig. 2). The mean (95% credible intervals, CI) population growth

224 rate (λ) = 0.89 (0.80–0.99), confirming a significant decline. At Dassen Island, λ = 0.98 (0.87–

225 1.09), suggesting moderate decline to stability (Fig. 2); the difference between the means (SD) of

226 41.3 (10.9) pairs for 1993–2004 and 52.2 (6.0) for 2005–2015 was marginally not significant

227 (Tukey's HSD: $p = 0.06$). The population at Stony Point increased from ~6 pairs in 1993 (1993–

228 2004 mean 12.3, SD 4.6 pairs) to ~60 pairs in 2009 (2005–2015 mean 36.3, SD 11.8 pairs; Fig. 2)

229 and $\lambda = 1.12$ (1.003–1.25). With the exception of Jutten and Dassen islands for 1993–2004 ($p =$

230 0.62), the mean differences between the colonies were all significant for the two regime periods (all

231 p-values < 0.01).

232

233 *Rock lobster availability*

234 Rock lobster availability was generally greatest around Stony Point, intermediate around Dassen

235 Island and least around Jutten Island at all distances (Fig. S1). For example, mean (SD) CPUE for

236 the 0–30 km interval was 2.3 (2.7) around Jutten Island, 15.4 (13.6) for Dassen Island, and 177.0

237 (54.9) at Stony Point. The differences between locations were significant at all four distances for

238 both CPUE and TCL (Tukey's HSD: all p-values < 0.002).

239

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

241 As rock lobster availability and bank cormorant numbers differed significantly (see above), we

242 modelled these relationships for each colony separately. For Jutten Island, no models showed

243 significant effects of rock lobster availability (all p-values > 0.05). At Dassen Island, two models

244 had good AICc support (Supporting Information); the cormorant local population responded

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positively to the proportion of TCL within 20 km (GAM: effective degrees of freedom (edf) = 1, F

246   = 6.7, p = 0.018, deviance explained [dev.] = 47.0%) and 30 km (edf = 1, F = 6.7, p = 0.018, dev. =

247   47.1%) of the colony (Fig. 4a). Regime was significant in both models (p = 0.005 and p = 0.006

248   respectively). The next best model (ΔAICc = 2.01) also contained a marginally significant linear

249   effect of TCL within 10 km (edf = 1, F = 4.5, p = 0.048). The deviance explained by TCL + Regime

250   at Dassen Island increased from ~38% at 5 km to ~47% at 20 and 30 km (Fig. 4b). At Stony Point, a

251   single model was well supported (Supporting Information). This model contained a significant

252   Regime effect (t = 7.7, p < 0.001) and a positive, non-linear response between the cormorants' local

253   population and TCL within 30 km (edf = 2.99, F = 4.6, p = 0.017, dev. = 80.5%; Fig. 4c).

254

Discussion

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

257   The positive response of bank cormorants to lobster availability at Dassen Island and Stony Point,

258   but not Jutten Island is consistent with the southward and eastward shift of marine resources and the

259   general deterioration of the coastal marine environment off north-west South Africa (e.g. Cockcroft

260   et al. 2008; Blamey et al. 2012; Crawford et al. 2015). The pattern of the responses also fits

261   theoretical expectations: an asymptotic-type response at Stony Point, where rock lobster was

262   consistently abundant (Fig. 4c), a linear response in the area of intermediate lobster abundance at

263   Dassen Island (Fig. 4a) and no response at Jutten Island, where regime shifts and fishing pressure

264   had already made rock lobster scarce by 1993 (Cockcroft & Mackenzie 1997; Cockcroft et al.

265   2008).

266

267   Marine predators often show asymptotic responses to changing prey availability (e.g. Moustahfid et

268   al. 2010; Cury et al. 2011) and many seabirds buffer severe decreases in their preferred prey by

269   switching to target other organisms (e.g. Smout et al. 2013). Together, these mechanisms can
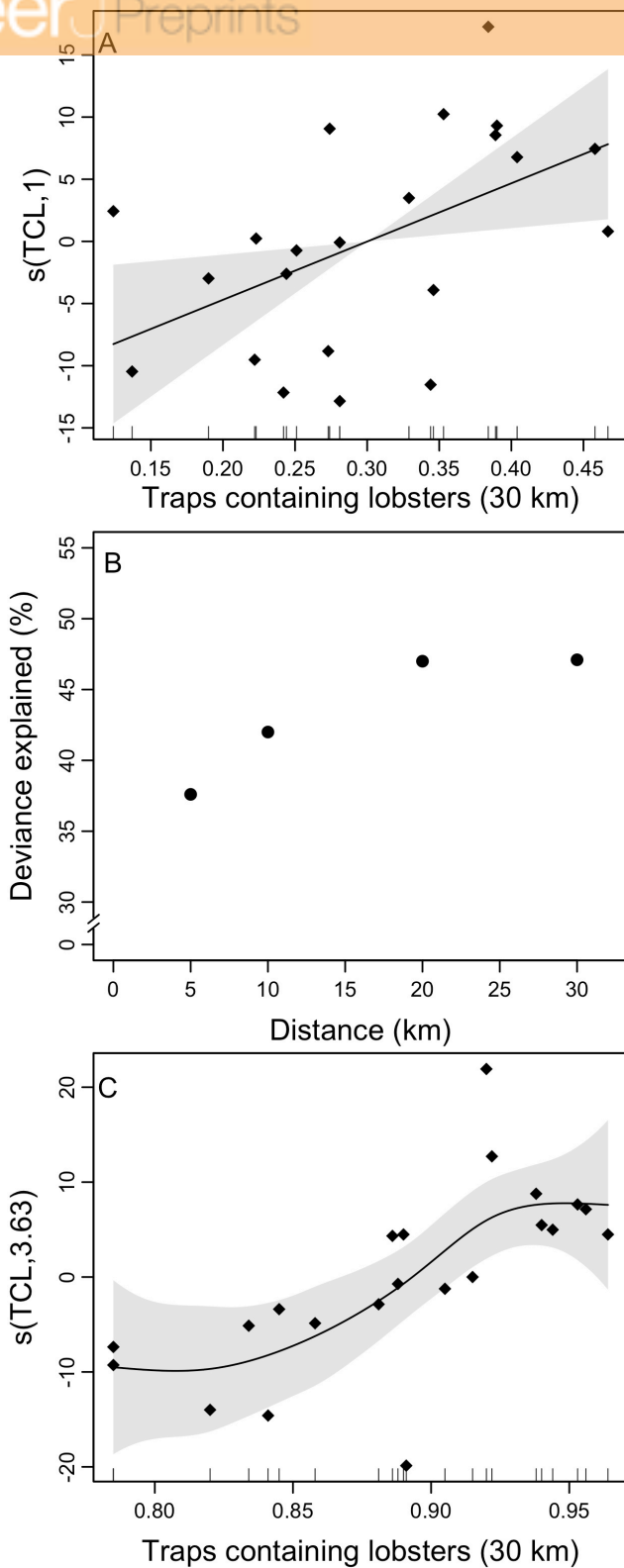
Figure 4. Results of GAM modelling of the effects of West Cost rock lobster availability on the estimated bank cormorant local population response (number breeding), 1993–2015. (A) The linear fit between bank cormorant pairs and the proportion of traps containing lobsters (TCL) within the 30 km (TCL 30) distance interval from the best fitting model for Dassen Island (dev. = 47.1%); (B) the percentage deviance in bank cormorant pairs explained by models containing the Regime covariate and TCL at the 5, 10, 20 and 30 km distance intervals around Dassen Island; (C) the relationship bank cormorant pairs and TCL 30 from the best fitting mode for Stony Point (dev. = 80.5%). In A and C, s(x,y) is the smoothing term, with x the explanatory variable and y the estimated degrees of freedom of the smoothing term. The pointwise 95% confidence intervals (grey area) and the partial residuals around the significant covariate effects (♦) are shown.

produce sigmoidal relationships between a species' response and the availability of its preferred prey (i.e. type III functional response; Fig. 5), particularly in demersal or benthic predators (Moustahfid et al. 2010). Indeed, bank cormorants will feed on other organisms when rock lobsters

13

299 are scarce (Crawford & Cooper 2005): at Jutten Island they now mainly eat Cape mantis shrimp

300 *Pterygosquilla capensis* and West Coast sole *Austroglossus microlepis* (BMD, unpubl. data), while

301 in Namibia they feed on bearded goby *Sufflogobius bibarbatus*, an abundant but poor quality prey

302 (Ludynia et al. 2010). Thus, prey switching may enable small colonies to persist in South Africa

303 (Crawford et al. 2008) and could have diluted any functional response to changing lobster

304 abundance at Jutten Island (cf. Smout et al. 2013; Fig. 5). In addition, once populations have

305 become small, the impact of other demographic drivers can make detecting responses to prey

306 availability difficult (Weller et al. 2016).
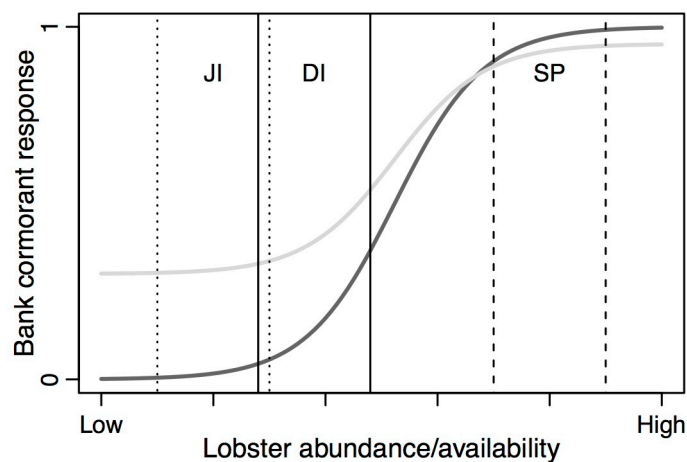
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308 Figure 5. Hypothetical type III functional response curves for the change in the proportion of West Coast

309 rock lobster in the diet of bank cormorants (dark grey curve) and the change in bank cormorant breeding

310 success (light grey curve) in relation to the abundance/availability of West Coast rock lobster. Across a

311 wide range of prey availability, sigmoidal predator-prey functional response curves can result from a

312 combination of mechanisms like predator satiation and prey switching (e.g. Moustahfid et al. 2010). The

313 vertical lines approximate the relative range of prey availability experienced by the bank cormorants at

314 Jutten Island (dotted lines), Dassen Island (solid lines) and Stony Point (dashed lines) during the study

315 period, as indexed by the proportion of traps containing lobsters (TCL).

316

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

318 The response to rock lobster availability at 30 km may result from the life-history traits of palinurid

319 lobsters. Bank cormorants predominately eat lobster < 60 mm carapace length (Cooper 1985),

14

320   which are generally found inshore. At ~60 mm carapace length, rock lobster begin to move to

321   deeper waters (Pollock & Beyers 1981) and ~95% of lobsters in FIMS traps were between 60–

322   90 mm carapace length (DAFF, unpubl. data). Hence the relationship between the local population

323   response and lobster availability beyond the foraging range of the cormorants (~10 km) may result

324   from the size class of lobsters most commonly caught in the traps tending to be associated with

325   deeper water, farther offshore.

326

327   Alternatively, or in addition to the above, the link at 30 km may relate to the importance of food

328   availability during the non-breeding period, which can affect seabird survival directly (Oro &

329   Furness 2002) or influence adult body condition and reproductive success (e.g. Salton et al. 2015).

330   As a result, prey availability over a larger spatial scale during the non-breeding season can cause

331   carry-over effects with important implications for population dynamics (e.g. Sherley et al. 2013;

332   Salton et al. 2015). Non-breeding adult bank cormorants likely extend their foraging range along the

333   coast, remaining within 20 km of shore (Cooper 1985). Indeed, the strong relationship at Dassen

334   Island may well be explained by the presence of shallow water reefs ~20–30 km north and south of

335   the island. Those to the north, in particular, are close to sites of high lobster peuruli settlement

336   (Groeneveld et al. 2010) and FIMS in this area consistently catch lobster of the size consumed by

337   bank cormorants (DAFF, unpubl. data).

338

339   *Implications for marine spatial planning*

340   Marine Protected Areas (MPAs) with no-catch zones can be powerful tools for managing reef-

341   dwelling organisms such as lobster (Moland et al. 2012), with strong benefits for fishing yields

342   expected through spillover effects (Kerwath et al. 2013; Edgar et al. 2014). Our results suggest that

343   implementing MPAs with no-take of lobster at a distances of 20 km around bank cormorant

344   colonies (see Supporting Information for an example) would also benefit the conservation of this

345   endangered seabird species, of which < 800 pairs remain in South Africa (Crawford et al. 2015).

15

346   Although the deterioration of the marine environment off north-west South Africa makes it unlikely

347   that no-take zones would have meaningful impacts north of this, our results, and the size of the

348   remaining populations at these localities, indicate that Dassen Island and Robben Island (Fig. 1)

349   should be priorities for such protection. The birds at Dassen Island responded strongly to rock

350   lobster availability, despite the regime shifts that have taken place (Fig. 4). Lobster landings in Area

351   7 and bank cormorants at Dassen Island (Fig. 1) both decreased between 1987 and 1994, after

352   which lobster catches increased to > 30% of total landings between 1997 and 2005, while

353   cormorant numbers remained low (Cockcroft et al. 2008; Crawford et al. 2008). At the same time,

354   the legal size limit for lobsters catches was reduced from 89 mm to 75 mm in 1993 (Pollock et al.

355   1997), increasing competition with the industry for the largest lobsters taken by the birds (lobsters

356   up to 82 mm have been recorded in [n = 281] diet samples; BMD and J. Cooper, unpubl. data). It is

357   likely, therefore, that fishing decreased the availability of rock lobster to bank cormorants at Dassen

358   Island during our study period (Crawford et al. 2008).

359

360   MPAs are increasingly designated to protect non-targeted marine predators, but their efficacy in this

361   regard is rarely assessed robustly and may be limited for wide-ranging species (Boersma & Parrish

362   1999; Sherley et al. 2015). Experimental 20 km purse-seine fishing closures around Dassen and

363   Robben islands are currently being assessed in South Africa. These appear to benefit Endangered

364   African penguins *Spheniscus demersus* (Sherley et al. 2015) and offer potential for Endangered

365   Cape cormorants *Phalacrocorax capensis*, which have a similar foraging range and diet (Cook et al.

366   2012). However, both species target highly mobile pelagic prey and move widely during their non-

367   breeding periods. Adult bank cormorants target relatively immobile, benthic prey and should remain

368   within a 20 km MPA year round (Cooper 1981). Hence they may show strong population-level

369   responses to spatial protection. Crucially, non-invasive methods exist to measure changes in their

370   breeding success and foraging behavior (Sherley et al. 2012; Botha 2014), allowing the impact of

371   closures to be assessed against baseline data or control sites relatively quickly (e.g. 3–4 years;

16

373 dynamics of non-harvested top predators would provide valuable information for MPA

374 management worldwide. Moreover, continuing to collect FIMS data inside and fisheries CPUE data

375 outside the MPA would quickly provide insights into potential 'spill-over' benefits for the fishery

376 (e.g. Moland et al. 2013, Kerwath et al. 2013). In addition, expanding FIMS sampling east of Cape

377 Point would provide a key, leading indicator of future changes in the inshore environment with

378 which to guide the future protection of breeding and foraging habitat for bank cormorants.

379

380 In conclusion, we have shown how time-series data on the population numbers of dependent-

381 predators and their prey can lead to models describing the functional link between the two, and in

382 doing so generate management recommendations. No-take zones for rock lobster on South Africa's

383 west coast would protect the year-round foraging habitat of endangered bank cormorants and likely

384 benefit the lobster population and its fishery, provided adequate quotas were effected in parallel

385 (Essington et al. 2015; Weller et al. 2016). They would make a significant contribution to an

386 ecosystems approach to fisheries management in South Africa. Moreover, assessment of their

387 impact could guide the creation of similar protected areas elsewhere in South Africa and globally,

388 providing resilience against the impacts of future environmental change on coastal marine

389 environments.

390

Supporting Information: JAGS code for the state-space model used in the analyses (Appendix S1), additional figures (Appendix S2), and the full candidate model set and model selection results (Appendix S3), are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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