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Fisheries bycatch mitigation measures as an efficient tool for the conservation of seabird populations

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## Abstract

1. The impact of industrial fisheries on marine biodiversity is conspicuous in large pelagic vertebrate's fisheries bycatch. In seabirds, this led to the decline of many populations since the 1980's following the rise of global fishing effort. Bycatch mitigation measures were implemented since the 2000's, but their effects on the concerned seabird populations remain poorly quantified and understood.

2. We studied the effects of bycatch mitigation measures on the demography of the white-chinned petrel, one of the most bycatch impacted seabirds whose populations suffered dramatic declines before the implementation of mitigation measures. To do so we 1) built multi-event capture-recapture models to estimate the demographic parameters of a population from Possession Island (southern Indian Ocean) over thirty years, 2) assessed the effect of climate and fishery covariates on demographic parameters, 3) built a population matrix model to estimate stochastic growth rate according to the management in fisheries bycatch, and 4) estimated changes in breeding population density using distance sampling data.

3. The population declined from the 1980's to the mid-2000's, while trawl and longline fisheries occurred with no bycatch mitigation measures. The negative effects of fishery bycatch through additive mortality and of rat predation on breeding success were likely the main drivers of this decline.

4. Both modelled population growth rate and observed breeding densities showed an increase since the mid-2000's. We explained this trend by the improvement in survival probability following implementation of fishery bycatch mitigation measures and in breeding success probability with the local control of the rat population and changes in sea ice conditions on foraging grounds.

6. Synthesis and applications: We provide a holistic approach to assess the effects of management measures by analysing datasets from sampling methods commonly employed in seabirds studies. Our conclusions should encourage the eradication of invasive predatory species in seabirds breeding areas and the strengthening of bycatch mitigation measures for the vulnerable seabird species, especially in international waters, but also the development of such measures considering the other marine large pelagic species

34 threatened by fisheries bycatch (sharks, rays, turtles and marine mammals) since it could be crucial to avoid  
35 populations' extinction.

36 **Keywords**

37 Conservation measures, demersal longline fisheries, population dynamics, capture-mark-recapture,  
38 procellariforms, southern Indian Ocean, white chinned petrel.

## 39 **Introduction**

40 Managing industrial fishing activities remains an urgent and crucial challenge for marine biodiversity  
41 conservation and food security (Zhou et al., 2010). Massive and selected marine resources exploitation  
42 causes a considerable impact on marine fish stocks and ecosystems' structures (Pauly et al., 2005), causing  
43 death by accidentally catching non-targeted species of pelagic vertebrate top-predators (sharks, turtles,  
44 marine mammals and seabirds) whose populations have severely declined in the last decades (Lewison et  
45 al., 2014; Nel et al., 2002; Stevens et al., 2000). Large marine vertebrates play a major role on the stability  
46 of trophic webs (Estes et al., 2011) and provide unique evolutionary innovations (Kelley & Pyenson, 2015).  
47 To reduce this impact, bycatch mitigation measures were developed, tested and implemented since the early  
48 2000's. They have led to substantial reductions in bycatch of large marine vertebrates in several fisheries  
49 worldwide (Cox et al., 2007; Phillips et al., 2016). However, the long-term efficiency of bycatch mitigation  
50 measures on trends and abundances of concerned populations may be challenging to estimate and has been  
51 poorly assessed.

52 Seabird conservation state is of concern with 28% of their species globally threatened (Croxall et al., 2012)  
53 and 66% of albatrosses and large petrels species actually listed by the Agreement on the Conservation of  
54 Albatrosses and Petrels (ACAP) as a priority (Phillips et al., 2016). Fishery bycatch has been identified as  
55 the most impacting threat on those species and alien species predation as the threat that affects the more  
56 numerous of those species (Dias et al., 2019). Many of them share their foraging areas with fishing vessels  
57 that they follow – because Procellariiforms use their sense of smell to track food – in order to take advantage  
58 of food opportunities such as fishing waste and baits. This increases hooking or entanglement risks and  
59 leads to the death of hundreds of thousands of seabirds every year (Tuck et al., 2003; Žydelis et al., 2013).  
60 This massive additive mortality is highly problematic for long-lived marine pelagic species such as seabirds  
61 characterised by slow demographic strategies due to long generation time, low fecundity and delayed  
62 maturity (Hamer et al., 2001). Their populations are sensitive to small variations in adult mortality (Caswell,  
63 2001). Since the early 2000's, the scientific community, the non-governmental organisations, the countries

64 that have ratified the ACAP and the Regional Fisheries Management Organisations (RFMOs) spent  
65 considerable efforts to develop and implement effective mitigation measures in order to significantly reduce  
66 or completely remove this threat. Measures include bird-scaring streamer lines, line weighting, night setting,  
67 and establishment of protected areas (Løkkeborg, 2011; Wolfaardt et al., 2016). Unfortunately, many  
68 threatened species do not yet benefit from sufficient mitigation measures implementation (Gilman et al.,  
69 2014).

70 Many studies showed the potential or direct efficacy of bycatch mitigation measures (Gilman, 2011; Maree  
71 et al., 2014), but little is known about their long-term effect on population dynamics and trends (Forney et  
72 al., 2020; van Beest et al., 2017). Furthermore, none of the studies investigated the retrospective efficiency  
73 of these measures on seabird demography and population dynamics. This knowledge is yet crucial to  
74 enhance the measures' implementation and to allow management optimisation of threatened populations  
75 (van Beest et al., 2017). Assessing the retrospective effect of bycatch mitigation measures could be  
76 challenging because of the complexity of the targeted species' phenology and their large scale at-sea  
77 distributions, the need of long-term monitoring data necessary to detect demographic changes, and the need  
78 to account for other factors that can potentially affect their population dynamics. Indeed, seabird populations  
79 can also be threatened by climate change, human disturbance, pollution, diseases and alien introduced  
80 predators (Croxall et al., 2012). Moreover, as long as fishing effort data remain sparse and inaccurate due  
81 to insufficient global fisheries control, especially in international waters, highlighting the effect of fishing  
82 activities on seabird populations remain difficult (Genovart et al., 2017) as well as the implementation of  
83 bycatch mitigation measures.

84 Our aim was to evaluate the impact of fishery bycatch and implementation of mitigation measures on a  
85 vulnerable seabird, the white-chinned petrel (*Procellaria aequinoctialis*), which is one of the most  
86 accidentally captured petrel in pelagic fisheries targeting tuna species in South Atlantic and Indian Oceans,  
87 and in demersal longline fisheries practices targeting Patagonian toothfish (*Dissostichus eleginoides*) in  
88 South Indian Ocean and in Southern Ocean (Weimerskirch et al., 1999). The species was also largely

89 threatened by trawl fisheries that occurred in their sub-tropical wintering areas (Croxall, 2008) and in  
90 subantarctic waters until the mid-1990's (Watkins et al., 2008; Weimerskirch et al., 2000).

91 We took advantage of long-term capture-recapture and population datasets of a white-chinned petrel  
92 population breeding at Possession Island, Crozet archipelago, to i) estimate demographic parameters before  
93 and after the implementation of bycatch mitigation measures in the subantarctic French exclusive economic  
94 zone (EEZ) and in waters managed by the Commission for the Conservation of Antarctic Marine Living  
95 Resources (CCAMLR); ii) test for temporal trends in demographic parameters and assess the relationship  
96 with fishing efforts and climate variables; iii) model the population dynamics and assess the effect of the  
97 implementation of bycatch mitigation measures and of the control of an introduced predator on the  
98 population growth rate; and iv) estimate breeding population density using distance sampling data from  
99 line-transect surveys conducted on land in 2011 and 2017.

100 There is evidence that longline fisheries bycatch, climate variability and introduced predators (black rat  
101 *Rattus rattus*) impact demographic parameters and population growth rate of the white-chinned petrels from  
102 the Crozet archipelago (Barbraud et al., 2008; Jouventin et al., 2003). The acceptance of fishery bycatch as  
103 a serious threat by the CCAMLR emerged in the early 1990's, followed by the implementation of strong  
104 bycatch mitigation measures since 2003 (Delord et al., 2010; Reid et al., 2010; Delord et al., 2005). In the  
105 meantime, the ACAP was ratified by 13 countries including France that integrated it in French law in 2005.

106 Under the hypothesis that bycatch was the main cause of the white-chinned petrel population's decline  
107 through additive mortality (Barbraud et al., 2008), and since numbers of white-chinned petrels caught in  
108 longlines strongly decreased following the implementation of mitigation measures (CCAMLR, 2020;  
109 Delord et al., 2010), we expected i) an increase in survival probability due to reduced direct bycatch  
110 mortality, ii) an increase in breeding success since a widowed parent due to its partner death in fisheries  
111 may fail to fledge the chick on its own, and iii) a stability or increase in the white-chinned petrel breeding  
112 population density.

113

## 114 **Material and Methods**

### 115 Study species and population monitoring

116 The Ethics Committee of IPEV and the Comité Environnement Polaire approved the field procedures for  
117 the French Southern Territories. White-chinned petrels were monitored at Possession island (46° S ; 51° E)  
118 (see Appendix S1 in Supporting Information) following two sampling approaches. First, 200 individually  
119 marked burrows were investigated each year from the breeding season 1985/1986 (hereafter 1985) to the  
120 breeding season 2017/2018 at the study colony of Station de Pompage. Each burrow was visited several  
121 times from egg laying (November) to chick fledging (April) to assess the presence of the occupying  
122 individuals, their identity, and their breeding status (breeder if an egg was laid, non-breeder otherwise).  
123 Each adult newly captured and all fledglings were marked with a stainless-steel ring on the leg (Barbraud  
124 et al., 2008, see Appendix S2). Black rats were introduced at Possession Island during the 19<sup>th</sup> century  
125 (Chapuis et al., 1994) and were poisoned yearly during each breeding season since 1994 at the study colony  
126 but not elsewhere on Possession Island (Jouventin et al., 2003). Second, in order to estimate breeding  
127 population density, line-transect distance sampling surveys were carried out in 2011 and 2017 at Pointe  
128 Basse, that hosts a large proportion (25-30%) of white-chinned petrels breeding on Possession Island with  
129 relatively high densities of burrows (Barbraud et al., 2008). Surveys were conducted during incubation  
130 (early December) and densities of occupied burrows were estimated from line transect distance sampling  
131 (see Appendix S3).

### 132 Modelling demographic parameters

134 For individuals marked as adults, their encounter history started at first capture. The 32-year time series  
135 (from 1986 to 2017) resulted in 842 individual capture histories. To model the transition of individuals in  
136 state  $i$  at time  $t$  to state  $j$  at time  $t+1$ , we estimated the following demographic parameters (Figure 1, Table  
137 1 S4): apparent survival probability ( $s$ ), the state-specific transitional probability of becoming or remaining  
138 a breeder (hereafter breeding probability) ( $\beta$ ), success probability ( $\gamma$ ), recapture probability ( $p$ ), and

139 assignment probability ( $\delta$ ). To do so, we constructed a multi-event capture-mark-recapture (MECMR)  
140 model (Pradel, 2005) to take account of uncertainty in breeding success, with four states consisting of one  
141 non-breeder state among adults (excluding subadults) (NB), two breeder states [failed breeder (FB),  
142 successful breeder (SB)], and the dead state ( $\dagger$ ) that was not observable. Capture histories were coded  
143 considering field observations: 0 = not observed, 1 = seen as NB, 2 = seen as FB, 3 = seen as SB, 4 = seen  
144 as breeder but status not ascertained. We started with a general model as the model that allowed the most  
145 numerous demographic parameters to be estimated independently for each step of time and for each state  
146 (see Appendix S4).

147 For individuals marked as chick, their encounter history started at the first return in the study population,  
148 from which they were considered as adults. Youngest individuals seen as breeders on the colony were five  
149 years old. To estimate juvenile survival and recruitment probabilities we used data from individuals that  
150 were marked as chicks only. Our dataset contained 979 individual capture histories of which 61 were seen  
151 recruiting. We estimated the following parameters: apparent survival probability ( $s_n$ ), the probability of first  
152 breeding ( $r_n$ ), as the probability that an individual breeds for the first time (Figure 1), and the recapture  
153 probability. To do so, we constructed a multi-state capture-mark-recapture (MSCMR) model (Lebreton et  
154 al., 2009; Pradel, 1996) with three states consisting of one juvenile state, one breeder state and the dead state  
155 (see Appendix S4). The goodness of fit tests (GOF) for MSCMR and MECMR models (Pradel et al., 2003)  
156 were performed using U-CARE 2.3.4 (Choquet et al., 2009) (see Appendix S4).

157

### 158 Modelling population dynamics

159 To model the dynamics of the white-chinned petrel population and the effects of different scenarios on the  
160 population growth rate ( $\lambda$ ), we built a female-only pre-breeding census matrix population model structured  
161 by age and breeding status (Caswell, 2001) with seven juvenile age classes and three adult classes according  
162 to breeding states (NB, SB and FB, see Appendix S5). From this matrix model we performed a sensitivity



163 analysis of  $\lambda$  to changes in demographic parameters, and a retrospective analysis to quantify the contribution  
164 of the vital rates to variability in  $\lambda$  (Caswell, 2001).

165 Then, we estimated  $\lambda$  using six management scenarios according to bycatch mitigation measure  
166 implementation and rat control (see Appendix S5, Table 1 S5). For each scenario the demographic  
167 parameters  $s$ ,  $\beta$  and  $\gamma$  differed following three periods: 1986-1993 (eight years), when trawl fishing occurred  
168 and no rat control occurred; 1994-2004 (11 years), when longline fishing occurred without mitigation  
169 measures and rat control occurred; 2005-2017 (13 years), when longline fishing occurred with mitigation  
170 measures and rat control occurred. All other parameters remained equal. The first three scenarios had no  
171 mitigation measures for fishery bycatch. Scenario (1) used  $s$ ,  $\beta$  and  $\gamma$  estimated from 1986 to 1993. Scenario  
172 (2) used  $s$  and  $\beta$  estimated from 1994 to 2004 and  $\gamma$  estimated from 1986 to 1993. Scenario (3) used  $s$ ,  $\beta$  and  
173  $\gamma$  estimated from 1994 to 2004. We then built three additional scenarios with mitigation measures for  
174 fisheries bycatch. We chose 2005 as the year-reference for the implementation of bycatch mitigation  
175 measures because France integrated the ACAP recommendations in the French law in 2005. Scenario (4)  
176 used  $s$  and  $\beta$  estimated from 2005 to 2017 and  $\gamma$  estimated from 1984 to 1993 (no rat control). Scenario (5)  
177 used  $s$ ,  $\beta$  and  $\gamma$  estimated from 2005 to 2017. Scenario (6) used  $\beta$  and  $\gamma$  estimated from 2005 to 2017, and  $s$   
178 for FB and SB individuals estimated as the intercept in the linear relationship between survival and demersal  
179 longline fishing effort. This last scenario reflected population dynamics without any additive effect of  
180 demersal longline fishing on adult survival.

181 Environmental stochasticity was modelled using the mean and process variance values of the demographic  
182 parameters. We calculated them from the values of demographic parameters estimated by MECMR model  
183 and following Gould & Nichols (1998), but ignoring the sampling covariance terms in the calculation of  
184 temporal variation in the demographic parameters.

185 We conducted random effect design Life Table Response Experiments (LTRE) in a retrospective analyses  
186 in order to estimate the contribution of each demographic parameter to the variability in the growth rate  $\lambda$ .

187 Following Jenouvrier et al., (2005), we approximated the contributions using the expression  $V(\lambda) \approx s(\theta)^2$   
188  $\text{var}(\theta)$ , where  $s(\theta)$  is the sensitivity of  $\lambda$  to the demographic parameter.

189

190

### 191 Effects of covariates on demographic parameters

192 We chose fisheries and climate covariates that were likely to have an influence on survival, reproduction or  
193 breeding parameters, according to white-chinned petrel breeding phenology, distribution at sea (see  
194 Appendix S6, Table 1 S6, Figures 1 S6, 2S6, 3 S6 & 4 S6) and previous knowledge of the studied population  
195 (Barbraud et al., 2008; Catard et al., 2000; Delord et al., 2013; Péron et al., 2010). Fishery covariates  
196 included fishing effort from demersal longline during the breeding season, pelagic longline during wintering  
197 (i.e. the non-breeding season), illegal, unreported and unregulated (IUU) from Crozet EEZ (CCAMLR,  
198 2018), and the quantity of hakes (*Merluccius spp.*) fished in Namibian EEZ used as a proxy of trawling  
199 effort. Climate data included sea surface temperature anomalies (SSTa) and sea surface temperature (SST)  
200 during the breeding and non-breeding seasons, sea ice concentration (SIC) during the breeding season, ,  
201 chlorophyll a concentration (Chla) during the non-breeding season, southern annular mode (SAM) and  
202 southern oscillation index (SOI) without lag and with a lag of one year (see Appendix S6, Figure 2 S6).

203 Relationships between covariates and demographic parameters were fitted using a logit link function:  
204  $\text{logit}(\theta) = B_0 + B_1 * X_n$  where  $\theta$  is the demographic trait,  $B_0$  is an intercept parameter,  $B_1$  is a slope  
205 parameter and  $X_n$  is the value of the covariate at year  $n$  (see Appendix S7). As demographic parameters  
206 may not respond linearly to a certain climate driver, we also tested for quadratic effects of climate covariates.  
207 When for a given demographic parameter a significant effect of a fishery and of a climate covariate was  
208 detected, we also tested for the effect of an interaction between the fishery and the climate covariate.  
209 Environmental variables were standardised by subtracting the mean and dividing by the standard error, in  
210 order to help with model fitting. We performed an environmental sensitivity analysis to assess to which  
211 covariate  $\lambda$  was the most sensitive (see Appendix S9).

212

## 213 **Results**

### 214 Breeding population density

215 Burrow occupancy rate was  $0.889 \pm 0.022$  (SE) in 2011 and  $0.921 \pm 0.017$  in 2017. Breeding population  
216 density at Pointe Basse was 6.54 active burrows/ha in 1983 and 3.09 active burrows/ha in 2004 (Marteau,  
217 2008). We found that breeding population density at Pointe Basse was  $5.65 \pm 0.89$  (N = 119) in 2011 and  
218  $5.68 \pm 1.07$  active burrows/ha (N = 126) in 2017 (see Appendix S3, Table 1 S3).

219

### 220 Demographic parameters

221 The GOF tests of the MECMR model did not indicate a lack of fit ( $\chi^2 = 432.700$ , df = 417, p = 0.288). The  
222 GOF tests of the MSCMR indicated a lack of fit ( $\chi^2 = 603.588$ , df = 82, p < 0.001) revealing a trap-  
223 dependence, so we used a coefficient of overdispersion ( $\hat{c} = 2.58$ ) for model selection.

224 The mean observed age at first breeding was  $7.3 \pm 1.5$  years old (median = 7), 82% of the first-time breeders  
225 were eight years old or less, 60.7% were seven years old or less and 34.4% were six years old or less.

226 MSCMR model selection suggested that recruitment started at age five and was  $0.061 \pm 0.030$ , increased at  
0.314  $\pm$  0.082 at six years old and was  $0.370 \pm 0.130$  at seven years old and older (Table 2 S4). The selected  
227 model suggested constant survival probability among age classes from seven years old at  $0.879 \pm 0.022$ .

228 Mean annual survival probability was estimated from fledging to five years old at  $0.781 \pm 0.028$ .

229 MECMR model selection indicated that recapture probability was time and state dependent, and was 0.785  
230  $\pm$  0.250 for successful breeders,  $0.863 \pm 0.180$  for failed breeders and  $0.047 \pm 0.006$  for non-breeders.

231 Assignment probability was  $0.971 \pm 0.004$  for failed breeders and was  $\approx 1$  for successful breeders.

232 Survival probability was time and state dependent (Figure 2). Mean survival probability of non-breeders  
233 was  $0.904 \pm 0.017$ ,  $0.870 \pm 0.099$  for successful breeders and  $0.844 \pm 0.106$  for failed breeders. No linear  
234 trend was detected in survival probabilities (Table 3 S4).

235

236 Breeding probability was time and state dependent and was higher for successful and failed breeders ( $0.870$   
237  $\pm 0.149$  and  $0.825 \pm 0.147$  respectively) than for non-breeders ( $0.350 \pm 0.253$ ) (Figure 2). A positive linear  
238 trend was detected for failed breeders (slope =  $0.391 \pm 0.147$ ) (Table 3 S4).

239 Success probabilities were time and state dependent (Figure 2). Mean success probabilities were  $0.544 \pm$   
240  $0.253$  for successful breeders,  $0.496 \pm 0.213$  for failed breeders and  $0.489 \pm 0.300$  for non-breeders.  
241 Breeding success probabilities showed significant positive linear trends for successful breeders (slope =  
242  $0.501 \pm 0.098$ ) and failed breeders (slope =  $0.363 \pm 0.112$ ) (Table 3 S4).

### 244 Population modelling

245 The stochastic  $\lambda$  obtained from the estimated demographic parameters (average rates for the entire 32-year  
246 period) was  $0.967 \pm 0.062$  and did not allow maintenance of the population.

247 Retrospective analyses indicated that survival of breeding individuals were the demographic parameters that  
248 contributed the most in the variability in  $\lambda$ , followed by breeding success of successful individuals and  
249 survival of non-breeders (Table 2). Elasticity of the population growth rate was the highest for adult survival,  
250 then to juvenile survival, to recruitment at seven years old, to breeding probabilities and to breeding success  
251 of breeders (Table 2).

252 Among the six scenarios combining conservation measures, population modelling indicated that when trawl  
253 fisheries operated and no rat control occurred [scenario (1), 1986-1993], and when longline fisheries  
254 operated without mitigation measures but rat control occurred [scenario (3), 1994-2004], stochastic  $\lambda$  did  
255 not allow maintenance of the population ( $\lambda = 0.925 \pm 0.071$  and  $0.954 \pm 0.060$  respectively).

256 When no rat control occurred, with or without implementation of bycatch mitigation measures in longline  
257 fisheries [scenario (4) and scenario (2) respectively, see Appendix S5, Figure 1 S5], the population growth  
258 rates were  $\lambda = 0.959 \pm 0.071$  and  $0.914 \pm 0.069$  respectively (Figure 3).

259 When longline fisheries with mitigation measures operated and rat control occurred [scenario (5), 2005-  
260 2016], the population slightly increased ( $\lambda = 1.014 \pm 0.062$ ) (Figure 3). The scenario with the highest  $\lambda$  was

261 the scenario where breeders' survival was modelled with no additive effect of longline fishery bycatch  
262 [scenario (6),  $\lambda = 1.035 \pm 0.062$ , Figure 3].

263

#### 264 Effect of covariates and environmental sensitivity

265 There was a significant negative effect of demersal fisheries effort in Crozet EEZ on annual survival  
266 probability (slope =  $-0.512 \pm 0.132$ , Figures 4 and 5). There was no significant effect of the climatic  
267 covariates on survival.

268 There was evidence for a positive linear effect of SIC in the foraging areas during chick rearing on breeding  
269 success of successful breeders (slope =  $0.311 \pm 0.073$ , Figure S8, Table S8), but no effect of detrended SIC  
270 was detected. A positive linear effect of SSTa in the wintering area and of SSTa in the breeding area was  
271 detected on breeding success of failed breeders (slope =  $0.352 \pm 0.092$ ) and of successful breeders (slope =  
272  $0.333 \pm 0.084$ ) respectively, as well as a negative linear effect of SSTa and of SST in Antarctic ice front  
273 area on breeding success of successful breeders (slope =  $-0.395 \pm 0.100$  and slope =  $-0.31 \pm 0.076$   
274 respectively, Figure S8, Table S8). There was also evidence for quadratic effects of SOI at t-1 on survival  
275 of successful breeders and of SIC on breeding success of successful breeders (Figure S8, Table S8).

276 Population growth rate was the most sensitive to demersal longline fisheries effort around Crozet (Table  
277 S9), followed by SIC, SST and SSTa, to which it was between 1.6 and 3.2 less sensitive (Table S9).

## 278 **Discussion**

279 While considerable efforts were made for the last two decades in the implementation of bycatch mitigation  
280 measures, this study is one of the few that assessed their effects on the demography and dynamic of a  
281 threatened population. Our results clearly suggest a positive effect of mitigation measures with i) an increase  
282 of the demographic parameter estimates after the implementation of bycatch mitigation measures, ii) a  
283 decrease followed by an increase and stabilization of breeding densities before and after implementation,  
284 respectively. Results indicated a higher sensitivity of population growth rate to demersal longline fishing  
285

286 effort compared to climate covariates. However, we found that control of invasive predators was also  
287 necessary in addition to bycatch mitigation measures to allow long-term persistence of the population.

288

### 289 Role of bycatch mitigation measures on population dynamics

290 As expected and following implementation of bycatch mitigation, in 2011 the white-chinned petrel breeding  
291 population of Pointe Basse seemed to have partly recovered its density of 1983. Despite large confidence  
292 intervals, this regain was still detected in 2017 and corresponded to an increase of 38% of the breeding  
293 population density between 2004 and 2017. A similar increase was found in populations of another highly  
294 accidentally caught large pelagic marine species, the porpoise (*Phocoena phocoena*) in California since the  
295 limitation of bycatch (Forney et al., 2020). Pointe Basse being the largest breeding colony of white-chinned  
296 petrels of Possession Island, we are convinced that this increase reflected the trend for the entire island  
297 breeding population. Supporting this and in spite of large confidence intervals of population growth rates  
298 that may assume stationary populations in all scenarios, population modelling indicated an increase of the  
299 population growth rate at the study colony of Station de Pompage from the scenario (3) to the scenario (5),  
300 that coincided with an increase in survival probability (from 0.87 to 0.91) and in breeding success  
301 probability (from 0.58 to 0.69) from the period 1995-2004 to the period 2005-2017. This corresponded to a  
302 change in longline fishery practices when bycatch mitigation measures were strongly reinforced in the  
303 French EEZ. However, our matrix population models did not include immigration which could not be  
304 estimated due to a lack of data. Thus we cannot exclude that the slight discrepancy between the observed  
305 population growth rate estimated from breeding densities between 2004 and 2011 (1.090) and the population  
306 growth rate obtained from scenario 6 (1.035) was partly due to immigration of white-chinned petrels to  
307 Pointe Basse.

308

309 In bycatch studies, much attention was focused on survival rates of threatened populations (Gianuca et al.,  
310 2019; Lewison & Crowder, 2003), because of the direct effect of bycatch on survival by additive mortality  
311 (Barbraud et al., 2008), which can have a major influence on population trends because of the strong

312 sensitivity of the populations growth rate to this parameter in long-lived species (Gianuca et al., 2019;  
313 Rolland et al., 2009; Jenouvrier et al., 2005). Our results are supportive of these statements since i) the  
314 highest survival probabilities of the white-chinned petrel population were observed after the implementation  
315 of bycatch mitigation measures, ii) this led to an increasing population, iii) population growth rate was more  
316 sensitive to demersal longline fishing effort than to climate covariates which impacted breeding parameters.  
317 Moreover, assessing the relationship between demersal longline fisheries effort and survival probability  
318 allowed us to estimate survival with no additive mortality due to fisheries bycatch ( $0.923 \pm 0.012$ ). This was  
319 very close to the survival probability estimated during the period with bycatch mitigation measures (2005-  
320 2017), but also to the survival of other closely related Procellariiform species (Gianuca et al., 2019; Oro et  
321 al., 2004). Strong site and mate fidelity in this population (Bried & Jouventin, 1999) and no evidence of ring  
322 loss suggest that adult survival estimates were poorly biased due to emigration.  
323 Although we did not find any significant relationship between breeding probability and fishing effort  
324 covariates, we cannot exclude that bycatch mitigation measures positively affected these demographic  
325 parameters and contributed to explain part of their increases between the periods 1995-2004 and 2005-2017.  
326 Indeed, bycatch may accentuate breeding failures in species with bi-parental care and may also decrease  
327 breeding probability due to widowing (Mills & Ryan, 2005).

### 328 329 Fisheries bycatch, rat predation and climate as drivers of population dynamics

330 According to our results and to Barbraud et al. (2008), the white-chinned petrel population from Possession  
331 Island declined when trawl fisheries (1986-1993, scenario (1)) and longline fisheries (1994-2004, scenario  
332 (2)) were operating in the Crozet EEZ without or with partial mitigation measures. Our results suggest that  
333 fisheries bycatch may have been the main driver of this decline, such as it was a serious threat for several  
334 albatross populations (Lewison & Crowder, 2003; Pardo et al., 2017) and sea turtles (Lewison et al., 2004).  
335 Indeed, we found a negative relationship between survival and longline fishing effort and low survival  
336 probability prior to the implementation of fisheries bycatch mitigation measures. The population growth

337 rate was most sensitive to this covariate, and population modelling indicated an increase in population  
338 growth rate when mitigation measures were implemented. In the Crozet EEZ, toothfish longline fisheries  
339 appeared in the mid-1990s and ended trawling fisheries. At that time there was no mitigation measure for  
340 seabird bycatch and IUU fisheries operated intensively until the early 2000s (Österblom & Sumaila, 2011).  
341 During the 1980s, tuna fishing effort increased in the South Indian Ocean and could also have affected the  
342 white-chinned petrel population [we observed the lowest survival probability (0.47) in 1991], as has been  
343 observed for albatross populations (Tuck et al. 2003; Nel et al., 2002). Low survival and breeding success  
344 probabilities estimated around 2000 may also be due to poor food availability and high fishing effort like it  
345 was found on albatross species (Pardo et al., 2017). Those major changes in fishing practices (Duhamel et  
346 al., 2011) that could have had contrasted effects on seabird populations and other large marine predators,  
347 and the lack of reliable fishing effort data from the RFMOs, in particular in tuna fishery practices (Gilman,  
348 2011; Rolland et al., 2009), could partly hinder the complete role of fisheries bycatch in population declines.  
349 The improvement and stabilisation of the white-chinned petrel breeding success was probably largely due  
350 to rat control in the study colony that occurred since 1994 (Jouventin et al., 2003). We found an increase  
351 from 21% to 58% in success probability after the implementation of rat control and before the  
352 implementation of fishery bycatch mitigation measures. Such an impact of rat predation on breeding success  
353 suggests that the white-chinned petrel population may be stable without rat control but could hardly increase,  
354 whether bycatch mitigation measures were implemented or not. As a consequence all population scenarios  
355 (3, 5, 6) in which the effect of rat control was taken into account lead to an increase in population growth  
356 rate compared to scenarios in which this effect was not accounted for. Rat control may have also benefited  
357 to the breeding probability since a high breeding success could favour site and partner fidelity (Bried &  
358 Jouventin, 1999).

359 Only breeding success was found to be affected by climate covariates, and the sensitivity of population  
360 growth rate to these covariates was lower than sensitivity to longline fishing effort. Our results suggest that  
361 the increase in breeding success during the study period was also likely due the increase of SIC from the



362 early 2000s. Although variations in SSTa affected breeding success, there was no temporal trend for these  
363 covariates.

364

### 365 Conservation implications

366 Showing improvement in a large pelagic marine population following the implementation of fisheries  
367 bycatch mitigation measures is encouraging. Such results highlight not only the efficacy of these measures,  
368 but how those populations recover after a relatively important decrease. Our results showed that after the  
369 control of rat predation, the implementation of bycatch mitigation measures was crucial for population  
370 maintenance and is likely to become more and more important with the rise of new threats such as climate  
371 change, diseases, or pollution. We view this study as an achievement of the significant efforts employed in  
372 the conservation of albatrosses and large petrels threatened by fisheries bycatch. This highlights the  
373 responsibilities that countries and RFMOs share for the conservation and management of endangered  
374 species (Beal et al., 2021). We hope that it will encourage not only the managers to maintain and reinforce  
375 protection measures, but also the scientific community to evaluate the demographic and population  
376 consequences of such measures.

377 Rats were introduced in many islands (Jones et al., 2008) and their presence is a well-known threat to  
378 seabirds (Croxall et al., 2012), including white-chinned petrels. Based on our results, we recommend rat  
379 eradication from Possession Island to allow the long-term persistence of this petrel population. Considering  
380 that different species may be impacted by the same threats but with different intensities, efforts in  
381 conservation should be important in eradicating rat predation simultaneously with serious fisheries bycatch  
382 mitigation management. Our adult survival estimate obtained with no additive mortality due to fisheries  
383 bycatch remains slightly higher than the average survival during the period 2005-2017. This may suggest  
384 that there is still some additional mortality due to bycatch within the at sea distribution of this white-chinned  
385 petrel population. Recent reports from the Crozet EEZ indicate extremely low bycatch mortality in legal  
386 longline fisheries [ $\leq 6$  white-chinned petrels per year in average, (CCAMLR, 2020)]. Therefore, it is likely

387 that additive mortality is still occurring in international waters where efforts are needed to implement  
388 effective mitigation measures.

389

### 390 **Authors' contributions**

391 All the authors conceived the ideas and designed methodology. KD, AC: data acquisition and preparation;  
392 AD, CB : data analysis and processing, led the writing of the manuscript. All authors edited and revised the  
393 manuscript and approved the final version. None of the author has conflict of interest related to this study.

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### 403 **Data availability statement**

404 Data are available online at the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1zcrjdfds>  
405 (Dasnon et al, 2022)

406

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595 **Tables**

596 Table 1: Mean demographic parameters ( $s$ : survival,  $\beta$ : breeding,  $\gamma$ : success) white-chinned petrels at  
 597 Possession Island and associated standard errors according to breeding state (SB: successful breeder, FB:  
 598 failed breeder) and to the selected study period.

Demographic parameter	State	All period	1986-1993	1994-2004	2005-2017
$s$	SB	$0.870 \pm 0.099$	$0.800 \pm 0.158$	$0.871 \pm 0.045$	$0.910 \pm 0.053$
	FB	$0.844 \pm 0.106$	$0.881 \pm 0.059$	$0.810 \pm 0.109$	$0.853 \pm 0.105$
	NB	$0.904 \pm 0.017$			
$\beta$	SB	$0.870 \pm 0.149$	$0.881 \pm 0.094$	$0.802 \pm 0.207$	$0.922 \pm 0.058$
	FB	$0.825 \pm 0.147$	$0.772 \pm 0.202$	$0.832 \pm 0.123$	$0.847 \pm 0.058$
	NB	$0.350 \pm 0.253$	$0.443 \pm 0.302$	$0.256 \pm 0.198$	$0.380 \pm 0.250$
$\gamma$	SB	$0.544 \pm 0.253$	$0.214 \pm 0.224$	$0.579 \pm 0.186$	$0.693 \pm 0.113$
	FB	$0.496 \pm 0.213$	$0.323 \pm 0.199$	$0.546 \pm 0.263$	$0.546 \pm 0.101$
	NB	$0.489 \pm 0.300$	$0.555 \pm 0.248$	$0.536 \pm 0.295$	$0.293 \pm 0.178$

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601 Table 2: Population growth rate sensitivities and elasticities to demographic parameters, and contribution  
 602 of demographic parameters to the variance ( $\text{Var}(\lambda) = 0.004$ ) in population growth rate for white-chinned  
 603 petrels at Possession Island, 1987-2017. SB: successful breeder, FB: failed breeder, NB: non-breeder,  $j_n$ :  
 604 juvenile of  $n$  years old.

Parameter	Status	Estimate	Temporal variance	Elasticity	Sensitivity	Contribution (%)
Juvenile survival	$j_1$	0.7		0.068	0.094	
	$j_2$	0.761		0.068	0.086	
	$j_3$	0.796		0.068	0.083	
	$j_4$	0.821		0.068	0.080	
	$j_5$	0.841		0.068	0.078	
	$j_6$	0.857		0.063	0.071	
	$j_7$	0.870		0.042	0.046	
Recruitment	$j_5$	0.062		<0.001	0.014	
	$j_6$	0.314		0.002	0.007	
	$j_7$	1		0.042	0.040	
Survival	SB	0.870	0.0095	0.200	0.223	28.0
	FB	0.844	0.0108	0.181	0.201	26.2
	NB	0.844	0.0108	0.108	0.126	10.1
Breeding	SB	0.870	0.0216	0.059	0.066	5.4
	FB	0.825	0.0204	0.049	0.062	4.8
	NB	0.350	0.0635	0.015	0.041	6.5
Success	SB	0.544	0.0635	0.031	0.056	11.9
	FB	0.496	0.0445	0.025	0.047	6.0
	NB	0.489	0.0835	0.008	0.016	1.2

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