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RESEARCH ARTICLE

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

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Anaïs Dasnon

Email: anaïs.dasnon@taaf.re**Handling Editor:** Maria Paniw**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 1980s following the rise of global fishing effort. Bycatch mitigation measures were implemented since the 2000s, 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 (a) built multi-event capture–recapture models to estimate the demographic parameters of a population from Possession Island (southern Indian Ocean) over 30 years, (b) assessed the effect of climate and fishery covariates on demographic parameters, (c) built a population matrix model to estimate stochastic growth rate according to the management in fisheries bycatch and (d) estimated changes in breeding population density using distance sampling data.
3. The population declined from the 1980s to the mid-2000s, 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-2000s. 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.
5. *Synthesis and applications.* We provide a holistic approach to assess the effects of management measures by analysing datasets from sampling methods commonly employed in seabird studies. Our conclusions should encourage the eradication of invasive predatory species in seabird 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

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the other marine large pelagic species threatened by fisheries bycatch (sharks, rays, turtles and marine mammals) since it could be crucial to avoid populations' extinction.

KEYWORDS

conservation measures capture–mark–recapture demersal longline fisheries population dynamics procellariiforms southern Indian Ocean white-chinned petrel.

1 | INTRODUCTION

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

Seabird conservation state is of concern with 28% of their species globally threatened (Croxall et al., 2012) and 66% of albatrosses and large petrels species actually listed by the Agreement on the Conservation of Albatrosses and Petrels (ACAP) as a priority (Phillips et al., 2016). Fishery bycatch has been identified as the most impacting threat on those species and alien species predation as the threat that affects the more numerous of those species (Dias et al., 2019). Many of them share their foraging areas with fishing vessels that they follow—because Procellariiforms use their sense of smell to track food—in order to take advantage of food opportunities such as fishing waste and baits. This increases hooking or entanglement risks and leads to the death of hundreds of thousands of seabirds every year (Tuck et al., 2003; Žydelis et al., 2013). This massive additive mortality is highly problematic for long-lived marine pelagic species such as seabirds characterised by slow demographic strategies due to long generation time, low fecundity and delayed maturity (Hamer et al., 2001). Their populations are sensitive to small variations in adult mortality (Caswell, 2001). Since the early 2000s, the scientific community, the non-governmental organisations, the countries that have ratified the ACAP and the Regional Fisheries Management Organisations (RFMOs) spent considerable efforts to develop and implement effective mitigation measures in order to significantly reduce or completely remove this threat. Measures

include bird-scaring streamer lines, line weighting, night setting and establishment of protected areas (Løkkeborg, 2011; Wolfaardt et al., 2016). Unfortunately, many threatened species do not yet benefit from sufficient mitigation measures implementation (Gilman et al., 2014).

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

Our aim was to evaluate the impact of fishery bycatch and implementation of mitigation measures on a vulnerable seabird, the white-chinned petrel *Procellaria aequinoctialis*, which is one of the most accidentally captured petrel in pelagic fisheries targeting tuna species in South Atlantic and Indian Oceans, and in demersal longline fisheries practices targeting Patagonian toothfish *Dissostichus eleginoides* in South Indian Ocean and in Southern Ocean (Weimerskirch et al., 1999). The species was also largely threatened by trawl fisheries that occurred in their sub-tropical wintering areas (Croxall, 2008) and in subantarctic waters until the mid-1990s (Watkins et al., 2008; Weimerskirch et al., 2000).

We took advantage of long-term capture–recapture and population datasets of a white-chinned petrel population breeding at Possession Island, Crozet archipelago, to (a) estimate demographic parameters before and after the implementation of bycatch mitigation measures in the subantarctic French exclusive economic zone (EEZ) and in waters

managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR); (b) test for temporal trends in demographic parameters and assess the relationship with fishing efforts and climate variables; (c) model the population dynamics and assess the effect of the implementation of bycatch mitigation measures and of the control of an introduced predator on the population growth rate; and (d) estimate breeding population density using distance sampling data from line-transect surveys conducted on land in 2011 and 2017.

There is evidence that longline fisheries bycatch, climate variability and introduced predators (black rat *Rattus rattus*) impact demographic parameters and population growth rate of the white-chinned petrels from the Crozet archipelago (Barbraud et al., 2008; Jouventin et al., 2003). The acceptance of fishery bycatch as a serious threat by the CCAMLR emerged in the early 1990s, followed by the implementation of strong bycatch mitigation measures since 2003 (Delord et al., 2005; Delord et al., 2010; Reid et al., 2010). In the meantime, the ACAP was ratified by 13 countries including France that integrated it in French law in 2005. Under the hypothesis that bycatch was the main cause of the white-chinned petrel population's decline through additive mortality (Barbraud et al., 2008), and since numbers of white-chinned petrels caught in longlines strongly decreased following the implementation of mitigation measures (CCAMLR, 2020; Delord et al., 2010), we expected (a) an increase in survival probability due to reduced direct bycatch mortality, (b) an increase in breeding success since a widowed parent due to its partner death in fisheries may fail to fledge the chick on its own and (c) a stability or increase in the white-chinned petrel breeding population density.

2 | MATERIAL AND METHODS

2.1 | Study species and population monitoring

The Ethics Committee of IPEV and the Comité Environnement Polaire approved the field procedures for the French Southern Territories. White-chinned petrels were monitored at Possession island (46°S;

51°E; see Appendix S1) following two sampling approaches. First, 200 individually marked burrows were investigated each year from the breeding season 1985/1986 (hereafter 1985) to the breeding season 2017/2018 at the study colony of Station de Pompage. Each burrow was visited several times from egg laying (November) to chick fledging (April) to assess the presence of the occupying individuals, their identity and their breeding status (breeder if an egg was laid, non-breeder otherwise). Each adult newly captured and all fledglings were marked with a stainless-steel ring on the leg (Barbraud et al., 2008, see Appendix S2). Black rats were introduced at Possession Island during the 19th century (Chapuis et al., 1994) and were poisoned yearly during each breeding season since 1994 at the study colony but not elsewhere on Possession Island (Jouventin et al., 2003). Second, in order to estimate breeding population density, line-transect distance sampling surveys were carried out in 2011 and 2017 at Pointe Basse, that hosts a large proportion (25%–30%) of white-chinned petrels breeding on Possession Island with relatively high densities of burrows (Barbraud et al., 2008). Surveys were conducted during incubation (early December) and densities of occupied burrows were estimated from line-transect distance sampling (see Appendix S3).

2.2 | Modelling demographic parameters

For individuals marked as adults, their encounter history started at first capture. The 32-year time series (from 1986 to 2017) resulted in 842 individual capture histories. To model the transition of individuals in state i at time t to state j at time $t + 1$, we estimated the following demographic parameters (Figure 1; Table 1 S4): apparent survival probability (s), the state-specific transitional probability of becoming or remaining a breeder (hereafter breeding probability; β), success probability (γ), recapture probability (p) and assignment probability (δ). To do so, we constructed a multi-event capture–mark–recapture (MECMR) model (Pradel, 2005) to take account of uncertainty in breeding success, with four states consisting of one non-breeder state among adults (excluding subadults; NB), two breeder states

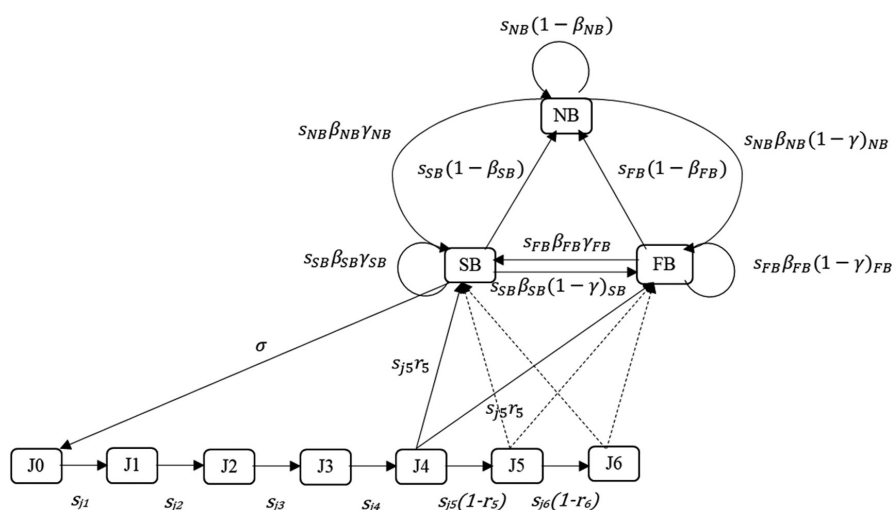


FIGURE 1 Life cycle of the white-chinned petrel. SB, Breeders that successfully raised a chick until fledging; FB, Breeders that failed to fledge a chick; NB, Non-breeders; j_n , juvenile (individual that did not yet attempt to breed) of n year(s) old; S , survival probability; β , breeding probability; γ , breeding success probability; σ , sex ratio; S_{jn} , survival probability for the transition between age $n - 1$ and age n , r_n , recruitment probability for the transition between juvenile of age n to breeder individual

[failed breeder (FB), successful breeder (SB)], and the dead state (\dagger) that was not observable. Capture histories were coded considering field observations: 0 = not observed, 1 = seen as NB, 2 = seen as FB, 3 = seen as SB, 4 = seen as breeder but status not ascertained. We started with a general model as the model that allowed the most numerous demographic parameters to be estimated independently for each step of time and for each state (see Appendix S4).

For individuals marked as chick, their encounter history started at the first return in the study population, from which they were considered as adults. Youngest individuals seen as breeders on the colony were 5 years old. To estimate juvenile survival and recruitment probabilities we used data from individuals that were marked as chicks only. Our dataset contained 979 individual capture histories of which 61 were seen recruiting. We estimated the following parameters: apparent survival probability (s_n), the probability of first breeding (r_n), as the probability that an individual breeds for the first time (Figure 1) and the recapture probability. To do so, we constructed a multi-state capture-mark-recapture (MSCMR) model (Lebreton et al., 2009; Pradel, 1996) with three states consisting of one juvenile state, one breeder state and the dead state (see Appendix S4). The goodness-of-fit (GOF) tests for MSCMR and MECMR models (Pradel et al., 2003) were performed using U-CARE 2.3.4 (Choquet et al., 2009; see Appendix S4).

2.3 | Modelling population dynamics

To model the dynamics of the white-chinned petrel population and the effects of different scenarios on the population growth rate (λ), we built a female-only pre-breeding census matrix population model structured by age and breeding status (Caswell, 2001) with seven juvenile age classes and three adult classes according to breeding states (NB, SB and FB, see Appendix S5). From this matrix model we performed a sensitivity analysis of λ to changes in demographic parameters, and a retrospective analysis to quantify the contribution of the vital rates to variability in λ (Caswell, 2001).

Then, we estimated λ using six management scenarios according to bycatch mitigation measure implementation and rat control (see Appendix S5, Table 1 S5). For each scenario the demographic parameters s , β and γ differed following three periods (Table 1): 1986–1993

(8 years), when trawl fishing occurred and no rat control occurred; 1994–2004 (11 years), when longline fishing occurred without mitigation measures and rat control occurred; 2005–2017 (13 years), when longline fishing occurred with mitigation measures and rat control occurred. All other parameters remained equal. The first three scenarios had no mitigation measures for fishery bycatch. Scenario (1) used s , β and γ estimated from 1986 to 1993. Scenario (2) used s and β estimated from 1994 to 2004 and γ estimated from 1986 to 1993. Scenario (3) used s , β and γ estimated from 1994 to 2004. We then built three additional scenarios with mitigation measures for fisheries bycatch. We chose 2005 as the year-reference for the implementation of bycatch mitigation measures because France integrated the ACAP recommendations in the French law in 2005. Scenario (4) used s and β estimated from 2005 to 2017 and γ estimated from 1984 to 1993 (no rat control). Scenario (5) used s , β and γ estimated from 2005 to 2017. Scenario (6) used β and γ estimated from 2005 to 2017, and s for FB and SB individuals estimated as the intercept in the linear relationship between survival and demersal longline fishing effort. This last scenario reflected population dynamics without any additive effect of demersal longline fishing on adult survival.

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

We conducted random effect design life table response experiments (LTREs) in a retrospective analyses in order to estimate the contribution of each demographic parameter to the variability in the growth rate λ . Following Jenouvrier et al. (2005), we approximated the contributions using the expression $V(\lambda) \approx s(\theta)^2 \text{var}(\theta)$, where $s(\theta)$ is the sensitivity of λ to the demographic parameter.

2.4 | Effects of covariates on demographic parameters

We chose fisheries and climate covariates that were likely to have an influence on survival, reproduction or breeding parameters,

TABLE 1 Mean demographic parameters (s , survival; β , breeding; γ , success) white-chinned petrels at Possession Island and associated standard errors according to breeding state (SB, successful breeder; FB, failed breeder) and to the selected study period

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

according to white-chinned petrel breeding phenology, distribution at sea (see Appendix S6, Table 1 S6, Figures 1 S6, 2 S6, 3 S6 and 4 S6) and previous knowledge of the studied population (Barbraud et al., 2008; Catard et al., 2000; Delord et al., 2013; Péron et al., 2010). Fishery covariates included fishing effort from demersal longline during the breeding season, pelagic longline during wintering (i.e. the non-breeding season), illegal, unreported and unregulated (IUU) from Crozet EEZ (CCAMLR, 2018), and the quantity of hakes (*Merluccius* spp.) fished in Namibian EEZ used as a proxy of trawling effort. Climate data included sea surface temperature anomalies (SSTa) and sea surface temperature (SST) during the breeding and non-breeding seasons, sea ice concentration (SIC) during the breeding season, chlorophyll a concentration (Chla) during the non-breeding season, southern annular mode (SAM) and southern oscillation index (SOI) without lag and with a lag of 1 year (see Appendix S6, Figure 2 S6).

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

3 | RESULTS

3.1 | Breeding population density

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

3.2 | Demographic parameters

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

The mean observed age at first breeding was 7.3 ± 1.5 years old (median = 7), 82% of the first-time breeders were 8 years old or

less, 60.7% were 7 years old or less and 34.4% were 6 years old or less. MSCMR model selection suggested that recruitment started at age 5 and was 0.061 ± 0.030 , increased at 0.314 ± 0.082 at 6 years old and was 0.370 ± 0.130 at 7 years old and older (Table 2 S4). The selected model suggested constant survival probability among age classes from 7 years old at 0.879 ± 0.022 . Mean annual survival probability was estimated from fledging to 5 years old at 0.781 ± 0.028 .

MECMR model selection indicated that recapture probability was time and state dependent, and was 0.785 ± 0.250 for successful breeders, 0.863 ± 0.180 for failed breeders and 0.047 ± 0.006 for non-breeders. Assignment probability was 0.971 ± 0.004 for failed breeders and was ≈ 1 for successful breeders.

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

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

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

3.3 | Population modelling

The stochastic λ obtained from the estimated demographic parameters (average rates for the entire 32-year period) was 0.967 ± 0.062 and did not allow maintenance of the population.

Retrospective analyses indicated that survival of breeding individuals was the demographic parameters that contributed the most in the variability in λ , followed by breeding success of successful individuals and survival of non-breeders (Table 2). Elasticity of the population growth rate was the highest for adult survival, then to juvenile survival, to recruitment at 7 years old, to breeding probabilities and to breeding success of breeders (Table 2).

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

When no rat control occurred, with or without implementation of bycatch mitigation measures in longline fisheries [scenario (4) and scenario (2) respectively, see Appendix S5, Figure 1 S5], the

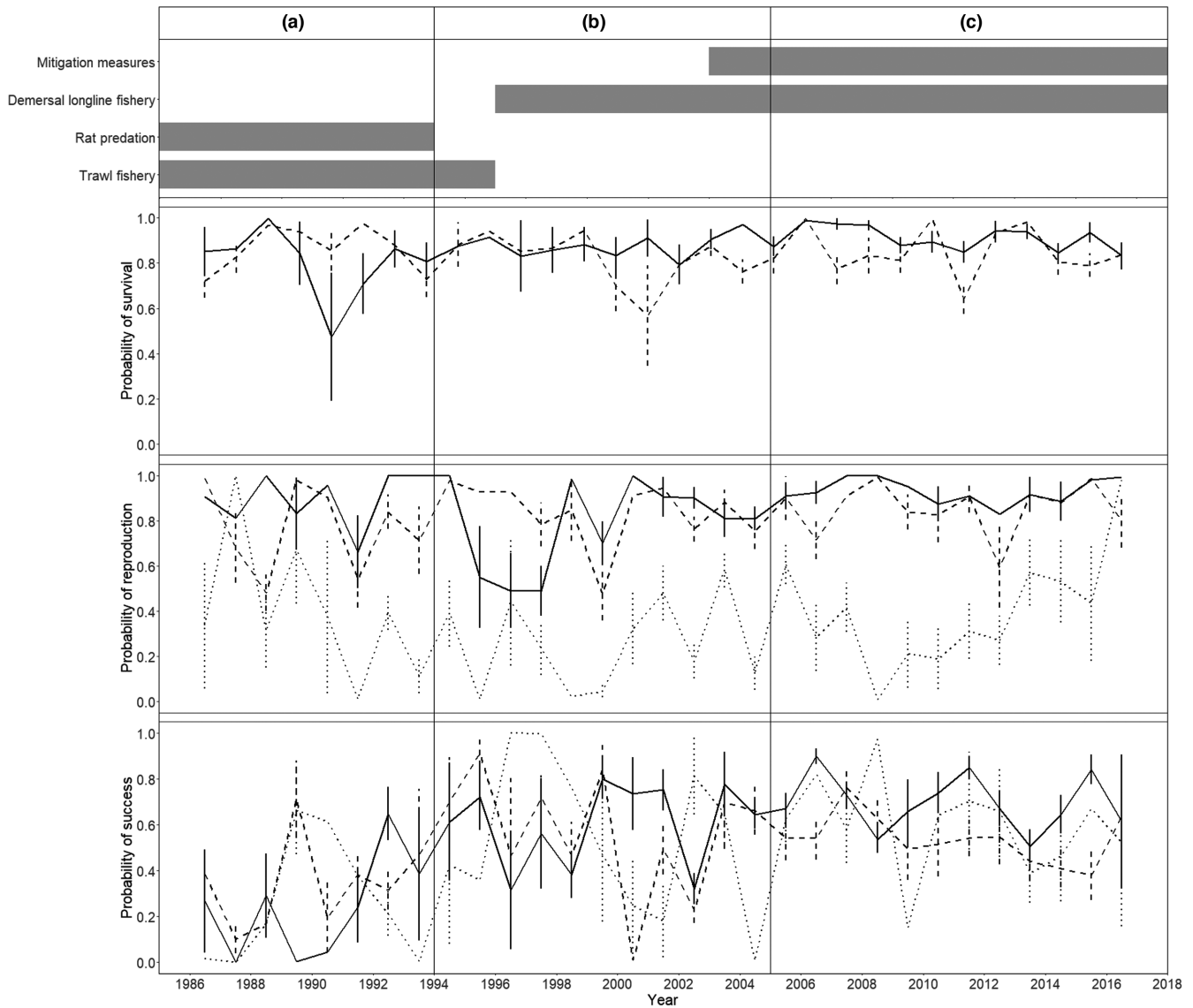


FIGURE 2 Timeline of fisheries and alien invasive predator (black rat, *Rattus rattus*) and their management in the Crozet EEZ in three periods: (a) 1986–1993, (b) 1994–2004 and (c) 2005–2017 (upper panel) and the demographic parameter estimates of white chinmed petrels from the study colony at Possession Island from 1987 to 2017. Solid line: successful breeder, dashed line: failed breeder, dotted line: non-breeder. Error bars are standard errors

population growth rates were $\lambda = 0.959 \pm 0.071$ and 0.914 ± 0.069 respectively (Figure 3).

When longline fisheries with mitigation measures operated and rat control occurred [scenario (5), 2005–2016], the population slightly increased ($\lambda = 1.014 \pm 0.062$; Figure 3). The scenario with the highest λ was the scenario where breeders' survival was modelled with no additive effect of longline fishery bycatch [scenario (6), $\lambda = 1.035 \pm 0.062$, Figure 3].

3.4 | Effect of covariates and environmental sensitivity

There was a significant negative effect of demersal fisheries effort in Crozet EEZ on annual survival probability (slope = -0.512 ± 0.132 ,

Figure 4). There was no significant effect of the climatic covariates on survival.

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

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

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

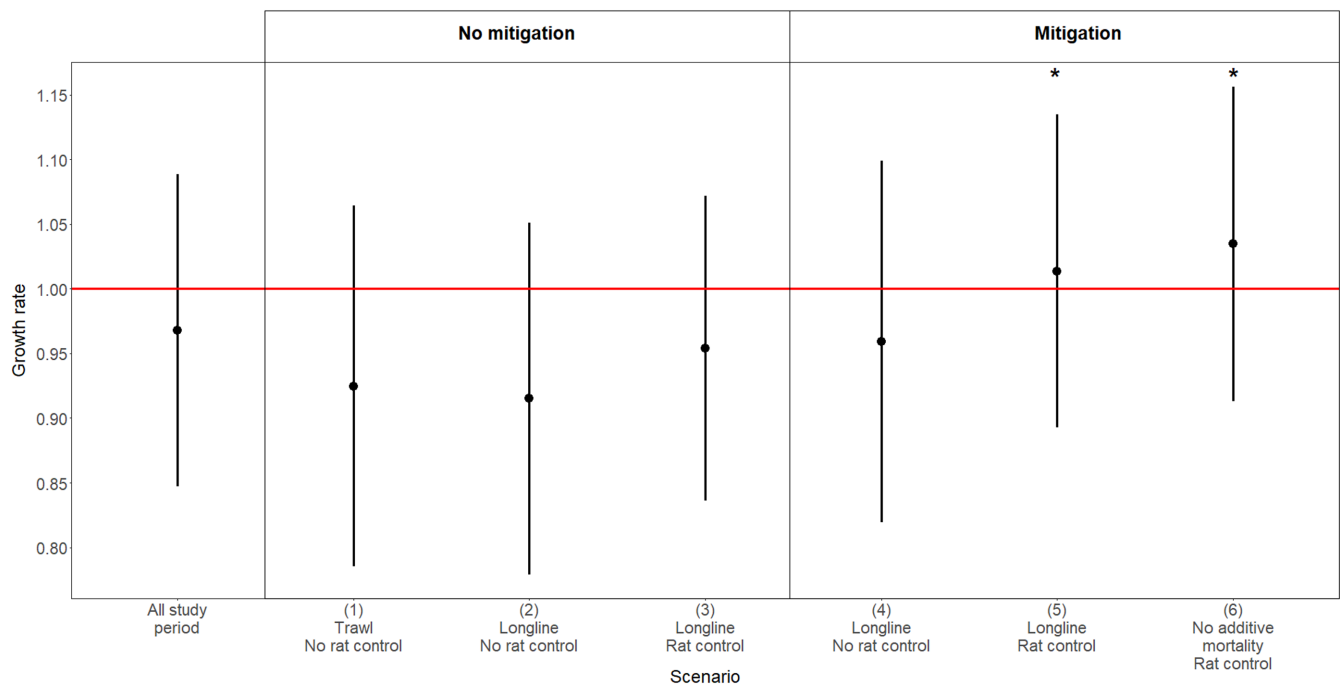


FIGURE 3 Stochastic population growth rate of white-chinned petrels at Possession Island according to six different management scenarios (see Methods). Error bars are 95% confidence intervals. No mitigation: no implementation of fishery bycatch mitigation measures in the Crozet EEZ, Mitigation: implementation of fishery bycatch mitigation measures in the Crozet EEZ. All study period: from 1986 to 2017. The asterisk (*) indicates that the population was not extinct after 100 years and the red line corresponds to the growth rate = 1

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

4 | DISCUSSION

While considerable efforts were made for the last two decades in the implementation of bycatch mitigation measures, this study is

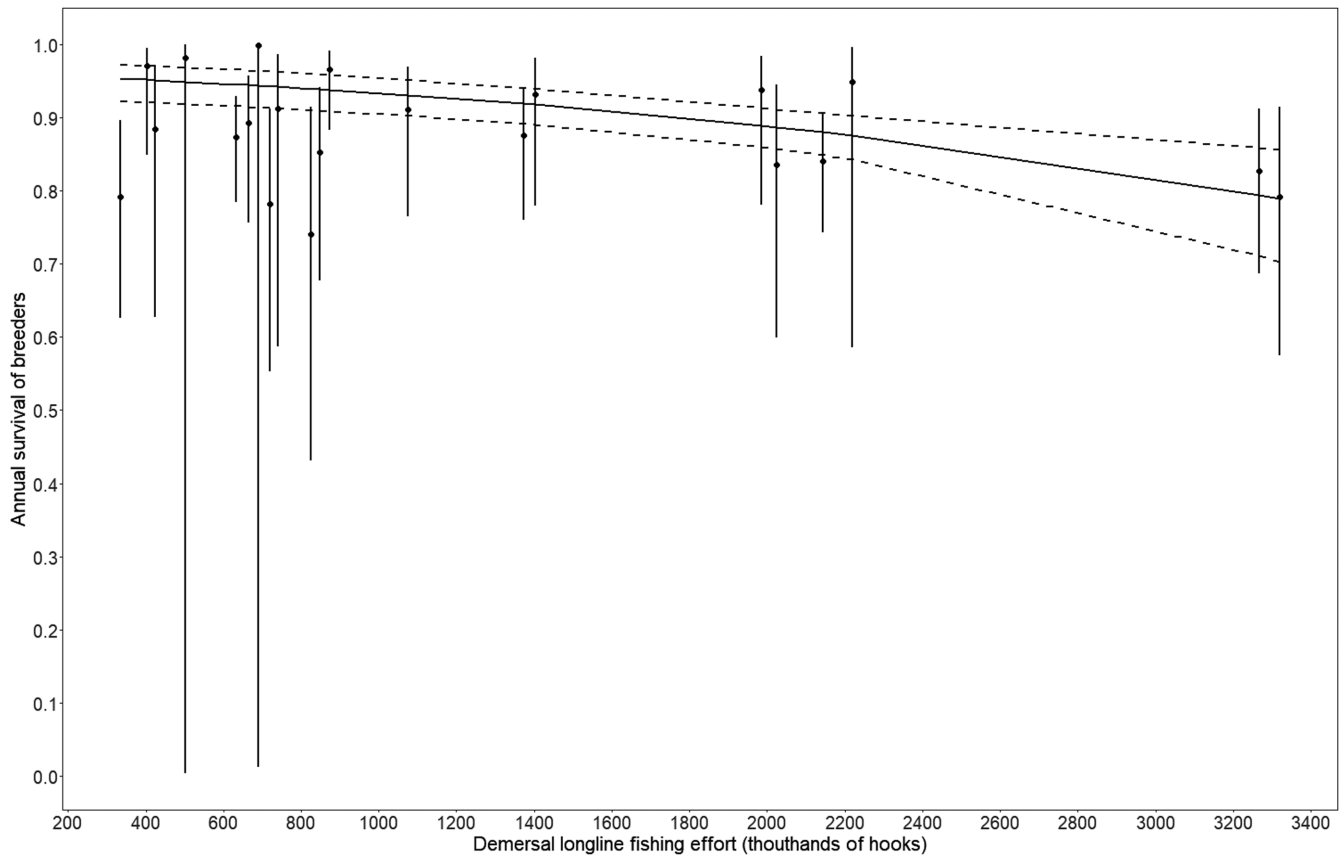


FIGURE 4 Relationship between annual survival probability of breeders and demersal longline fishing effort (in number of hooks) in the Crozet EEZ. Error bars indicate 95% confidence intervals. The modelled relationship between adult survival and fishing effort is indicated by the black line (intercept = 2.490 ± 0.173 , slope = -0.512 ± 0.130 , in logit scale). Dotted lines indicate 95% confidence intervals

one of the few that assessed their effects on the demography and dynamic of a threatened population. Our results clearly suggest a positive effect of mitigation measures with (a) an increase in the demographic parameter estimates after the implementation of bycatch mitigation measures, (b) a decrease followed by an increase and stabilisation of breeding densities before and after implementation respectively. Results indicated a higher sensitivity of population growth rate to demersal longline fishing effort compared to climate covariates. However, we found that control of invasive predators was also necessary in addition to bycatch mitigation measures to allow long-term persistence of the population.

4.1 | Role of bycatch mitigation measures on population dynamics

As expected and following implementation of bycatch mitigation, in 2011 the white-chinned petrel breeding population of Pointe Basse seemed to have partly recovered its density of 1983. Despite large confidence intervals, this regain was still detected in 2017 and corresponded to an increase of 38% of the breeding population density between 2004 and 2017. A similar increase was found in populations of another highly accidentally caught large pelagic marine species, the porpoise *Phocoena phocoena* in California since

the limitation of bycatch (Forney et al., 2020). Pointe Basse being the largest breeding colony of white-chinned petrels of Possession Island, we are convinced that this increase reflected the trend for the entire island breeding population. Supporting this and in spite of large confidence intervals of population growth rates that may assume stationary populations in all scenarios, population modelling indicated an increase in the population growth rate at the study colony of Station de Pompage from the scenario (3) to the scenario (5), that coincided with an increase in survival probability (from 0.87 to 0.91) and in breeding success probability (from 0.58 to 0.69) from the period 1995–2004 to the period 2005–2017. This corresponded to a change in longline fishery practices when bycatch mitigation measures were strongly reinforced in the French EEZ. However, our matrix population models did not include immigration which could not be estimated due to a lack of data. Thus we cannot exclude that the slight discrepancy between the observed population growth rate estimated from breeding densities between 2004 and 2011 (1.090) and the population growth rate obtained from scenario 6 (1.035) was partly due to immigration of white-chinned petrels to Pointe Basse.

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

influence on population trends because of the strong sensitivity of the populations growth rate to this parameter in long-lived species (Gianuca et al., 2019; Jenouvrier et al., 2005; Rolland et al., 2009). Our results are supportive of these statements since i) the highest survival probabilities of the white-chinned petrel population were observed after the implementation of bycatch mitigation measures, ii) this led to an increasing population, iii) population growth rate was more sensitive to demersal longline fishing effort than to climate covariates which impacted breeding parameters. Moreover, assessing the relationship between demersal longline fisheries effort and survival probability allowed us to estimate survival with no additive mortality due to fisheries bycatch (0.923 ± 0.012). This was very close to the survival probability estimated during the period with bycatch mitigation measures (2005–2017), but also to the survival of other closely related Procellariiform species (Gianuca et al., 2019; Oro et al., 2004). Strong site and mate fidelity in this population (Bried & Jouventin, 1999) and no evidence of ring loss suggest that adult survival estimates were poorly biased due to emigration.

Although we did not find any significant relationship between breeding probability and fishing effort covariates, we cannot exclude that bycatch mitigation measures positively affected these demographic parameters and contributed to explain part of their increases between the periods 1995–2004 and 2005–2017. Indeed, bycatch may accentuate breeding failures in species with bi-parental care and may also decrease breeding probability due to widowling (Mills & Ryan, 2005).

4.2 | Fisheries bycatch, rat predation and climate as drivers of population dynamics

According to our results and to Barbraud et al. (2008), the white-chinned petrel population from Possession Island declined when trawl fisheries (1986–1993, scenario (1)) and longline fisheries (1994–2004, scenario (2)) were operating in the Crozet EEZ without or with partial mitigation measures. Our results suggest that fisheries bycatch may have been the main driver of this decline, such as it was a serious threat for several albatross populations (Lewison & Crowder, 2003; Pardo et al., 2017) and sea turtles (Lewison et al., 2004). Indeed, we found a negative relationship between survival and longline fishing effort and low survival probability prior to the implementation of fisheries bycatch mitigation measures. The population growth rate was most sensitive to this covariate, and population modelling indicated an increase in population growth rate when mitigation measures were implemented. In the Crozet EEZ, toothfish longline fisheries appeared in the mid-1990s and ended trawling fisheries. At that time there was no mitigation measure for seabird bycatch and IUU fisheries operated intensively until the early 2000s (Österblom & Sumaila, 2011). During the 1980s, tuna fishing effort increased in the South Indian Ocean and could also have affected the white-chinned petrel population [we observed the lowest survival probability (0.47) in 1991], as has been observed

for albatross populations (Nel et al., 2002; Tuck et al., 2003). Low survival and breeding success probabilities estimated around 2000 may also be due to poor food availability and high fishing effort like it was found on albatross species (Pardo et al., 2017). Those major changes in fishing practices (Duhamel et al., 2011) that could have had contrasted effects on seabird populations and other large marine predators, and the lack of reliable fishing effort data from the RFMOs, in particular in tuna fishery practices (Gilman, 2011; Rolland et al., 2009), could partly hinder the complete role of fisheries bycatch in population declines.

The improvement and stabilisation of the white-chinned petrel breeding success was probably largely due to rat control in the study colony that occurred since 1994 (Jouventin et al., 2003). We found an increase from 21% to 58% in success probability after the implementation of rat control and before the implementation of fishery bycatch mitigation measures. Such an impact of rat predation on breeding success suggests that the white-chinned petrel population may be stable without rat control but could hardly increase, whether bycatch mitigation measures were implemented or not. As a consequence all population scenarios (3, 5, 6) in which the effect of rat control was taken into account lead to an increase in population growth rate compared to scenarios in which this effect was not accounted for. Rat control may have also benefited to the breeding probability since a high breeding success could favour site and partner fidelity (Bried & Jouventin, 1999).

Only breeding success was found to be affected by climate covariates, and the sensitivity of population growth rate to these covariates was lower than sensitivity to longline fishing effort. Our results suggest that the increase in breeding success during the study period was also likely due the increase in SIC from the early 2000s. Although variations in SSTa affected breeding success, there was no temporal trend for these covariates.

4.3 | Conservation implications

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

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

AUTHORS' CONTRIBUTIONS

All the authors conceived the ideas and designed methodology; K.D. and A.C. were involved in data acquisition and preparation; A.D. and C.B. were involved in data analysis and processing, and led the writing of the manuscript. All authors edited and revised the manuscript and approved the final version. None of the author has conflict of interest related to this study.

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DATA AVAILABILITY STATEMENT

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

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