



The demography of the White-headed Petrel at Mayes Island, Kerguelen

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Abstract

The demography and factors affecting the population dynamics of gadfly petrels (*Pterodroma* spp.) remain poorly known, although they constitute the most diverse genus of Procellariiformes and many species are threaten. Using a long-term individual monitoring dataset over 35 years, this study provides estimates of state-specific demographic parameters of the White-headed Petrel (*Pterodroma lessonii*) from Mayes Island, Kerguelen archipelago, and tests for the effects of environmental factors. Age at first breeding was 8.7 ± 2.6 years and apparent adult annual survival was 0.941 ± 0.058 . Annual breeding probability was 0.356 ± 0.036 for successful breeders and 0.988 ± 0.054 for individuals that took a sabbatical year after a successful breeding event. Successful breeders that bred during two consecutive years had a lower breeding success (0.574 ± 0.048) than individuals that bred after a sabbatical year (0.655 ± 0.036). The realized population growth rate (1.073 ± 0.011) suggested that the population is increasing. There was a slight evidence for a positive effect of the Southern Annular Mode on the breeding probability of successful breeders, but no effect of sea surface temperature, chlorophyll *a* or wind was detected on demographic parameters. This study revealed that White-headed Petrels had a particularly high adult survival coherent with a quasi-biennial strategy and late age at first breeding. According to life history theory, populations of White-headed Petrel are thus likely to be very sensitive to small variations in adult survival, and anthropogenic factors causing additive mortality such as introduced predators will constitute serious threats for this species.

Keywords Adult survival · Breeding · Capture-mark-recapture · Population growth rate · *Pterodroma lessonii* · Seabird

Zusammenfassung

Die Demografie des Weißkopf-Sturmvogels auf der Mayes-Insel, Kerguelen-Archipel

Die Demografie und die Faktoren, die die Populationsdynamik der Sturmvögel (*Pterodroma* spp.) beeinflussen, sind nach wie vor kaum bekannt, obwohl sie die artenreichste Gattung der Procellariiformes bilden und viele der Arten bedroht sind. Auf der Grundlage einer Langzeitbeobachtung von Individuen über einen Zeitraum von 35 Jahren werden in dieser Studie statusspezifische demografische Parameter des Weißkopf-Sturmvogels (*Pterodroma lessonii*) auf der Mayes-Insel im Kerguelen-Archipel eingeschätzt und die Auswirkungen von Umweltfaktoren untersucht. Das Alter bei der ersten Brut betrug $8,7 \pm 2,6$ Jahre, die jährliche Überlebensrate der erwachsenen Tiere lag bei $0,941 \pm 0,058$. Die jährliche Brutwahrscheinlichkeit betrug $0,356 \pm 0,036$ für erfolgreiche Brütende und $0,988 \pm 0,054$ für Individuen, die nach erfolgreichem Brüten in einem Jahr für ein Jahr aussetzten. Die festgestellte Wachstumsrate der Population ($1,073 \pm 0,011$) deutet darauf hin, dass die Bevölkerung wächst. Es gab leichte Hinweise auf eine positive Auswirkung des Southern Annular Mode auf die Brutwahrscheinlichkeit erfolgreicher Brüter, aber es wurden keine Auswirkung von Meeresoberflächentemperatur, Chlorophyll *a* oder Wind auf

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die demografischen Parameter festgestellt. Die Untersuchung ergab, dass adulte Weißkopf-Sturmvögel eine besonders hohe Überlebensrate haben, die mit einer nahezu Zweijahres-Strategie und einem höheren Alter bei der ersten Brut zusammenhängt. Entsprechend der Lebensgeschichte-Theorie dürften die Populationen des Weißkopf-Sturmvogels daher sehr empfindlich auf kleine Schwankungen im Überleben der Erwachsenen reagieren, und anthropogene Faktoren wie z. B. eingeführte Prädatoren, die eine zusätzliche Sterblichkeit verursachen, stellen eine ernsthafte Bedrohung für diese Art dar.

Introduction

Gadfly petrels (*Pterodroma* spp.) are amongst the most truly oceanic of birds, and is the most diverse genus of Procellariiformes seabirds with 35 species living in all water masses of the World Ocean, but the high-Arctic (Brooke 2004; Harrison et al. 2021). Yet they are neither well-known nor well-studied. Several new species have recently been discovered and most gadfly petrels are threatened with extinction (Dias et al. 2019). Although our understanding of the at sea ecology of gadfly petrels have improved in recent years (Rayner et al. 2008, 2012; Pinet et al. 2012; Clay et al. 2017; Ramos et al. 2017; Taylor et al. 2020), their demography and factors affecting their population dynamics remain very poorly known. For example, survival rates and age at primiparity have been estimated for only a handful of species (Schreiber and Burger 2002; Nicoll et al. 2017).

Although many gadfly petrels occur in areas where important climate and oceanographic changes have been reported during the last decades, such as in the Southern Hemisphere (Sydeman et al. 2015), a consequence of the scarcity of demographic studies among gadfly petrels is that we have a very insufficient understanding of the effects of environmental variability on their population dynamics compared to other seabird families such as albatrosses, penguins or auks (Orgeret et al. 2022). Yet, environmental factors affecting the demography of gadfly petrels may differ from those affecting other seabird species. For example, gadfly petrels are less attracted by fishing vessels than albatrosses or fulmarine petrels, their diets poorly overlap with forage fish targeted by industrial fisheries, and thus may be less vulnerable to bycatch or overfishing (Dias et al. 2019). Gadfly petrels may also be more sensitive to predation by invasive alien species or natural predators due to their relatively small size compared to larger seabird species. There is, therefore, a need for studies quantifying the demographic parameters and population growth rates of gadfly petrel populations, and investigating the effects of environmental drivers on their demography.

Among gadfly petrels, the White-headed Petrel *Pterodroma lessonii* movements and foraging ecology were recently investigated (Taylor et al. 2020; Chérel et al. 2022), but demographic processes and population dynamics have been little studied, and how environmental variation affects its vital rates remains unknown. Although the White-headed Petrel is listed as Least Concern, based on its large population sizes and widespread breeding distribution, some

populations are declining (Dias et al. 2019). On land, the major threat to White-headed Petrels is thought to be from invasive mammalian species at the breeding sites (Taylor 2013), whereas threats at sea are poorly understood.

Unique amongst Procellariidae, the White-headed Petrel was described as a biennial breeder (Zotier 1990; Chastel 1995). At Kerguelen, Zotier (1990) found that 93% of the birds that successfully fledged a chick did not breed the following breeding season, while 80% of the burrows where breeding failed were occupied the following summer. Using a larger dataset Chastel (1995) found that 13% of successful breeders returned to nest two years in a row, whereas 86% of failed breeders returned the following year. At Adams Island, Taylor et al. (2020) found that one out of ten birds tracked using geolocators reared chicks two years in a row, then skipped breeding in the third season. However, return rates reported in these studies did not correct for detectability issues, which may have biased estimates of breeding frequency. For example, Taylor et al. (2020) and Chérel et al. (2022) reported the behaviour of White-headed Petrels tracked using miniature geolocators that returned from distant foraging areas to spend just a day or so ashore during the courtship period, then departed again to sea to take a season off. It is thus possible that visits to burrows by birds that subsequently skipped breeding were overlooked and that estimates of breeding frequency were biased. Therefore, the breeding strategy of White-headed Petrels remains insufficiently known, which given its unicity among Procellariidae, limits our understanding of the evolution of breeding strategies in seabirds.

Such a breeding strategy offers an interesting opportunity to test predictions from life-history theory that individuals trade-off investment in survival and reproduction to maximize fitness, such that greater investment in one of these traits may result in reduced investment in others (Williams 1966; Stearns 1992). Indeed, as some successful individuals breed the following year while others skip a breeding year, one may predict that if reproduction is costly, skipping individuals should have higher survival and/or reproductive performances than individuals breeding during two consecutive years. Such costs of reproduction have been investigated in several seabird species with ambiguous empirical support (Aubry et al. 2011; Cruz-Flores et al. 2021).

This paper provides the first detailed examination of White-headed Petrel demography and effects of environmental parameters on demographic parameters. Using long-term individual monitoring over 35 years, we first estimated

state-specific demographic parameters including apparent adult survival, breeding probability, success probability, as well as population growth rate, age at first return and age at first breeding. We then investigated how climate variation and natural predators on land could influence vital rates.

Methods

Species, study site and monitoring

The White-headed Petrel is the largest species among the *Pterodroma* genus weighing in average ~700 g (Weimerskirch et al. 1989). The species breeds on sub-Antarctic islands of the Southern Ocean between Crozet Islands to the west and Antipodes Islands to the east (Marchant and Higgins 1990). At Kerguelen, where several tens of thousands of pairs breed in scattered groups (Weimerskirch et al. 1989), the species nest in 1–2 m long burrows generally dug in dry soil from near sea-level to 100 m asl (Zotier 1990).

White-headed Petrels were studied at Mayes Island (49° 28' S, 69° 57' E), a 3-km uninhabited island in the Morbihan Gulf of the Kerguelen archipelago. No invasive mammalian predator occurs on the island except house mouse (*Mus musculus*). Breeding adults arrive at the colonies in late August–September to copulate before departing to sea for an 80 days pre-laying exodus (mid-October to mid-November). Females lay a single egg in late November–early December, hatching occurs at the end of January after 50–60 days of incubation, and chicks fledge in May–early June following a chick rearing period of 100–110 days (Barre 1976; Jouventin et al. 1985; Zotier 1990; Brooke 2004; Taylor et al. 2020). White-headed Petrels are considered migratory with birds moving away from the colony during the inter-breeding period (Taylor et al. 2020; Cherel et al. 2022). During the breeding season (late September to late April) White-headed Petrels from Mayes Island forage over an area surrounding Kerguelen Island and east and southeast of the Kerguelen–Heard plateau between the South Subtropical Front and the Polar Front, between 40° E–100° E and 42° S–55° S (Cherel et al. 2022). During the non-breeding season (April–August–September), White-headed Petrels distribute over a larger area extending from the southern Atlantic Ocean across the Indian Ocean to the West of Australia, between 20° W–100° E and 35° S–60° S (Cherel et al. 2022). White-headed Petrels feed primarily on mesopelagic fish in the sub-tropical and sub-Antarctic zones, mainly myctophids and melamphoids, and also significantly on cephalopods, while crustaceans constitute a minor prey group (Cherel et al. 2022). White-headed Petrels do not tend to follow ships (Griffiths 1982) and are not impacted by bycatch in fishing gear (Waugh et al. 2008). Return rates of individuals monitored at Mayes Island indicate that

White-headed Petrels exhibit a quasi-biennial breeding strategy with only ~13% of the successful breeders breeding the following year and ~58% of the breeders returning two or more years later (Zotier 1990; Chastel 1995).

From 1986 to 2020, between 12 and 100 individually marked burrows (average \pm SD: 60 ± 23), were inspected annually during breeding. All monitored burrows were fitted with an observation window (a hole was dug between the burrow entrance and the nest chamber and was covered with a removable trap between nest inspections) to allow the capture of individuals, to assess their breeding status and to capture fledglings. Two to three burrow inspections were made in late December and early January just after laying to check for eggs and to record marked adults, one inspection was made in mid-February to record hatched eggs, and one inspection was made in late April before fledging. Every year, all new adult birds captured in the study burrows during egg incubation, and all chicks just before fledging were marked with a stainless steel band. Birds were captured by hand in their burrows and replaced in their burrow immediately after handling. Handling time usually took less than 3–4 min. Bands for which numbers had started to wear off were replaced to avoid band loss. The breeding status of marked birds recaptured each year was determined. Individuals were considered as successful breeders (SB) if they laid an egg and raised a chick to fledging and as failed breeders (FB) if they laid an egg that did not hatch or if their chick died. Individuals were not sexed and there is no sexual size or plumage dimorphism.

From 2000 to 2020, as part of another study on smaller-sized petrels breeding on Mayes Island, mist nets were set at night within the same area than the monitored burrows of White-headed Petrels. Two to four nylon mist nets 2 m high and 12 m long (3 shelves, mesh size 20 mm) were settled during 26 nights in average (SD = 14; min: 6; max: 68) between mid-November and end of April each year and from one hour after sunset until three hours after sunset. All captured White-headed Petrels were removed from the mist net within less than 5 min, and the presence or absence of a brood patch was noted. Newly captured individuals were banded with a stainless steel leg band and measured. Individuals recaptured during successive mist-netting sessions were identified. Individuals were not sexed and we did not use lure calls during mist-netting sessions.

Estimation of survival, breeding and success probabilities from burrow monitoring

Capture–recapture data from individuals monitored in burrows were analysed using multistate capture–recapture models [MSMR, Brownie et al. (1993); Lebreton and Pradel (2002)]. For individuals marked as adults their capture history started at first capture. For those marked as chicks their

capture history started at the first return in the study population, from which they were considered as adults. Youngest individuals seen as breeders in monitored burrows were four years old. The 35-year time series (1986–2020) resulted in 714 capture histories, from which 697 corresponded to individuals marked as adults. Therefore, there were too few recruits to estimate juvenile survival and recruitment probabilities in a capture–recapture framework. Since White-headed Petrels exhibit a quasi-biennial breeding strategy, we used a MSMR developed by Hunter and Caswell (2009) for biennial breeders and adapted for quasi-biennial breeders in Barbraud and Weimerskirch (2012). This model distinguishes with four states: two observable states consisting of failed breeders and successful breeders, and two unobservable states consisting of non-breeders whose previous breeding attempt failed (post-failed breeders, PFB) and non-breeders whose previous breeding attempt was successful (post-successful breeders, PSB). The unobservable states account for temporary absence corresponding to birds that skip breeding after breeding unsuccessfully or successfully. This MSMR model requires that states are assessed with certainty, which was the case for our study. We thus considered five states (FB, SB, PFB, PSB, and dead which was not observed). Models were parameterised in terms of the probability of survival (s), the probability of breeding given survival (β), and the probability of success given breeding (γ), and the recapture probability (p). Transition probabilities between states were thus modelled with a three-step procedure where survival, breeding and success are considered as three successive steps in transition matrices. Several constraints were made to ensure that our initial model did not contain redundant parameters. The state dead being explicitly included in the model but being never encountered its recapture probability was fixed to 0, and transition probabilities from the state dead to the other states were fixed to 0. The probability of seeing individuals in unobservable states and transitions between unobservable states were constrained to zero. Since some individuals were observed breeding in the year consecutive to a successful breeding event, we did not constrain β to 0. To limit redundancy in survival parameters, we did not consider models where survival probabilities all varied separately. More specifically, survival of FB and PFB states were constrained to be equal, as well as survival of SB and PSB states. Survival, breeding and success probabilities were constrained to be time independent. Recapture probability was state and time dependent. We then tested several hypotheses by considering constrained models for each parameter type. We tested for time and state variation in recapture probability. For survival, breeding and success probabilities we tested for state variation, but not for time variation as a preliminary model indicated that several parameters were not identifiable when these parameters varied as a function of time. We tested for

heterogeneity in recapture probabilities by incorporating an individual random effect on recapture probabilities (Gimenez and Choquet 2010). We tested for the null hypothesis of homogeneity vs. the alternative hypothesis of heterogeneity in recapture probability using a likelihood ratio test between models where recapture probability was modelled or not as a random effect following Gimenez and Choquet (2010).

Estimation of survival and realised population growth rate from mist-netting

Capture–recapture data collected using mist-nets were analysed using Cormack–Jolly–Seber models (Lebreton et al. 1992) to estimate adult survival while taking into account imperfect detectability. The 21-year time series (2000–2020) resulted in 297 capture histories of birds marked as adults and 27 recaptures. Several constraints were made to ensure that our initial model did not contain redundant parameters. Since the number of recaptures was relatively small we constrained survival to be constant. Then, we compared models where recapture probabilities were constant or time dependent. We also tested for heterogeneity in recapture probabilities as described above.

Due to the very low return rates of individuals marked as chicks (see below), we were not able to estimate age-specific survival and recruitment rates needed to parameterize a matrix population model, which could have been used to model population dynamics. We thus estimated the realised population growth rate (λ) from capture–recapture data collected with mist-nets and using the Link and Barker (2005) reparameterization of Pradel models (Pradel 1996). Several constraints were made to ensure that our initial Link–Barker model did not contain redundant parameters: we constrained survival ϕ and recruitment f to be constant. We parameterised the structure on p from the selected CJS model. λ , the rate of change of the population between year i and year $i + 1$, was obtained as a derived parameter from apparent survival ϕ and recruitment f .

Goodness-of-fit tests and model selection

The goodness-of-fit tests (GOF) for MSMR models (Pradel et al. 2003) and CJS models (Lebreton et al. 1992) were performed using U-CARE 2.3.4 (Choquet et al. 2009a). For the MSMR model we ran the test on the JollyMoVe (Brownie et al. 1993) umbrella model for multistate data. We based inference on information-theoretic model selection using AICc (Burnham and Anderson 2002). Data analyses were completed using program E-SURGE 2.1.4 (Choquet et al. 2009b) and MARK 9.0 (White and Burnham 1999). To check the identifiability of parameters and existence of local minima in MSMR models we used the EM(20) + Quasi-Newton algorithm in E-SURGE, checked that the number of

mathematical parameters was equal to the model rank, used the multiple random option with 10 random initial values and finally checked the Hessian eigenvalues.

Environmental covariates

Selection of environmental covariates was based on previous knowledge on seabirds and White-headed Petrel ecology (Barbraud et al. 2012; Oro 2014; Cherel et al. 2022). To investigate effects on survival probability, breeding probability and success probability, we used a large-scale climatic index, the southern annular mode (SAM). SAM is the dominant mode of atmospheric variability in the Southern Hemisphere and is characterized by the displacements of atmospheric masses between polar and mid-latitudes (Marshall 2003, 2007). SAM is related to changes in temperature and in sea surface temperature (SST) of the Southern Ocean. A positive SAM is associated with a significant increase in wind anomalies over the Antarctic Zone and Polar Frontal Zone, which generate northward Ekman transport of SST and chlorophyll *a* (Chl *a*) anomalies in the region between the Polar Front and the Sub Antarctic Front (Lovenduski and Gruber 2005), corresponding to the latitudinal distribution area of White-headed Petrels (Cherel et al. 2022). We thus predicted that the positive phases of SAM, potentially leading to enhanced food availability in the areas used by White-headed Petrels, would have positive impacts on demographic parameters.

We also used local oceanographic covariates on foraging areas of White-headed Petrels on different temporal and spatial scales: the sea surface temperature anomaly (SSTa) during the pre-breeding, breeding and non-breeding season, as well as the surface Chl *a* concentration during the breeding season. SSTa reflects local oceanographic conditions that influence the whole marine food web. High SST generally reduces vertical mixing and provides poor growing conditions for zooplankton communities, which, through bottom-up mechanisms, induces reduced trophic resources for seabirds (Barbraud et al. 2012; Sydeman et al. 2015). Therefore, we predicted that high SSTa would negatively affect overwinter survival and breeding parameters of petrels. The SSTa data were downloaded from the National Oceanic and

Atmospheric Administration (data: NOAA NCEP EMC CMB GLOBAL Reyn_SmithOIv2 monthly ssta). Chlorophyll *a* is found in phytoplankton that lies at the bottom of the marine food web and provides resources for higher trophic levels. Because White-headed Petrel feed their chick mainly with fish feeding at low trophic levels (Cherel et al. 2022), we predicted that high concentrations of Chl *a* would be favourable to the breeding success of petrels. The Chl *a* data were downloaded from the NASA Ocean Data with a 9 km mapped concentration data of chlorophyll *a* for the years 1997–2001 and from the NASA Earth Observation (NEO AQUA/MODIS data) monthly for the years 2002 to 2020. For local climate covariates (SSTa, Chl *a*), we calculated the average values of the covariates in the areas in which petrels were located for a specific time period [pre-breeding 40° E–100° E/42° S–55° S; breeding 40° E–100° E/42° S–55° S; non-breeding 20° W–100° E/35° S–60° S; chick-rearing 60° E–90° E/60° S–70° S; Cherel et al. (2022)] during which the environment might affect the demographic parameters under investigation (Table 1).

As wind intensity may affect breeding success of dynamic soaring seabirds such as albatross and petrels through enhanced water mixing, nutrient supply and primary productivity, but also by reducing the commuting costs and hence accessibility of foraging areas (Ventura et al. 2021), we used intensity as a covariate. Monthly wind speed (m/s) was calculated from wind meridional and zonal components NCEP-NCAR reanalysis at 1000 mb pressure on a 2.5 spatial grid scale (http://iridl.ldeo.columbia.edu/maproom/Global/Atm_Circulation/Wind_SST.html). We calculated the averaged values of wind zonal, meridional and overall wind speed in the area in which petrels were located during the breeding period (40° E–100° E/42° S–55° S).

Finally, to test for predation effects we used the annual number of breeding pairs of brown skuas *Catharacta lönnerbergi* monitored annually on Mayes Island since 1995 (Quéroué et al. 2021). Although brown skuas feed mainly on smaller-sized burrowing petrels on Mayes Island (Pacoureaux et al. 2019), they also feed on adult and chick White-headed Petrels (Mougeot et al. 1998) which may constitute their main prey at other localities (Jones 1980; Moors 1980). We thus tested whether apparent adult survival and breeding

Table 1 Summary of the covariates tested in the demographic parameters of White-headed Petrels at Mayes Island, Kerguelen from 1986 to 2020

Parameter	Covariates tested	Time period
Adult apparent survival, <i>s</i>	SAM SSTa Pred	Non-breeding (May–August)
Breeding probability, <i>β</i>	SAM SSTa	Pre-breeding (October–November)
Success probability, <i>γ</i>	SAM SSTa Chl <i>a</i> Pred Wind	Breeding (December–April)
Success probability, <i>γ</i>	Wind	Chick-rearing (February–mid May)

SAM southern annular mode, SSTa sea surface temperature anomalies, Chl *a* chlorophyll *a* concentration, Pred number of breeding pairs of skuas

success of White-headed Petrels was related to the number of breeding pairs of Brown Skuas.

Modelling the effects of climate covariates on demographic parameters

For survival, breeding and success probabilities we used the structure of the selected MSMR model that best described the multi-state capture recapture data to which covariates were added. Relationships between covariates and demographic parameters were fitted using linear logit link functions $\text{logit}(\theta) = b_0 + b_1 \times X_n$ 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 . We also fitted quadratic logit link functions to test for non-linear relationships. We performed an analysis of deviance [ANODEV, Grosbois et al. (2008)] to assess the fit of a covariate model to that of the constant and the time-dependent models and to test the significance of each relationship. The proportion of deviance explained by covariates (R^2) was estimated following Skalski (1996). To avoid spurious correlations with covariates in the presence of temporal trends, linear trends in demographic parameters were investigated using ANODEV tests, and in environmental covariates in R with linear regression. If temporal trends were detected we followed the procedure in Grosbois et al. (2008), i.e., using residuals of the linear regression of the covariates to test whether the covariates accounted for a significant variation in the demographic parameter about the trend. Each environmental covariate was standardized to have a zero mean and unit variance.

Results

Age at first return and first breeding

A total of 17 individuals ringed as fledglings we re-observed in study burrows out of 469 marked (3.6%). The mean age at first observed return was 7.6 ± 2.7 years (min: 4, max: 12). Of these, seven were observed as first time breeding giving a mean age at first observed breeding of 8.7 ± 2.6 years (min: 4, max: 12).

Demographic parameters

Goodness-of-fit tests of the MSMR model did not indicate a lack of fit (Table 2). Model selection indicated that recapture probability of White-headed Petrels monitored in burrows was time but not state dependent (M3 vs. M1 and M2, Table 3), success probability was state dependent (M3 vs. M4 and M5), breeding probability was state dependant (M3 vs. M6 and M7), and survival probability was constant (M8 vs. M3). No temporal trend was detected for survival, breeding and success

Table 2 Results from the goodness-of-fit tests for the JollyMoVe model used to assess the fit of the multistate model

Test	χ^2	df	P value
WBWA	21.1	43	0.998
3G.SR	47.8	55	0.742
3G.Sm	100.6	160	1.000
M.ITEC	66.7	53	0.098
M.LTEC	44.6	32	0.068
Global	280.9	343	0.994

probabilities (Table 4), although significant positive slopes were found for breeding probability of successful breeders (slope = 0.328, 95% CI = 0.046–0.610) and post-failed breeders (slope = 0.716, 95% CI = 0.044–1.388), suggesting the breeding probability increased during the study period (ANODEV: $F_{3,64} = 2.468$, $P = 0.070$). Parameters estimates obtained from the best model are shown in Table 5. Mean recapture probability was 0.578 (95% CI 0.514–0.639, Fig. 1) and we found evidence for heterogeneity in recapture probability (LRT M9 vs. M8 $0.5\chi^2(0) + 0.5\chi^2(1) = 8.03$, $P = 0.002$; $\sigma_p = 0.783$ (0.204)).

Goodness-of-fit indicated that the CJS model fitted the data (Table 6). Model selection indicated that recapture probability of White-headed Petrels monitored using mist nets was not time dependant (M1 vs. M2, Table 7). However, there was heterogeneity in recapture probability (LRT M2 vs. M3 $0.5\chi^2(0) + 0.5\chi^2(1) = 3.9$, $P = 0.024$). Apparent adult survival was 0.941 (se = 0.058, 95% CI 0.673–0.992) and recapture probability was 0.010 (se = 0.007, 95% CI 0.003–0.037, $\sigma_p = 1.307$ (0.472)). The realized population growth rate estimated using the Link and Barker model was 1.073 (se = 0.011, 95% CI 1.053–1.094) and the recruitment rate was 0.172 (0.052, 95% CI 0.097–0.306).

Effect of environmental covariates

No significant effect of environmental covariates was found on demographic parameters (Table 8). Although the slope of the relationship between the breeding probability of successful breeders and the southern annular mode was positive (slope = 0.343, 95% CI = 0.036–0.650) suggesting a positive effect of SAM on breeding success, the ANODEV testing for an effect of SAM on breeding probability of successful breeders was not significant ($F_{1,32} = 1.860$, $P = 0.182$).

Discussion

Results from this long-term study highlighted the singular breeding strategy of the White-headed Petrel, with 64.4% of the individuals breeding successfully in a given year skipping breeding the following year. Accordingly, the breeding probability of skipping individuals was close to one. There was evidence that the study population is increasing,

Table 3 Modelling survival, breeding and success probabilities in White-headed Petrels at Mayes Island, Kerguelen from 1986 to 2020

Model	Survival	Breeding	Success	Detection	<i>k</i>	Dev	AICc
M1	F/S	R	R	r.t	79	4598.7	4769.1
M2	F/S	r	R	r	13	4749.3	4775.6
M3	F/S	r	R	t	45	4669.8	4763.7
M4	F/S	r	cst	t	42	4676.9	4764.4
M5	F/S	r	F/S	t	43	4673.2	4762.7
M6	F/S	cst	R	t	42	4813.5	4900.9
M7	F/S	F/S	R	t	43	4774.2	4863.89
M8	cst	r	R	t	44	4670.8	4762.6
M9	cst	r	R	t + rand	45	4662.8	4756.7

M2 and M3 test for time and state effects on recapture probability (p), M4 and M5 test for state effects on success probability (γ), M6 and M7 test for state effects on breeding probability (β) and M8 test for state effect on survival probability (s). Results include the number of mathematical parameters (k), the deviance (Dev), Akaike Information Criterion adjusted for sample size (AICc). cst indicates constant, t indicates time, r indicates that the trait varied according to all previous states, F/S indicates that failed breeders and post-failed breeders were pooled together as well as successful and post-successful breeders. The selected model is indicated in bold. All models were full rank

Table 4 Testing for linear and quadratic trends on demographic parameters for White-headed Petrels at Mayes Island, Kerguelen between 1986 and 2020

Parameter	Hypothesis tested	<i>J</i>	Dev	<i>F</i>	<i>P</i>	<i>R</i> ²
<i>S</i>	Linear	2	4670.6	0.322	0.574	0.01
	Quadratic	3	4670.2	0.334	0.719	0.02
	Time reference model	77	4643.6			
	Constant reference model	44	4670.8			
β	Linear	8	4656.7	1.287	0.262	0.07
	Quadratic	12	4654.0	0.957	0.489	0.08
	Time reference model	174	4455.7			
	Constant reference model	44	4670.8			
γ	Linear	8	4665.7	0.441	0.875	0.02
	Quadratic	12	4656.8	0.779	0.660	0.06
	Time reference model	176	4454.2			
	Constant reference model	44	4670.8			

Results include the number of parameters used to model the effect of trends (J), the deviance (Dev), the ANODEV test (F and P), and the proportion of deviance explained (R^2)

coinciding with a positive trend in breeding probability for successful breeders and post-failed breeders. None of the environmental factors investigated affected the demographic parameters, except a slight evidence for a positive effect of the southern annular mode on breeding probability of successful breeders which only explained 5.5% of the deviance.

Parameter estimates obtained from the multi-state model using 35 years dataset revealed the quasi-biennial breeding strategy in the White-headed Petrel. Most individuals that bred successfully during a given year skipped breeding the following year. However, contrary to biennial albatrosses, White-headed Petrels that bred successfully had a larger probability of breeding the following year [0.356 in the White-headed Petrel; 0.045–0.069 in the Wandering Albatross *Diomedea exulans* at Crozet Islands, Barbraud and Weimerskirch (2012); 0.01 in the Grey-headed Albatross

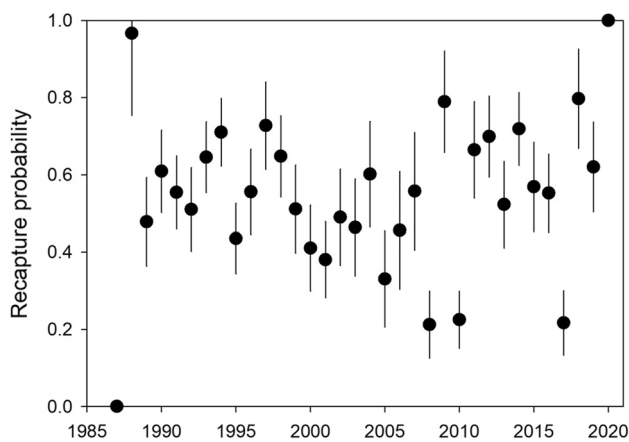
Thalassarche chrysostoma at South Georgia, Prince et al. (1994)]. The breeding frequency of White-headed Petrels is thus situated at an intermediate position [as the grey headed albatross at Marion Island, Converse et al. (2009)] on a continuum between seabird populations in which successful breeders have a very high probability of breeding the following year [e.g. Grey Petrel *Procellaria cinerea*, White-chinned Petrel *P. aequinoctialis*; Chastel (1995)] and populations in which successful breeders have a very low probability of breeding the following year [e.g., Wandering Albatross, Grey-headed Albatross; Warham (1990); Prince et al. (1994); Barbraud and Weimerskirch (2012)]. In seabirds, biennial breeding is mainly attributed to the duration of the entire breeding activity and the constraint of feather moult (Warham 1990; Chastel 1995; Hamer et al. 2001), and to the high energy requirements of each preventing

Table 5 Estimates of survival, breeding and success probabilities for White-headed Petrels at Mayes Island, Kerguelen between 1986 and 2020 obtained from model M9

Parameter	Estimate	95% confidence interval
s	0.873 (0.016)	0.838–0.902
β_{FB}	0.790 (0.043)	0.695–0.862
β_{SB}	0.356 (0.036)	0.288–0.430
β_{PFB}	0.061 (0.062)	0.008–0.351
β_{PSB}	0.988 (0.054)	0.008–1.000
γ_{FB}	0.533 (0.037)	0.459–0.604
γ_{SB}	0.574 (0.048)	0.479–0.664
γ_{PFB}	0.167 (0.251)	0.006–0.873
γ_{PSB}	0.655 (0.036)	0.581–0.722

Numbers in parentheses are se

s survival probability, β breeding probability, γ success probability, FB failed breeder, SB successful breeder, PFB post-failed breeder, PSB post-successful breeder

**Fig. 1** Recapture probability of White-headed Petrel at Mayes Island, Kerguelen from 1986 to 2020. Error bars are ± 1 se. Estimates are from model M9 (Table 3)**Table 6** Results from the goodness-of-fit tests for the CJS model

Test	χ^2	df	P value
3.SR	5.5	8	0.703
3.SM	1	0	1
2.CT	2.6	8	0.958
2.CI	1.4	9	0.998
Global	9.5	29	0.999
z for transience	1.412	1	0.079
z for trap-dependence	-0.456	1	0.649

birds to accomplish both activities at the same time. Chastel (1995) suggested most White-headed Petrels breed biennially because they fledge their young at the end of the austral summer (May) and must moult during the winter when food

Table 7 Modelling survival probabilities in White-headed Petrels at Mayes Island, Kerguelen from 1986 to 2020

Model	s	p	k	Dev	AICc
M1	cst	t	21	93.3	300.1
M2	cst	cst	2	114.3	279.8
M3	cst	rand	3	110.4	278.0

M2 tests for time effect on recapture probability (p), M3 test for random effect on p . Results include the number of mathematical parameters (k), the deviance (Dev), Akaike Information Criterion adjusted for sample size (AICc). cst indicates constant, t indicates time, rand indicates random effect. The selected model is indicated in bold

Table 8 Testing for the effects of environmental covariates on demographic parameter for White-headed Petrels at Mayes Island, Kerguelen between 1986 and 2020

Parameter	Models	Dev	J	F -statistic	P value
s	SAM	4670.33	2	0.590	0.448
	SAM ²	4670.33	3	0.288	0.752
	SSTa	4670.79	2	0.041	0.841
	SSTa ²	4669.67	3	0.685	0.512
	Pred	4669.77	2	0.670	0.422
β	SAM	4665.14	8	0.497	0.835
	SAM ²	4657.91	12	0.720	0.718
	SSTa	4665.02	8	0.507	0.828
	SSTa ²	4662.63	12	0.447	0.931
	γ	SAM	4668.99	8	0.156
γ	SAM ²	4668.16	12	0.140	0.999
	SSTa	4666.07	8	0.410	0.895
	SSTa ²	4664.69	12	0.328	0.978
	Chlo a	4653.73	8	0.353	0.924
	Chlo a^2	4650.69	12	0.396	0.950
	Wind	4663.91	8	0.603	0.752
	Pred	4661.59	8	0.695	0.676

Results include the number of parameters used to model the effect of covariates (J), the deviance (Dev) and the ANODEV test (F -statistic and P -value)

availability is low, which slows the moult process. In line with this hypothesis, recent activity data from geolocators showed that the duration of the breeding season is relatively long in the White-headed Petrel (nearly 8 months from arrival on breeding grounds to departure with a particularly long pre-laying period), and that birds moult wing feathers right after breeding (July–August) in both the sub-Antarctic zone and the subtropical zone (Taylor et al. 2020; Cheral et al. 2022), thus in areas with relatively low primary productivity during the austral winter (Torres et al. 2015; Jones et al. 2021). Note, however, that our estimate of breeding probability for successful breeders (0.356) differs substantially from the estimate (0.132) obtained by Chastel (1995). As these estimates were obtained from the same population

and since no temporal trend was detected in state-specific breeding probabilities, this difference likely originates from the analytical procedure as we explicitly took into account detection probability and used a multi-state capture-mark-recapture model developed for biennially breeding species (Hunter and Caswell 2009). This suggests that a significant proportion of individuals that bred successfully are able to moult and accumulate sufficient body reserves during the winter to initiate breeding the following summer. The nature of the intrinsic factors differentiating these individuals from others remains an open area of research.

Contrary to successful individuals that bred the subsequent year, White-headed Petrels that skipped breeding had a higher probability of breeding and a higher probability of success during their following breeding attempt. According to our estimates, the probability of performing two consecutive successful breeding attempts was 0.204 in White-headed Petrels, whereas the probability for a skipped breeder to become a successful breeder the following year was 0.647, mainly due to a high breeding probability (0.988). Such differences were also found in the Wandering Albatross in which successful breeders that bred the following year and attempted to breed during two consecutive years experienced a lower breeding success than individuals that skipped breeding (Barbraud and Weimerskirch 2012). This suggests that in both species individuals that do not skip breeding after a successful breeding attempt may experience higher costs of reproduction than those that skipped breeding. Those results indicate that rearing a chick for White-headed Petrels is very costly and most individuals cannot breed successfully annually, contrary to other similar sized Procellariiformes. Accordingly, in the White-headed Petrel, breeding probabilities for individuals that failed during their previous breeding attempt, and thus experienced lower breeding effort, was intermediate between those of successful breeders and individuals that skipped breeding following successful breeding. From an evolutionary point of view, the maintenance of this quasi-biennial breeding strategy in the White-headed Petrel, with a relatively high proportion of successful individuals breeding during consecutive years, may appear paradoxical. Indeed, on average a White-headed Petrel breeding successfully every year would produce two fledglings during a 10 year period, whereas an individual that would systematically skip breeding after a successful breeding attempt would produce 3.2 fledglings during the same period. This suggests that intrinsic factors such as sex, individual quality and age may play a role in individual breeding frequency as observed in other species (Hamer et al. 2001; Barbraud and Weimerskirch 2012), as well as moulting and environmental conditions in the wintering areas used by individuals. Indeed, movement data of White-headed Petrels tracked year round revealed important inter-individual variations in migration routes and wintering

areas (Taylor et al. 2020; Chérel et al. 2022). Therefore, one may hypothesise that some individuals moult and spend the winter in more productive areas than others, allowing them to accomplish their moult and replenish their body condition after a successful breeding attempt, and therefore to breed the following year.

Surprisingly, apparent adult survival probability estimated from birds captured in monitored burrows differed from the one estimated using mist nests. Although the difference may appear substantial ($\approx 7\%$), it could not be explained by differences in localities as both monitoring methods were used in the same area of Mayes Island where White-headed Petrels breed. Survival estimates obtained from mist net data may be biased due to low recapture probability (Abadi et al. 2013). However, survival tends to be underestimated when recapture probability is low (which would further enhance the difference between survival obtained from mist net data and burrow monitoring), and explicitly modelling capture heterogeneity, as we did, considerably reduces bias in survival (Abadi et al. 2013). Thus, we are confident about the accuracy of survival estimates obtained from modelling mist net data, although their precision was likely poor due to low recapture probability (Abadi et al. 2013). It is also unlikely that individuals captured in mist nets were immature birds with a different survival from breeding adults as the majority (64%) of mist netted birds had a brood patch. Rather, we suspect that adult survival of birds monitored in burrows was underestimated for at least two reasons. First, a survival probability of 0.873 appears incompatible with a population growth rate higher than 1 for a species with a quasi-biennially breeding strategy. Indeed, adult survival for stable populations of annually-breeding or biennial Procellariiforme species is expected to vary between 0.93 and 0.96 depending on population-specific mean age at first breeding (Dillingham and Fletcher 2011). Second, White-headed Petrel burrows on Mayes Island are often several meters long and may have two or more tunnels branching after the main entrance connecting to two or more nest chambers. Therefore, we strongly suspect that some birds shifted burrows and/or nest chambers and became inaccessible for capture, generating apparent permanent emigration and thus underestimating adult survival. Caution should thus be taken with the survival estimate obtained from individual captured in burrows. The apparent adult survival rate obtained from individuals captured in mist-nests appears less biased and much closer to what can be expected in a quasi-biennially breeding Procellariiforme.

Although White-headed Petrels from Kerguelen started breeding at 4 years old, the observed mean age at first breeding was relatively high for a *Pterodroma* species (Warham 1990). Since age at first return and at first breeding were estimated without taking into account detectability of individuals, as there was too few individuals to estimate these

parameters in a capture-mark-recapture framework, it is possible that both parameters were slightly overestimated.

Although inter-annual variability in adult apparent survival was low, breeding probability and success probability were more variable (Fig. 2), as expected for a long-lived species (Gaillard and Yoccoz 2003). This suggests that environmental factors drive variability in breeding probability and success probability. However, none of the environmental factors investigated seemed to affect demographic parameters of White-headed Petrels breeding at Mayes Island, except a slight effect of the southern annular mode on breeding probability of successful breeders, which only explained a small part of the deviance. Although the ANODEV did not indicate a significant effect of SAM, the positive slope between SAM and this demographic parameter provided slight evidence for an effect. In the foraging area of White-headed Petrels during the pre-breeding period, a positive phase of SAM leads to a decrease in sea surface temperature and an increase in the abundance of phytoplankton (Lovenduski and Gruber 2005). SAM in the positive phase may thus

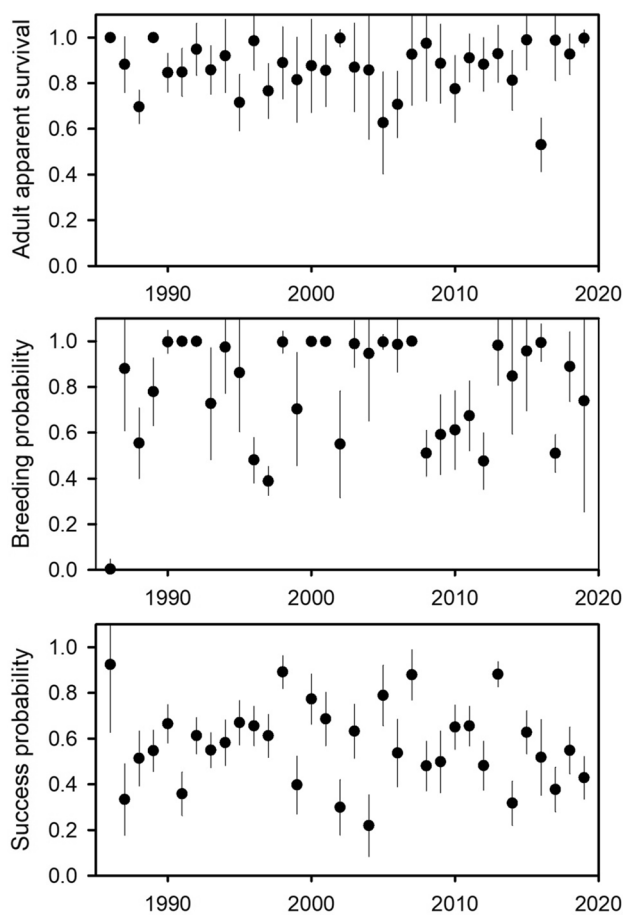


Fig. 2 Survival, breeding and success probability of White-headed Petrel at Mayes Island, Kerguelen from 1986 to 2020. Error bars are ± 1 se. Estimates are from time reference models (Table 4)

allow an increase in the abundance of resources for White-headed Petrels, thus increasing their probability of breeding. Although little information is available to understand the underlying mechanisms linking SAM to the demography of southern seabird populations, the effects of this climate index have been reported for several species [Snow Petrel *Pagodroma nivea* Sauser et al. (2018); Cape Petrel *Daption capense* Sauser et al. (2022); Emperor Penguin *Aptenodytes forsteri* Abadi et al. (2017); wandering albatross Fay et al. (2017); Southern Giant Petrel *Macronectes giganteus* Gianuca et al. (2019)], revealing its importance as a driver of southern ocean top predator populations.

To conclude, prior to this study there was very few information available about the demography of the White-headed Petrel and how environmental factors affected demographic parameters. Long-term monitoring at Mayes Island indicated a high adult survival coherent with a quasi-biennial strategy, late age at first breeding, and rearing a chick is very costly. As a consequence populations of White-headed Petrel are likely to be very sensitive to small variations in adult survival, and anthropogenic factors causing additive mortality will constitute serious threats. This is, for example, the case for White-headed Petrels breeding on the main island of Kerguelen which suffer predation from Feral Cats *Felis catus*, constituting 18% of the prey species consumed (Pontier et al. 2002). At Mayes Island, the population appears to be increasing despite the presence of house mouse, suggesting no or very little impact of this introduced species on White-headed Petrels. Despite a relatively large global population size (Brooke 2004), major populations of White-headed Petrels are potentially threatened by introduced predators [Feral Cats, House mice *Mus musculus*, Feral Pig *Sus scrofa*; Russell et al. (2020)]. The particularly slow life history strategy of White-headed Petrels demonstrated here calls for further studies quantifying the impact of these introduced predators on the population dynamics of White-headed Petrels.

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