RESEARCH ARTICLE

Modeling the demography and population dynamics of a subtropical seabird, and the influence of environmental factors

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ABSTRACT

The use of long-term ecological datasets to explore the importance of the effects of environmental variability on higher predator populations has been focused mainly on high-latitude areas. We modeled the population dynamics of the Westland Petrel (*Procellaria westlandica*), which spends its time mostly in subtropical waters during both breeding and the interbreeding migration across the Pacific Ocean. We found that the population has slowly increased since the early 1970s, a result of high adult survival, high fecundity (0.6 of all eggs laid survived to fledge) and moderate mean age at first return to the colony (7.7 yr; a recruitment age typical for this genus), strong recruitment rate of juveniles, and negligible emigration. The modeled population trends were supported by similar rates of increase in nest occupancy since 2001 and nest density since 2007. Annual adult survival for breeders was the same for both sexes (0.954, 95% CI: 0.918–0.975) and constant across years. However, nonbreeders had lower survival rates than breeders, and, among nonbreeders, males tended to survive better (0.926, 95% CI: 0.917–0.934) than females (0.917, 95% CI: 0.900–0.931). Breeders transitioned to the nonbreeding state at a rate of 0.232 and nonbreeders to the breeding state at a rate of 0.295. Sea-surface temperature anomalies had a negative effect on adult survival during the breeding period and a positive effect on survival outside the breeding season. Local marine productivity as measured by fishery catches was strongly correlated with adult survival: Years with a greater fish catch were also years of higher adult survival. Despite many threats operating throughout the breeding and foraging range of Westland Petrels, it appears that marine environmental change is a strongly influential factor for the species, with uncertainty in population growth due to predicted increases in sea-surface temperature in the future.

Keywords: population model, survival, environmental effects, Hoki fishery, sea-surface temperature anomalies, recruitment, Westland Petrel, *Procellaria westlandica*

Modélisation de la démographie et de la dynamique des populations d'un oiseau de mer subtropical et de l'influence des facteurs environnementaux

RÉSUMÉ

L'utilisation d'ensembles de données écologiques à long terme pour explorer l'importance de la variabilité environnementale sur les populations de grands prédateurs s'est principalement concentrée dans les zones en haute latitude. Nous avons modélisé la dynamique des populations de *Procellaria westlandica*, une espèce qui passe presque tout son temps dans les eaux subtropicales durant la reproduction et la migration inter-reproduction à travers l'océan Pacifique. Nous avons découvert que la population avait lentement augmenté depuis le début des années 1970 en conséquence de la survie élevée des adultes, de la grande fécondité (0,6 de tous les œufs pondus ont survécu jusqu'à l'envol) et de l'âge moyen au premier retour à la colonie (7,7 années) – un âge de recrutement typique pour ce genre, un fort taux de recrutement des juvéniles et une émigration négligeable. Les tendances démographiques modélisées étaient supportées par des taux d'augmentation similaires de l'occupation des nids depuis 2001 et de densité de nids depuis 2007. La survie annuelle des adultes nicheurs était la même chez les deux sexes (0,954 [0,918–0,975, IC 95 %]) et

constante entre les années. Toutefois, les adultes non nicheurs avaient des taux de survie inférieurs aux adultes nicheurs, et parmi les non nicheurs, les mâles tendaient à survivre mieux (0,926 [0,917–0,934]) que les femelles (0,917 [0,900–0,931]). Les adultes nicheurs font la transition vers l'état de non nicheurs au taux de 0,232 et les non nicheurs vers l'état de nicheurs au taux de 0,295. Les anomalies de la température à la surface de la mer influaient négativement sur la survie des adultes au cours de la période de reproduction et positivement sur la survie en dehors de la saison de reproduction. La productivité marine locale mesurée par les prises des pêcheurs était fortement corrélée avec la survie des adultes; les années avec plus de captures de poissons étaient également des années de plus grande survie des adultes. Malgré de nombreuses menaces présentes à travers l'aire de reproduction et d'alimentation de *P. westlandica*, il semble que les modifications de l'environnement marin soient un facteur influant fortement sur l'espèce, avec une incertitude dans la croissance de la population en raison des augmentations prévues de la température de la surface de la mer dans le futur.

Mots-clés: modèle de population, survie, effets environnementaux, pêche au hoki, anomalies de la température à la surface de la mer, recrutement, Puffin du Westland, *Procellaria westlandica*

INTRODUCTION

Seabirds are good indicators of environmental change, as their position at the slow end of the slow–fast continuum of life-history variation (Stearns 1992, Sæther and Bakke 2000) results in adult survival and breeding frequency being sensitive to pressures in the environment. Climate variability influences seabirds across several families (e.g., Alcidae, Votier et al. 2008; Sulidae, Cubaynes et al. 2011; Laridae, Frederiksen et al. 2004; Procellariidae, Veit et al. 1997, Scott et al. 2008; and Diomedeidae, Rolland et al. 2008, 2009, Weimerskirch et al. 2012). Effects vary from small-scale deferment of recruitment to breeding populations (Cubaynes et al. 2011) and phenological changes (Chambers et al. 2013) to long-term effects such as decreased adult survival in response to increased sea-surface temperatures and fisheries bycatch (Rolland et al. 2009, Barbraud et al. 2012).

Many seabirds live for two or more decades, so long-term datasets are required to accurately estimate population parameters, including recruitment, breeding frequency, and survival across contrasting environmental conditions, but these datasets can also be used to detect system-level changes in marine ecosystems (Reid and Croxall 2001, Schreiber 2001, Péron et al. 2010). Until now, such studies have focused mainly on high-latitude ecosystems, including the sub-Antarctic or Antarctic, where distinctive summer breeding seasons result from rich but short-lived food resources (Grosbois et al. 2008, Barbraud et al. 2012). However, research at the community scale in subtropical systems suggests that changes here may be as marked, or even more so, as those in sub-Antarctic areas (Péron et al. 2010).

Recent meta-analysis of seabird demographic responses to climate change in the Southern Ocean showed that most studies reported a negative effect of sea-surface temperature anomalies (SSTA) on demographic parameters (Barbraud et al. 2012), a finding mirrored in other regions of the globe (Veit et al. 1997, Kitaysky and Golubova 2000, Durant et al. 2003, Frederiksen et al. 2004, Harris et al. 2005). When fisheries are also considered, complex interrelationships result among survival, population growth, breeding decision, and environmental influences (Barbraud et al. 2012). For example, Rolland et al. (2008) showed that, for Black-browed Albatrosses (*Thalassarche melanophris*), adult survival increased with SSTA during the incubation period, but there was a negative effect of tuna longline fisheries (through bycatch) in the wintering grounds in the same years. By modeling a broader set of demographic parameters for the same population, including juvenile and prebreeder survival and breeding success of first-time and experienced breeders, Rolland et al. (2009) showed that the population trajectory was most sensitive to environmental influences on adult survival, particularly that of experienced breeders, and least sensitive to breeding and juvenile survival parameters. Similar results were demonstrated for Sooty Shearwaters (*Puffinus griseus*), with adult survival varying the least but also most influencing population growth compared with other parameters (Hunter et al. 2000), as is common across other vertebrate groups (Stibly et al. 2003).

To test how a subtropical population of long-lived seabird responded to environmental change, we studied the population biology of Westland Petrels (*Procellaria westlandica*) over the period of 1970–2012 using mark–recapture techniques, with data on colony size and nesting density collected during 2001–2014. The species spends its entire lifecycle in the South Subtropical Convergence province (Longhurst 1998), and, like all procellariiform seabirds, has slow maturation, a maximum of one offspring per year, and high adult survival (Warham 1990, Schreiber and Burger 2001, Waugh et al. 2006). We aimed to estimate the key demographic parameters for the population and to model population growth, emigration, and recruitment for the first time. As nonbreeding individuals may represent a considerable proportion of procellariiform populations (Bradley et al. 2000, Pardo et al. 2013) and contribute to population growth only once they transition to breeding status, we estimated survival rates in relation to breeding

TABLE 1. Study periods relative to different parameters estimated or to sexing methods used for Westland Petrels at Punakaiki, West Coast, New Zealand.

Parameter estimated	Years
Adult survival	1970–2012
Emigration	1970–1997
Band loss	1970–1997
Sexing by cloacal examination	1970–2002
Environmental effects on adult survival	1970–2012
Banding for recruitment and juvenile survival	1977–1988
Age at first return (proxy for age at first breeding)	1977–2012
Breeding success	1993–2003, 2012
Breeding frequency	1995–2012
Burrow occupancy	2001–2014
Burrow density	2007–2014
Sexing by genetics, laying dates, and morphometrics	2004–2012
Population size at the breeding colony	2011

state and transition rates between breeding and nonbreeding states. We tested for the effects of local marine oceanographic conditions (SSTA) and local ocean productivity (via fish catch indices) on adult survival for both breeding and nonbreeding birds, to identify which variables might be most useful for predicting how the petrel's population will adjust to changing climate in the future.

METHODS

Study Species and Field Procedures

We studied a burrow-nesting seabird endemic to New Zealand, the Westland Petrel (~1200 g; Landers et al. 2011a), which breeds in lowland rainforest on the mainland of New Zealand (~50–200 m elevation). Birds attend breeding colonies from March to November (Marchant and Higgins 1990, S. Waugh and K.-J. Wilson personal observation). The world population of ~4,000 pairs nests mainly within a 1,600-ha protected area near the village of Punakaiki (Agreement on the Conservation of Albatrosses and Petrels 2012, Wood and Otley 2013). The species has "Vulnerable" status under the threat ranking system of the International Union for the Conservation of Nature (IUCN 2013).

Adults feed mainly around the New Zealand continental shelf south of Cook Strait in the breeding season, whether breeding or not. They migrate annually to western South American waters and some birds visit the Patagonian Shelf (Landers et al. 2011b). Juveniles migrate to western coastal South American waters after fledging and return to New Zealand waters before first breeding (recruitment) several

years later, as shown by band recoveries (Marchant and Higgins 1990).

Our study was conducted principally at the Scotsman Creek colony (hereafter called the study colony) near Punakaiki, West Coast, New Zealand (42.712°S, 170.969°E), which is the largest known colony of the species (Best and Owen 1976, Wood and Otley 2013). Years of study with data collection for different parameters are detailed in Table 1. Monitoring of the petrels began in 1969, with colony reconnaissance and the establishment of study burrows from 1970. From 1970 onward, birds were identified by stainless steel numbered leg bands. Inspection hatches were fitted to study burrows. Birds were captured and recaptured in the nest by hand or on the ground surface when frequenting the colony at night; thus, breeding and nonbreeding birds, as well as birds of unknown status, were included in the study. Surface-captured birds were classified as unknown status. Confirmed nonbreeders were birds found in burrows, but with no egg or chick. During 1981–1997, double-banding of birds established in study burrows was undertaken to assess band wear.

Birds were sexed at each recapture by cloacal examination from 1970 to 2002 following O'Dwyer et al. (2006). Genetic analyses from blood sampling were used to sex some birds starting in 2005 (T. Landers, S. Waugh, and L. Shepherd personal observation) and, where these data were not available, observations of attendance during laying and morphometric measures of both members of a pair were used to sex birds (Landers et al. 2011b, S. Waugh personal observation).

We identified a total of 1,941 adult Westland Petrels using between 20 and 108 study burrows each year, or birds caught nearby on the ground. Most birds were captured during the prebreeding period (1977–1991) and the incubation period (1992–2012), with between 1 and 26 days of effort per year, or an average of 12 days per year. However, in 1971, 1974, 2004, and 2006 no fieldwork was undertaken; and in 1992 and 2005, fewer than 10 birds were recaptured on fewer than 5 days or nights. In other years, 46–667 birds per year were recaptured in the study area. During 1981–1997, colony areas were checked each night that observers were present, to ensure a high capture rate of adults on the surface. During 2002–2013, nest monitoring was conducted mainly by checking burrow contents during the day, with a few night visits each year to catch birds on the surface.

To establish a known-aged sample of individuals for estimating recruitment and juvenile survival, 1,054 fledglings were banded at the study colony. Of these, 323 were from study nests or nests central to the study colony and 731 were from other areas, including nearby small colonies, during 1977–1988.

Estimating Study Population Size, Burrow Occupancy, and Density

In 2011, just after the end of laying (first week of June), we assessed the size of the breeding population at the study colony, with repeated counts by 2–3 independent observers in each of 5 zones within the colony. From 2011 to 2014, burrow occupancy was estimated in midincubation using a set of 15–31 randomly selected burrows, which were examined by burrowscope (Sextant Technology 2013) in each of 2–5 zones. Burrows were classified as either 'occupied' (where a single bird, a pair of birds, or bird and egg were present) or 'empty,' following previous methodology for the same area (Waugh et al. [2003] for 2001 estimates, and Baker et al. [2011] for 2008 estimates). The density of burrows within the study colony was estimated in 2014, following the methodology of Baker et al. (2011). Transect (15–56 m long) surveys were conducted in all zones of the study colony. The transects in 2014 were shorter but more numerous than those of Baker et al. (2011), and covered comparable areas of the colony. Transect length was recorded on a handheld Garmin 605X Global Positioning System (GPS) unit (Garmin, Olathe, Kansas, USA) in the field and estimated by plotting the start and end points of each transect in Google Earth, version 5.1.3533.1731 (Google Earth, Mountain View, California, USA). Field GPS data were recorded with an accuracy of ± 10 m in most cases.

Estimating Breeding Success, Recruitment, and Juvenile Survival

Annual breeding success was estimated from the sample of 20–60 marked burrows as the proportion of eggs that fledged a chick during 1995–2003 and in 2012.

Chicks ($n = 323$) were banded in study burrows and in nearby burrows within the study colony between 1977 and 1988. Of these, 139 birds were resighted up to 2012. Given that only a small proportion of the banded chicks were observed as first breeders, we estimated age at first return (using raw data) as a proxy for age at first breeding. Juvenile survival was estimated from the capture histories of the 323 individuals marked as fledglings using a multistate capture–mark–recapture (CMR) model with two states (Lebreton et al. 2009): one immature state (1) and one adult state (2). Breeding status was known for only a small proportion of the recaptured individuals (i.e. those captured within burrows where egg or chick presence was noted). For birds recaptured at the surface (the majority of recaptures), breeding status could not be ascertained. Therefore, we approximated adult state (defined as first recapture by default), which was structured by time. The transition from adult to immature state was fixed at 0. To account for the period when young petrels are at sea before returning to breeding areas, and hence are unobservable, juvenile survival probability was fixed at 1 from year 2 to year 3 of

life after fledging, and capture probability was fixed at 0. Capture probability was also fixed at 0 for years when no captures were conducted. Given the large number of parameters of this model, we imposed further constraints to make sure that our data would support the model. Survival and transition probabilities were modeled as constant. Our initial model was thus $\phi_{a1,a2-3=1,a4+}^{st} \psi^{st} p_t^{st}$, where the survival probability (ϕ) and the probability of transitioning from one state to the other (ψ) varied with the state ($st = 1$ or 2), whereas capture probability (p) was time- and state-dependent. From this initial model, we tested for time variation in capture probability and built models where ψ was age-dependent.

Estimating Adult Survival and Breeding Probabilities

A previous study of the congeneric White-chinned Petrel (*Procellaria aequinoctialis*) showed that recapture of nonbreeders was rare (Barbraud et al. 2008). In contrast, Westland Petrel nonbreeders were commonly recaptured, along with birds whose breeding status was unknown. We used this information to estimate sex- and state-specific adult survival using multi-event CMR models (Pradel et al. 2005; Appendix). Our most general model included sex (s), breeding status (st), time (t), and interactions between sex, state, and time for apparent survival probability (ϕ), transition probability (ψ) from breeder to nonbreeder (given survival) and vice versa, encounter probability (ε), probability of sexing an individual (δ) given that it was encountered, probability of correctly sexing an individual (γ) given that it was encountered and sexed (correctness probability), and probability of assigning a breeding state (η) to an individual given it was encountered. We notated this model as $\phi_{s.t}^{st} \psi_{s.t}^{st} \varepsilon_{s.t}^{st} \delta_{s.t}^{st} \gamma_{s.t}^{st} \eta_{s.t}^{st}$.

Several constraints were made to ensure that the model did not contain redundant parameters. Specific constraints relative to the state "dead" being explicitly included in the model were also made (see Pradel et al. 2005). This general model had many parameters and a priori we did not believe that our data would support all interaction terms due to our sample size. To minimize the number of parameters in the model, survival, transition, correctness, and state assignment probabilities were not allowed to vary between years. Our initial model was thus $\phi_s^{st} \psi_s^{st} \varepsilon_{s.t}^{st} \delta_{s.t}^{st} \gamma_s^{st} \eta_s^{st}$. Further constraints were made on this model to ensure parameter identifiability (Appendix). Once we identified the best model structure for these parameters, we constructed models in which survival and transition probabilities were modeled as constant or as a function of sex or state only.

Adult survival and breeding probabilities were estimated from a sample size of 1,941 individual capture histories. Over a 20-yr period, no band wear or loss was found, so we assumed that band loss was negligible.

The modeling procedure described above was performed on the entire dataset from 1970 to 2012, including all individuals captured in study burrows or elsewhere in the study colony; however, because many individuals were captured on the ground outside burrows and these may have been short-term visitors to the colony or breeding in burrows which were not monitored, we suspected that our transition probabilities between breeding states might have been underestimated. Therefore, in a second step we performed the same modeling procedure on marked individuals captured in monitored burrows only, so as to obtain more reliable transition probability estimates between states. Since the monitoring of study burrows was better documented from 1995 onward, we chose the period of 1995–2012 for this second analysis of transition probabilities, which used 283 individual capture histories.

Testing for Environmental Effects on Adult Survival

Adult annual survival relationships could be examined in detail in relation to environmental variables due to the complex nature of the dataset (Appendix). However, the datasets used to estimate juvenile survival and recruitment were too small to allow for time-dependency in parameters, and the dataset used to estimate breeding success was too short and interrupted, so the testing of these parameters against environmental variables was considered unfeasible.

Because environmental processes operate over decadal timescales, and survival is a key driver of population growth in many species, particularly long-lived ones such as Procellariiformes, we opted to examine adult survival only in relation to climate and ocean productivity indices. We started from the model structure selected in the previous step and constructed a model in which we allowed survival to vary between years, using the 42-yr survival dataset. This approach enabled us to examine interannual fluctuations in adult survival while taking into consideration the limitations of the dataset, which would not allow individual year estimates for all sex and stage groups.

Based on our knowledge of the ecology of the Westland Petrel and of the effect of climate on Procellariiformes, we tested the effect of the following covariates. First, we considered the hoki (*Macruronus novaezelandiae*) fishery catch in areas exploited by Westland Petrels during the breeding season using data published by the Ministry for Primary Industries (2012). Fishery catch was considered an appropriate proxy for marine productivity because: (a) the fishery is a spawning fishery and its catch is closely monitored by government observers; (b) the fishery waste and discards are heavily exploited by Westland Petrels during chick-rearing, with fishery discards constituting up to 63% of the solid food fed to chicks (Freeman 1998, Freeman et al. 2001); (c) there is negligible incidental

bycatch of Westland Petrels in this fishery and therefore we expected a positive effect of this fishery catch on survival; and (d) the total catch of this fishery has varied by a factor of 4 over the past 20 years, up to 20,900 tons (recorded as up to 19,000 metric tonnes) per year in the area used by the petrels, while other fisheries in the same region have a relatively small total tonnage (Ministry for Primary Industries 2012). The hoki fish stock is managed as several independent stocks, geographically spread around New Zealand's southern waters. For the western stock of this fishery, which overlaps the area used by the petrels, year-class strength (cohort population size) is correlated with cooler sea-surface temperatures (SST), and negatively correlates with the Southern Oscillation Index (SOI; Bull and Livingston 2001). Similar results have been shown for the red cod (*Pseudophycis bachus*) fishery in this region (Beentjes and Renwick 2001), suggesting some generalization of improved marine productivity in cooler SST years in this marine system. Although the fishery started in 1969, the effect of the fishery catch (in tons) was tested for the period 1989–2012, since catch documentation to area level was poor prior to 1989 (Ministry for Primary Industries 2012). The more classically used SeaWIFs chlorophyll-*a* measures in this zone showed a poor correlation with station-recorded measures in the New Zealand area (Murphy et al. 2001). In consequence, the SOI and remotely sensed chlorophyll-*a* measures for this zone correlate poorly and are not recommended as indicators of variability (Murphy et al. 2001).

Second, we considered sea-surface temperature anomalies (SSTA) in the areas used by Westland Petrels during the breeding season (mean SSTA from April to October in the area 168°E–175°E and 40°S–45°S, in southern New Zealand; Landers et al. 2011b, S. Waugh personal observation) and nonbreeding season (mean SSTA from December to March in the areas 72°W–78°W and 35°S–45°S, west of southern Chile, and 64°W–68°W and 50°S–55°S, in the southern Patagonian Shelf off the coast of Argentina; Landers et al. 2011a). SSTA reflected oceanographic variability in the main foraging areas and data were obtained from the IRI Data Library (http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.monthly/.ssta/).

Third, we used two global climate indices: the mean SOI and the mean Southern Annular Mode (SAM), both calculated from October to March. The SOI is defined as the normalized pressure difference between Tahiti, French Polynesia, and Darwin, Australia. In association with the El Niño–La Niña Oscillation (Kwok and Comiso 2002), the SOI describes global environmental variability across the Pacific Ocean. SOI data were obtained from the Australian Bureau of Meteorology (ftp://ftp.bom.gov.au/anon/home/ncc/www/sco/soi/soiplaintext.html). The SAM is defined as the difference in the normalized monthly zonal mean
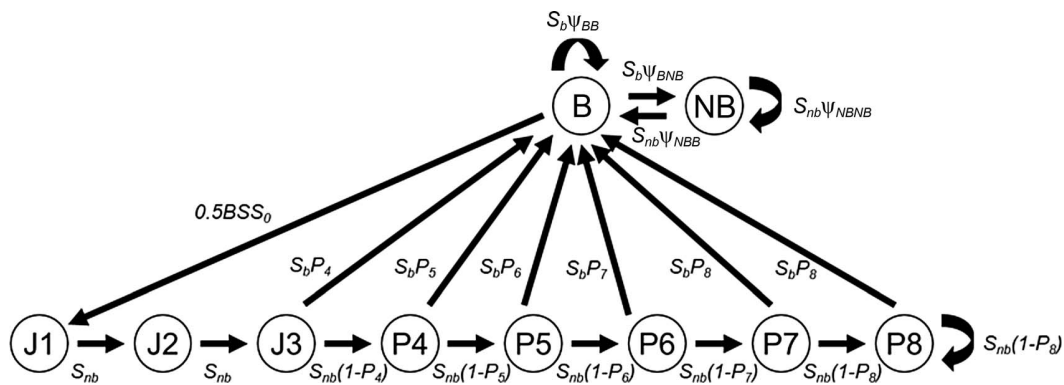
FIGURE 1. Lifetime diagram for the Westland Petrel at Punakaiki, West Coast, New Zealand. Stages are: Ji for i-year-old juveniles; Pi for i-year-old prebreeders; B for adult breeders; and NB for adult nonbreeders or skipped breeders. We consider the minimum age at first breeding to be 4 yr. The probability of breeding for the first time is $S_{nb}P_i$, where S_{nb} is the survival of nonbreeders and P_i is the probability of breeding for the first time at i yr old. Once recruited, birds reproduce every year with the probability $S_b\psi_{BB}$, where S_b is the survival of birds in the breeder state and ψ_{BB} is the probability of remaining in the breeder state, or may skip breeding with the probability $S_b\psi_{BNB}$. Skipped breeders may remain nonbreeders with the probability $S_{nb}\psi_{NBNB}$, or may breed with the probability $S_{nb}\psi_{NBB}$. BS is overall breeding success, and S_0 is survival during the first year at sea.

sea-level pressure between 40°S and 65°S (Gong and Wang 1999). The SAM is the leading mode of atmospheric circulation variability in the Southern Hemisphere, affecting wind speed and predominant direction in the Southern Ocean (Marshall 2003). Previous studies have shown that changes in wind regime over the Southern Ocean influence the foraging ecology and life-history traits of seabirds (Weimerskirch et al. 2012). SAM data were selected from the online database of the British Antarctic Survey (http://www.nerc-bas.ac.uk/icd/gjma/sam.html).

Goodness-of-Fit and Model Selection

Goodness-of-fit of the initial CMR models was assessed using U-CARE 2.5 (Choquet et al. 2009a) for multistate models. There is currently no goodness-of-fit test applicable to multi-event models (Kendall 2009). Thus, we assessed the fit of a multistate model that only retained information regarding whether an individual was encountered as a breeder or as a nonbreeder, or not encountered. On the basis of goodness-of-fit results, we calculated a variance inflation factor to be used for the models. Multistate models were fitted using program MARK (White and Burnham 1999) and multi-event models with program E-SURGE 1.8.5 (Choquet et al. 2009b). Model selection was based on Akaike's Information Criterion for small samples (AIC$_c$), corrected for overdispersion (QAIC$_c$) when necessary (Burnham and Anderson 2002).

Population Modeling

We constructed a female-based population model using a prebreeding matrix (Caswell 2001) structured by age and reproductive status classes (Figure 1). Parameters entering the model were age-specific recruitment probabilities and juvenile survival (estimated from the multistate model),

breeder vs. nonbreeder survival and breeding probabilities (estimated from the multi-event model), and breeding success (Table 2). We used a sex ratio of 1:1. Minimum age at first breeding was considered to be 4 yr (see Results). Therefore, juvenile life history was parameterized to allow individuals to move through 3 years following fledging (called J1, J2, and J3) with identical parameters, in which annual survival was equal to the survival of nonbreeding adults. From 4 to 8 yr, parameters were estimated from CMR models (see Estimating Adult Survival and Breeding Probabilities, above). Individuals survived and started to recruit as breeders with age-specific recruitment probabilities (from model-averaged estimates from the multistate model). Once recruited, birds could alternate between the breeder and nonbreeder stages with stage-specific survival and transition probabilities. We ignored immigration in the matrix population model as rates were negligible (see Appendix).

We first built a deterministic matrix model that included the mean values of the demographic parameters (see Results). We estimated the deterministic growth rate (λ) and the stable age distribution. We then focused on a stochastic matrix model to estimate the stochastic growth rate (λ_{stoch}) and to estimate the sensitivities of λ to variations in demographic rates, θ ($\partial\lambda/\partial\theta$; Caswell 2001). We used sensitivities, log-scaled sensitivities (elasticities), and arcsine-scaled sensitivities for the vital rates sensitivities, because all demographic parameters were bounded by 0 and 1 (Link and Doherty 2002). Environmental stochasticity was incorporated in the matrix model by sampling the yearly values of survival and reproductive rates from a beta distribution and a log-normal distribution, respectively (Morris and Doak 2002), mean and variance of which were set equal to those previously

TABLE 2. Modeling juvenile survival (ϕ), recruitment probability (ψ), and recapture (p) probabilities for Westland Petrels in New Zealand between 1977 and 2012. For each model, we present the model description, effect tested, deviance, number of estimable parameters (K), $\Delta QAIC_c$ (the difference in quasi–Akaike's Information Criterion from the top model), and Akaike weight (w_i).

Model[a]	Hypothesis tested	Deviance	K	$\Delta QAIC_c$	w_i
$\phi^{st}_{a1,a2-3=1,a4+} \psi^{st}_{a5} p^{st}_t$	Five age classes	1,063.42	27	0.00 [b]	0.483
$\phi^{st}_{a1,a2-3=1,a4+} \psi^{st}_{a7} p^{st}_t$	Seven age classes	1,060.76	29	1.70	0.206
$\phi^{st}_{a1,a2-3=1,a4+} \psi^{st}_{a6} p^{st}_t$	Six age classes	1,063.94	28	2.69	0.126
$\phi^{st}_{a1,a2-3=1,a4+} \psi^{st}_{a8} p^{st}_t$	Eight age classes	1,060.33	30	3.46	0.086
$\phi^{st}_{a1,a2-3=1,a4+} \psi^{st}_{a4} p^{st}_t$	Four age classes	1,069.43	26	3.83	0.071
$\phi^{st}_{a1,a2-3=1,a4+} \psi^{st}_{a9} p^{st}_t$	Nine age classes	1,060.31	31	5.64	0.029
$\phi^{st}_{a1,a2-3=1,a4+} \psi^{st} p^{st}_t$	—	1,105.23	26	39.64	0.000
$\phi^{st}_{a1,a2-3=1,a4+} \psi^{st} p^{st}$	Constant capture probability	1,359.85	4	248.13	0.000

[a] $a1$ estimates S_0, survival during the first year at sea; $a2-3=1$ was a necessary constraint to estimate S_0; and $a4+$ estimates survival for individuals 4 yr old and older.
[b] The $QAIC_c$ value of the top model = 1,984.83.

estimated. The stochastic matrix population model was analyzed by Monte Carlo simulations (1,000 iterations) using the package 'popbio' (Stubben and Milligan 2007) implemented in program R (R Development Core Team 2011). Initial stage abundances corresponded to the stable age distribution based on the number of breeders actually observed in the study colony in 2011, data that were accessible and verified at the time of modeling. All values are reported ± SE unless otherwise stated.

RESULTS

Population Size, Breeding Success, Nest Occupancy, and Density

We estimated the size of the study colony in 2011 at 998 (95% CI: 856–1,121) burrows, with an occupancy rate of 0.33 ± 0.07 ($n = 6$ areas measured for occupancy with 94 nests checked; Table 3 summarizes data from previous studies and information from this study). This equated to ~330 (95% CI: 194–437) breeding pairs in 2011 during the midincubation period. Burrow occupancy fluctuated during 2001–2011, then increased from 2011 to 2014, with an overall increase throughout the study period ($\beta = 0.0095 \pm 0.0048$; linear regression: Wald-statistic = 3.946, $P = 0.047$). Similarly, burrow density increased from 2007–2008 to

2014, although uncertainty was higher in the latter period ($\beta = 0.0067 \pm 0.0037$, Wald-statistic = 3.169, $P = 0.075$). The mean breeding success across all years, 1995–2003 and 2012, was 0.607 (± 0.119 SD).

Age at First Return and Juvenile Survival

The mean observed age at first return was 7.7 ± 1.1 (SD) yr old (mode = 6, $n = 139$, range = 4–15 yr; Figure 2). For the juvenile survival analyses, the initial model ($\phi^{st}_{a1,a2-3=1,a4+} \psi^{st} p^{st}_t$) was accepted ($\chi^2_{41} = 36.6$, $P = 0.668$). Detection probability was best modeled as time dependent (Table 2). There was model selection uncertainty for the transition probability from the juvenile to the adult stage (Table 2). Given our modeling of the probability of first reproduction, recruitment probability was model-averaged over 8 age classes (Figure 3). Model-averaged survival of juveniles from fledging to first return was estimated to be 0.359 ± 0.032 (95% CI: 0.300–0.423).

Adult Survival and Breeding Probability

Goodness-of-fit tests showed that a two-state (breeding and nonbreeding) model did not fit the data ($\chi^2 = 825.4$, df = 484, $P < 0.001$). We thus used a variance inflation factor (1.705) for model selection. The best model (Table 4) showed that survival probability differed between sexes

TABLE 3. Burrow occupancy (occupied burrows) and density measures for the Westland Petrel study colony at Scotsman Creek near Punakaiki, West Coast, New Zealand, during 2001–2014. '—' indicates no data.

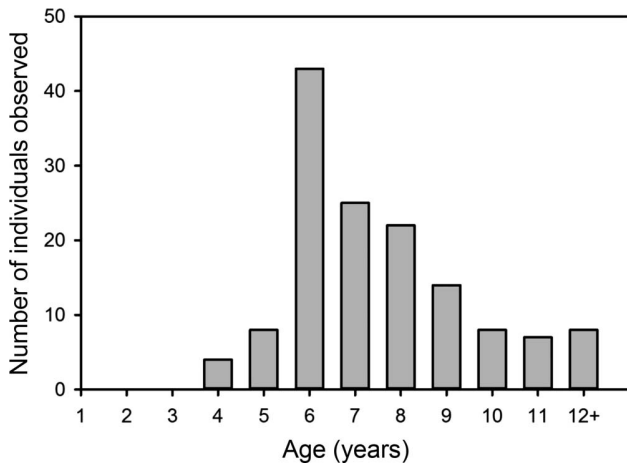| Year	Burrow occupancy ± SD (n)	Burrow density (m²) ± SD (n)	Source
2001	0.21 ± 0.28 (2)	—	Waugh et al. (2003)
2007	—	0.15 ± 0.05 (8)	Baker et al. (2011)
2008	0.37 ± 0.56 (2)	0.11 ± 0.05 (8)	Baker et al. (2011)
2011	0.33 ± 0.06 (5)	—	This study
2012	0.52 ± 0.08 (5)	—	This study
2013	0.43 ± 0.11 (5)	—	This study
2014	0.43 ± 0.07 (5)	0.18 ± 0.11 (19)	This study

FIGURE 2. Distribution of observed age at first return, used as a proxy for first breeding, of 139 Westland Petrels banded at the study colony at Scotsman Creek near Punakaiki, West Coast, New Zealand, during 13 years between 1970 and 1988.

and states (Table 5). Breeders had a higher survival rate than nonbreeders, and nonbreeding females tended to have lower survival than nonbreeding males, although confidence intervals broadly overlapped between nonbreeding males and nonbreeding females (initial model M1 vs. selected model M8; Table 4). Birds transitioned from breeding to nonbreeding states at different rates depending on sex and state. Females tended to be less likely to remain in the breeding state from one year to the next (0.608, 95% CI: 0.524–0.687) than males (0.722, 95% CI: 0.662–0.774). Nonbreeding males had a lower probability of returning to breed at $t + 1$ compared with nonbreeding females (Table 5).

We further tested these transition rates using survival data from 1995 to 2012, which included birds captured at least once in a study burrow and hence reduced bias
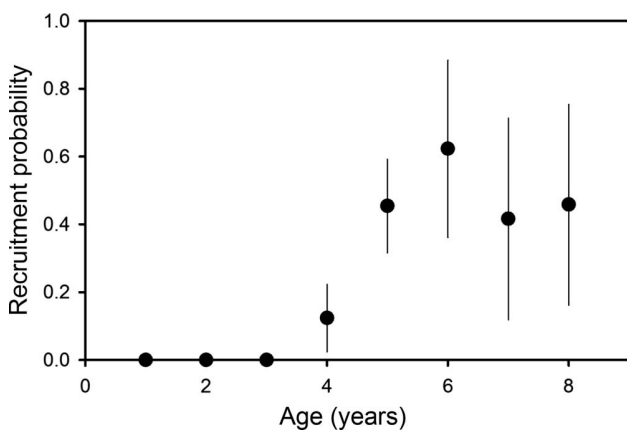

FIGURE 3. Model-averaged age-dependent recruitment probability for Westland Petrels at Punakaiki, West Coast, New Zealand. Error bars indicate SE.

associated with recapture rates for non-nesting birds (see model selection results in Appendix Table 6). The best model for this dataset, as for the longer dataset (above), showed that breeders had higher survival than nonbreeders and that nonbreeding females had lower survival than nonbreeding males. However, for this model with reduced bias, birds were found to transition from breeding to nonbreeding states at different rates depending on state only. Birds that previously bred were likely to skip breeding in the following year with a probability of 0.232 (95% CI: 0.156–0.330) for both sexes. The probability of birds classified as nonbreeders in one year breeding in the following year was 0.295 (95% CI: 0.190–0.426). The probability estimated from the capture–recapture model was that 77% of breeders bred again, given that they survived until the following year.

Testing for Environmental Effects on Adult Survival

Model M9, in which adult survival of breeders, female nonbreeders, and male nonbreeders was time dependent and additive on the logit scale, was favored compared with model M8 ($\Delta QAIC_c = 15.4$), suggesting that the survival of these groups of birds varied in parallel between years. Survival remained high for almost the entire study period, except during 2002–2004 when it was lower than 0.80 (Figure 4). Adult survival increased when the hoki fishery catch increased ($\beta = 0.695 \pm 0.214$; ANODEV: $F_{3,22} = 2.822$, one-sided $P = 0.031$). This covariate explained 28% of the variation in survival. Adult survival was negatively related to sea-surface temperature anomalies (SSTA) in New Zealand waters used by Westland Petrels ($\beta = -0.942 \pm 0.130$; $F_{3,29} = 8.644$, $P < 0.001$), but was positively related to SSTA west of southern Chile ($\beta = 1.176 \pm 0.143$; $F_{3,29} = 15.302$, $P < 0.001$). These slopes did not differ significantly ($z = 1.211$, $P = 0.113$). These two covariates explained 62% of the variation in survival, but most of this variation (61%) was explained by SSTA west of southern Chile. There was no significant effect of the Southern Oscillation Index ($P = 0.769$) or the Southern Annular Mode ($P = 0.376$) on adult survival.

Population Modeling

The deterministic population growth rate was 1.034, indicating ~3% population growth per year, with a generation time of 19.8 yr. The stochastic population growth rate was 1.018 (95% CI: 1.018–1.019), or 1.8% per year, again indicating a positive population trend, in accordance with the positive trends in observed burrow occupancy and density. Sensitivity analyses indicated that the population growth rate showed the highest sensitivity to the survival of breeders, then nonbreeders and juveniles, in descending order (Table 7). The probability of remaining in the breeding state, moving from the nonbreeding to the breeding state, and breeding success

TABLE 4. Modeling encounter, sexing, survival, and breeding state transition probabilities in male and female Westland Petrels in New Zealand between 1970 and 2012. Sexing probability is the probability that the bird, caught in the field, is attributed to the right sex. For each model, we present the model description, effect tested, deviance, number of estimable parameters (K), $\Delta QAIC_c$ (the difference in quasi–Akaike's Information Criterion from the top model), and Akaike weight (w_i). The reference model, i.e. our initial model for adult survival, was model M1. The top model is highlighted in bold font.

Model	Hypothesis tested	Deviance	K	$\Delta QAIC_c$	w_i
M8	**No sex effect on breeders' survival**	**35,831.77**	**324**	**0.00[a]**	**0.748**
M1	—	35,831.65	325	2.18	0.252
M5	No state effect on survival	36,189.82	323	205.56	0.000
M4	No sex effect on survival	36,763.16	323	541.83	0.000
M7	No state effect on transition	36,872.00	323	605.67	0.000
M6	No sex effect on transition	37,235.84	321	814.56	0.000
M3	Constant encounter probability	37,992.94	173	934.67	0.000
M2	Constant sexing probability	39,215.50	189	1,636.34	0.000

[a] The $QAIC_c$ value of the top model = 21,703.44.

had lower sensitivities, with age-specific recruitment probabilities having the lowest sensitivities. The vital rates that most influenced the population growth rate showed the lowest variability (Table 7), and adult survival had both the lowest variability and the highest sensitivity. Anecdotal information about the study colony suggests that there has been an increase in colony area, with a new area near the upper extremity having been colonized since the mid-1990s (J. A. Bartle, A. Freeman, K.-J. Wilson, and S. Waugh personal observation).

DISCUSSION

We described the demography and population dynamics of the Westland Petrel, a top-level predator in the subtropical marine system, and examined some environmental influences on the population. The species spends its entire life cycle between the Subtropical Convergence and the Subantarctic Front in marine systems spanning predom-inantly the South Pacific and, less frequently, West Atlantic oceans (Brinkley et al. 2000, Landers et al. 2011a, J. Arnould and S. Waugh personal observation). Its breeding season, in the austral fall, winter, and spring, corresponds to the period of highest chlorophyll-*a* production for this zone (Longhurst 1998). In the interbreeding (austral summer) period, Westland Petrels migrate to the Humboldt Current and Patagonian Shelf areas (Brinkley et al. 2000, Landers et al. 2011b), a time of year when ocean productivity in the southern New Zealand area is relatively low, while that of the Shelf and upwelling systems around the southern South American continent is highest (Longhurst 1998).

Using capture–mark–recapture (CMR) data gathered between 1970 and 2012, and state-of-the-art CMR models, we estimated the population growth rate and adult survival of Westland Petrels, and modeled the relationships with environmental factors, particularly sea-surface temperature anomalies (SSTA) and local marine productivity

TABLE 5. Probabilities (mean and 95% CI) of adult survival and transition between breeding states for male and female Westland Petrels in New Zealand using the entire dataset from 1970 to 2012 and using the reduced dataset from 1995 to 2012 for individuals captured in burrows.

	Survival probability	Transition probability to the breeder state
All colony, 1970–2012		
Male		
Breeder	0.954 (0.918–0.975)	0.722 (0.662–0.774)
Nonbreeder	0.926 (0.917–0.934)	0.023 (0.019–0.028)
Female		
Breeder	0.954 (0.918–0.975)	0.608 (0.524–0.687)
Nonbreeder	0.917 (0.900–0.931)	0.047 (0.036–0.062)
Burrows only, 1995–2012		
Male		
Breeder	0.934 (0.842–0.974)	0.768 (0.670–0.844)
Nonbreeder	0.737 (0.643–0.813)	0.295 (0.190–0.426)
Female		
Breeder	0.934 (0.842–0.974)	0.768 (0.670–0.844)
Nonbreeder	0.436 (0.247–0.645)	0.295 (0.190–0.426)

TABLE 7. Sensitivity of the population growth rate to changes in demographic parameters for Westland Petrels in New Zealand, and relative variability of demographic parameters (corrected CV at its maximum possible value, given the mean following Morris and Doak [2002]). See Figure 1 for demographic parameter definitions.

Demographic parameter	Mean value (SE)	Sensitivity			CV, corrected
		Standard	Log scale	Sin^{-1} scale	
S_b	0.954 (0.014)	0.504	0.474	0.105	0.067
S_{nb}	0.917 (0.008)	0.331	0.298	0.090	0.029
S_0	0.357 (0.031)	0.164	0.058	0.078	0.065
BS	0.607 (0.040)	0.098	0.058	0.048	0.082
ψ_{BB}	0.768 (0.045)	0.125	0.095	0.057	0.134
ψ_{NBB}	0.295 (0.061)	0.074	0.021	0.031	0.107
P_4	0.124 (0.074)	0.013	0.001	0.004	0.225
P_5	0.454 (0.127)	0.009	0.004	0.004	0.255
P_6	0.623 (0.128)	0.006	0.003	0.003	0.264
P_7	0.416 (0.097)	0.002	0.001	0.001	0.197
P_8	0.458 (0.139)	0.002	0.001	0.001	0.279

around the breeding area. Our results enabled the population trend for this species (1.8% increase per annum) to be described for the first time, along with juvenile survival rates. Survival parameters and breeding transition probabilities were estimated with more certainty than in previous work (Waugh et al. 2006), and showed that, annually, up to 54% of the population on average is in a nonbreeding state. In the best models assessed, an important level of heterogeneity was found in survival

between breeding and nonbreeding individuals, but without significant sex differences.

Adult Survival and Breeding Probabilities

As the main drivers of population growth in long-lived animals, the importance of survival and breeding probability was examined in detail. Although Westland Petrel adult breeder survival was high at 0.954, compared with many other procellariiform seabirds (Shreiber and Burger
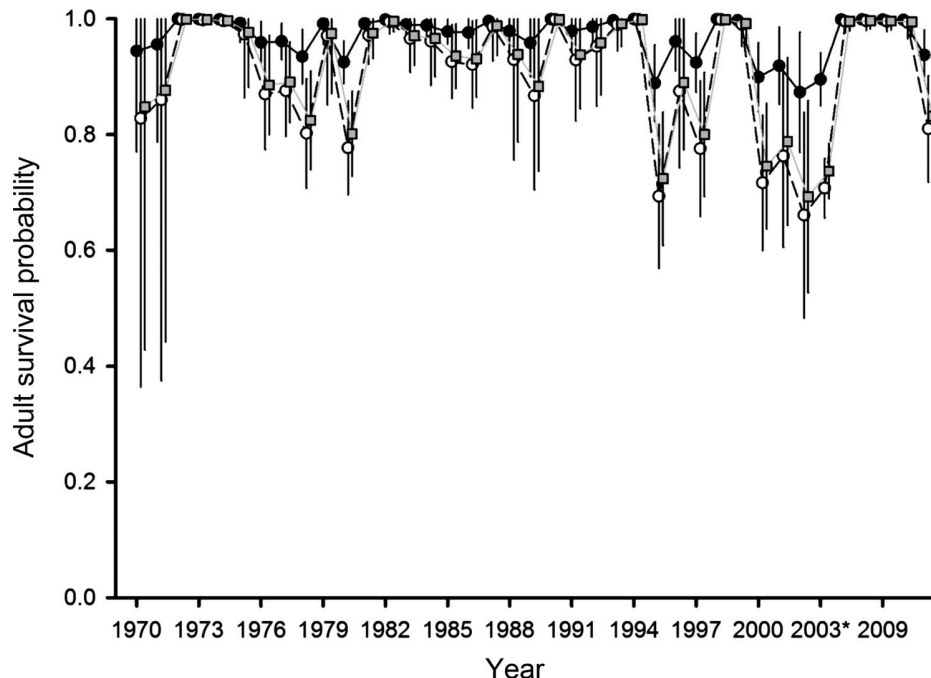
FIGURE 4. Adult annual survival of Westland Petrels at Punakaiki, West Coast, New Zealand, obtained from the same structure as model M8 (Table 4), but with an additive time effect on survival. Filled circles and black line indicate breeders, empty circles and dashed line indicate female nonbreeders, and gray squares and gray line indicate male nonbreeders. Error bars indicate SE. 2003* indicates that survival was constrained to be identical for the years 2003, 2004, 2005, and 2006 due to the absence of or very low recapture efforts in these years.

2001, Barbraud et al. 2014, Agreement on the Conservation of Albatrosses and Petrels 2015), nonbreeders (including birds that had previously bred and prebreeding birds) had significantly lower survival rates. As emigration from the study colony was extremely low (Appendix), it can be ruled out as a downward bias on the survival rates estimated. In the context of rates of survival estimated for other *Procellaria* petrels, Westland Petrel survival is moderate: higher than the congeneric White-chinned Petrel (0.895) population that is in decline on the Crozet Islands (Barbraud et al. 2008), and marginally lower than the increasing population of Spectacled Petrels (*P. conspicillata*; 0.970) on Inaccessible Island (Ryan et al. 2006). These rates show how variable population parameters for the genus can be, and the role of the environment in influencing these different factors warrants further examination, as does the role of phylogenetic constraint in determining life histories (Abadi et al. 2014). Estimating survival in nocturnal, burrow-nesting birds with widespread breeding populations presents a particular challenge for researchers and, to date, only one or two studies for each species have been reported. However, the ability to estimate differential breeder and nonbreeder survival rates is important to enable the potential impacts of environmental effects on specific parts of the population to be examined.

Our analyses of the transition rates from breeding to nonbreeding state and vice versa confirmed that adults frequently miss breeding seasons: Birds remained in the breeding state with a probability of 0.768, and returned to breeding after a nonbreeding year with a probability of 0.295. This outcome was similar to that previously noted (38% of birds deferred breeding, as estimated by Waugh et al. [2006]; the occurrence of frequent breeding deferral was noted by Warham [1990]). Currently the proximate causes of low rebreeding rates are unknown. It remains to be tested whether body condition, physiological factors, and previous breeding outcomes, among other factors, are good indicators of future breeding decisions. In exceptional cases birds were observed to breed in up to 11 consecutive years, showing that high breeding frequency over long time periods was possible, at least for some individuals. The proportions of birds breeding in consecutive years were similar to those found for the White-chinned Petrel (0.766 for breeders in one year returning to breed in the next and 0.178 for nonbreeders in one year rebreeding in the next; Barbraud et al. 2008). Bradley et al. (2000) found similar rates of missed breeding seasons for Short-tailed Shearwaters (*Puffinus tenuirostris*) in Tasmania, Australia, with up to 29% of the adult population not breeding per year. These nonbreeding birds, although difficult to study at the breeding colony due to their reduced attendance and lower recapture probability, make up an important part of procellariiform populations—54%

in the case of the Westland Petrel, based on our matrix model outcomes—and thus can strongly influence the size of the breeding population between years.

We were confident that state transition probability estimates obtained with the 1995–2012 dataset were more reliable than those obtained with the full dataset (Table 5). First, survival probabilities were not significantly different between these datasets. It is thus unlikely that survival decreased and transition probabilities increased due to life-history tradeoffs. Second, state assignment probabilities were nuisance parameters in our case, needed only to make use of the entire dataset (i.e. including birds of known and unknown status). State assignment probability is conditional on apparent survival and does not address the problem of temporary or permanent emigration. Consequently, we suspect that the differences in transition probabilities between the two datasets originated from birds captured on the surface of the colony, rather than being attributed to a burrow, and moving outside the capture area. Finally, the analysis of the reduced dataset was restricted to birds captured in burrows, for which breeding status was most often known, and for which temporary or permanent emigration was less likely to occur than for birds captured at the surface due to the strong fidelity to a nest site.

Recruitment and Age at First Return

The mean age of first return of Westland Petrels in this study (7.7 yr) was lower than that previously described for Westland Petrels (5–12 yr for age at first return to minimum age at first breeding, as noted by J. A. Bartle; see Marchant and Higgins 1990), but compares well with age at first breeding of White-chinned Petrels (6.1 yr; Barbraud et al. 2008). Forty-eight percent of Westland Petrel chicks banded and recovered at the breeding site were aged between 4 and 7 yr, which indicates that the age of first return is a little higher than that for the declining White-chinned Petrel population on the Crozet Islands, where 87% were observed breeding at these ages (Barbraud et al. 2008).

Population Dynamics and Sensitivities

For the single, large breeding colony of Westland Petrels, with ~330 pairs or just under 10% of the annual breeding population of ~4,000 pairs (Baker et al. 2011, Wood and Otley 2013), the modeled stochastic population growth rate was 1.8% per year for the period 1970–2012. This growth rate was due to high adult breeder survival, high fecundity, very low emigration, and the positive effect of environmental variables during the study period. This finding of slow positive population growth was corroborated by analyses of burrow densities (a trend of +0.67% per year) and occupancy (+0.95% per year) at the study colony over 7- and 13-yr periods, respectively, to 2014.

These independent measures indicate a positive population trend for the Westland Petrel, although certainty for these factors will be improved by more intensive sampling and longer time-series of data in future analyses.

However, it is possible that the population growth rate has not been constant throughout the study period. Anecdotal reports suggest a rapid increase in petrel numbers during the 1970s and 1980s, as industrial fishing activity increased (J. A. Bartle personal communication). The degree to which these possible increases would have been offset by incidental mortality in earlier periods, when fisheries (particularly tuna longline fisheries in the region) were largely unregulated and unmitigated, is unknown. Without solid evidence for either possibility, our parsimonious approach is that the outcome of processes over the several decades of the study has been a slowly increasing population through time.

Unfortunately, analyzing interdecadal population trend data via previously published population estimates was not feasible, as early reports did not detail their survey methodology (Jackson 1958, Best and Owen 1976) and more recent studies varied significantly in their approaches (Baker et al. 2011, Wood and Otley 2013). However, the latter two studies and more quantitative estimates both reported a population size at the study colony of 300–500 birds, estimates that compare well with the 330 pairs estimated in this study. Further, our work has shown that the Baker et al. (2011) methodology for surveying density and occupancy is readily repeatable and therefore provides a sound basis for future population trend analysis.

The ways in which particular years of low survival for nonbreeders may have influenced the population is uncertain. If a large mortality event of nonbreeding birds had occurred during one or several years, the results would have manifested as a reduction in recruitment, along with a possible increase in the proportion of birds breeding in one or more years (as the nonbreeding proportion of the population would have been reduced), and the overall effect would have been to reduce population growth over a long period. A sudden identifiable decrease in the breeding population would not have been evident. While it is not possible, retrospectively, to assess the impacts of this type of effect, these factors should be considered for any future studies on the petrels.

As has been found for other long-lived avian species (Pfister 1998, Hunter et al. 2000, Sæther and Bakke 2000), sensitivities and log-scaled sensitivities of the population growth rate to adult survival were very high, and the relative variability of adult survival was low compared with the relative variability of other demographic parameters. Although the same result was true for arcsine-scaled variance-stabilized sensitivities of the population growth rate to adult survival, these types of sensitivities of the population growth rate to juvenile survival, breeding

success, and the probability of remaining in the breeding state were also relatively high. This suggests that further data collection to estimate these parameters with increased accuracy is warranted, as they can be important to determining population trends (Link and Doherty 2002).

Environmental Effects on Adult Survival

Studies modeling seabird population responses to changing environmental conditions have demonstrated the complex nature of demographic outcomes and their drivers (Rolland et al. 2009, Barbraud et al. 2011), but survival has been consistently identified as a sensitive indicator of the pressure on populations (Hunter et al. 2000, Schreiber 2001, Weimerskirch et al. 2003). For Westland Petrels, adult survival decreased when sea-surface temperature anomalies (SSTA) increased in the zone exploited during the breeding season. Sea-surface temperature in this area is expected to increase (Rhein et al. 2013), an outcome that would most likely not favor the adult survival of breeding petrels.

Conversely, there was a significant positive relationship of adult survival with SSTA in the interbreeding, summer foraging areas off the coast of southern Chile. Several mortality events were evident in the survival data, particularly for nonbreeding birds during the 1990s and early 2000s. While zooplankton biomass was higher when the upper boundary of the oxygen minimum zone was at shallow depths in the southern South American area, which corresponded to upwelling conditions (Escribano and Schneider 2007), the relationship between SSTA and these processes was not investigated over multiple years. These events, although irregular, may have a significant influence on population stability for higher predators. Westland Petrels may be sensitive to these effects. A high proportion (over 50% of birds) in any one year are nonbreeders that appear to be affected by oceanographic factors.

Mortality of seabirds in fisheries has been widely examined in New Zealand waters (Waugh et al. 2008, Abraham and Thompson 2011) and globally (Anderson et al. 2011). However, for the commercial trawling and longline fisheries consistently observed in New Zealand coastal waters, fisheries observers have recorded very few Westland Petrels caught (Richard and Abraham 2013). While modeling of the overlap of the species' foraging zones and fishing activity signals the potential for fishing-related mortality to negatively influence the Westland Petrel population (Richard and Abraham 2013), considerable uncertainty remains regarding whether this potential is realized (Ministry for Primary Industries 2013). There may be substantial benefits to seabirds from feeding on fishery discards (Thompson 1992, Furness et al. 2007), and these discards have been shown to be a common food source for Westland Petrels, particularly those from the

hoki trawl fishery (Freeman 1997, 1998, Freeman et al. 2001). While fishery waste is known to be common in the diet of chick-rearing adults, it may result in only short-term benefits to the species (such as boosting chick growth) and may not necessarily result in higher productivity in a sustained manner across the lifetime of an individual adult (Grémillet et al. 2008). Our results show that adult survival is the key driver of population growth, whereas fledging success has a relatively minor influence on population growth. Rather than suggesting a direct, negative effect of the fishery on adult survival, as would be expected with fisheries mortality on this group, our results relating to covariation of fishery catch and adult survival suggest that fish catch for hoki is better used as a measure of local marine productivity—Conditions that favor high fish catches also favor the fitness of adult petrels. A range of fisheries in this area have been shown to have increased productivity with lower sea-surface temperatures (Beentjes and Renwick 2001, Bull and Livingston 2001).

The extremely low survival estimated for the early 2000s, and particularly 2004, remains unexplained by the covariates that we tested (SSTA in the breeding and nonbreeding areas and fishery outputs). However, we cannot rule out mortality in illegal, unknown, and unreported fisheries in the nonbreeding foraging areas in South America, nor the effects of other climatic or oceanographic covariates not investigated here.

Conclusions

The mark–recapture and modeling study that we conducted has enabled a complex and structured population dynamic to be described for a top-trophic-level seabird, the Westland Petrel, in the subtropical ocean ecosystem of the South Pacific. We found strong relationships between adult survival and local oceanic productivity in the breeding area and with sea-surface temperature anomalies in both the breeding and nonbreeding areas. While high levels of adult survival would be expected for birds in this family, there were significant differences between rates for breeders and nonbreeders in any given year, with nonbreeder survival varying in response to environmental conditions more strongly than breeder survival, and lower overall. As individual birds transition between breeding states, low survival of nonbreeders could potentially impact strongly on the population growth rate over time. For example, high mortality of nonbreeders would reduce the pool of potential breeders in the population in future years, when conditions might be more favorable for a higher proportion of the population to breed. However, our ability to detect between-year differences in these factors was limited, and this remains an area of high interest for future research on this species and system. Although the modeled population growth was slightly positive, with direct observations of nest density and occupancy confirming the modeled trend over the period of the study, this trend is not assured for the future. A potential increase in anomalies in sea-surface temperature in the breeding and nonbreeding areas over the coming years is likely to create more unfavorable conditions for the population. Finally, the proximate causes for relatively high mortality events remain unknown.

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APPENDIX

Estimation of Demographic and Detection Parameters Used in Modeling the Westland Petrel Population

Methods. *Emigration and immigration*. To assess emigration and immigration rates, the exact location of all birds marked or recaptured during the period 1970–1997 was recorded at each colony. During this period 3,002 adults and fledglings were marked on the slopes at, above, and around the study colony, including within the areas used for intensive mark–recapture work. A further 941 adults and fledglings were marked in neighboring colonies from 300 m to 1,200 m from the study colony. While the majority of these colonies were within the same river catchment, two of the colonies were in the adjacent catchment of Liddy's Creek, to the south of the Scotsman Creek study colony. From these data anecdotal information was gathered about emigration rates among colonies. Although emigration and immigration rates can be estimated with capture–mark–recapture (CMR) models, too few individuals dispersed from their colonies to allow a CMR approach.

To assess our ability to detect the emigration of birds from study nests, we used two series of consecutive years of study burrow breeding data to assess changes in breeding burrow by individuals.

Estimating adult survival and breeding probabilities. In multi-event models observations do not necessarily correspond to states, which allows the handling of state uncertainty, and the state "dead" is explicitly included. The state "dead" is an absorbing state representing death or permanent emigration from the study area. We thus considered 5 states: female breeder (FB), male breeder (MB), female nonbreeder (FNB), male nonbreeder (MNB), and dead. States occupied are not directly observed; rather, at each occasion t, an event happens and is recorded, leading to an observed encounter history. In our case, we thus considered 10 events: 0 = "not observed"; 1 = "seen as FB"; 2 = "seen as MB"; 3 = "seen as breeder but sex not determined"; 4 = "seen as FNB"; 5 = "seen as MNB"; 6 = "seen as a nonbreeder but sex not determined"; 7 = "seen as female but status not determined"; 8 = "seen as male but status not determined"; 9 = "seen but sex and status not determined." Birds were assigned to breeder, nonbreeder, and unknown breeder to describe the status of birds depending on whether they were found with eggs or chicks, without these but inside a burrow, or always away from burrows, respectively.

Sex assessment was uncertain for a number of individuals. Sex data were groomed so that a bird's sex was fixed within a year, based on the majority of sexing outcomes within the year, as male, female, or unknown, and allowed to vary among years. We allowed these observations (sex and breeding state) to change, as there was uncertainty in each, and individuals were not assigned arbitrarily to any category.

Encounter, sexing, and correctness probabilities were fixed at 0 in years when no recaptures occurred, and sexing and correctness probabilities were fixed at 0 in years when no individuals were sexed. From this initial model, modeled correctness, and sexing, encounter, and state

APPENDIX TABLE 6. Modeling encounter, sexing, survival, and state transition probabilities of male and female Westland Petrels in New Zealand between 1995 and 2012. Sexing is the probability that the bird, caught in the field, is attributed to the right sex. For each model, we present the model description, effect tested, deviance, number of estimable parameters (K), $\Delta QAIC_c$ (the difference in quasi–Akaike's Information Criterion from the top model), and Akaike weights (w_i). The reference model, i.e. our initial model for adult survival, was model M1. The best model is highlighted in bold font.

Model	Hypothesis tested	Deviance	K	$\Delta QAIC_c$	w_i
M1	—	3,341.79	135	2.92	0.129
M2	Constant sexing probability	3,773.46	81	285.20	0.000
M3	Constant encounter probability	3,580.51	83	97.34	0.000
M4	No sex effect on survival	3,348.68	133	3.79	0.083
M5	No state effect on survival	3,374.54	133	29.65	0.000
M6	No sex effect on transition	3,378.34	131	27.48	0.000
M7	No state effect on transition	3,346.61	133	1.73	0.233
M8	**No sex effect on breeder survival**	**3,347.88**	**132**	**0.00[a]**	**0.554**

[a] The $QAIC_c$ value of the top model = 3,670.79.

assignment probabilities were modeled as constant or as a function of state or sex only.

Testing for environmental effects on adult survival. To test for the effect of a covariate on survival, we built a CMR model in which survival was modeled as a function of a covariate using a logit link function: $\text{logit}(\phi) = a + b \times co$, where a is an intercept, b is a slope, and co is a time-varying covariate. This CMR model was built from the model retained following model selection on adult survival. We then performed an analysis of deviance with a Fisher-Snedecor distribution (ANODEV; Skalski et al. 1993, Grosbois et al. 2008) by comparing the amount of deviance between the model assuming full time dependence (t), the model including the covariate (co), and the model assuming no time variation (cst) through the ratio F-test $= \left(\frac{Dev_{cst}-Dev_{co}}{j-1}\right) / \left(\frac{Dev_{co}-Dev_t}{n-j}\right)$, where $n =$ the number of survival estimates obtained from the time-dependent model and $j =$ the number of parameters required to describe the relationship between survival and the covariate. The percentage of variation explained by a covariate (r^2) was estimated as: $r^2 = \frac{(Dev_{cst}-Dev_{co})}{(Dev_{cst}-Dev_t)}$. Because we expected a positive effect of the hoki fishery catch, we used a one-sided P-value for this covariate.

Results. *Emigration.* Movement among subcolonies was negligible. Only 1 (male) fledgling of 1,054 banded at the study colony was recorded breeding elsewhere. Similarly, of the 463 fledglings banded in the neighboring colonies, only 1 (male) was observed breeding in the study colony. No intercolony movement was found among adults.

In the 9 yr from 1995 to 2003, an average of 0.3% of individuals changed burrows in a year, or 9 out of 350 bird-breeding years observed. Similarly, in the period 2010 to 2013, 1% of individuals changed nest per year, or 7 out of 167 birds.

Modeling encounter, sexing, and state assignment probabilities. Using the entire dataset, model selection (Table 4) indicated that the best model (M8) had a constant encounter probability of 0.573 ± 0.050 for breeding females, 0.554 ± 0.047 for breeding males, 0.097 ± 0.012 for nonbreeding females, and 0.148 ± 0.019 for nonbreeding males. For less favored models, encounter probability (model M1 vs. M3) and sexing probability (M1 vs. M2) varied among years. For breeders, encounter probability increased from the beginning of the study until ca. 1988 and was then relatively stable (Appendix Figure 5). The opposite pattern was observed for nonbreeders. Average sexing probability (the probability that a bird was sexed when caught) varied from 0.638 ± 0.058 for nonbreeding females to 0.788 ± 0.043 for breeding males (Appendix Figure 6). The probability of correctly sexing an individual (correctness probability) was 0.939 ± 0.019 for breeding females, 0.906 ± 0.016 for breeding males, 0.998 ± 0.009 for nonbreeding females, and 0.981 ± 0.005 for nonbreeding males.

State assignment probabilities varied between states and sexes and were 0.951 ± 0.025 for breeding females, 0.953 ± 0.022 for breeding males, 0.866 ± 0.035 for unsexed breeders, 0.394 ± 0.025 for nonbreeding females, 0.441 ± 0.013 for nonbreeding males, and 0.251 ± 0.017 for unsexed nonbreeders.
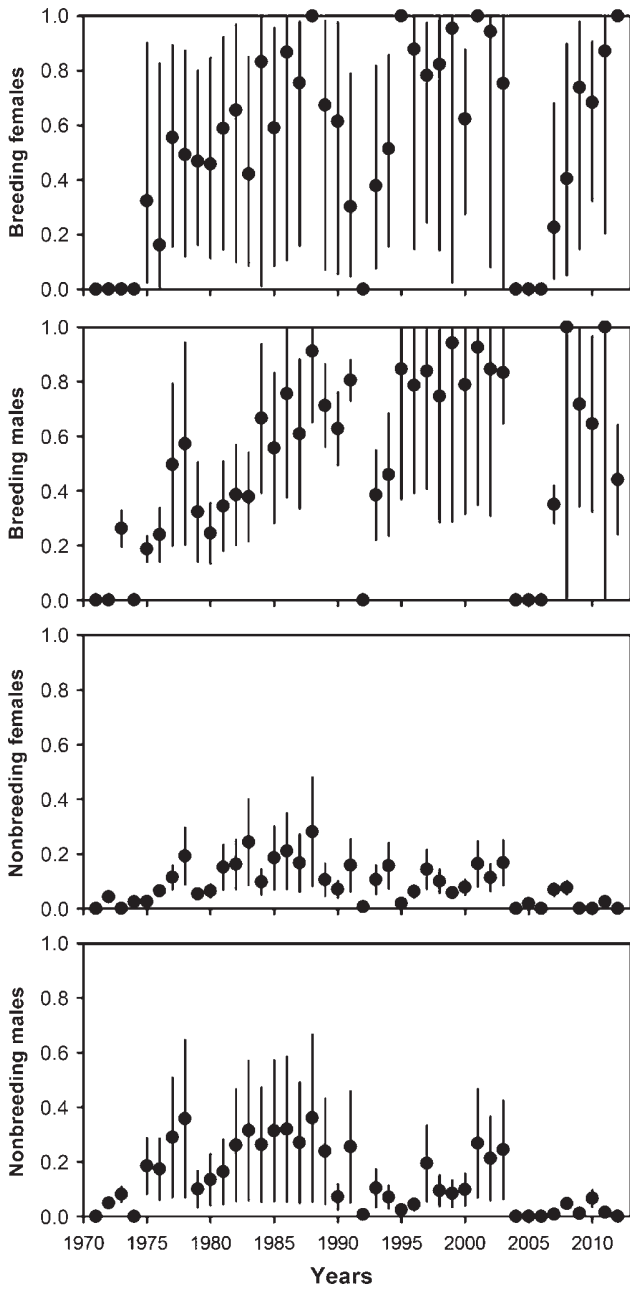
APPENDIX FIGURE 5. Encounter probabilities of Westland Petrels at Punakaiki, West Coast, New Zealand, obtained from model M8 (Table 4). Error bars indicate 95% CI.
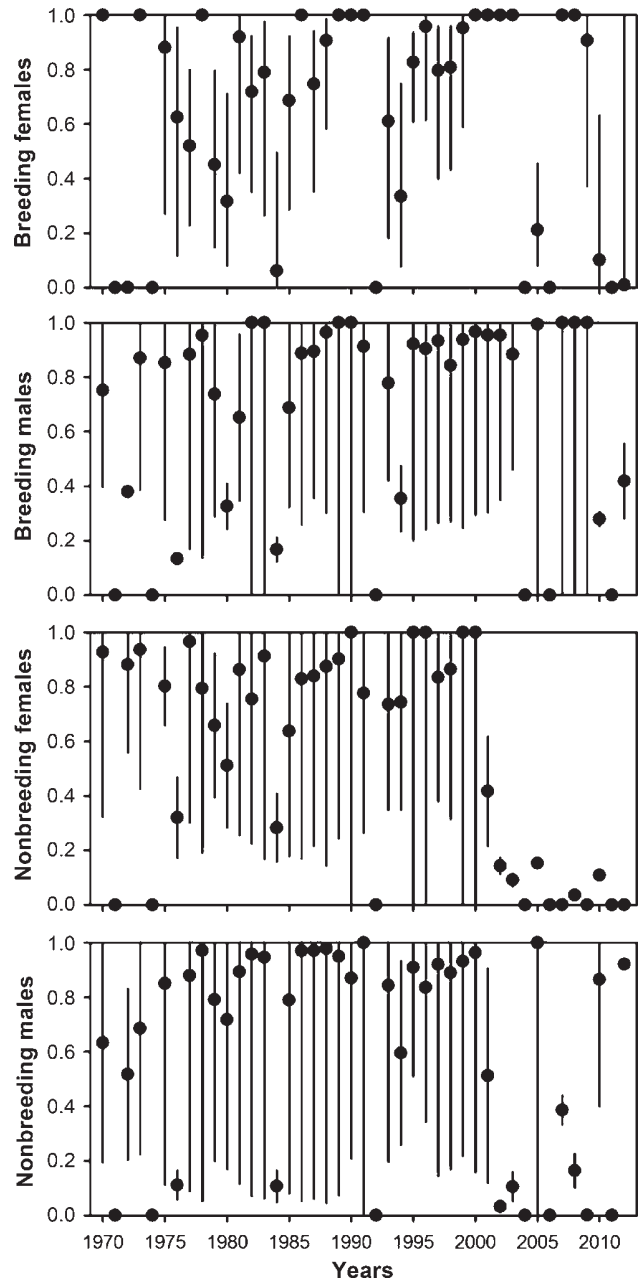
APPENDIX FIGURE 6. Sexing probabilities (the probability that a bird, caught in the field, was sexed) of Westland Petrels at Punakaiki, West Coast, New Zealand, obtained from model M8 (Table 4). Error bars indicate 95% CI.